

Northwest Atlantic



Fisheries Organization

Serial No. N934

NAFO SCR Doc. 84/IX/125

SCIENTIFIC COUNCIL MEETING - SEPTIMEBER 1984

The Respiratory Metabolism and Swimming Performance  
of the Squid, *Illex illecebrosus*

by

D. M. Webber and R. K. O'Dor

Department of Biology, Dalhousie University  
Halifax, Nova Scotia, Canada, B3H 4J1

ABSTRACT

Pressure transducers, measuring intra-mantle pressure allowed monitoring of total P-V work associated with swimming and respiration in cannulated and free-swimming squid (*Illex illecebrosus*). Squid were "calibrated" in a Brett-type tunnel respirometer by simultaneously measuring pressure and oxygen consumption at various swimming speeds. Oxygen consumption increased logarithmically with swimming speed. The maximum or critical velocity, as defined by Brett (1964), a squid can swim is between 0.70 and 0.80 ms<sup>-1</sup>, approximately 2 body lengths s<sup>-1</sup>. Values for oxygen consumption were the highest recorded for marine poikilotherms at this size and temperature; 303 mlO<sub>2</sub>Kg<sup>-1</sup>h<sup>-1</sup> for standard metabolism and 1080 mlO<sub>2</sub>Kg<sup>-1</sup>h<sup>-1</sup> for maximum velocity for a 0.400 Kg animal at 15 °C. The relation predicting oxygen consumption at various combinations of weight and velocity is:  $OxCons(mlO_2h^{-1}) = 1.58 Mass(g)^{0.725} 1.016 Vel(cm/s)$  (r=0.88) (n=97). At a body length of 0.40 m *I. illecebrosus* uses 6.0 times more energy per unit distance than a sockeye salmon (*Oncorhynchus nerka*) of approximately the same length at 15 °C. Oxygen consumption increased linearly with the average pressure generated in the mantle cavity resulting from both increasing jet frequency and pressure. The oxygen-pressure relation for individual animals was highly correlated over a wide range of velocities (r=0.90 to 0.99). The relation predicting oxygen consumption over a wide range of pressure for all the animals is:  $OxCons.(mlO_2h^{-1}) = -109.3 + 18.8 Pre(10^2 Nm^{-2}) + 0.495 Mass(g)$  (r=0.93). A telemetering ultrasonic pressure transducer measuring intra-mantle pressure was used in free-swimming squid in the 15 m

Aquatron Pool Tank. The results indicate that the oxygen-pressure relation has great promise as a means of studying the activity and bioenergetics of cephalopods in nature.

#### INTRODUCTION

Illex illecebrosus is similar to pelagic teleosts in that it is fast swimming, carnivorous and is believed to engage in extensive migrations (Squires, 1957; Dawe et al., 1981). It also undergoes vertical migrations over hundreds of meters (Roper and Young, 1975; Lu and Roper, 1979). However there are few data to allow description of the energetics of these activities.

There are data describing the metabolism and swimming performance of numerous fish over a wide range of activity and environmental conditions and behaviours (Brett and Groves, 1980). To date the only data on the energetics of swimming cephalopods where activity is quantified in terms of swimming or walking velocities are from O'Dor (1982) for Loligo opalescens and Wells et al. (1983) for Octopus vulgaris. Studies like these allow prediction of metabolic costs of closely documented behaviour in nature, for example for river migrating salmon (Brett, 1970); however, estimating energetics of other species, i.e. oceanic fish and squid, that have less well known behaviours and energy saving strategies, is not practical.

These lab studies are necessary, but it remains a challenge to devise a means of measuring more accurately rates of energy expenditure of free-moving animals in nature. The best approximations to the activity and metabolism of fish in nature were by Priede and Young (1977), Ross et al. (1981) and Priede (1983), by continuous monitoring of heart rate and tailbeat frequency using ultrasonic telemetry. These methods are not perfect because of heart stroke-volume changes and the poor correlation between tailbeat frequency and swimming velocity.

I. illecebrosus swims by producing a jet for thrust and at the same time forces water over its gills for respiration. At high velocities the jet produces all the thrust and at lower velocities a high proportion of the forward momentum is derived from the jet with a small contribution from the fins. By measuring jet pressure and correlating this to 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 1982-83 squid were captured in a mackerel box trap at Mill Cove (St. Margaret's Bay), Halifax County and transferred to the 15 m diameter Aquatron pool as described by O'Dor (1977). While in captivity the animals were fed on a daily diet of live fish (Fundulus heteroclitus) and frozen shrimp and kept under a controlled light-dark cycle. Weight and length of animals used was 0.200 to 0.550 Kg and 0.25 to 0.50 m.

The respirometer was a recirculating water tunnel constructed of acrylic plastic (0.192 m inside diameter) (Farmer and Beamish, 1969). Total volume was 92 liters. The swimming chamber was 0.85 m in length and enclosed by honeycomb grids and a wire screen designed to reduce vertical velocity perturbations and create a uniform, microturbulent velocity profile. New water was introduced by gravity flow through a heat exchanger into the respirometer. During oxygen measurement the system was "closed" and water was recirculated. An oxygen probe ( $O_2$ -Beckman Model 0260 Oxygen Analyzer) was inserted in a separate line with a constant flow rate. Temperature was controlled at  $15 \pm 0.2^\circ C$ . All animals were swum "tail" first.

To continuously monitor intra-mantle pressure of animals swimming in the respirometer a cannula was inserted through the mantle and attached to a Statham Model P23AC pressure transducer. The transducer was attached to an integrating analog to digital converter (ADALAB) with 12 bit accuracy, sampling at a rate of  $22 s^{-1}$ .

A telemetry system was employed for continuous monitoring of intra-mantle pressure of free-swimming animals. Pressure was measured by a sub-miniature ultrasonic pressure transducer designed with Vemco Engineering, Shad Bay, N.S. The transducer (5.3cm \* 1.4cm \* 1.4cm) was positioned inside the mantle cavity ventral to the body organs. The signal (69 KHz) was transmitted to a hydrophone-receiver and transformed to a digital signal for input to a microcomputer. The frequency of the digital signal was proportional to pressure. For both methods (cannula and ultrasonic) jet pressure was integrated and an average value for pressure was computed for each swimming velocity. The average pressure value accounts for both jet pressure and frequency.

Test squid were not fed for a 24 hour period prior to being transferred to the respirometer. The animal was conditioned at rest in the respirometer for one to three hours until it was calm. If an animal was not cannulated it was swum "Brett style" (Brett, 1964) in successive 60 minute increments of increasing velocity ( $0.10 \text{ m s}^{-1}$ ) yielding a maximum swimming speed or critical velocity as defined by Brett (1964). Animals that were cannulated were swum 30-40 minutes at each velocity. An effort was made to minimize excitement by reducing movement and light intensity and inserting a one-way mirror between the observer and the animal. In many cases video recordings of swimming animals were also made using a Beta-1 cassette recorder and low light intensity camera.

Regression analyses were performed on an Apple microcomputer using a microcomputer statistical package (MISP) developed by Hilborn (1981). Programs to measure analog pressure, ultrasonic pressure data and to integrate raw pressure data were developed by the authors.

## RESULTS

### Metabolic Rate-Velocity Relations

In a typical trial a squid was swum through a series of increasing water speeds until they collapsed against the screen. The water speed was then lowered to  $0.07 \text{ m s}^{-1}$  and the animal would drop to the bottom and respire deeply and rapidly for a few minutes. The time for recovery for a 0.400 Kg animal is listed in Table 1. In most cases the animal stayed in resting posture and respiratory frequency dropped to a stable pre-trial level within 0.5 to 1 hours. As swimming speed increased the strength and frequency of mantle contractions increased and use of the fins decreased. At the higher speeds ( $0.50$  to  $0.90 \text{ m s}^{-1}$ ) the animal frequently tucked its fins down under and against the mantle to minimize drag. Under these conditions the jet controls both the angle of attack and the forward momentum. I. illecebrosus is negatively buoyant (3-4%), so to counteract the effect of gravity the jet angles the body upward. At low speeds the fin action angles the body upwards in between jets and may also contribute to a small proportion of the forward momentum.

The critical velocity measured for "Brett" style swimming for 5 animals

ranged from 62 to 88 cm s<sup>-1</sup>. The highest critical velocity was attained by the largest squid (0.445 m). Relative to body length (L), velocities ranged from 1.60 to 2.21 L s<sup>-1</sup> for animals of 0.257 and 0.235 Kg respectively.

There was no apparent relation between critical velocity and body length for the small sample.

Oxygen consumption was observed to increase exponentially with swimming velocity (Figure 1). Most studies of fish metabolism in respirometers have also observed the relation to be exponential (Jones and Randall 1978). Often the oxygen value for the maximum sustained velocity, near collapse, was lower than predicted by regression. This has been observed in other studies and probably reflects an anaerobic contribution to energy for swimming. The regression predicting oxygen consumption at various velocities for 24 animals is;

$$\text{Ox.Cons. (ml O}_2 \text{ h}^{-1}) = 102.0 * 1.016^{\text{Vel (cm s}^{-1})}. \quad (1)$$

This relation explains 53 % of the variation (r = 0.73; n = 97). Including weight as another independent variable gives the relation;

$$\text{Ox.Cons. (ml O}_2 \text{ h}^{-1}) = 1.58 \text{ Mass (g)}^{0.725} * 1.016^{\text{Vel (cm s}^{-1})}. \quad (2)$$

This relation explains 77% of the variation (r = 0.88; n = 97).

From this equation it is possible to calculate the standard rate of metabolism (extrapolated oxygen consumption at 0 velocity) and the active metabolism (extrapolated value at critical velocity) as derived by Brett (1964) for sockeye salmon (Oncorhynchus nerka). The difference between these is the metabolic scope for locomotion, an indication of the capacity of the animal to do work.

Table 1 illustrates comparisons of I. illecebrosus to sockeye salmon, a fish of high aerobic capacity. The total and net metabolic costs were used to calculate the gross and net cost of transport. The actual or effective swimming weight of a 0.400 Kg I. illecebrosus is comparable to a 0.500 Kg salmon since jet propulsion requires a squid to carry water in its mantle while swimming. Based on data for mantle radius changes during L. opalescens jets (Gosline and Shadwick 1983) and using 200 ml of water as a maximum mantle volume from video analysis, an average mantle volume was calculated in order to compute an effective swimming weight (0.500 Kg) of a 0.400 Kg squid.

The cost of transport of I. illecebrosus at various velocities is shown in Figure 2. The shape of this relation is similar to that for Brett's data for sockeye salmon (Webb 1975a) and for O'Dor's data for L. opalescens (O'Dor 1982). From this study, the most economical speeds for transport for I illecebrosus (0.34-0.50 m) are those greater than  $0.30 \text{ m s}^{-1}$ .

Whenever possible, oxygen consumption was also determined for animals resting on the bottom of the tube in a resting posture described by Bradbury and Aldrich (1969). Not all animals would rest and only the oxygen measurements for animals ranging from complete rest to 2 to 3 spontaneous jets per minute were used. The relation predicting resting rates at various weights is;

$$\text{Ox.Cons.}(\text{ml O}_2 \text{ h}^{-1}) = 12.0 * \text{Mass}(\text{g})^{0.329}. \quad (3)$$

In this regression the independent variable accounts for only 27 % of the variation ( $r = 0.52$ ;  $n = 25$ ). The high variability may be due to the narrow range of weights used (0.204 to 0.496 Kg), spontaneous activity, and to inherent individual variability. Also, individuals in captivity have been observed to exhibit high feeding variability related to a hierarchy within the school (Hirtle et al. 1981). Much of the variability also occurs in the smaller animals whose spontaneous activity is more difficult to control. It is interesting to note that the predicted resting rate is always lower than the extrapolated value at 0 velocity for a particular weight indicating an energetic cost for "hovering".

#### Pressure-Metabolic Rate Relations

Average pressure generated in the mantle cavity increased linearly with oxygen consumption as a result of both increasing jet frequency and pressure. Jet pressure for a velocity can vary from consistent for a "smooth" swimmer to oscillatory for an animal that has difficulty maintaining position. The oxygen pressure relation for individual animals was highly correlated (0.90 to 1.0) over a wide range of average pressures ( $2.6 * 10^2 \text{ N m}^{-2}$  to  $13.4 * 10^2 \text{ N m}^{-2}$ ). Figure 3 shows the oxygen pressure relation for a 0.293 Kg animal. The relation predicting oxygen at various pressures for all 14 cannulated animals is;

$$\text{Ox.Cons.}(\text{ml O}_2 \text{ h}^{-1}) = 34.5 + 20.2 \text{ Pre}(10^2 \text{ N m}^{-2}). \quad (4)$$

In this case pressure explains only 48% of the variation ( $r = 0.68$ ;  $n = 69$ ).

Including mass as another independent variable gives the relation ;

$$\text{Ox.Cons. (ml O}_2 \text{ h}^{-1}) = -109.3 + 18.6 \text{ Pre}(10^2 \text{ N m}^{-2}) + 0.495 \text{ Mass(g)}. \quad (5)$$

This relation explains 87% of the variation ( $r = 0.93$ ;  $n = 69$ ). The range of pressures is considerable allowing for prediction of oxygen consumption over a wide range of activity. For a 0.100 Kg increase in mass, oxygen consumption increases by 49.5 ml O<sub>2</sub> h<sup>-1</sup>.

#### Pressures in Free-Swimming Squid

Due to the limited availability of large healthy squid in 1983, the ultrasonic pressure transducer was used in only one 0.550 Kg female squid (maturity stage III; from Durward et al. (1979)) which was swum both in the respirometer and in the pool. At maximum mantle radius the transducer displaced 4% of the mantle cavity volume. Figure 4 shows pressure records for this animal swimming in both the respirometer and the pool at 11.5 °C. The animal consumed 199 ml O<sub>2</sub> h<sup>-1</sup> and produced an average pressure of  $4.3 * 10^2 \text{ N m}^{-2}$  at  $0.35 \text{ m s}^{-1}$  in the respirometer (Fig. 4<sup>(a)</sup>). At this pressure equation 5 predicts an oxygen consumption of 243 ml O<sub>2</sub> h<sup>-1</sup>. This value is not directly comparable to the measured oxygen consumption since equation 5 was developed for animals at 15 °C, but is a reasonable consumption for an animal of this size at this speed at 15° according to equation 2. When adjusted for temperature using Demont's (1981) short-term Q<sub>10</sub> of 1.6, the predicted value is 196 ml O<sub>2</sub> h<sup>-1</sup>, very close to the measured value.

Given this good correspondence, it should be possible to make similar extrapolations from pressure data collected for the animal swimming freely in the pool. The animal behaved normally in the pool moving at highly variable speeds. The segment reproduced in Figure 4<sup>(b)</sup> was taken just after a net had been placed in the water. The animal was moving away from the net in a typical avoidance reaction, but was not using a full escape response. Although swimming is clearly less regular than in the respirometer, the average pressure of  $9.9 * 10^2 \text{ N m}^{-2}$  predicts an average oxygen consumption of 347 ml O<sub>2</sub> h<sup>-1</sup> (at 15°C, eq.5) and an average speed of  $0.51 \text{ m s}^{-1}$  (eq.2). This is 1 body length s<sup>-1</sup> for this animal, a value considered a typical cruising speed for most aquatic animals. The predicted oxygen consumption must, of course, be adjusted down for temperature as above, giving a value of 295 ml O<sub>2</sub> h<sup>-1</sup>.

## DISCUSSION

I. illecebrosus has the highest metabolic rate known for a fish or cephalopod at this size and temperature. This result is consistent with its lifestyle of high growth rates and maturity in one year (Squires 1967 ; O'Dor et al. 1980 ; Hirtle et al. 1981).

A study by Demont and O'Dor (1984) predicts oxygen consumption for I. illecebrosus at various levels of weight, temperature and activity. They quantified activity as the percentage of time not spent in resting posture. Most of the data in the present study are at the extreme end of their extrapolations but their predicted values for a 0.400 Kg animal at 15 °C at rest (0% activity) and continuously jetting (100% activity) were 454 and 1823 ml O<sub>2</sub> Kg<sup>-1</sup> h<sup>-1</sup>. These compare to 303 and 1080 ml O<sub>2</sub> Kg<sup>-1</sup> h<sup>-1</sup> for 0 and 80 cm s<sup>-1</sup> respectively, in the present study. The differences at the higher levels of activity may be accounted for, in part, by differences in experimental methods of describing activity. An animal in Demont's study, at 100% activity, could be burst jetting and under stress. Also, his study contained only a few measurements above 13 °C and 50% activity (n = 5) varying from 1198 to 1595 ml O<sub>2</sub> Kg<sup>-1</sup> h<sup>-1</sup>. It is worth noting that two animals in the present study showed very high rates of oxygen consumption of 1372 (0.235 Kg) and 1417 (0.320 Kg) ml O<sub>2</sub> Kg<sup>-1</sup> h<sup>-1</sup> approaching his predicted values, but the major problem is probably a very high and perhaps unrealistic Q<sub>10</sub> of 6.6 generated by the earlier regressions. More extensive studies on the effects of long-term temperature changes on squid metabolism are needed.

The results from O'Dor (1982) using Loligo opalescens, the only other study on squid energetics at precise swimming velocities, were similar to this study. L. opalescens has a lower metabolic rate (862 ml O<sub>2</sub> Kg<sup>-1</sup> h<sup>-1</sup>) at a maximum sustained velocity of 0.36 m s<sup>-1</sup>. Relative to body length both I. illecebrosus and L. opalescens have similar critical speeds, 1.60 to 2.21 body lengths s<sup>-1</sup> versus 1.84 body lengths s<sup>-1</sup> respectively. This compares to 3.7 body lengths s<sup>-1</sup> for a sockeye salmon of 0.500 Kg.

Compared to sockeye salmon, I. illecebrosus has a lower sustained critical swimming velocity and consumes twice as much energy at the critical velocity (Table 1). I. illecebrosus uses three to four times more energy per unit distance to swim at the critical velocity than sockeye salmon of the same swimming weight but slightly lower length (0.37m vs. 0.42m). In terms of relative swimming speed (body lengths s<sup>-1</sup>) I. illecebrosus uses 6.0 times more energy per unit



distance for speeds between 1.0 and 2.0  $L \cdot s^{-1}$  (data from figure 2 and from Brett (1965a)). L. opalescens shows an even higher cost of transport than I. illecebrosus, 12.5 (from O'Dor 1982) versus 7.3  $J \cdot Kg^{-1} \cdot m^{-1}$  respectively. These figures show 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 since they must accelerate much less water to a much higher velocity to achieve the same thrust as a fish. They also suggest the cost of transport for jet propelled squid decreases with size 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 11% of their body weight per day to sustain an extensive migration. The situation for I. illecebrosus appears to be considerably more favourable but the costs are still very high. Squid may reduce their costs by swimming in favourable currents and by climb and glide swimming, suggested by Weihs (1973) as a means for a negatively bouyant 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 is significant for fish (Webb 1975). A squid may also travel more efficiently in schools than in isolation.

The high correlation between oxygen consumption and jet pressure for individual animals and for combined data from all animals shows 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 used for measuring fish activity and energetics because it accounts for both amplitude and frequency changes during swimming. It is obvious that this approach is necessary to achieve an overall bioenergetic model for this species incorporating daily and seasonal activity patterns. Future plans are to insert jet pressure, depth pressure and temperature sensing ultrasonic transmitters into animals within the same school. It should then be possible to answer questions such as: Do squid vertically migrate and use climb and glide swimming as a means of cutting costs? How do these costs compare to those of horizontal swimming? How fast do squid travel while migrating and how much does it cost? How often do squid burst jet or rest on the bottom and do they exhibit temperature preferences which reduce their apparently staggering energy costs?

#### REFERENCES

- Alexander, R.McN. 1975. Swimming. In "Mechanics and energetics of animal locomotion" (R.McN. Alexander and G. Goldspink, ed.), pp.222-248. Chapman and Hall, London.

- Bradbury, H.E., and F.A. Aldrich. 1969. Observations on locomotion of the short-finned squid, I. illecebrosus (Lesueur, 1821), in captivity. Can. J. Zool. 47: 741-744.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183-1226.
1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can. 22: 1491-1501.
- 1970a. Fish—the energy cost of living. In "Marine Aquaculture" (W.J. McNeil, ed), pp. 37-51.
- Brett, J.R., and T.D.D. Groves. 1980. Physiological energetics. In "Fish physiology Vol. VIII. Bioenergetics and growth" (W.S. Hoar, D.J. Randall and J.R. Brett, ed), pp. 279-352. Academic Press, New York, N.Y.
- Dawe, E.G., P.C. Beck, H.J. Drew, and G.H. Winters. 1981. Long-distance migration of a short-finned squid (Illex illecebrosus). NAFO SCR Doc. 81/VI/24, Ser. No.N303, 4 p.
- Demont, M.E. 1981. The effects of activity, temperature and mass on the respiratory metabolism of the squid, Illex illecebrosus. M. Sc. Thesis. Dalhousie University.
- Demont, M.E., and R.K. O'Dor. 1984. The effects of activity, temperature and mass on the respiratory metabolism of the squid, Illex illecebrosus. J. Mar. Biol. Ass. U.K. 64: 535-543.
- Durward, R.D., T. Amaratunga, and R.K. O'Dor. 1979. Maturation index and fecundity for female squid, Illex illecebrosus (Lesueur, 1821). Int. Comm. Northwest Atl. Fish. Res. Bull. 14: 67-72.
- Elliott, J.M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19: 195-201.
- Farmer, G.J., and F.W.H. Beamish. 1969. Oxygen consumption of Tilapia nilotica in relation to swimming speed and salinity. J. Fish. Res. Board Can. 26: 2807-2821.
- Gosline, J.M., and R.E. Shadwick. 1983. The role of elastic energy storage mechanisms in swimming: an analysis of mantle elasticity in escape jetting in the squid, Loligo opalescens. Can. J. Zool. 61: 1421-1431.
- Hilborn, R. 1981. Microcomputer interactive statistics and plotting (MISP) :57 pp.
- Hirtle, R. W. M., M.E. Demont, and R. K. O'Dor. 1981. Feeding, growth and metabolic rates in captive short-finned squid, Illex illecebrosus, in relation to the natural population. J. Shell. Res. 1; No.2: 187-192.

- Jones, D.R., and D.J. Randall. 1978. The respiratory and circulatory systems during exercises. In "Fish physiology Vol. VII. Locomotion" (W.S. Hoar and D.J. Randall, ed.) pp. 425-501. Academic Press, New York, N.Y.
- Lu, C.C., and C.F.E. Roper. 1979. Cephalopods from deepwater dumpsite 106 (Western Atlantic) : vertical distribution and seasonal abundance. Smith. Contrib. Zool. 288: 36 pp.
- O'Dor, R.K. 1982. Respiratory metabolism and swimming performance of the squid, Loligo opalescens . Can. J. Fish. Aquat. Sci. 39: 580-587.
- O'Dor, R.K., R.D. Durward, and N. Balch. 1977. Maintenance and maturation of squid ( Illex illecebrosus ) in a 15 meter diameter circular pool. Biol. Bull. 153: 322-335.
- O'Dor, R.K., R.D. Durward, E. Vessey, and T. Amaratunga. 1980a. Feeding and growth in captive squid, Illex illecebrosus , and the influence of food availability on growth in the natural population. ICNAF Sel. Pap. 6: 15-21.
- Priede, I.G. 1983. Heart rate telemetry from fish in the natural environment. Comp. Biochem. Physiol. 76a: 515-524.
- Priede, I.G., and A.H. Young. 1977. The ultrasonic telemetry of cardiac rhythms of wild brown trout ( Salmo trutta L. ) as an indicator of bio-energetics and behaviour. J. Fish Biol. 10: 299-318.
- Roper, C.F.E., and R.F. Young. 1975. Vertical distribution of pelagic cephalopods. Smithsonian. Contrib. Zool. 209: 1-51.
- Ross, L.G., W. Watts, and A.H. Young. 1981. An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. J. Fish Biol. 18: 479-490.
- Squires, H.J. 1957. Squid, Illex illecebrosus (Lesueur) in the Newfoundland fishing area. J. Fish. Res. Board Can. 14: 693-728.
1967. Growth and hypothetical age of the Newfoundland bait squid Illex illecebrosus illecebrosus . J. Fish. Res. Board Can. 24: 1209-1217.
- Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190: 158p.
- Weih, D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. J. Mar. Res. 31: 194-209.
- Wells, M.J., R.K. O'Dor, K. Mangold, and J. Wells. 1983. Oxygen consumption in movement by Octopus . Mar. Behav. Physiol. 9: 275-287.

Table 1. Comparison of swimming performance and respiratory metabolism for the squid Illex illecebrosus and sockeye salmon Oncorhynchus nerka (Brett 1965).

	Squid	Salmon
Temperature ( $^{\circ}\text{C}$ )	15	15
Total length (m)	0.42	0.37
Total weight (g)	400	500
Critical speed ( $\text{m}\cdot\text{s}^{-1}$ )	0.80	1.35
Active metabolism ( $\text{ml O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ )	1080	480
Standard metabolism ( $\text{ml O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ )	303	40
Rest metabolism ( $\text{ml O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ )	212	—
Scope for activity ( $\text{ml O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ )	777	440
Gross cost of transport ( $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ )	7.3	1.9
Net cost of transport ( $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ )	5.2	1.7
Oxygen debt		
Time for recovery (h)	0.5-1	3-4

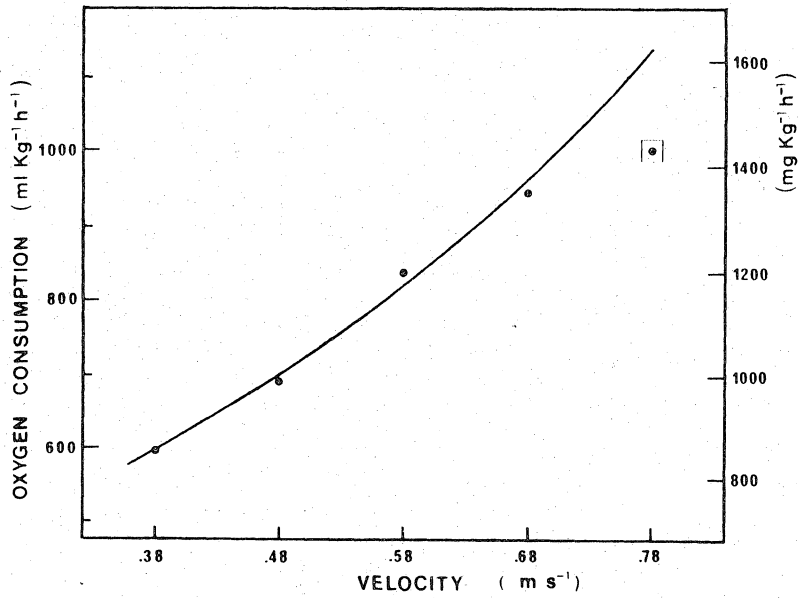


Fig. 1. The influence of velocity on the metabolic rate of a typical swimming squid, *Illex illecebrosus*, (0.406 Kg) at 15°C. The value in the square was not used to determine the line of best fit. The critical swimming velocity for this animal was 0.70 m s<sup>-1</sup>.

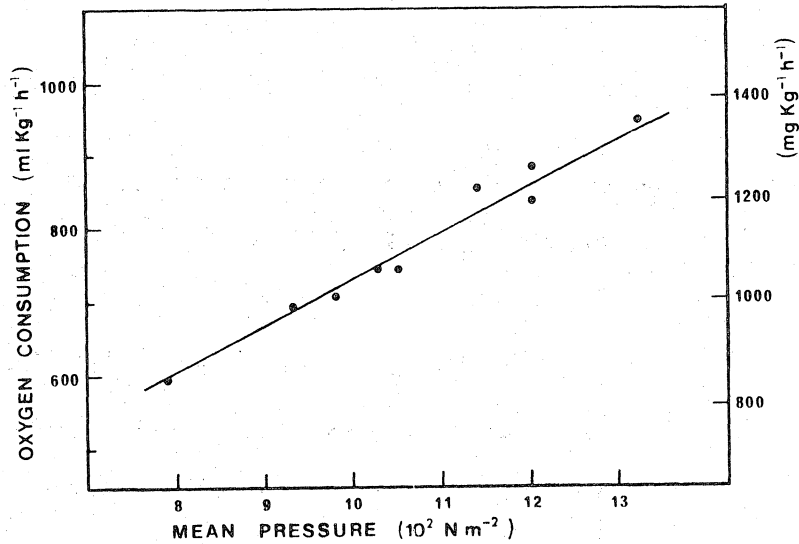


Fig. 2. The effect of average pressure, generated in the mantle cavity, on the rate of oxygen consumption of a cannulated squid, *Illex illecebrosus*, (0.293 Kg) at 15°C. The animal was forced to swim from 0.28 to 0.68 m s<sup>-1</sup>.

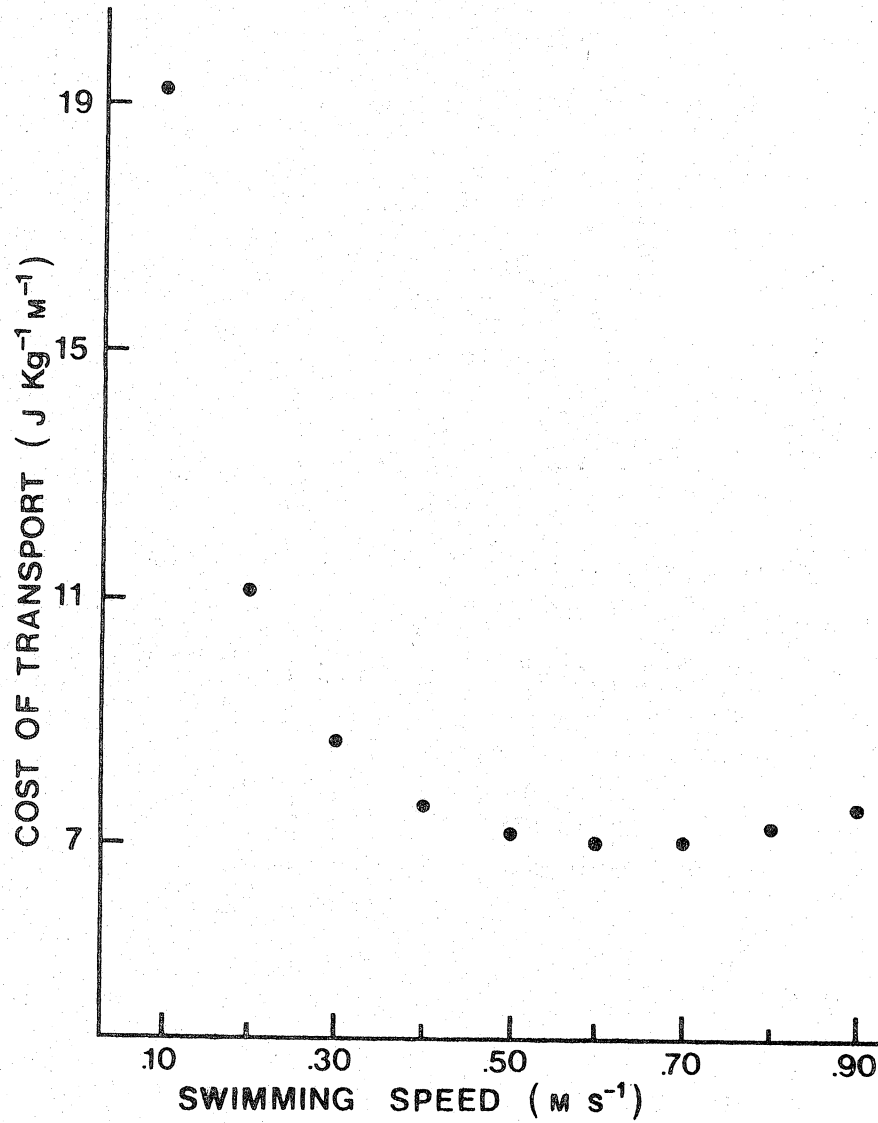


Fig. 3. The cost of transport of a 0.400 kg squid, Illex illecebrosus, at various velocities at 15 °C. Oxygen consumption values were estimated from eq.2 and were converted to energy equivalents using 1.0 ml O<sub>2</sub>=4.63 cal (from Elliott and Davison 1975).

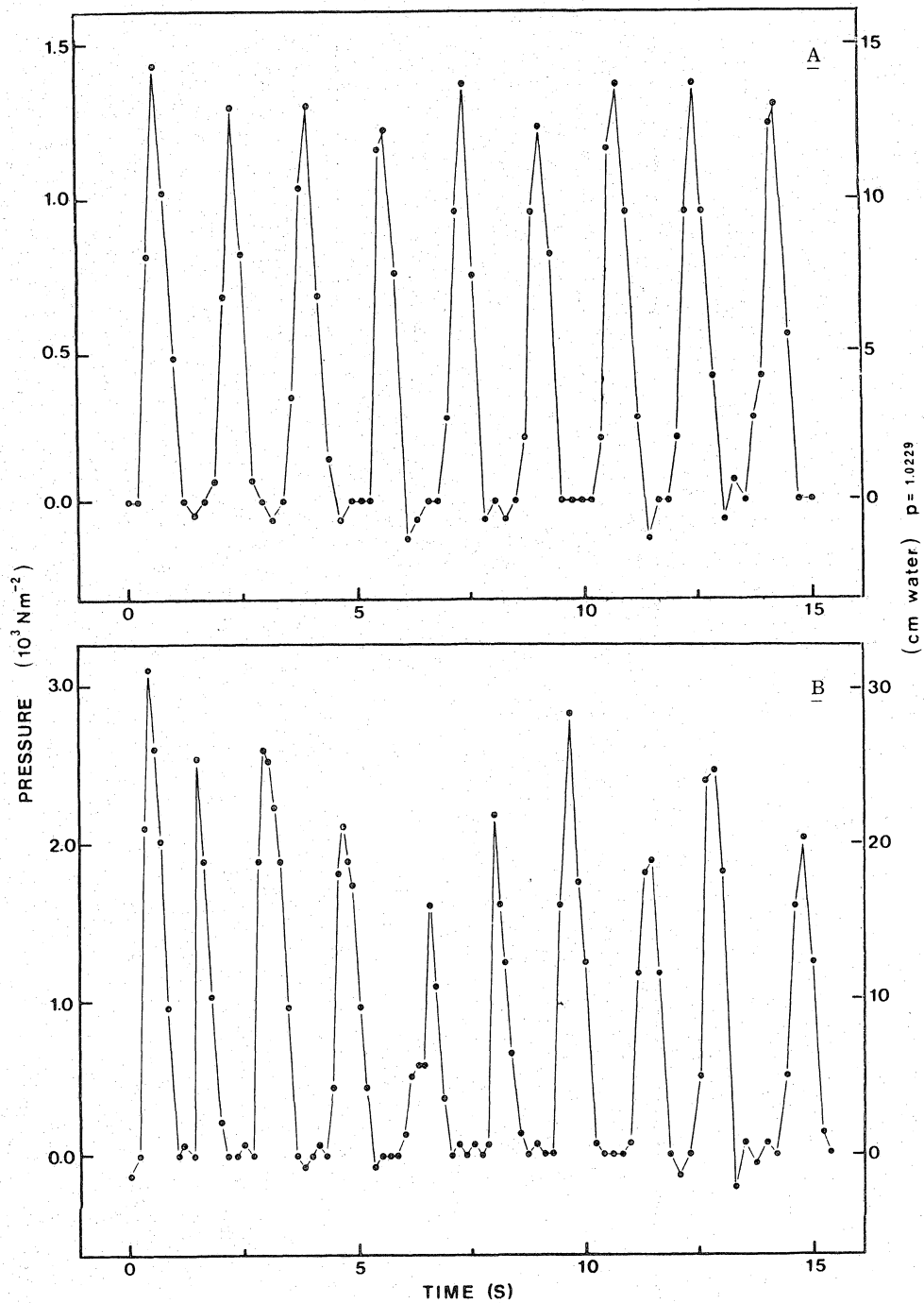


Fig. 4. Records of pressure generated in the mantle cavity of a squid, Illex illecebrosus, (0.550 Kg) swimming with the ultrasonic pressure transducer at  $11.5^{\circ}\text{C}$ . (a) free-swimming in the Aquatron pool tank exhibiting a net avoidance reaction. Average pressure was  $9.9 \times 10^2 \text{ N m}^{-2}$ . (b) forced to swim  $0.35 \text{ m s}^{-1}$  in a water tunnel. Average pressure was  $4.3 \times 10^2 \text{ N m}^{-2}$ .

