

Respiration and Swimming Performance of Short-finned Squid (*Illex illecebrosus*)

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Abstract

Intramantle pressure transducers allowed the monitoring of respiration and swimming performance of cannulated and free-swimming squid (*Illex illecebrosus*). Jet pressure and oxygen consumption of individual squid were measured simultaneously in a tunnel respirometer at various swimming speeds. The rate of oxygen consumption increased logarithmically with swimming speed up to critical speeds of 70–90 cm/sec (about two body lengths per second). Oxygen consumption values for a 400 g squid at 15° C were the highest that have been recorded for marine poikilotherms at this size and temperature: 313 ml/kg/hr for standard metabolism and 1,047 ml/kg/hr for active metabolism at maximum speed. A 40-cm squid (total length) uses about six times more energy per unit distance than a sockeye salmon of similar length at 15° C. The rate of oxygen consumption increased linearly with average jet pressure generated in the mantle cavity and the relationship was highly correlated for speeds of 0.15–0.80 cm/sec. The results from telemetric monitoring of jet pressure generated by a free-swimming squid in a 15-m pool and the oxygen-pressure relationship show great promise for studying the activity and bioenergetics of squid in nature.

Introduction

Short-finned squid (*Illex illecebrosus*) are similar to pelagic teleosts in that they are fast-swimming, carnivorous animals which engage in extensive horizontal migrations (Squires, 1957; Dawe *et al.*, 1981). They also undergo vertical migrations of hundreds of meters (Roper and Young, 1975; Lu and Roper, 1979). However, there are few data on the energetics of these activities. Although the metabolism and swimming performance of many fish species over a wide range of activity, environmental conditions and behavior have been described (Brett and Groves, 1980), the only reports on the energetics of mobile cephalopods, where activity is quantified in terms of swimming speeds, are by O'Dor (1982) for *Loligo opalescens* and Wells *et al.* (1983) for *Octopus vulgaris*. Studies like these allow prediction of metabolic costs for species with well documented behavior in nature, e.g. for river-migrating salmon (Brett, 1970), but estimation of the energetics for oceanic species (i.e. some fishes and squids) with less well known behaviors and energy-saving strategies is not practical. While such laboratory studies are necessary, it remains a challenge to devise a means of measuring accurately the rates of energy expenditure of free-moving animals in nature. The best approximations of the activity and metabolism of fish in nature were obtained by Priede and Young (1977), Ross *et al.* (1981), and Priede (1983) by continuously monitoring the heart rate and tail-beat frequency with ultrasonic telemetry. These methods are not perfect because of heart-stroke-volume changes and the poor correlation between tail-beat frequency and swimming speed.

I. illecebrosus swims by producing a jet of water for thrust and, at the same time, forces water over its gills for respiration. At high speeds, the jet produces all the thrust, but, at lower speeds, most of the forward momentum is derived from the jet with a small contribution from the fins. By measuring jet pressure and correlating this with oxygen consumption at various swimming speeds, it should be possible to use telemetering ultrasonic pressure transducers to measure metabolic rates and monitor activity of free-swimming squid in nature. The purpose of this study was to measure the energetics of *I. illecebrosus* at various levels of activity with existing techniques and to develop a unique method for determining metabolic costs of free-swimming squid in nature.

Materials and Methods

From August to November of 1982 and 1983, squid were captured in a mackerel trap in St. Margaret's Bay, Nova Scotia, and transferred in tanks of seawater to the 15-m diameter pool at the Aquatron Laboratory, Dalhousie University. In captivity, the squid were fed daily on live fish (*Fundulus heteroclitus*) and frozen shrimp (*Pandalus borealis*) and were maintained as described by O'Dor *et al.* (1977). The weights of the squid ranged from 200 to 550 g and total lengths (dorsal mantle length equals 64% of total length) from 25 to 50 cm.

The respirometer was a recirculating water tunnel, constructed of acrylic plastic, with inside diameter of 19.2 cm (Farmer and Beamish, 1969). Total volume was 92 liters. The swimming chamber (85 cm in length) was

enclosed by honeycomb grids and a wire screen, which were designed to reduce vertical speed perturbations and to create a uniform microturbulent flow profile. New water was introduced to the respirometer by gravity flow through a heat exchanger. When oxygen measurements were being made, the system was "closed" and the water was recirculated. The oxygen probe (Beckman Model 0260 Oxygen Analyzer) was inserted in a separate water line with constant flow rate. The experiments simulated backward (tail first) swimming of the squid. Temperature was maintained at $15 \pm 0.2^\circ \text{C}$.

To continuously monitor intramantle pressure of animals swimming in the respirometer, a cannula was inserted through the mantle and attached to a pressure transducer (Statham Model P23AC). The transducer was connected to an integrating analog digital converter (ADALAB) with 12-bit accuracy and sampled at a rate of 22/sec. For continuous monitoring of intramantle pressure of free-swimming animals, a telemetric system was used. Pressure was measured by a subminiature ultrasonic pressure transducer which was designed by Vemco Engineering, Shad Bay, Nova Scotia. The transducer ($5.3 \times 1.4 \times 1.4 \text{ cm}$) was positioned ventrally to the body organs in the mantle cavity. The signal (69 KHz) was transmitted to a hydrophone-receiver and transformed to a digital signal for input to the microcomputer. The frequency of the digital signal was proportional to pressure to the limit of the calibration technique ($\pm 1\%$). For both methods (cannula and ultrasonic), jet pressure was integrated and an average value was computed for each swimming speed. The average pressure value accounts for both jet pressure and frequency.

Squid which were used in the tests were not fed during the 24-hr period prior to being transferred to the respirometer. Each animal was conditioned at rest for 1–3 hr until it was calm. Animals that were not cannulated were swum in successive 60-min stages of increasing speed (10 cm/sec per stage), yielding a maximum sustained swimming speed or critical speed, as described by Brett (1964). Animals that were cannulated were swum for 30–40 min at each speed. An effort was made to minimize excitement by reducing movement and light intensity and by inserting a one-way mirror between the observer and the animal. In many cases, video recordings of swimming animals were made with a low light intensity camera and a Beta-1 cassette recorder.

Regression analyses were performed on a microcomputer with standard statistical procedures (Ott, 1977). Programs to measure analog pressure and ultrasonic pressure data and to integrate the raw pressure data were developed by the authors.

Results

Metabolic rate and swimming speed

In a typical trial, a squid was forced to swim continuously through a series of increasing water speeds in the respirometer until it collapsed against the screen. With decrease in water speed to 7 cm/sec, the animal dropped to the bottom and respired deeply and rapidly for a few minutes. In most cases, the squid stayed in resting posture and the respiratory frequency declined to the stable pretrial level in 30–60 min. In six cases, it was possible to measure the oxygen debt accumulated by measuring the elevated respiration during this resting period. These ranged from 132 to 267 ml O_2/kg , with average and standard deviation of 167 ± 58 . As swimming speeds increased, the strength and frequency of mantle contractions increased and the use of fins decreased. At the higher speeds (50–90 cm/sec), the fins were rolled down against the body to minimize drag. Under these conditions, the jet controls both the angle of attack and the forward (tail first) momentum. Because the squid is negatively buoyant (3–4%), the jet angles the body slightly upward in order to counteract the effect of gravity. At low swimming speeds, the fin action angles the body upward between jet thrusts and may also contribute a small portion of the forward momentum. The critical swimming speeds for five squid, as measured by the method of Brett (1964) were 62–88 cm/sec, the highest value being attained by the largest animal (44.5 cm TL). However, there was no apparent relationship between critical swimming speed and total length for the small sample. Relative to total length, the critical speeds ranged from 1.6 to 2.2 body lengths per second, the extreme values being for animals which weighed 257 and 235 g respectively.

The rate of oxygen consumption was observed to increase exponentially with swimming speed to near the critical level, as indicated by the trend for a 353 g squid (Fig. 1). Most studies of fish metabolism in respirometers have also indicated exponential relationships (Jones and Randall, 1978). However, the oxygen consumption at maximum sustained swimming speed (near collapse) for squid was often lower than the predicted regression value. This has been observed in other studies and probably reflects an anaerobic contribution to energy for swimming, which causes the accumulation of the oxygen debt. The relationship between oxygen consumption rate (O_2 , ml/hr) and swimming speeds (S , cm/sec) for 24 squid is

$$\text{O}_2 = 102.0 \times 1.016^S \quad (r = 0.73, n = 97) \quad (1)$$

The inclusion of animal weight (W , g) as an independent variable in the multiple regression gives the relationship

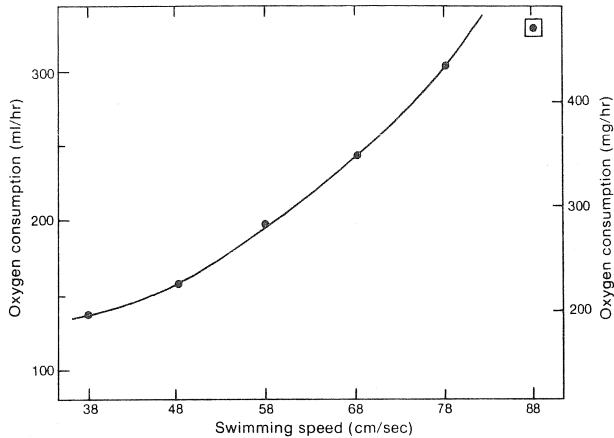


Fig. 1. Influence of swimming speed on the metabolic rate of a typical *I. illecebrosus* (353 g) with water temperature at 15°C. (Swimming speed at collapse was 88 cm/sec.)

$$O_2 = 1.58W^{0.725} \times 1.016^S \quad (r = 0.88, n = 97) \quad (2)$$

Thus, the inclusion of animal weight results in an increase in the proportion of the variance of oxygen consumption that can be attributed to its regression on swimming speed from 53% in equation (1) to 77% in equation (2).

From the latter equation, it is possible to calculate the average standard rate of metabolism (extrapolated oxygen consumption at zero speed) and the average active metabolism (extrapolated oxygen consumption at critical swimming speed), as derived by Brett (1964) from a similar relationship for sockeye salmon (*Oncorhynchus nerka*). The difference between these values is the metabolic scope for activity or an indication of the capacity of the animal to work, which is considerably higher in short-finned squid than in sockeye salmon of comparable size (Table 1). The actual or effective swimming weight of a 400 g squid is comparable to a 500 g salmon, because jet propulsion requires the squid to carry water in its mantle while swimming. The difference represents the average weight of water in the mantle cavity, based on observations of changes in mantle radius of *L. opalescens* (Gosline and Shadwick, 1983) and an estimate of 200 ml as the maximum volume of water in the mantle cavity of *I. illecebrosus* from analysis of video-recordings. The gross and net costs of transport per unit weight are evidently much higher in squid than in salmon (Table 1) but the oxygen debt is much lower.

The costs of transport of *I. illecebrosus* at various swimming speeds were calculated from equation (2) for an animal weighing 400 g (Fig. 2). Oxygen consumption values were converted to energy equivalents by the factor that 1.0 ml $O_2 = 4.63$ cal (Elliott and Davison, 1975). The resultant normalized curves indicate that the most economical speeds of transport for *I.*

TABLE 1. Comparison of swimming performance and respiratory metabolism at 15°C for short-finned squid (*Illex illecebrosus*) and sockeye salmon (*Oncorhynchus nerka*). (Salmon data from Brett, 1965.)

Parameter	<i>Illex illecebrosus</i>	<i>Oncorhynchus nerka</i>
Total length (cm)	42	37
Total weight (g)	400	500
Critical speed (cm/sec)	76	135
Active metabolism (ml O_2 /kg/hr)	1,047	480
Standard metabolism (ml O_2 /kg/hr)	313	40
Scope of activity (ml O_2 /kg/hr)	734	440
Rest metabolism (ml O_2 /kg/hr)	202	—
Gross cost of transport (J/kg/m)	7.6	1.9
Net cost of transport (J/kg/m)	5.4	1.7
Oxygen debt (ml/kg)	167	329
Time for recovery (hr)	0.5–1	3–4

illecebrosus are between 50 and 70 cm/sec. The shape of the relationship is similar to those for *O. nerka* (Brett, 1965; Brett and Glass, 1973) and *L. opalescens* (O'Dor, 1982), but the cost is much higher for squids.

Whenever possible, the rate of oxygen consumption was determined for squid in a resting posture on the bottom of the respirometer, as described by Bradbury and Aldrich (1969). Not all animals assumed a complete resting posture, and only the oxygen measurements for animals in resting or near-resting posture (2–3 spontaneous jets per minute) were used to determine the relationship between oxygen consumption (O_2 , ml/hr) and body weight (W , g) for animals in the range of 204–496 g, as

$$O_2 = 12.0 W^{0.329} \quad (r = 0.52, n = 24) \quad (3)$$

In this regression, only 27% of the variation in oxygen consumption is attributable to variation in body weight. The high variability may have been due to spontaneous activity and inherent differences among animals. Hirtle *et al.* (1981) noted that captive *I. illecebrosus* exhibited high feeding variability which seemed to be related to the hierarchy within the school. Much of the variability may have been due to the difficulty of controlling the spontaneous activity of the smaller animals in the sample. For squid larger than 200 g, the predicted rate of oxygen consumption at rest (equation 3) is always lower than the extrapolated value at zero speed (equation 2), indicating an energetic cost for "hovering".

Jet pressure and metabolic rate

The rate of oxygen consumption increased linearly with average pressure due to the increase in jet frequency with swimming speed, as illustrated by data for a 293 g cannulated squid which was forced to swim at speeds from 28 to 68 m/sec (Fig. 3). Although jet pressure at a particular swimming speed varied from

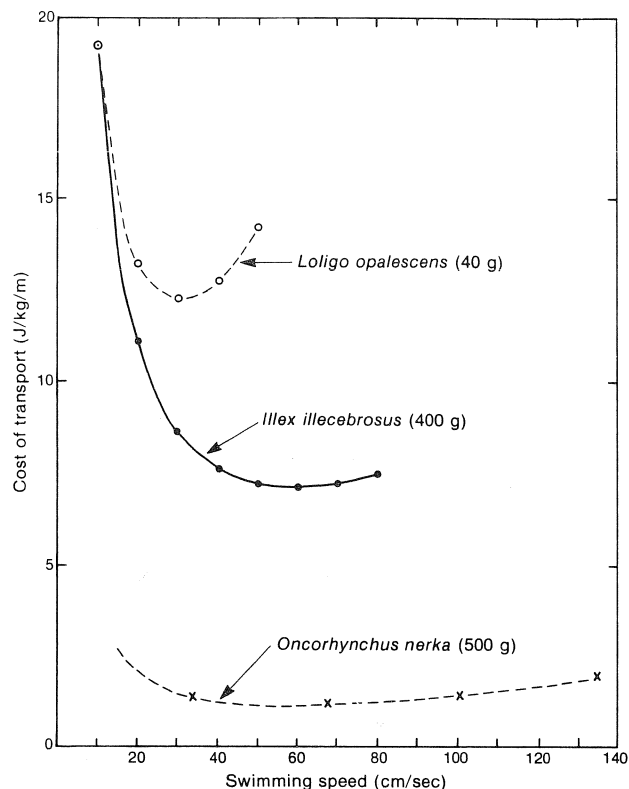


Fig. 2. Trends in costs of transport for *I. illecebrosus* weighing 400 g at increasing swimming speeds and with water temperature at 15°C, together with data for *L. opalescens* weighing 40 g at 14°C (O'Dor, 1982) and for *O. nerka* weighing 500 g at 15°C (Brett, 1965; Brett and Glass, 1973).

being consistent for a "smooth" swimmer to oscillatory for an animal that had difficulty in maintaining position, the oxygen pressure relationship for each of 14 cannulated squid was highly correlated ($r > 0.90$). The relationship between the rate of oxygen consumption (O_2 , ml/hr) and average pressure (P , newtons/100 cm²) for all 14 cannulated squid at 15°C over a wide range of average pressure (2.6 – 13.4 N/100 cm²) is

$$O_2 = 20.2 P + 34.5 \quad (r = 0.68, n = 69) \quad (4)$$

In this regression, pressure explains only 48% of the variation in rate of oxygen consumption. The inclusion of animal weight (W , g) as an independent variable in the multiple regression gives the relationship

$$O_2 = 18.6 P + 0.495 W - 109.3 \quad (r = 0.93, n = 69) \quad (5)$$

In this case, 87% of the variation in rate of oxygen consumption is attributable to variation in pressure. The wide range of pressure allows prediction of the rate of oxygen consumption over a wide range of activity. For each 100 g increase in animal weight, rate of oxygen consumption increases by 49.5 ml/hr at a given level of pressure.

Jet pressure in free-swimming squid

The limited availability of large healthy squid after the ultrasonic pressure transducer became available in

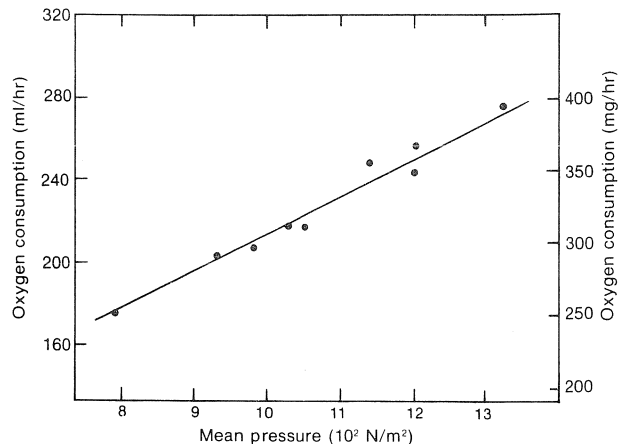


Fig. 3. Relationship between rate of oxygen consumption and average pressure generated in the mantle cavity of a cannulated *I. illecebrosus* (293 g) with water temperature at 15°C. (The squid was forced to swim at speeds of 28–68 cm/sec.)

1983 resulted in its use in only one animal (female, 550 g, maturity stage III according to the scale of Durward *et al.*, 1979), which was tested in both the respirometer and the Aquatron pool at 11.5°C. The transducer displaced about 4% of the water in the mantle cavity at maximum mantle expansion. Pressure records for this squid from forced swimming in the respirometer at 35 cm/sec and forced free-swimming (exhibiting net avoidance) in the Aquatron pool are illustrated in Fig. 4. In the respirometer at constant swimming speed, the jet pulses were quite regular, with average pressure of 4.3 N/100 cm² and oxygen consumption rate of 199 ml/hr (Fig. 4A). At this pressure, equation (5) predicts an oxygen consumption rate of 243 ml/hr. This predicted value is not directly comparable to the measured rate of oxygen consumption because equation (5) was developed for animals that were tested at 15°C, but it is a reasonable value for an animal of this size at a speed of 35 cm/sec according to equation (2). Adjustment of the predicted rate of oxygen consumption (243 ml/hr) for the temperature difference, by using a short-term Q_{10} value of 1.6 (Demont, MS 1981), gives a value of 196 ml/hr which is very close to the measured value.

When the same squid, with the ultrasonic transducer, was transferred to the Aquatron pool, it behaved normally and moved about at highly variable speeds. The segment of pressure data in Fig. 4B was recorded just after a net had been placed in the pool. The squid moved away from the net in a typical avoidance response but it did not exhibit a full escape reaction. Although the jet pulses were clearly less regular than in the respirometer, the average pressure was 9.9 N/100 cm². This value predicts an average oxygen consumption rate of 347 ml/hr at 15°C from equation (5) and an average swimming speed of 51 cm/sec from equation (2). This speed is approximately one body length per second, which is considered as the typical cruising speed for most aquatic animals. The predicted rate of oxygen consumption must, of course, be adjusted

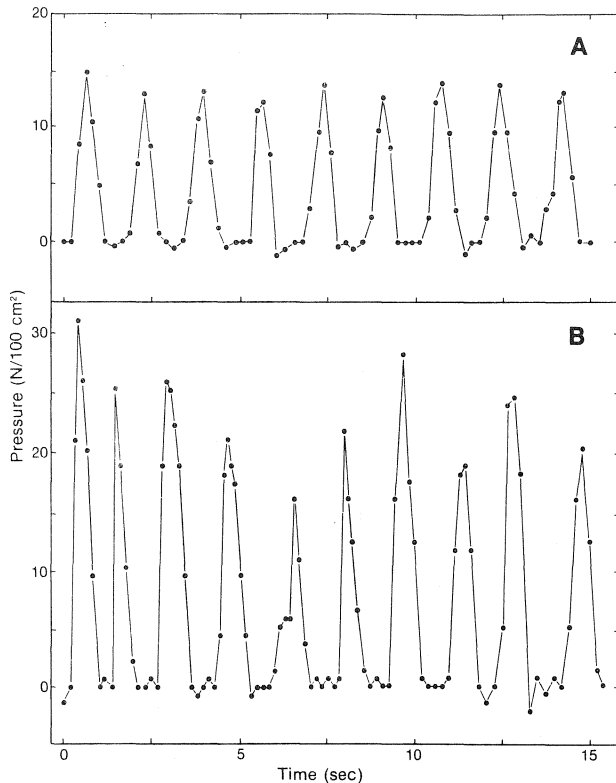


Fig. 4. Records of pressure generated in the mantle cavity of an *I. illecebrosus* (550 g) with an ultrasonic pressure transducer from (A) forced swimming in the respirometer at 35 cm/sec, and (B) net avoidance reaction during free-swimming in the Aquatron pool. (Water temperature was 11.5°C in both cases.)

downward to account for the temperature difference, the resultant value being 295 ml/hr.

Discussion

At similar temperatures, *I. illecebrosus* has the highest known metabolic rate among fishes and other cephalopods of comparable size. This is consistent with its life-style of high growth rates and maturation within a short life-cycle of a year (Squires, 1967; O'Dor *et al.*, 1980; Hirtle *et al.*, 1981).

Demont and O'Dor (1984) studied the oxygen consumption of *I. illecebrosus* at various levels of temperature, activity and squid size. They quantified activity as the percentage of time not spent in resting posture. In terms of oxygen consumption per kilogram of body weight, their predicted values for a 400 g squid at rest (0% activity) and continuously jetting (100% activity) were 454 and 1,823 ml/hr respectively at 15°C. In the present study, relative oxygen consumption values at 15°C were 354 and 1,047 ml/hr at swimming speeds of 0 and 80 cm/sec respectively. The difference at the higher levels of activity may be accounted for in part by

differences in experimental methods and definition of maximum activity. In the study by Demont and O'Dor (1984), an animal at 100% could have been burst-jetting and under stress. Also, their study involved few measurements at activity levels above 50% and at temperatures above 13°C, the range of oxygen consumption per kilogram of body weight being 1,198–1,595 ml/hr for five specimens. In the present study it is worth noting that two animals (235 and 320 g) had very high rates of oxygen consumption (1,372 and 1,417 ml/hr), which are within the above-noted range for five specimens. However, the major reason for the differences between the two studies may be the very high, and perhaps unrealistic, Q_{10} value (6.6) that is generated by the regression in Demont's (MS 1981) study. More extensive studies of the effects of long-term temperature changes on squid metabolism are needed.

Results from the only other study on squid energetics at precise swimming speeds, i.e. *L. opalescens* by O'Dor (1982), were rather similar to those of the present study. Although *L. opalescens* has a lower metabolic rate per kilogram of weight (862 ml O_2 /hr) at a maximum sustained speed of 36 m/sec, the critical swimming speeds (relative to body length, BL) were similar, being 1.60–2.20 BL/sec for *I. illecebrosus* and 1.84 BL/sec for *L. opalescens*. The sustained critical swimming speed for a 500 g sockeye salmon (*O. nerka*) is higher at 3.7 BL/sec.

I. illecebrosus has a lower sustained critical swimming speed than sockeye salmon and uses twice as much energy at the critical speed (Table 1). *I. illecebrosus* uses 3–4 times more energy per unit distance to swim at the critical speed than sockeye salmon of the same swimming weight but slightly lower total length. In terms of relative swimming speed (BL/sec), *I. illecebrosus* uses 6 times more energy per unit distance for speeds between 1.0 and 2.0 BL/sec (data from Fig. 2 and from Brett, 1965). The cost of transport for *L. opalescens* (12.5 J/kg/m) (O'Dor, 1982) is even higher than that for *I. illecebrosus* in this study (7.3 J/kg/m). These data indicate that squid are inefficient swimmers, compared to fish, and support Alexander's (1977) prediction, based on a theoretical analysis of jet propulsion, that squid should be inefficient because they must accelerate much less water to a much higher speed to achieve the same thrust as fish. The data also indicate that the cost of transport for a jet-propelled squid decreases with increasing size of animal in much the same way as it does for undulatory swimmers. O'Dor (1982) suggested that *L. opalescens* would have to be voracious predators, eating the equivalent of 11% of their body weight per day, in order to sustain an extensive migration. The situation for *I. illecebrosus* appears to be considerably more favorable but the costs are still very high. Squid may reduce their costs

of transport by swimming in favorable currents and by climb-and-glide swimming, which was suggested by Weihs (1973) as a means for a negatively-buoyant animal to reduce its cost of transport up to 50%. It should also be realized that an animal in a respirometer is subjected to microturbulent water, whereas water flow in nature is laminar. This difference may be significant for fish (Webb, 1975). Squid may also travel more efficiently in schools than in isolation.

The high correlation between oxygen consumption and jet pressure for individual squid and for the combined data indicates that the pressure telemetry method has great promise for determining metabolic rates and activity patterns of free-swimming squid in nature. The method is more accurate than those that are used for measuring fish activity and energetics because it accounts for both amplitude and frequency changes during swimming.

It should be possible to monitor swimming patterns and metabolic rates of *I. illecebrosus* under natural conditions in near-shore waters. Jet-pressure, depth-pressure and temperature-sensing ultrasonic transmitters could be inserted in the mantle cavity of animals from the same school in a localized area and their activity monitored for extended periods of time. Possible energy-saving strategies, such as vertical migrations, climb and glide swimming (Weihs, 1973) and temperature preferences could be investigated. In addition, it may be possible to measure metabolic costs of short and long distance migrations.

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