MONITORING THE METABOLIC RATE AND ACTIVITY OF FREE-SWIMMING SQUID WITH TELEMETERED JET PRESSURE

BY D. M. WEBBER AND R. K. O'DOR

Biology Department and Aquatron Laboratory, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

SUMMARY

1. Measurements of oxygen consumption ($\dot{V}_{O_2}$, ml h^{-1}) and mantle cavity pressure (P, kPa) of squid, *Illex illecebrosus*, of various masses (M, kg), swimming at various speeds (U, m s^{-1}) in a tunnel respirometer yielded two relationships:

(a) $$\dot{V}_{O_2} = 245M^{0.73} e^{1.59U}$$

(b) $$\dot{V}_{O_2} = 555M^{0.75} P^{0.77}.$$

2. Both jet frequency and peak pressures increase with increasing speed. Patterns varied considerably between individuals, but total area under the pressure curve (P) was well correlated with oxygen consumption and speed.

3. A differential pressure transducer linked to an ultrasonic transmitter carrying average pressure data encoded on impulse frequency was designed to be carried inside the mantle cavity. It was tested in both the swim-tunnel and in video-taped free-swimming animals.

4. The relationships above held over a range of speeds from 0 to 1·4 m s^{-1}, the maximum speed observed, indicating that such transducers could provide direct estimates of both the metabolic rates and activities of these pelagic carnivores in nature; their use to test hypotheses about several energy-saving strategies is discussed.

5. Average thrusts, calculated from pressure data, are consistent with rigid body drag predictions and with overall locomotor efficiencies of 5%, which are also consistent with the relative costs of transport and efficiency estimates for fish.

INTRODUCTION

Several recent studies (O'Dor, 1982; Freadman, Hernandez & Scharold, 1984; Webber & O'Dor, 1985) have now shown that the energetics of squid can be studied in swim-tunnel respirometers like those used for fish. Such dynamic swimming invites an examination of the relationship between the intra-mantle pressures and thrust during squid swimming suggested by Johnson, Soden & Trueman (1972) based on Trueman & Packard's (1968) studies of tethered cephalopods. The present experiments examine the key role of pressure generation in the mantle during

dynamic swimming using telemetered pressures from both squid in respirometers and freely swimming squid. The mechanics of the mantle musculature producing this pressure is now reasonably clear (Gosline, Steeves, Harman & DeMont, 1983; Gosline & Shadwick, 1983; Bone, Pulsford & Chubb, 1981), and evidence will be presented that nearly every aspect of squid locomotion, in contrast to that of fish, is subject to direct analysis. Although this paper deals primarily with the empirical observations, the telemetering differential pressure transducer that is described here should allow detailed analysis of the bioenergetics of this nektonic predator from the level of muscle mechanics to natural behaviour in the sea. Squid and fish have many functional similarities (Packard, 1972), but recent studies have shown that they have dramatically different energy strategies (O'Dor & Webber, 1986). Detailed studies of squid locomotion should not only provide insights into squid life history strategies, but also, by comparison, into those of fish, which use a propulsion system much less easily studied in either the laboratory (Blake, 1983) or nature (Rogers, Church, Weatherly & Pincock, 1984; Priede, 1983; Bainbridge, 1958).

MATERIALS AND METHODS

Animals

Squid, *Illex illecebrosus*, LeSueur 1821, were obtained from mackerel box traps between August & November, from 1982 to 1985, from Mill Cove, St Margaret's Bay, Nova Scotia. They were gently removed from the pursed trap by dipnet and placed either in portable aerated 250 l polyethylene tanks (20 per tank) or in 70 l buckets surrounded with ice (five per bucket) containing sea water at 1–3 °C previously saturated with oxygen for the 1-h trip to the Aquatron Laboratory. The icing technique 'calmed' the squid, was more convenient, and gave at least as good a survival rate (70–100 %) as the ambient temperature method. At the laboratory, the animals were maintained in a pool tank of 700 m^3 volume and 15 m diameter under conditions previously described (O'Dor, Durward & Balch, 1977).

Mass and length of the 37 animals used ranged from 0·204–0·672 kg and 0·34–0·52 m. Females constituted 75 % of the animals used and ranged in mass from 0·244 to 0·672 kg. Males ranged from 0·204–0·496 kg. Maximum mantle cavity volume was estimated by filling the mantle cavity of anaesthetized squid with water. A 1·5 % solution of ethanol in sea water was used to anaesthetize the animals for this and for cannula and transmitter insertion.

Apparatus

The respirometer was designed by the Department of Engineering, Guelph University as a recirculating water tunnel constructed of acrylic plastic (19·2 cm i.d.). The original design (see Farmer & Beamish, 1969) was extensively modified for squid swimming and respiration measurements. Total volume was reduced from 166 to 92 l and the swimming chamber extended to 85 cm in length to accommodate large animals better. Since the maximum cross-sectional area of the largest squid measured (551 g) did not exceed 11 % of the cross-sectional area of the swimming chamber and

most animals did not exceed 8 % of the cross-sectional area, an adjustment for swimming speed was not required. Details of respirometer operation and oxygen consumption measurements are given elsewhere (Webber, 1985; Webber & O'Dor, 1985).

Continuous monitoring of intra-mantle pressures of animals swimming in the respirometer was done with cannulae (1·1 mm i.d. polyethylene tubing) 50–70 cm long inserted through the mantle, positioned lateroventrally, 3–4 cm posterior to the edge of the mantle and inhalant aperture (Fig. 1). Two tightly fitting rubber washers (0·8 cm diameter) on either side of the mantle prevented the cannula from slipping. The cannula was attached to a Statham Model P23AC pressure transducer which was connected to an integrating analogue-to-digital (A/D) converter (ADALAB from Interactive Microware Inc., State College, Pennsylvania) with 12 bit accuracy (−2048 to +2048), sampling at a rate of 22 analogue measurements per second. A microcomputer (Apple II+) continuously recorded pressure data. The frequency response of the transducer and cannula ranged from 30 to 25 Hz for a cannula of 50–70 cm, respectively.

A telemetry system was developed to monitor continuously intra-mantle pressure of free-swimming animals. Pressure was measured differentially using a semi-conductor strain gauge bridge mounted in a stainless-steel housing filled with light mineral oil. The diaphragm faced into the mantle and external pressure caused by
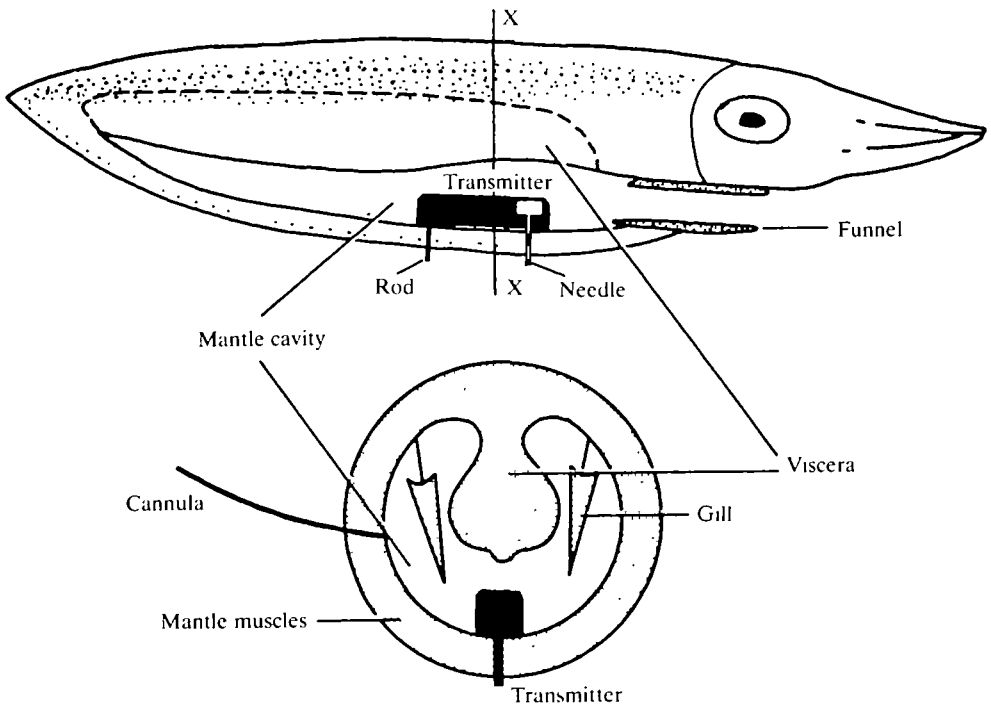

Fig. 1. Diagram of a longitudinal and a cross section of a squid illustrating the positions of insertion of the cannula and the ultrasonic pressure transmitter. (Modified from Trueman, 1975.)

depth was compensated for by pressure transferred through an oil-filled 22 gauge needle, as shown in Fig. 1. Output from the transducer was integrated electronically and telemetered ultrasonically at 69 kHz by a miniature transmitter (Voegeli & Pincock, 1981) designed with Vemco Ltd, Shad Bay, Nova Scotia. The transducer ($5\cdot3\times1\cdot4\times1\cdot4$ cm) was positioned inside the mantle cavity ventral to the organs, 4–6 cm posterior to the edge of the mantle with the needle and a threaded rod protruding through the mantle as anchors (Fig. 1). A signal at 69 kHz was transmitted to a CR-40 hydrophone-receiver (Communication Associates, Inc., Huntington Station, NY) which sent a digital signal to the microcomputer. The interval between successive signals was proportional to pressure. A 1000 Hz digital timer in the microcomputer was used to measure the interval between digital signals. The transducer was made neutrally buoyant by gluing a strip of rigid plastic foam along each side. This increased the width to 2·0 cm and gave a total volume of 17·5 ml. The transmitter displaced 12·7–6·1 % of the maximum mantle volume for animals ranging in weight from 0·348 to 0·672 kg.

Both methods (cannula and ultrasonic) were calibrated in kiloPascals (1 kPa = $10^3\,\mathrm{N\,m^{-2}} = 10\cdot2\,\mathrm{cmH_2O}$) using a water column of known height. The cannula system was calibrated four or five times for each animal. The calibration was linear and did not change during this time. For normal and burst swimming the gain on the amplifier was set at $2\cdot4\times10^{-3}$ V and $9\cdot8\times10^{-4}$ V for a pressure change of 0·1 kPa. This resulted in a change of 10 and 4 decimal units, respectively, after conversion by the A/D converter. For the ultrasonic transmitter, a pressure change from 0 to 20 kPa resulted in a frequency change from 4·2 to 16·7 Hz, respectively. For both methods, jet pressure was integrated and an average value for pressure was computed for each swimming speed by dividing the sum of pressures by the total number of measurements. The average pressure value accounts for both jet pressure and frequency.

Experimental procedures

All experimental animals were fasted for 24 h before being transferred in water from the pool tank to the respirometer. The digestion time for *I. illecebrosus* was 16 h for average meals (Wallace, O'Dor & Amaratunga, 1981). The 24-h interval should be sufficient to ensure that oxygen consumption was no longer elevated because of digestion. An effort was made to minimize excitement by reducing movements in the room and reducing light intensity. To allow comparisons of the energetics and swimming performance of squid and fish, the routine used by O'Dor (1982) for *Loligo opalescens*, which was a shorter version of that developed by Brett (1964) for fish, was adopted. After a brief exposure to the full range of speeds (0 to 0·88 m s^{-1}), the speed was decreased to 0·07 m s^{-1}, and the animal either settled to the bottom in the 'resting posture' (Bradbury & Aldrich, 1969) or swam spontaneously for 2–3 h. After this rest period the squid were forced to swim for 60-min periods at fixed speeds. Commencing at 0·28 m s^{-1} the speed was increased in increments of

$0.10 \, \mathrm{m \, s^{-1}}$ until the animal collapsed against the downstream grid. Whenever possible, oxygen consumptions and pressures were recorded for each animal in resting posture before and after recovery from exercise. In several cases, video recordings of swimming animals were made using a Sony SLO-323 recorder and an RCA TC2011/N low-light camera. Continuous recordings of mantle cavity pressure were synchronized with filmed swimming movements by voice audio and by audio output from the ultrasonic receiver. This method enabled frame-by-frame (30 Hz) video analyses of individual jet cycles and fin activity to be made. Trials in the respirometer were all at 15 °C except for squid with transmitters. To allow direct comparison between respirometer and tank, the ambient temperature in the pool was used in these cases.

Squid with transmitters were released in the pool tank for recovery and observation before swim-tunnel trials. A thin, $1.0 \, \mathrm{cm^2}$ aluminized reflector was attached with cyano-acrylate glue to the dorsal surface of the head to aid in recognition when the squid rejoined the school, which generally required only a few minutes. At intervals during this period the animal and the school were restricted to one half of the pool covered by a ceiling-mounted, low-light video camera with a wide-angle lens. During these periods mantle cavity pressure was continuously recorded. To determine swimming speed, a $2.0 \, \mathrm{m}$ grid was marked on the pool bottom. As well, a $2.0 \, \mathrm{m}$ stick was positioned at various locations, within the viewing field of the camera, $2 \, \mathrm{m}$ from the bottom and on the surface. This calibration was necessary to account for the parallax effect of the camera lens. Data were first collected for 1–3 h while the animals were cruising at speeds between 0.10 and $0.20 \, \mathrm{m \, s^{-1}}$. Then the animals were disturbed by waving a dipnet in the water, and data were collected at swimming speeds greater than $0.20 \, \mathrm{m \, s^{-1}}$.

A 0.412-kg animal was used to compare the cannula and the transmitter methods. The animal was anaesthetized and both a cannula and transmitter were inserted. The signal from the Statham transducer (cannula) was split into both the A/D converter and a Gould thermal recorder (Model TA 600) with a frequency response of $1.2 \, \mathrm{kHz}$. This permitted a direct comparison of jet cycles measured by the Gould thermal recorder and the A/D converter (Fig. 2A). Despite the lower frequency response of the A/D converter (22 Hz), the peak pressure and shape of the pressure curve were similar for both methods for jets of various sizes. It was also possible to compare jets measured by the Gould recorder and the transmitter (Fig. 2B). During this test the frequency response of the transmitter was only 2 Hz at 0 kPa. The peak pressures and shapes of individual jet cycles were different for the two methods, but the integrated pressure values were similar. The ultrasonic transmitter integrates pressure before it is transmitted, and, since average pressure is derived from the integration of a jet cycle, it is the same for a cycle measured by the Gould recorder or the transmitter.

Regression analyses were performed using Minitab (Ryan, Joiner & Ryan, 1976). Programs to measure analogue pressure and ultrasonic pressure data and to integrate raw pressure data were developed by DMW and may be obtained by writing to the authors.
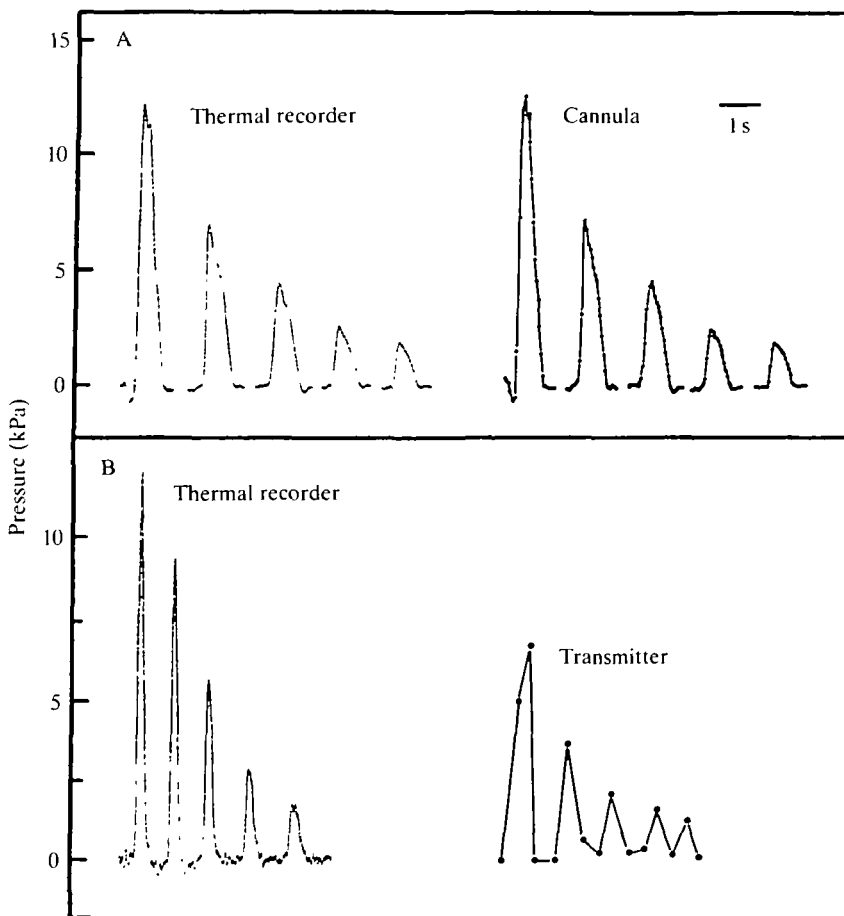
Fig. 2. Comparisons of different pressure recording techniques used. (A) Jets measured *via* a cannula with a Statham Model P23AC pressure transducer (frequency response = 25–30 Hz) attached to an analogue-to-digital integrating converter (sampling rate = $22 s^{-1}$). (B) Jets measured with an integrating ultrasonic pressure transducer-transmitter (frequency response = 2 Hz at 0 kPa and 8 Hz at 10 kPa). Each of these responses is compared to the output from a Gould thermal recorder (frequency response = 1.2 kHz).

RESULTS

Swimming behaviour

Illex illecebrosus is negatively buoyant and apparently uses its small fins primarily for control. During normal cruising it maintains its body at an angle such that the thrust from its jet is balanced between pushing the body fins-forward through the water and countering gravity. In the tube, at speeds below $0.28 m s^{-1}$, the animal would either drop to the bottom in resting posture or swim gently with the body angled upwards, the arms touching the bottom of the tube and the posterior tip of the mantle striking the upstream grid. Thus, no accurate data could be obtained for the metabolic cost of low-speed swimming using the respirometer. At higher speeds, swimming was oscillatory and varied considerably among animals, but most swam

relatively uniformly after the pre-trial conditioning period, seldom bumping against either grid. Most animals avoided contact with the tube, remaining in the area of microturbulent flow, and almost all animals swam horizontally. Even the few animals whose fins angled upwards seldom rubbed against the tube. At speeds from 0.28 to $0.38\,\mathrm{m\,s^{-1}}$, most animals used the fins at or near the jet frequency. As swimming speed increased, the strength and frequency of mantle contractions increased and the use of the fins usually decreased. At the higher speeds (0.48–$0.88\,\mathrm{m\,s^{-1}}$), animals frequently tucked their fins under and against the mantle, probably to minimize drag. This behaviour was also observed during high-speed swimming in the pool. Under these conditions, the jet alone controls both the angle of attack and the forward momentum.

For smooth swimmers, jet frequency usually increased most dramatically at speeds from 0.28 to $0.48\,\mathrm{m\,s^{-1}}$. At higher speeds, frequency usually either increased less or reached an asymptotic value. Frequencies ranged from 0.60 to $1.17\,\mathrm{jets\,s^{-1}}$ for animals from 0.220 to $0.491\,\mathrm{kg}$ (Table 1). Generally, smaller animals exhibited higher frequencies than larger animals, for a particular speed. Analysis using the ultrasonic transmitter permitted determination of jet frequency for a 0.491-kg animal freely swimming in the respirometer and in the pool, for a wide range of speeds from 0.12 to $1.22\,\mathrm{m\,s^{-1}}$ (Fig. 3). For this animal, jet frequency increased as speed increased for low speeds but reached an asymptote at speeds above approximately $0.70\,\mathrm{m\,s^{-1}}$.

Swimming performance and oxygen consumption

A detailed analysis of swimming performance and aerobic metabolism at various swimming speeds from these experiments has been given elsewhere (Webber & O'Dor, 1985), but the results are summarized in Table 2 for later use in the comparison of oxygen consumption and pressure data as indices of metabolic rate. The table includes data on a well-studied fish for reference; the comparison of a

Table 1. *Jet frequency (s^{-1}) of eight cannulated squid ($15°C$) and one squid with an ultrasonic transmitter ($10°C$) exercised in a swim-tunnel at various speeds determined from continuous pressure records*

Speed (m s^{-1})	Mass (kg)								
	0·220	0·293	0·303	0·304	0·305	0·391	0·406	0·496	0·491*
0·28	0·93	0·84	0·74	0·78	—	—	—	0·76	0·60
0·35	—	—	—	—	—	0·73	—	—	0·64
0·38	0·98	0·89	0·79	0·83	0·83	—	0·83	0·71	—
0·45	—	—	—	—	—	—	—	—	0·66
0·48	1·06	1·00	0·85	0·74	0·88	0·79	0·88	0·77	—
0·55	—	—	—	—	—	—	—	—	0·69
0·58	1·02	1·15	0·94	0·76	0·90	0·85	0·89	0·76	—
0·68	1·17	1·16	—	—	—	0·91	0·87	0·82	0·69
0·78	—	—	—	—	—	—	0·87	—	—

* Squid with ultrasonic transmitter.

0·4-kg squid to a 0·5-kg salmon was chosen because the average mass of water carried in the squid's mantle is about 0·1 kg. Fish can swim nearly twice as fast using less than half the energy required by squid, as reflected in the cost of transport figures. Maximum oxygen consumption in this squid is higher than any marine poikilotherm of this size range (M, kg) and temperature reported in the literature. As has been reported in most empirical studies on fish (Jones & Randall, 1978), oxygen consumption ($\dot{V}_{O_2}$, ml O_2 h^{-1}) increased exponentially with swimming speed (U, m s^{-1}).
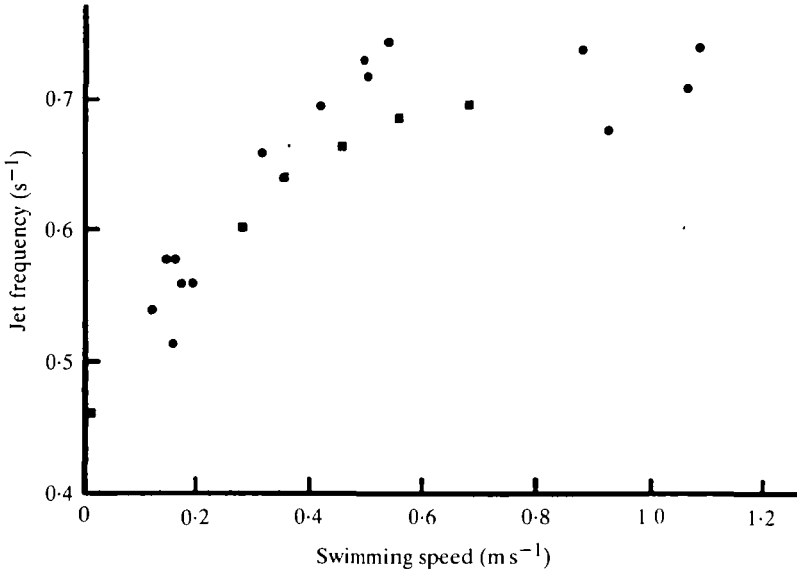

Fig. 3. Increase in jet frequency with swimming speed for a 0·491-kg *Illex illecebrosus* exercised in a swim-tunnel (squares) and freely swimming in a 4×15 m diameter sea water pool with an ultrasonic pressure transmitter (circles), both at 10°C. Jet frequency was measured from pressure records.

Table 2. *Comparison of swimming performance and respiratory metabolism for sockeye salmon,* Oncorhynchus nerka, *and for the squid,* Illex illecebrosus

	O. nerka	I. illecebrosus
Temperature (°C)	15	15
Total length (m)	0·37	0·42
Mass (g)	500	400
Critical speed (m s^{-1})	1·35	0·76
Active metabolism (ml O_2 kg^{-1} h^{-1})	480	1047
Standard metabolism (ml O_2 kg^{-1} h^{-1})	40	313
Rest metabolism (ml O_2 kg^{-1} h^{-1})	—	202
Scope for activity (ml O_2 kg^{-1} h^{-1})	440	734
Gross cost of transport (J kg^{-1} m^{-1})	1·9	7·6
Net cost of transport (J kg^{-1} m^{-1})	1·7	5·4

Salmon data from Brett (1965) and Brett & Glass (1973).
Cost of transport calculated after Schmidt-Neilsen (1972).

Since the exponential relationship resulted in a higher correlation coefficient (r) than the linear or power relationships for individuals, this form has been adopted for squid (r always $> +0.92$ and $> +0.98$ in a majority of cases). The values given in Table 2 are calculated from a multiple regression for 97 determinations of oxygen consumption at various speeds in 24 squid. This yielded the relationship:

$$\dot{V}_{O_2} = 245M^{0.73}e^{1.59U}. \tag{1}$$

This relationship explains 77% of the variation ($r = 0.88$). Most of the residual variation is simply the result of differences in the ability of individual animals to adapt to swimming in the tube, but there was also some variability due to the year of the experiment and the inclusion of the cannulated animals in the data set. The cannulae probably slightly increased the oxygen consumption at higher speeds due to the added drag they caused; however, rejection of these animals was not justified statistically.

The standard rate of metabolism (extrapolated oxygen consumption at $0\,m\,s^{-1}$) and the active metabolism (extrapolated value at critical speed), as derived by Brett (1964), can be calculated from equation 1. The difference between these is the metabolic scope for locomotion, an indication of the capacity of the animal to do work. Oxygen consumption for an animal resting on the bottom of the tube was always lower than the standard rate of metabolism, presumably reflecting the energetic cost of 'hovering' for the negatively buoyant squid. The regression lines for 0.2- and 0.5-kg squid are plotted in Fig. 5B to allow estimations of swimming speeds from pressure.

A similar line for 0.5 kg is also plotted in Fig. 5B for a regression based on nine determinations in three additional squid (0.380–0.519 kg) carrying transducer-transmitters for which oxygen consumptions were measured in the swim-tunnel for speeds ranging from 0.28 to 0.78 m s^{-1}:

$$\dot{V}_{O_2} = 238M^{0.82}e^{1.28U}. \tag{2}$$

Although the number of animals is low ($r = 0.83$), the transducer does not appear to cause any marked shift in the cost of locomotion. The lower costs at high speeds may again reflect the increased drag in the cannulated animals included in the other regression. Since the transducer is completely inside the mantle cavity it would not have this effect.

Pressure–metabolic rate relationships

The speed of the A/D converter (22 Hz) allowed characterization of the pressure waveform developed in the mantle cavity for jet cycles at various swimming speeds. Fig. 4 illustrates the pressure of a smooth swimmer. Animals that had difficulty maintaining position gave more variable patterns, but *Illex illecebrosus* can clearly generate graded pressure jets. Pressure reaches a maximum in 0.09–0.13 s for all jets and then quickly falls to zero. At this point in the cycle, the mantle cavity is at minimum volume (Gosline & Shadwick, 1983). Both the rise and fall of pressure occur during the contraction phase and the period of this phase appears to decrease

slightly as swimming speed increases. The recoil of compressed 'collagen springs' (Gosline *et al.* 1983) then causes pressure to become negative for a brief period (0·06–0·09 s). The magnitude of the negative pressure increases with the pressure of the preceding jet. The negative pressure presumably occurs before the inhalant apertures fully open to allow water into the mantle cavity. The mantle cavity then refills while the pressure is zero before the start of the next jet. A squid increases both jet frequency (Fig. 3) and jet pressure (Fig. 4) with increasing swimming speed. The increase in frequency is primarily the result of a shorter refilling phase (Table 3). Thrust can be increased by increasing the volume of water in the jet, but, since there is little pressure differential to drive refilling, the maximum effective frequency
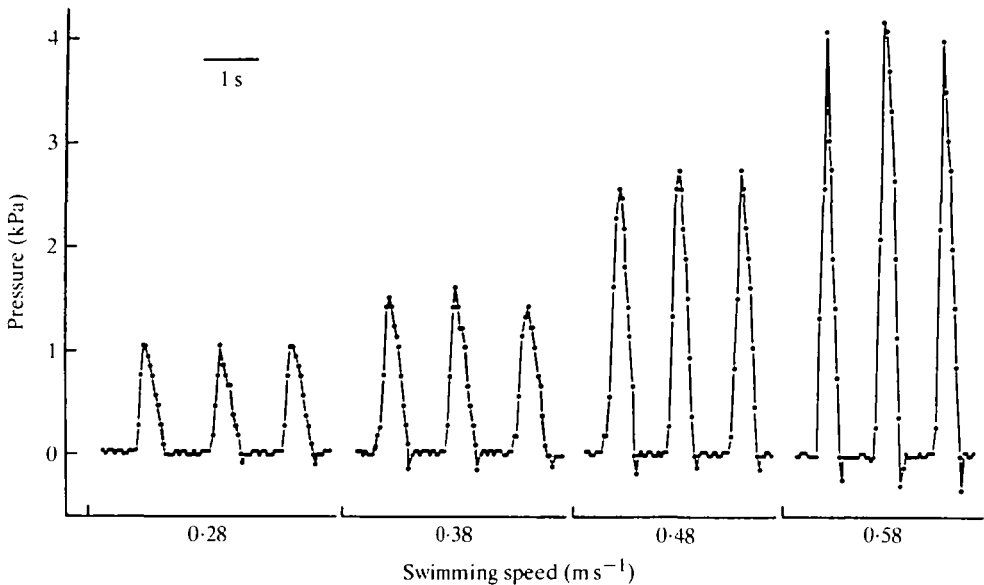

Fig. 4. Record of pressure generated in the mantle cavity of a cannulated squid, *Illex illecebrosus* (0·303 kg) exercised at various speeds in a swim-tunnel at 15 °C. Three jet cycles are shown for each speed. Sampling frequency was 22 analogue-to-digital measurements s^{-1}.

Table 3. *The duration of the refilling and contraction phases of jet cycles for a cannulated squid (0·323 kg) swimming smoothly at various speeds in the swim-tunnel*

Speed (m s^{-1})	Average pressure (kPa)	Peak pressure (kPa)	Jet frequency (s^{-1})	Refill time (s)	Pressure stroke time* (s)
0·28	0·28	1·2	0·74	0·831	0·521
0·38	0·43	1·7	0·79	0·754	0·508
0·48	0·79	3·4	0·85	0·691	0·480
0·58	1·09	5·3	0·94	0·603	0·464

* The pressure stroke is from 0 to peak to 0 pressure.

(Table 1) will be limited by a balance between the amount of water taken in per cycle and the number of cycles. Thrust can also be increased by the higher jet velocities produced at higher pressures, and this seems to be the most important factor at higher speeds. It remains unclear how such graded pressures are produced by the 'all-or-none (non-facilitating, non-summating) response' (Packard & Trueman, 1974; Wilson, 1960) normally associated with the squid giant fibre system, but control of funnel diameter may contribute.

Although the combination of jet frequency and pressure used at a particular speed varied greatly between individuals, average pressure calculated from the area under the pressure curve increased consistently with oxygen consumption. Over the range of average pressures (0·26–1·66 kPa) at sub-critical speeds in the respirometer, a linear relationship between average pressure and speed gave an adequate fit and was used by Webber & O'Dor (1985). Animal mass clearly influenced the relationship, however, and the linear multiple regression of mass, pressure and oxygen consumption gave negative oxygen consumptions on extrapolation to $0 \, \mathrm{m \, s^{-1}}$. When the data were fitted to non-linear models, however, this problem was avoided. The correlation coefficient for a power relationship was the same as for the linear relationship ($r = 0·93$) and higher than for an exponential relationship ($r = 0·85$). The relationship predicting $\dot{V}_{O_2}$ at various pressures and masses based on 69 determinations in 14 animals is:

$$\dot{V}_{O_2} = 555 M^{0·75} P^{0·77}. \tag{3}$$

Curves from this relationship are plotted in Fig. 5A for masses of 0·2 and 0·5 kg, the approximate upper and lower mass limits of the animals tested. Data for two of the smallest squid (0·220 and 0·227 kg) and for the largest squid (0·496 kg) are plotted on the figure and indicate the degree of variability and the predictive value of the relationship.

Pressures in freely swimming squid

The transducer-transmitter has been used in 10 squid, and caused little apparent trauma. Two animals died under the anaesthetic, but seven of the eight remaining were exercised in both the respirometer and the pool tank. In the respirometer, speeds up to $0·78 \, \mathrm{m \, s^{-1}}$ were attained. Swimming behaviour in the tube was the same as that for non-cannulated and cannulated animals except that squid had difficulty maintaining higher speeds (0·58 and $0·78 \, \mathrm{m \, s^{-1}}$) for the full hour, probably because of the reduced mantle cavity volume. When returned to the pool after respirometer trials, the animals swam with the school, were active and fed for up to three days until experiments were terminated due to battery failure.

Complete analysis of these results is in progress, including video analysis of changes in mantle volume and the interaction of fins and jet in a variety of natural behaviour patterns, but only data from a representative animal are presented here to show correspondence between respirometer results and those in free-swimming
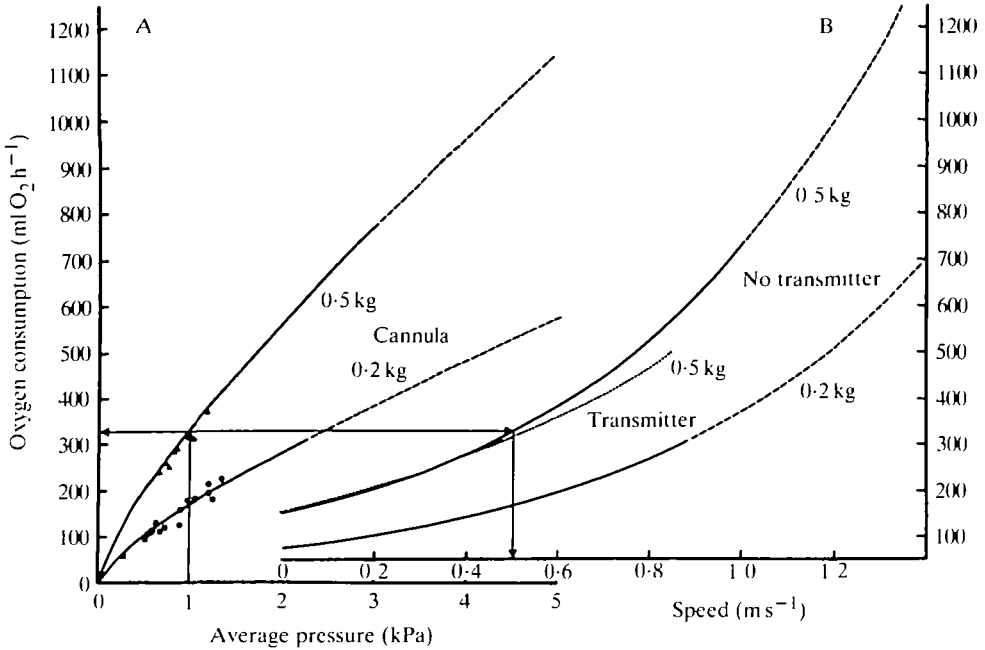
Fig. 5. Interrelationships between oxygen consumption, swimming speed and mantle cavity pressure for *Illex illecebrosus*. (A) The regressions for equation 3 (oxygen–pressure) calculated for squid of 0·2 and 0·5 kg with data for animals of approximately these masses (triangles, 0·496; circles, 0·227; squares, 0·220 kg). (B) Similar solutions for equation 1 (oxygen–speed relationship for intact and cannulated squid, solid curve) compared with the solution for equation 2 (oxygen–speed relationship for squid carrying a transducer-transmitter, dotted curve) at 0·5 kg. The arrows indicate how average pressure data can be used to predict both oxygen consumption and swimming speed from the figure. The dashed portions of the curves are extrapolations to unrealistic oxygen consumptions which are included because the resultant pressure–speed relationships are consistent with direct measurements (see Fig. 7).

squid. A single 0·491-kg animal swam in the respirometer at speeds from 0·28 to 0·68 m s^{-1}. In the pool, it swam from 0·12 m s^{-1} to 1·4 m s^{-1} using consecutive escape jets. Although others performed similarly, this animal gave the most complete range of results in both the respirometer and the pool and it has been used in the analysis that follows. Fig. 6 shows pressure records for this animal swimming in the pool at 10°C. The shape of the pressure curve is the same as that produced by the cannulation method. The negative pressure is also apparent in the pool. The number of data points describing the pressure curve is less for the transmitter than for the cannula method; however, since the digital circuitry for both methods integrates pressure over time the value for average pressure is comparable for the two methods. As observed with the cannula method, both jet pressure and frequency increased as swimming speed increased.

The average pressures for swimming in the respirometer and pool are plotted against swimming speed in Fig. 7. The swimming speeds in the pool were calculated as the change in horizontal distance per unit time, and, since the video analysis did

not detect vertical displacement, they may be slightly underestimated. The solid line in Fig. 7 is the relationship between pressure and speed derived from equations 1 and 3 for a squid of 0·5 kg by eliminating oxygen consumption as a variable:

$$P = 0·35e^{2·1U}. \tag{4}$$

Mass was included in this calculation, but the mass exponents in the equations are very close. The speed produced by a particular pressure is probably independent of the size of the squid. Although the speed–pressure relationship for this individual did not correspond perfectly to that derived from the regressions, it was close over the full range of speeds. The regressions seem quite robust since they yield reasonable predictions both above and below the speeds actually testable in the respirometer. The pressure needed to swim in the microturbulent flow of the respirometer for a particular speed differs little from that needed at the same speed under laminar conditions in the pool. The extrapolations of oxygen consumption in Fig. 5 at the higher speeds are clearly well beyond even the high capacities of squid, but they are probably reasonable estimates of the energy produced by anaerobic metabolism and subsequently made up as an oxygen debt (Webber & O'Dor, 1985).
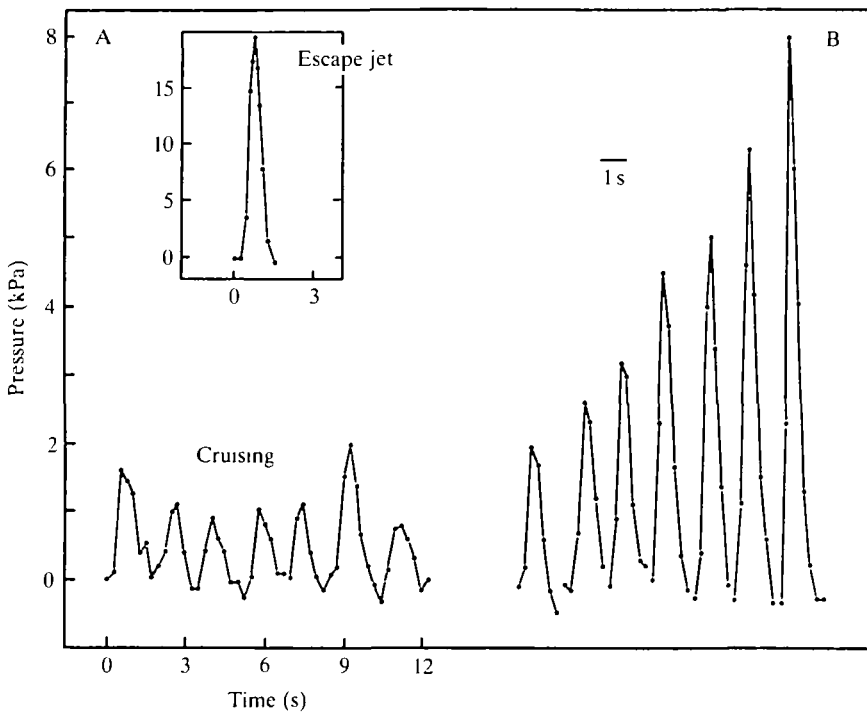

Fig. 6. Records of pressure generated in the mantle cavity of a squid, *Illex illecebrosus* (0·491 kg), freely swimming in a 4×15 m diameter sea water pool with the ultrasonic pressure transducer at 10°C. (A) A continuous pressure record at a cruising speed of (0·15 m s⁻¹) and (B) typical pressure jets of the animal swimming at sub-maximal speeds. The jet in the inset is a maximal escape jet.
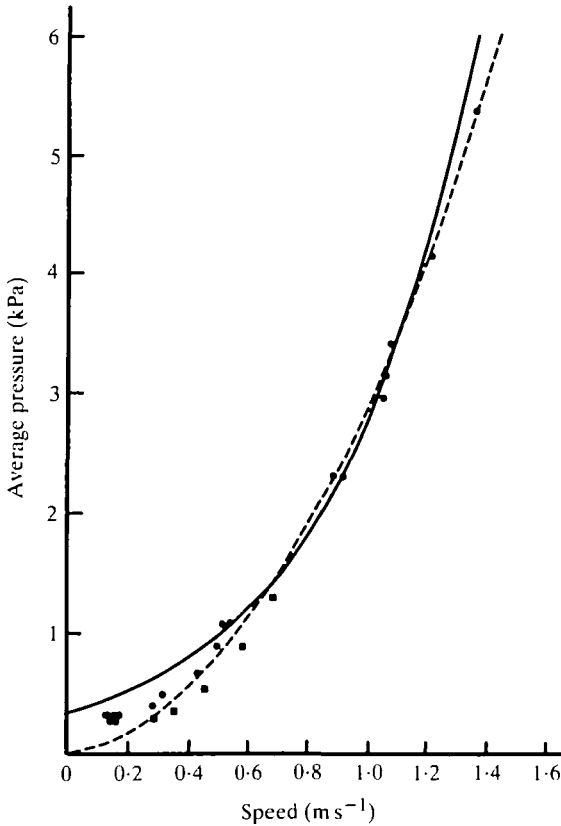
Fig. 7. Influence of swimming speed on average pressure generated in the mantle cavity of *Illex illecebrosus* (0·491 kg) exercised in a swim-tunnel (squares) and freely swimming in a 4×15 m diameter sea water pool (circles) with an ultrasonic pressure transducer at 10°C. The solid line is the predicted relationship from solution of equations 1 and 3 at 0·5 kg for comparison. The dashed line is the estimated pressure required to produce the thrust necessary to overcome drag assuming 20 % efficiency (see text).

Energy budget for captive squid

Given these correlations, it should be possible to estimate energy consumption from pressure data collected for this animal swimming freely in the pool. In the pool the school cruises almost without interruption producing average pressures of 0·38 kPa. The cruising speed calculated from sequences of video images ranged from 0·12 to 0·19 m s^{-1}. The predicted oxygen consumption for this pressure at 15°C is 160 ml O_2 h^{-1}. The appropriate correction to 10°C is still problematical, but, using an energy value for oxygen of 19 J ml^{-1} (Brett & Groves, 1980) and for typical crustacean prey one of 3800 J g^{-1} (O'Dor, 1982), this equates to a daily food intake of 3·8 % body mass. At 15°C squid in this size range may consume as much as 6·7 % body mass per day and have a gross conversion efficiency of 35 % (O'Dor & Wells, 1986). This leaves a small proportion of food intake to support higher level activities such as escape and attack jetting, feeding and interactions within the school which video records indicate may occupy 5–10 % of a squid's time.

DISCUSSION

Their high metabolic rates, voracious feeding, rapid growth and semelparous reproductive pattern all indicate that squid 'live fast and die young'. This life history pattern may be a consequence of their inherently inefficient jet locomotion, which requires power outputs nearly quadruple those of fish to achieve similar speeds. It has been suggested that the resting rate of a metabolism adapted to produce such high output may also be proportionately higher. The resultant 'hyperactivity' may suit squid to life histories that take advantage of short-term variability in the ecosystem while their competitors, fish, live more economically, have adapted to longer lives and use more stable resources (O'Dor & Webber, 1986). The initial stimulus for quantitative studies on squid locomotion was a need for a better understanding of the 'rules' for the competition between squid and fish (O'Dor, 1982). The three studies to date (O'Dor, 1982; Freadman *et al.* 1984; Webber & O'Dor, 1985) all make it clear that squid have a severe handicap in their economy of locomotion. The present study was undertaken to develop a means of determining how and to what extent the natural behaviour patterns of squid compensate for this handicap.

As an example of the need for economy, there is clear evidence that *Illex illecebrosus* and the very similar *Todarodes pacificus*, which occur off Japan, make spawning migrations exceeding 2000 km at average speeds of as high as $0.37 \, \text{m s}^{-1}$ (Dawe, Beck, Drew & Winters, 1981; Hurley & Dawe, 1980; Shevtsov, 1973). If locomotion takes as much energy as respirometer studies suggest, such travel would require that an *Illex* consume 6·5 % of its body mass in prey per day. This is its *ad libitum* feeding rate in captivity (Hirtle, DeMont & O'Dor, 1981), and field data suggest that, even on the feeding grounds, such high rates rarely occur (O'Dor, Durward, Vessey & Amaratunga, 1980). If the squid resort to cannibalism, which is common among squid, and fuel their migration by eating others in the school, only 1 % of the squid could survive for 2000 km (O'Dor & Wells, 1986).

Many mechanisms of energy conservation have been suggested for fish, but few could be tested directly because fish do work against a large volume of water outside their bodies. The difference in the locomotor systems means that some mechanisms proposed for fish, such as the potential advantage produced by interacting vortices in properly spaced schools suggested by Weihs (1974), will not apply to squid. However, other mechanisms, such as retaining laminar flow or climb-and-glide swimming (Weihs, 1973), can be directly tested for squid with the system described here. Such tests will not only indicate how squid behave, but should also improve our understanding of the basic energy requirements of nektonic organisms. The potential for biomechanical and hydrodynamic modelling of squid is also high, but a complete analysis is beyond the scope of this paper.

The same feature which makes squid easy to study makes them inefficient. It is much easier to measure the work done pressurizing a small volume of water inside the mantle than to measure the work done on all the water surrounding a fish, but, since the motion of the animal results from an exchange of momentum between it and the

water, the squid must accelerate the small volume of water in its mantle to very high speeds. This causes a low Froude efficiency (Alexander, 1977). As a first approximation, average pressure may be substituted for variable pressure in the approach of Johnson et al. (1972). From the Bernoulli equation the jet speed (U_j, $m\,s^{-1}$) can be calculated from pressure (P, Pa) and density ($d = 1023\,kg\,m^{-3}$) as:

$$U_j = (2P/d)^{0.5}. \tag{5}$$

From Fig. 5, a 0·5-kg squid at $0.5\,m\,s^{-1}$ would have $P = 1000\,Pa$, giving $U_j = 1.4\,m\,s^{-1}$. A 0·5-kg squid has a funnel diameter of about 0·0011 m, giving an area (a) of 0·000 095 m^2 and a flow (Q) of 0·000 133 $m^3\,s^{-1}$. The product PQ is the power equivalent of pressure–volume work and equals the power output of the muscles, 0·132 W. The power consumed can be calculated from $\dot{V}_{O_2}$, also given in Fig. 5. At 19 J ml^{-1} O_2 the difference between the oxygen consumption at $0.5\,m\,s^{-1}$ (330 ml h^{-1}) and that at rest (100 ml h^{-1}, from Table 2) gives a power consumption of 1·21 W and a muscle efficiency of 11 %. This is a reasonable *in situ* muscle efficiency at a low speed (Goldspink, 1977), particularly considering that some of the muscle work goes to load the collagen springs used during refilling (Gosline *et al.* 1983). Knowing the speed of the squid (U), the Froude efficiency (FE) can be calculated as:

$$FE = \frac{U}{U + 0.5U_j}. \tag{6}$$

In the example above this gives a Froude efficiency of 42 % and a combined efficiency for the production of available power of 4·6 %.

The net cost of transport should reflect the efficiency of the locomotor process. From Table 2, the cost of transport for squid is 3·2 times that of salmon. If efficiencies are in the same ratio, the fish has an efficiency of about 15 %. Although it has not been possible to measure fish efficiency directly because of the diffuse power output, this is the generally accepted value based on a variety of indirect estimates (Blake, 1983; Alexander, 1977; Webb, 1975).

Estimating the power needed to propel a fish has also been difficult, because the undulating body is constantly changing its profile and its drag. Although the mantle diameter in squid changes as it swims, the effect on drag appears to be much smaller than that of fish undulations. The dashed line in Fig. 7 is based on standard equations for rigid body drag, assuming a turbulent boundary layer and including the correction for pressure drag (Blake, 1983). The wetted surface area of a 0·491-kg squid, 0·42 m long and 0·047 m average diameter at the widest point, was calculated as 0·036 m^2. To allow drag force to be compared to pressure, the pressure (P) necessary to produce a thrust (T) was calculated following Johnson *et al.* (1972) as:

$$P = \frac{T}{2a}. \tag{7}$$

The dashed line in Fig. 7, which fits the speed–pressure data for the squid well at high speeds, uses values of T equal to five times the calculated drag. This implies that drag consumes about 20 % of power output. Since the low Froude efficiency

means that only about 40 % of power output is available, the calculated rigid body drag accounts for half of the available power. In contrast, similar calculations account for only 15 % of the power in fish. Presumably, the remaining power in squid goes to induced drag associated with the lift needed to overcome the negative buoyancy of the squid and to accelerate the water taken into the mantle to the speed of the squid.

The pressures required for squid to swim at low speeds are somewhat higher than those predicted by the drag equation. This is probably due to the additional power required for the 'acceleration reaction' (Daniel, 1984). The oscillatory character of squid locomotion means that they are constantly accelerating and decelerating which increases power requirements. This effect is complex because the amount of boundary layer water that must be accelerated also changes with velocity. Daniel (1984) suggested that the overall effect may be smaller in fast-moving squid than in other slow animals using oscillatory modes of locomotion, but these data indicate that it may be significant for squid at cruising speeds. It is also interesting to note that these low speeds are the ones where the fins are used most. More evidence is certainly required, but, since pressures are relatively higher at low speeds, it could be argued that the jet, not the fins, is still the major contributor to locomotion, even at low speed.

Alexander (1977) has argued that the microturbulent flow in swim-tunnels should have little effect on the boundary layer turbulence, that conventional assumptions about laminar and turbulent flow at a particular Reynolds numbers apply, and that the power required to swim in static water should be no lower than that in a swim-tunnel. Earlier workers suggested that swimming costs in nature under laminar conditions might be lower than those in the tunnel (Brett, 1963; Webb, 1975). Fig. 7 provides the first direct evidence on this controversy. The analysis above for squid assumes a turbulent boundary layer, even though the Reynolds number of the slowest squid studied was only 150 000, below the transition speed for even a bluff body. Deciding which drag equation is appropriate would require a careful analysis of all the other factors outlined above and considerably more data; however, the pressure required to swim in the tunnel actually appears to be *less* than that required in the pool. This is not consistent with either assumption about drag. One explanation may be that the microturbulence in the tunnel thins the boundary layer and reduces the volume of water involved in the acceleration reaction. If this is true, the result could not be applied to fish which maintain a steady speed. This difference could also relate to the vertical component of swimming in the pool which was not accounted for but could be in future studies using this technique.

Although these experiments have, perhaps, produced more questions than answers so far, it seems clear that direct measurement of pressure–flow power output in freely swimming squid can provide key information for an analysis of the energetics of squid locomotion under both laboratory and field conditions. The relationship between power consumption (oxygen consumption) and power output (pressure) can be characterized for a variety of conditions, the alternation of powered vertical swimming with passive gliding, for example. Even without a complete

analysis, the approach presented in Fig. 5 allows one to estimate the speed and oxygen consumption of squid based only on the average pressure data relayed by the transducer-transmitter. A reasonable approximation of average energy expenditure by squid in nature could be developed by simply releasing several squid carrying transducers in a small bay and recording pressure data over several days. For more detailed analysis, a system of sonobuoys, radio-linked to a shore-based computer, is under development which will also continuously triangulate the position of the squid. This system will allow individual squid to be 'calibrated' and compared. Pressure–oxygen relationships for an individual squid with a transducer can be measured in the field using a small portable respirometer of the sort described by DeMont & O'Dor (1984) before it is released. The pressure–speed relationship for this squid can then be established based on returned position and pressure data. Once these relationships for an individual are established, calibration curves like those in Fig. 5 can be drawn for subsequent analysis. A complete picture of energy consumption also requires information on vertical movement and ambient temperature; these data might also be collected by simultaneously releasing other squid, carrying depth, pressure and temperature transducers, as part of the same school.

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