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THE LOCOMOTION AND ENERGETICS OF HATCHLING SQUID, *ILLEX ILLECEBROSUS*

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ABSTRACT

Although never seen in nature, gelatinous egg masses up to 1 m in diameter containing 10,000 to 100,000 eggs have been produced in captivity by female *Illex illecebrosus* swimming in mid-water in the 15 m diameter Aquatron pool. When incubated at temperatures between 13 and 26°C these masses produced viable hatchlings whose behaviours were observed and recorded. The hatchlings sink at 5 mm s⁻¹, swim vertically at speeds up to 26 mm s⁻¹, hover and avoid both the surface and the bottom. Metabolic rates estimated from rates of yolk utilization and calculated values for swimming costs were used to predict "critical periods" or survival times for unfed hatchlings in various temperature and activity regimes. These are discussed in relation to the hypothesized role of the Gulf Stream in distribution of the hatchlings of this commercially important but still poorly understood squid species. Potential benefits from vertical migration are suggested and a comparison with *Loligo opalescens* made.

The ommastrephid squid, *Illex illecebrosus* (Lesueur), occurs in the western North Atlantic Ocean from the Labrador Sea south at least to central Florida, and has produced catches exceeding 100,000 metric tons in its northern range during several recent years. Its life cycle is not well known, but there is evidence that the major stocks which feed during the summer on the Scotian Shelf and Grand Banks come from juveniles found in late winter in the upwelling zone along the northern edge of the Gulf Stream (O'Dor, 1983) and that adults from these stocks migrate south in the fall (Dawe *et al.*, 1981). This is probably a spawning migration to warm waters since eggs fail to develop at temperatures below 12°C (O'Dor *et al.*, 1982), and, as this report indicates, develop well at temperatures up to 26°C. The spawning sites are unknown, and while earlier literature suggests demersal spawning (Hamabe, 1962; 1963), recent observations suggest that mid-water spawning of large neutrally buoyant egg masses in the Gulf Stream is a plausible alternative (O'Dor and Balch, 1985).

The behaviours and metabolic patterns required to survive in the open ocean at 20 - 25°C should be quite different from those required to survive near the bottom on the continental shelf at 13°C. This study examines the behaviour of newly hatched *I. illecebrosus* in the laboratory and uses data

on yolk absorption rates, standard metabolic rates and swimming speeds to estimate the "critical periods" of hatchlings under a variety of temperature and activity regimes. The consequences for animals in nature are then briefly considered. Similar data for *Loligo opalescens* Berry are examined and compared to test the applicability of the approach.

MATERIALS AND METHODS

ANIMALS

Adult squid were held in the 15 m diameter, 3 m deep pool at the Aquatron Laboratory under conditions that induce precocious maturation and spawning (O'Dor *et al.*, 1977). Reports on the characteristics of the tenuous gelatinous egg masses, which are typically spherical and between 0.5 and 1.0 m in diameter, have appeared elsewhere (Durward *et al.*, 1980; O'Dor and Balch, 1985). Intact egg masses can be collected from the pool and incubated at controlled temperatures. A long-handled triangular sheet-metal funnel, 1 m on a side at the outside edge, was used to "scoop" a mass off the bottom and direct it into a bag, 0.5 m in diameter and 1 m long, made of black nylon window screen. The bag

was attached to the funnel with Velcro; once a mass had been raised near the surface it was detached and the open end sealed with the Velcro. A polyethylene drum liner (200 l) was lowered beneath the enclosed mass, and an entire mass, still suspended in water, could be lifted out using a crane. For studies of egg development rate, an enclosed mass was left suspended in the liner and a gentle flow of constant temperature water introduced (16, 21, and 26°C).

Newly hatched squid have a mantle length of about 1.2 mm and easily escaped through the screen around the mass. The overflow from the liner was allowed to flow upward through a 1 l settling cone covered with 0.5 mm mesh nylon netting to retain the hatchlings. The velocity gradient produced as the water ascended the cone allowed the squid to find a level where they could swim comfortably. At intervals squid were removed and placed in other holding tanks or experimental systems.

TECHNIQUES

Behavioural observations were recorded in either a standard 20 l glass aquarium through a 50 mm lens or in a vertical flow-through swim chamber (3 mm square and 78 mm high, made from microscope slides) through a Zeiss dissecting microscope at 5x with the ocular replaced by an RCA TC 2011/N low-light video camera which was connected to a Sony SLO-323 Beta recorder. A Vicon Industries Model V240 Date/Time Display Generator was used to add a time base to the nearest 0.1 s to the recording. Frame-by-frame analysis was used to calculate swimming velocities. Squid at various stages, both pre- and posthatch, were photographed in plastic petri dishes through a Zeiss inverted microscope from top and side views, and the volume of yolk remaining calculated by summing the volumes of various segments (usually cylinders or cones) representing the yolk mass using standard mensuration formulae.

CALCULATIONS

Direct measurements of the cost of locomotion in hatchlings has not yet been possible, but Daniel (1983) has given a detailed analysis of medusan jet propulsion that resembles that of *I. illecebrosus* hatchlings. The Reynolds numbers (R_e) for the squid are in the same range (1 to 500), and the drag coefficient (C_d) can therefore be estimated from the equation:

$$C_d = 24/R_e^{0.7}$$

From this the drag force (D), the major force the squid have to overcome, can be estimated from the equation:

$$D = 0.5 C_d \rho S u^2.$$

Where ρ is the density of water, S is the frontal surface area and u the velocity of the squid. The power consumption (P) to overcome drag is then:

$$P = D u$$

Solutions of these equations in S.I. units gives power in watts that have been converted in calories per day for comparison with other biological data (1 watt = 20,635 cal d⁻¹). The metabolic energy consumed is not, of course, equal to mechanical output, so these values must be adjusted for efficiency. Daniel found typical efficiencies in medusae in the

range of 5 to 10%, while O'Dor (1982) found efficiencies for adult squid of about 4%; here 5% efficiencies have been assumed for hatchlings.

The only direct measurements of metabolic rates in hatchling squid are those of Hurley (1976) which are for "routinely" active *Loligo opalescens*. These values are similar to routine weight-specific metabolic rates for adult *L. opalescens*, and it appears reasonable to assume the same metabolic rates in other hatchlings as in adults of the same species since in many cases the weight exponents for squid have not proved to be significantly different from 1.0 (O'Dor and Wells, 1985). On this basis, standard metabolic rates at 15°C of 303 and 257 ml O₂ kg⁻¹h⁻¹ for *I. illecebrosus* (Webber and O'Dor, 1985) and *L. opalescens*, respectively, have been used for hatchlings. Assuming 1 ml O₂ equals 4.6 cal and no diel changes, this equals 33.4 cal g⁻¹d⁻¹ for *I. illecebrosus* and 28.4 for *L. opalescens*.

RESULTS

OBSERVATIONS OF PRE- AND POSTHATCH *I. ILLECEBROSUS*

Once the embryos reached stage XVII of development (O'Dor *et al.*, 1982), some activity was seen inside the egg. Mantle contractions occurred in bursts of 7 to 14 followed by a period of rest. There appeared to be no preferred orientation in the egg; the embryos rotated in a figure-eight, powered by a combination of ciliary motion, weak mantle contractions and an occasional jet. As the embryos developed further, the mantle contractions become stronger but less spasmodic. Animals that hatched before stage XX of development still had weak mantle contractions and were not sufficiently coordinated to produce jetting sequences. Consequently, these animals could not leave the bottom of the container. Stage XX hatchlings jetted up through the water column to the surface at speeds up to 26 mm s⁻¹ (the maximum speed measured during a single jet was 52 mm s⁻¹), but averaged about 10 mm s⁻¹. They could hover in one place by bobbing up and down, but had very limited ability to control lateral movements. The fins always point toward the surface, whether the animal is jetting or sinking. This orientation may be due to the position of the two statoliths in the head behind the optic lobes which would have a higher density than tissue. When a hatchling was not jetting it would sink at about 5 mm s⁻¹ and, upon touching the bottom, immediately jet upward. The first contact with the bottom was with the proboscis (fused tentacles peculiar to young of the family Ommastrephidae, which appeared to extend and push the animal off like a pogo-stick. When a hatchling touched the water surface it relaxed and passively sank for a time before jetting again.

TEMPERATURE EFFECTS

Earlier experiments showed that *I. illecebrosus* eggs will not develop at temperatures below about 13°C (O'Dor *et al.*, 1982), and the present experiments show that they develop at temperatures at least as high as 26°C. In fact,

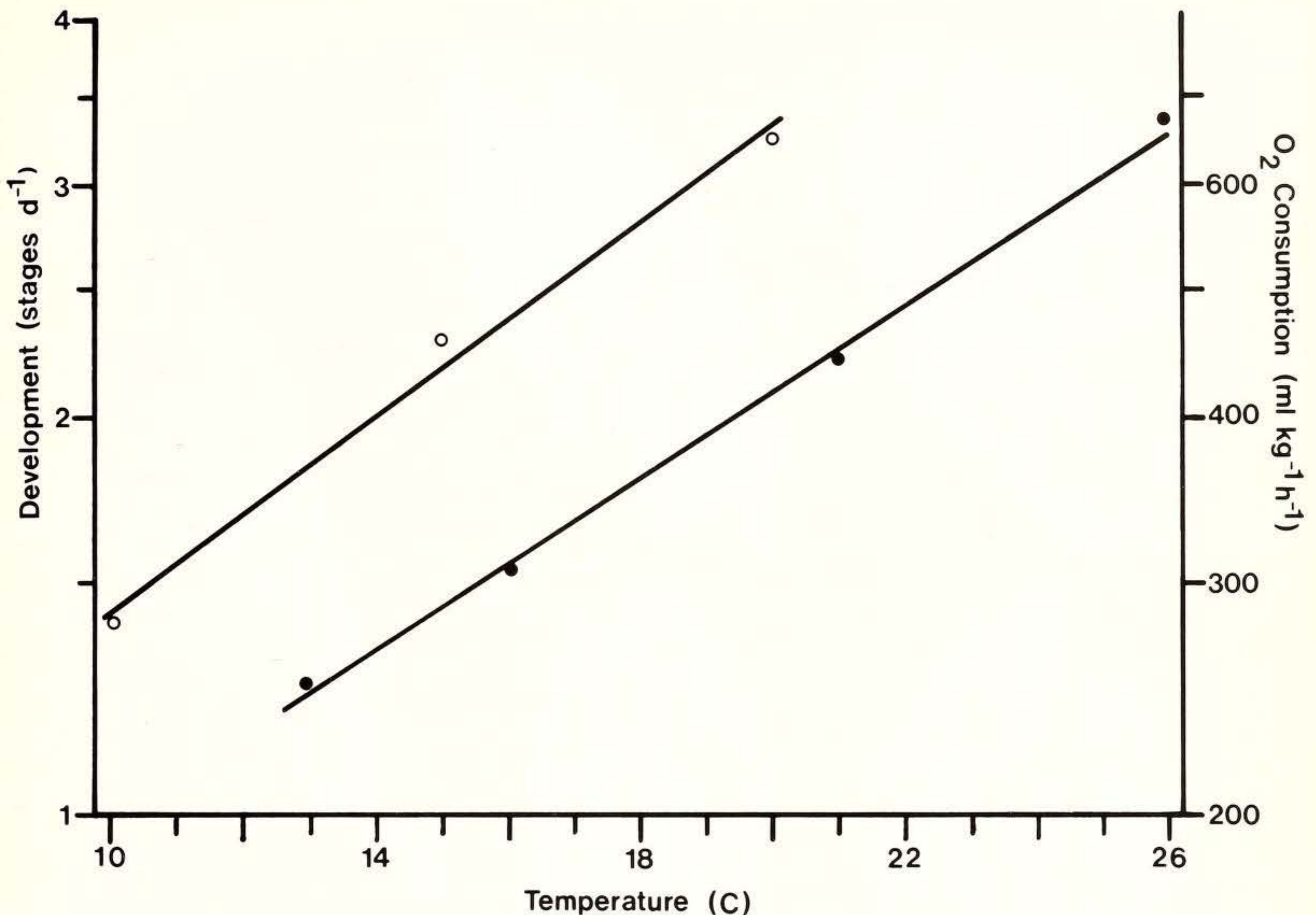


Fig. 1. Temperature effects on development and metabolic rates in newly-hatched squid. Development rates (filled circles) are for *L. illecebrosus* and are given in stages per day (20 stages divided by the number of days to hatching; staging and some data from O'Dor *et al.*, 1982). Oxygen consumptions (open circles) are for *L. opalescens* from Hurley (1976). Lines are regressions of the form $R = B(A)^T$. For development, A is 1.0782 (equal to a Q_{10} of 2.12), B is 0.460 and r is 0.9995. For metabolic rate, A is 1.0879 (equal to a Q_{10} of 2.32), B is 123.7 and r is 0.995.

they appear to do better at these higher temperatures. The number of viable hatchlings from the egg mass at 26°C was higher than from any mass observed to date, and they appeared to be more fully developed at hatching. The buccal mass was fully formed and operational, for example, which was typically seen only several days post-hatch in earlier experiments. Records of earlier hatchlings are not precise enough to be sure whether there is really a better coordination of development of all systems at the higher temperatures or whether there was simply a higher proportion of premature hatching at the lower temperatures. In most egg masses at lower temperatures, a fungus develops in the gel after about a week, and as the gel collapses the expanded chorions of the later stages (O'Dor *et al.*, 1982) are more easily ruptured causing premature hatching.

Whether high temperatures ultimately produce more viable squid depends upon several factors. Premature hatching is one, but if the metabolic rate increases faster than the development rate, high temperatures could produce well-

formed, fully developed hatchlings which would, however, lack the yolk reserves to sustain them until they begin to feed. Figure 1 shows the development rate (R_D) over the entire range of temperatures (T), and compares this effect to the change in metabolic rate (R_M) seen in hatchling *L. opalescens* (Hurley, 1976). R_D is calculated in stages per day based on the day the first swimming stage XX hatchlings appeared: 6, 9, 13 and 16 days at 26, 21, 16 and 13°C, respectively (O'Dor *et al.*, 1982). A regression of rate against log temperature gives the following relation when back-transformed:

$$R = B(A)^T$$

For development, back-transformed regression coefficients A and B are 1.0782 and 0.46, respectively; this means the time to hatch is approximately halved by a 10°C rise in temperature and that the development rate has a Q_{10} of 2.1 (1.0782¹⁰). For metabolic rate, A is 1.0879 and B is 123.7 giving a Q_{10} of 2.3. Thus, both development and metabolic rates increase similarly with temperature, and there is no major



Fig. 2. *Illex illecebrosus* embryo and hatchling photographs used to calculate yolk volume. a) and b) are top and side views of Stage XVII embryos. c) and d) are recently hatched Stage XX embryos. e) is one of the most advanced hatchlings seen to date seven days post-hatching. Its yolk reserve is nearly developed, and it is near starvation.

disadvantage to development at high temperature.

YOLK ENERGY PARTITIONING

Until a newly hatched animal begins to feed, the yolk reserves must meet three requirements: 1) material for further development, 2) energy to meet the demands of standard metabolism and 3) energy for activity. This report attempts to estimate the relative importance of each of these under various natural regimes of temperature and activity and to predict the maximum time available for hatchlings to find and learn to capture food.

The only direct measure of energy consumption available for *I. illecebrosus* hatchlings is the rate of yolk utilization. The precocious hatchlings in Figure 2 a to d were kept at 15°C and photographed 2 days apart at stages XVII and XX of development as indicated. The photographs showing the internal yolk sac were diagrammed and yolk volumes determined as described in Materials and Methods. Assuming a density of 1.036 g cm⁻³ (slightly greater than Aquatron seawater), the weights of yolk at stages XVII and XX were estimated at 113 and 87 μg, respectively. If its caloric value is 1.71 Kcal g⁻¹ as in *L. opalescens* (Giese, 1969), the yolk consumed contained 0.045 cal and at stage XX a hatchling

would contain 0.148 cal in yolk. After about 7 days at this temperature a hatchling would be devoid of yolk and would starve (Fig. 2e) unless feeding had commenced. Extrapolating from the rate for adults given in Materials and Methods predicts a standard metabolic rate of 0.0050 cal d⁻¹ for a 150 µg embryo. When this is deducted it leaves 0.017 cal d⁻¹ for growth of developing tissues. The balance is similar in the hatchlings; activity raises the routine metabolic rate to 0.0055 (see Table 1) which accounts for 0.037 cal in 7 days, leaving 0.016 cal d⁻¹ for development.

Table 1. Estimates of total metabolism and survival times for *I. illecebrosus* hatchlings at various temperatures and activity levels.

Velocity (mm s ⁻¹)	Hovering	10	26
Active Metabolism (cal d ⁻¹)	0.00007	0.00053	0.0048
Standard Metabolism (cal d ⁻¹)	Total Metabolism(cal d ⁻¹)/Survival Time(d)		
0.0033 at 10°C	0.0034 12	0.0038 11	0.0081 5
0.0050 at 15°C	0.0051 8	0.0055 7	0.0098 4
0.0065 at 18°C	0.0066 6	0.0070 6	0.0113 3
0.0127 at 26°C	0.0128 3	0.0132 3	0.0175 2

Table 1 gives the standard metabolic rates at various temperatures, based on a Q₁₀ of 2.3, and the calculated costs of swimming at maximum and routine speeds and of hovering. The value for hovering was estimated from the average upward velocity (6.2 mm s⁻¹) and the fraction of each cycle spent moving up (40%). In the matrix of the table, total metabolic rates and estimated survival times under each condition are given. The survival times assume that the same amount of yolk always goes to development, which is reasonable where the temperature effect on standard metabolic rate predominates, since development rate increases in parallel, but may lead to underestimation at high activity where yolk might be used for energy before development could occur.

DISCUSSION

COMPARISON WITH OTHER SQUID

This report brings together all the data available on hatchling *I. illecebrosus* energetics, but, given the rather meager data base, it seems desirable to have some verification of the approach before discussing the conclusions and implications. Table 2 summarizes some basic data for *I. illecebrosus* and compares them to similar values for *L. opalescens* and *L. vulgaris* hatchlings, giving the sources of data and indicating how estimates were made. The three data sets are complimentary, each having some directly measured

data that the others lack; thus calculated values can be tested. The difference between standard and routine metabolic rates for *L. opalescens* is 20 cal g⁻¹d⁻¹ which would allow a routine speed of 25 mm s⁻¹. This is 2.5 times the speed observed for *I. illecebrosus*, and since *L. opalescens* is 2.5 times longer, this suggests that "cruising" speed scales directly with length as is found in fish. The calculated speed is comparable to the observed speeds of *L. vulgaris* hatchlings.

Table 2. Summary of data on locomotion and energetics in hatchling squid of three species at 15°C. Values in parentheses are new estimates for the table; unless indicated by a letter, other data are either original observations, calculations from the text or direct unit conversions. Reference sources are: a) Fields, 1966. b) Hurley, 1976. c) Mangold-Wirz, 1963. d) O'Dor, 1982. e) Packard, 1969. f) Webber and O'Dor, 1985.

	<i>Illex illecebrosus</i>	<i>Loligo opalescens</i>	<i>Loligo vulgaris</i>
EGGS			
Size (mm)	0.9x0.6	2.3x1.5a	2.0x1.5c
Weight (mg)	0.21	3.0a	2.6c
HATCHLINGS			
Weight (mg)	0.15	3.4b	3.6e
Total length (mm)	1.8	4.4b	6.0e
Maximum velocity (mm s ⁻¹)	50	(130)	160e
Routine velocity (mm s ⁻¹)	10	(25)	30e
Standard metabolism (m10 kg ⁻¹ h ⁻¹)	303f	257d	—
(cal ² g ⁻¹ d ⁻¹)	33	28	—
Routine metabolism (cal g ⁻¹ d ⁻¹)	38	48b	—
(cal d ⁻¹)	0.006	0.16	—
Yolk content (cal)	0.148	3.05a	—
Yolk available (cal)	0.039	(0.81)	—
Survival time (d)	7	5	—

The predicted survival time for starving *L. opalescens* is short, but not unreasonably so. Fields (1965) reports that at 15°C hatchlings that were apparently not feeding all died in less than 10 days. In any case, the assumption that *L. opalescens* hatchlings use the same proportion of yolk for growth and development as *I. illecebrosus* is probably the least defensible argument in the analysis since *L. opalescens* hatchlings are much more highly developed at hatching and essentially able to function as miniature adults.

A final observation suggesting that the calculations of the cost of locomotion are reasonable is that a regression of weight on cost of transport for *L. opalescens* and *I. illecebrosus* in the range of 40 to 400 g predicts values for the hatchlings of both species differing by less than 10% from the values calculated from drag estimates.

DISTRIBUTIONAL IMPLICATIONS

The observations on *I. illecebrosus* seem to raise a dilemma. Egg development proceeds most efficiently at temperatures as high as 26°C, but hatchlings have fewer than three days to find food and learn to capture it at these temperatures. Since learning may require some time

(Hurley, 1976), this could be a serious problem in relatively oligotrophic waters where such temperatures exist in winter when the major stocks of *I. illecebrosus* are spawned. The requirement for warm temperatures is consistent with recent observations of captive squid spawning nearly neutrally buoyant egg masses while swimming (O'Dor and Balch, 1985); thus allowing them to spawn in the warm surface waters and the egg masses to remain above the thermocline long enough for the eggs to develop. But what happens to the hatchlings? Since the hatchlings can swim vertically at reasonable speeds and costs, the trade-off between the rate of yolk utilization and the period to attain feeding success may be optimized by vertical migrations. This tactic has long been proposed for zooplankters in general (McLaren, 1963). Although it has not been possible to demonstrate negative or positive phototaxis in captive hatchlings, in nature there is some evidence that vertical migrations of early juveniles may occur (O'Dor, 1983).

There may be several advantages to such behaviour for the squid. If the present analysis is correct hatchlings could, for example, sink over 200 m in 12 h and ascend the same distance in 6 h at their typical speed with a cost of less than 0.0003 cal d⁻¹. The standard metabolic rate at 26°C is so high that the energy saved in 20 min. at 10°C or 30 min. at 18°C would fuel the trip. The actual rate of ascent or descent may be determined by the need to stay with their prey; they are easily able to match the vertical migration rates of most other zooplankters (Hardy and Bainbridge, 1954; Mileikovsky, 1973). Such vertical movement would be particularly important if the Gulf Stream plays a major role in distributing *I. illecebrosus* hatchlings (Trites, 1983; O'Dor and Balch, 1985). The warm Gulf Stream provides good conditions for eggs and would carry them toward rich upwelling areas along the northern edge of the Stream. Descent beneath the Stream would not only move hatchlings to lower temperatures but also dramatically change their horizontal velocity, providing them with some control over their distribution. There is even some evidence to suggest that it would put them directly into the source of water moving into the mixing zone where food is most plentiful (Yoder *et al.*, 1981). Such behaviours are not yet documented and it is unclear what cues the squid might use to regulate them, but, as Trites (1983) has shown, small changes in the position of animals in the Stream can have dramatic effects on their eventual distribution. With the swimming abilities shown here the hatchlings may be less at the mercy of the sea than expected.

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