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# Aerobic respiratory costs of swimming in the negatively buoyant brief squid *Lolliguncula brevis*

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## Summary

Because of the inherent inefficiency of jet propulsion, squid are considered to be at a competitive disadvantage compared with fishes, which generally depend on forms of undulatory/oscillatory locomotion. Some squid, such as the brief squid *Lolliguncula brevis*, swim at low speeds in shallow-water complex environments, relying heavily on fin activity. Consequently, their swimming costs may be lower than those of the faster, more pelagic squid studied previously and competitive with those of ecologically relevant fishes. To examine aerobic respiratory swimming costs, $O_2$ consumption rates were measured for *L. brevis* of various sizes (2–9 cm dorsal mantle length, *DML*) swimming over a range of speeds (3–30 cm s$^{-1}$) in swim tunnel respirometers, while their behavior was videotaped. Using kinematic data from swimming squid and force data from models, power curves were also generated. Many squid demonstrated partial (**J**-shaped) or full (**U**-shaped) parabolic patterns of $O_2$ consumption rate as a function of swimming speed, with $O_2$ consumption minima at 0.5–1.5 *DML* s$^{-1}$. Power curves derived from hydrodynamic data plotted as a function of swimming speed were also parabolic, with power minima

at 1.2–1.7 *DML* s$^{-1}$. The parabolic relationship between $O_2$ consumption rate/power and speed, which is also found in aerial flyers such as birds, bats and insects but rarely in aquatic swimmers because of the difficulties associated with low-speed respirometry, is the result of the high cost of generating lift and maintaining stability at low speeds and overcoming drag at high speeds. *L. brevis* has a lower rate of $O_2$ consumption than the squid *Illex illecebrosus* and *Loligo opalescens* studied in swim tunnel respirometers and is energetically competitive (especially at $O_2$ consumption minima) with fishes, such as striped bass, mullet and flounder. Therefore, the results of this study indicate that, like aerial flyers, some negatively buoyant nekton have parabolic patterns of $O_2$ consumption rate/power as a function of speed and that certain shallow-water squid using considerable fin activity have swimming costs that are competitive with those of ecologically relevant fishes.

Key words: squid, respiration, power, negative buoyancy, swimming, *Lolliguncula brevis*, locomotion.

## Introduction

Many squid rely on jet propulsion for locomotion, which is inherently less efficient than the undulatory/oscillatory locomotion employed by many fishes (Vogel, 1994). Jet propulsion is thought to be inefficient because jetters, such as squid, fill a cavity of limited volume with water and eject that water through an orifice, thus expelling relatively small volumes of water backwards with each jet pulse. Undulatory/oscillatory swimmers drive significantly larger volumes of water backwards with each sweep of the body, tail and/or fins, and the mass of water directed backwards is not constrained by internal morphology. Since thrust is the rate of momentum transfer (momentum being equal to mass × velocity of fluid expelled backwards) and jet-propelled organisms cannot substantially increase the mass of water because of internal volume limitations, jet locomotors must expel the water at high

velocity. This is costly because the energy required for thrust increases with velocity squared ($E=\frac{1}{2}mv^2$, where $E$ is energy, $m$ is mass and $v$ is velocity) (O'Dor and Webber, 1991; Vogel, 1994). Not surprisingly, direct comparisons between fish, such as *Salmo* spp., and certain squid that rely heavily on jet propulsion for locomotion, such as *Illex illecebrosus* and *Loligo opalescens*, show that squid typically have $O_2$ consumption rates 5–7 times higher than those of fish (O'Dor, 1982; Webber and O'Dor, 1986; O'Dor and Webber, 1986; O'Dor and Webber, 1991). As a result, O'Dor and Webber (O'Dor and Webber, 1986) conclude that 'squid are not so much competing with fish as trying to stay out of their way'.

The assumption that all squid, the most mobile of the cephalopods, are not competitive with fishes because of the inefficiency of jet propulsion may be too simplistic. Squid, like

fishes, are diverse and have evolved many behavioral and physiological mechanisms that allow them to compete in a variety of environments. One species, the brief squid *Lolliguncula brevis*, is particularly distinctive from the squid *Loligo opalescens* and *Illex illecebrosus* considered in previous studies. Brief squid have small rounded bodies, large rounded fins, heavily keeled third (III) arms, and may live in shallow, complex, temporally variable environments (Hixon, 1980; Bartol et al., 2001a). Conversely, *Loligo opalescens* and *Illex illecebrosus* are larger, more elongate and pelagic (Hixon, 1980; Hixon, 1983; O'Dor, 1983; Hanlon and Messenger, 1996). Brief squid swim at low speeds, at which the costs of jet propulsion are reduced, and they use significant fin movement, avoiding the volume limitations of jet propulsion. Thus, the inherent inefficiencies of jet propulsion may not be as pronounced for *L. brevis*. *Loligo opalescens* and *Illex illecebrosus* swim at moderate to high speeds and use their fins primarily for steering and maneuvering (O'Dor, 1988a; Hoar et al., 1994). *L. brevis* is also the only cephalopod to invade the inshore, euryhaline waters of the Chesapeake Bay, where it is abundant [ranking in the upper 10 % of annual nektonic trawl catches (Bartol et al., 2001a)] and competes as a predator with bay fauna that number in the hundreds of species.

Aside from jet propulsion, squid are distinct from many pelagic nekton because they are often negatively buoyant. Birds, which are negatively buoyant in air, expend considerable energy staying aloft at low speeds, when lift forces are minimal, and overcoming drag forces at high speeds (drag increases exponentially with speed). Oxygen consumption/power is low at intermediate speeds when lift forces are greater than at low speeds because of increased flow over the body and wings and when drag forces are less important than at high speeds. The resulting $O_2$ consumption/power *versus* speed curve is U-shaped [see Tucker (Tucker, 1968; Tucker, 1973) and Pennycuick (Pennycuick, 1968; Pennycuick, 1989)]. A similar relationship may exist in negatively buoyant squid because they also presumably have high lift generation costs at low speeds and substantial drag costs at high speeds. Parabolic power *versus* speed relationships have been detected in the negatively buoyant mandarin fish *Synchiropus picturatus* (Blake, 1979a). No such relationship has been observed previously in squid, but low speeds (1–10 cm s$^{-1}$), speeds frequently used by brief squid and when lift generation costs are highest, have not yet been examined.

*L. brevis* is morphologically, ecologically and physiologically unlike many cephalopods, especially those considered in previous comparisons between squid and fishes, and may swim differently. The reliance of brief squid on fin motion and their preference for low-speed swimming may minimize the inefficiencies of jet propulsion and therefore reduce the costs of swimming. Moreover, negative buoyancy and the costs associated with maintaining vertical position in the water column may influence the relationship between $O_2$ consumption/power and speed, such that costs are lower at intermediate speeds than at high or low speeds. Brief squid that

swim at these intermediate speeds may be more competitive with fish than is presently thought. Therefore, $O_2$ consumption rates and power estimates for *L. brevis* of various sizes swimming over a continuum of speeds were measured (i) to characterize the $O_2$ consumption/power *versus* speed relationship and (ii) to compare their energetics with those of other ecologically comparable nekton.

## Materials and methods
### Experimental animals

*Lolliguncula brevis* (Blainville) (2.9–8.8 cm dorsal mantle length, *DML*,; 1.7–48.3 g) were captured by trawl both within embayments along the seaside of Virginia's Eastern Shore and in the York River, Virginia, a sub-estuary of the Chesapeake Bay. Squid captured along the Eastern Shore of Virginia were transported to the Virginia Institute of Marine Science (VIMS) Eastern Shore Laboratory located in Wachapreague, Virginia, while squid captured in the York River were transported to the VIMS main campus located in Gloucester Point, Virginia. Squid were kept alive in the field using 114 l coolers equipped with filtration and aeration systems, which were powered by sealed rechargeable batteries. At both Wachapreague and Gloucester Point, squid were kept in flow-through raceway tanks and fed *ad libitum* a diet of grass shrimp, *Palaemonetes pugio*. All squid considered in this study were kept in captivity for at least 1 week prior to experimentation and were not fed for 24 h before trials so that digestion (specific dynamic action) was not reflected in $O_2$ measurements. Experiments were performed on three squid 2.9–3.9 cm in *DML*, four squid 4.0–4.9 cm in *DML*, four squid 5.0–5.9 cm in *DML*, six squid 6.0–6.9 cm in *DML*, five squid 7.0–7.9 cm in *DML* and five squid 8.0–8.9 cm in *DML*. After experimentation, some squid were released; others were over-anesthetized in an isotonic solution of MgCl$_2$ (7.5 % MgCl$_2$.6H$_2$O) and sea water (Messenger et al., 1985) and transferred to 10 % buffered formalin for future morphological examination.

### $O_2$ consumption measurements

Two separate swim tunnel respirometers, one with a capacity of 15.6 l and the other with a capacity of 3.8 l, were used. Within each swim tunnel respirometer, flow velocity was controlled using two propellers attached to a stainless-steel shaft in a rotor-stator configuration driven by a 187 W (0.25 horse power) variable-speed motor with a belt and pulleys. To keep the water temperature as constant as possible within the respirometer and to facilitate the removal of air bubbles, each of the tunnels was completely submerged in a 378 l aquarium filled with aerated sea water. During the experiments, water from within the respirometers was pumped to a submerged microcell using a peristaltic pump, and dissolved $O_2$ levels were measured using a Strathkelvin 1302 $O_2$ electrode and Strathkelvin 78 L $O_2$ meter. Electrode output was expressed as percentage $O_2$ saturation and recorded continuously over the speed trials using a Kipp and Zonen BD 41 strip chart recorder.

*Lolliguncula brevis* shorter than 4 cm in *DML* were examined in the 3.8 l respirometer, and *L. brevis* 4 cm or more in *DML* were tested in the 15.6 l respirometer. Each squid was placed in the respirometer and allowed to acclimate for 40 min. Flow was set at $3 \, cm \, s^{-1}$ during the initial 10 min and final 20 min of the acclimation period. During an interim 10 min period, flow speeds were gradually elevated to $18–21 \, cm \, s^{-1}$ to allow the squid to acclimate to higher flow speeds. The 40 min acclimation/training period was selected on the basis of recovery times from exercise and stress, which are extremely short in squid (Pörtner et al., 1993), and acclimation periods used for *L. brevis* in other studies (Finke et al., 1996; Zielinski et al., 2000). After the 40 min adjustment period, the respirometer lid was closed, $O_2$ levels were recorded for 15 min while the squid swam at $3 \, cm \, s^{-1}$, and the respirometer was then opened, allowing water from the surrounding waterbath to enter the respirometer. This flushing procedure was carried out for 10 min to ensure that fresh, oxygenated water was present in the system for the next trial. This procedure was repeated for speeds of 6, 9, 12, 15, 18, 21, 24, 27 and $30 \, cm \, s^{-1}$ or until the squid could no longer keep pace with flow velocity. Because of high behavioral variation and high $O_2$ consumption rates at the lowest speed tested, repeat measurements at $3 \, cm \, s^{-1}$ were periodically performed following an intermediate speed $(9–12 \, cm \, s^{-1})$ flushing period. When low-speed $O_2$ consumption rates measured at the beginning and at an intermediate stage in the trial differed significantly, the trial was terminated.

During each trial, swimming behavior was recorded using a Sony Hi-8 video camera. After the final trial, each squid was measured (*DML*) (±0.1 cm) and weighed (±0.01 g), and blanks were run to correct for bacterial $O_2$ consumption, electrode drift and/or the endogenous $O_2$ consumption of the electrode. Rates of $O_2$ consumption were determined from the slope of percentage $O_2$ saturation *versus* time curves (corrected for background components and/or electrode drift) recorded over the final 10 min period of each speed range. Mean water temperature and salinity for this study were 24.5±2.0 °C and 29.2±5.6 ‰ (means ± S.E.M.), respectively.

### Video analysis

Portions of the video footage were analyzed on a Peak Motus v.3.0 motion measurement system (Peak Performance Technologies, Englewood, CO, USA) to account for some of the variability in swimming behavior. For all squid tested, two representative minutes of footage at each speed were examined. Mantle angle (±1 °), arm angle (±1 °) and the distance from the eye to the respirometer floor (±0.1 cm) were recorded every second within the 2 min video sequence. Changes in position along the axis parallel to flow and the number of fin beats per second were also recorded. For all squid, the mean overall body angle of attack (which was simply the mean of the mantle and arm angles), the mean distance from the bottom of the respirometer, the mean number of fin beats per second and the mean horizontal change in position during each 2 min video sequence were computed. Using an acoustic Doppler velocimeter (Son-Tek, Inc., San Diego, CA, USA), bottom flow profiles were recorded in each swim tunnel for the range of speeds considered in this study. These measurements were used in conjunction with mean height above the bottom and mean horizontal change in position to calculate actual swimming velocities. A few squid exceeded 10 % of the cross-sectional area of the tunnel; speed adjustments were made for these squid to account for blocking effects (Webb, 1975).

### Statistical procedures

Polynomial regression analysis was performed both on data pooled by size class (size classes: 2.9–3.9, 4.0–4.9, 5.0–5.9, 6.0–6.9, 7.0–7.9 and 8.0–8.9 cm *DML*) and on data collected for individual squid. Regression analysis involved fitting the data initially to a linear regression and subsequently to higher-degree polynomial regressions when additional terms significantly improved the accuracy of the prediction of dependent values (Zar, 1984; Sokal and Rohlf, 1981). Unfortunately, regression analyses performed on pooled data did little to characterize the nature of patterns apparent in scatter plots for individual squid. This was because high variability among individuals masked underlying relationships. Furthermore, when the data were analyzed separately for each squid, the limited number of data points precluded the consistent detection of significant linear or curvilinear relationships.

Because of this high variation among individual squid, an additional procedure was employed to determine whether a significant parabolic relationship existed between $O_2$ consumption rates and speed, i.e. were $O_2$ consumption rates at intermediate speeds lower than those at low and high speeds? For each squid tested, the data were divided into three speed ranges: $<0.5 \, DML \, s^{-1}$, $0.5–1.5 \, DML \, s^{-1}$ and $>1.5 \, DML \, s^{-1}$. A speed of $0.5 \, DML \, s^{-1}$ was a logical low-end cut-off because the squid demonstrated greater lateral variation about a given point at speeds below $0.5 \, DML \, s^{-1}$ (mean lateral deviation 4.16±4.53 cm, mean ± S.D., *N*=19) compared with speeds of $0.5 \, DML \, s^{-1}$ or above (mean lateral deviation 1.78±1.67 cm, mean ± S.D., *N*=19). A speed of $1.5 \, DML \, s^{-1}$ was a reasonable high-end cut-off because anaerobic end products may begin to accumulate in *L. brevis* at speeds above $1.5 \, DML \, s^{-1}$ (Finke et al., 1996). Mean $O_2$ consumption rates were calculated for each speed range for each squid tested, and a randomized-block analysis of variance (ANOVA), treating each squid as a block, was used to determine whether there was an overall significant difference in $O_2$ consumption rate for the three speed ranges. A randomized-block ANOVA (also called an ANOVA with repeated measures) was used because repeated measurements ($O_2$ consumption rates) were collected from the same squid over time and blocking subjects helped account for variation among squid. Level differences were determined using Newman–Keuls multiple-comparison tests for randomized-block ANOVAs (Zar, 1984).

Mean wet masses and mean mass-specific $O_2$ consumption rates for the three speed ranges were calculated for the six size

classes. To characterize the metabolic scaling relationship in brief squid, a power-law regression of mean mass-specific $O_2$ consumption rates pooled across the three speed ranges *versus* mean wet masses for the six size classes was performed. (Data from the three speed ranges were pooled because there was little difference in power-law relationships among the speed ranges.) The power-law function was defined as:

$$R = aM^b,$$

where $R$ is mass-specific rate of $O_2$ consumption, $a$ is the mass coefficient, $M$ is wet mass and $b$ is the mass exponent.

### Power and efficiency calculations

Power curves for two *Lolligunucla brevis*, one measuring 4.4 cm in *DML* and the other measuring 7.6 cm in *DML*, were generated to determine the nature of the hydrodynamic power/speed relationship. The power curves were based on kinematic and force data presented in the companion manuscript published in this volume (Bartol et al., 2001b), to which we refer the reader for detailed descriptions of the forces discussed below. Five power terms were calculated: (i) induced power, the power required by the fins to generate lift to keep the squid up in the water column; (ii) vertical jet power, the power needed by the jet to generate lift to keep the squid up in the water column; (iii) parasite/profile power, the power required to overcome pressure and friction drag on the fins, body and arms; (iv) refilling power, the power required to overcome mantle refilling forces; and (v) total power, the sum of the above power terms. Induced power (W) was computed by multiplying predicted vertical fin thrust (N) by induced velocity (m s$^{-1}$), the only term in this section not described in Bartol et al. (Bartol et al., 2001b). Induced velocity, which is the velocity of fluid passing through an area swept out by the fins (Pennycuick, 1972; Blake, 1979b; Norberg, 1990), was determined by high-speed (250 frames s$^{-1}$) videotaping of the two squid swimming in a flume seeded with brine shrimp eggs (see Bartol et al., 2001b) and measuring fin flapping speeds and particle trajectories underneath the fins during downstrokes. At low speeds, the vertical components of fin flapping speed and particle speed were reasonably consistent, but at higher speeds the vertical speed component of particle trajectories was much lower than that of the fins because translational flow had a large effect on induced velocity. Consequently, only particle trajectories were used to determine induced velocity at speeds above 6 cm s$^{-1}$. More precise methods of measuring induced power, which are based on vortex theory and circulation

measurements [see Rayner (Rayner, 1979), Spedding (Spedding, 1987) and Norberg (Norberg, 1990)], were beyond the scope of this project. Moreover, induced power estimates using Rankine–Froude axial momentum jet theory are known significantly to underestimate induced power at low speeds because non-steady effects are not considered (Norberg, 1990). Vertical jet power (W) was the product of vertical jet thrust (N) and the vertical component of jet speed (m s$^{-1}$), parasite/profile power (W) was the product of total drag (N) on the body, fins and arms and swimming speed (m s$^{-1}$), and refilling power (W) was the product of refilling force (N) and swimming speed (m s$^{-1}$).

Using power estimates from a 4.4 and 7.6 cm *DML* squid and $O_2$ consumption rates from a 4.5 and 7.5 cm *DML* squid, respectively, aerobic efficiencies ($N_a$) were calculated for a range of speeds. Aerobic efficiency was defined as the ratio of the power required to move the squid through the water [i.e. power output, which is simply total power (W) calculated as above divided by wet mass (kg)] to the aerobically supplied
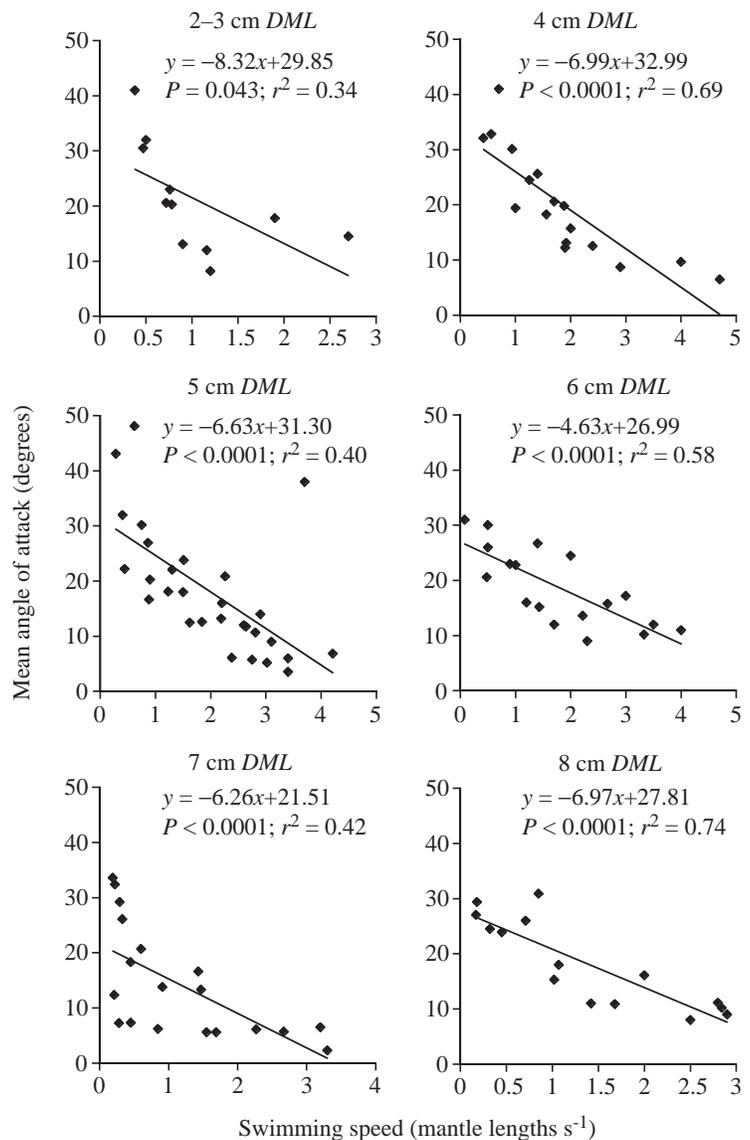


Fig. 1. Linear regressions of mean body angle of attack (degrees) *versus* swimming speed (mantle lengths s$^{-1}$) for six size classes of *Lolliguncula brevis*: 2.9–3.9, 4.0–4.9, 5.0–5.9, 6.0–6.9, 7.0–7.9 and 8.0–8.9 cm dorsal mantle length, *DML*. Regression equations, *P*-values and $r^2$ values are included for each size class.

power (i.e. power input, which is based on active metabolic rate). Active metabolic rate ($ml\,O_2\,kg^{-1}\,h^{-1}$) was converted to power input using the common assumption that 1 ml of $O_2$ yields 20 J and multiplying by $1/3600\,s$ to arrive at $J\,s^{-1}\,kg^{-1}$ ($W\,kg^{-1}$). For aerobic efficiency comparisons with other cephalopods, it was necessary to generate gross cost of transport (COT) curves and to determine $U_{mr}$ (the speed of maximum range), which is the minimum of the COT curve. For hydrodynamic estimates of COT ($J\,kg^{-1}\,m^{-1}$), power output ($W\,kg^{-1}$) calculated as above was divided by speed ($m\,s^{-1}$). For aerobic estimates of COT, power input ($W\,kg^{-1}$) calculated as above was divided by speed ($m\,s^{-1}$).

## Results

### Swimming behavior

In the swim tunnel respirometers, brief squid were capable of both arms-first swimming, in which the arms extend in front in a streamlined, conical arrangement while the mantle and fins trail behind, and tail-first swimming, in which the mantle and fins are forward while the arms form a sharp trailing edge. Upon initial placement within either respirometer (during the acclimation period), most squid oriented arms-first in the direction of flow. However, during exposure to higher speeds, brief squid frequently shifted to tail-first swimming, which allowed them to keep pace with flow more effectively. The majority of data reported here were collected during tail-first swimming periods because tail-first swimming appeared to be the preferred mode of swimming throughout the speed range tested. However, many squid would not swim exclusively in either mode at low speeds ($<6\,cm\,s^{-1}$), and thus low-speed $O_2$ consumption rates often reflected both modes of swimming. Oxygen consumption rates during tail-first and arms-first swimming were not separated at low speeds because squid switched erratically between tail-first and arms-first modes, making it difficult to extract consistent linear relationships from the strip chart data for a particular swimming mode.

For all size classes, there was a clear decline in mean angle of attack and number of fin beats per second with increased swimming velocity (Fig. 1, Fig. 2). Most squid tested were capable of detecting areas of lower flow within the tunnel respirometer and consistently swam at speeds lower than the target velocity. Moreover, several behaviors were employed by some to aid swimming and presumably to reduce swimming costs. A number of squid remained on the tunnel floor either in a horizontal orientation, with the body and appendages aligned parallel to flow, or in an

inverted V-posture, with the tips of the mantle and arms touching the tunnel floor and the head projected upwards. Since these squid were in contact with the bottom, they were not actually swimming. Other squid frequently pushed off the bottom and/or downstream collimator with their arms during trials to assist locomotion. Some squid even swam with their body and fin pressed against the respirometer side wall to exploit low flows near the wall and to help maintain horizontal and vertical position. These behaviors were most prevalent during low- and high-speed trials when squid had the most difficulty matching free-stream flow.

Speed trials in which the above behaviors were used more than 30% of the time were eliminated. This cut-off was selected because there was generally a clear division between cooperative and uncooperative swimming at the 30% time division at most speeds, with the majority of squid either 'cheating' more than 90% or less than 10% of the time. For eight squid, this resulted in no measurements at speeds below
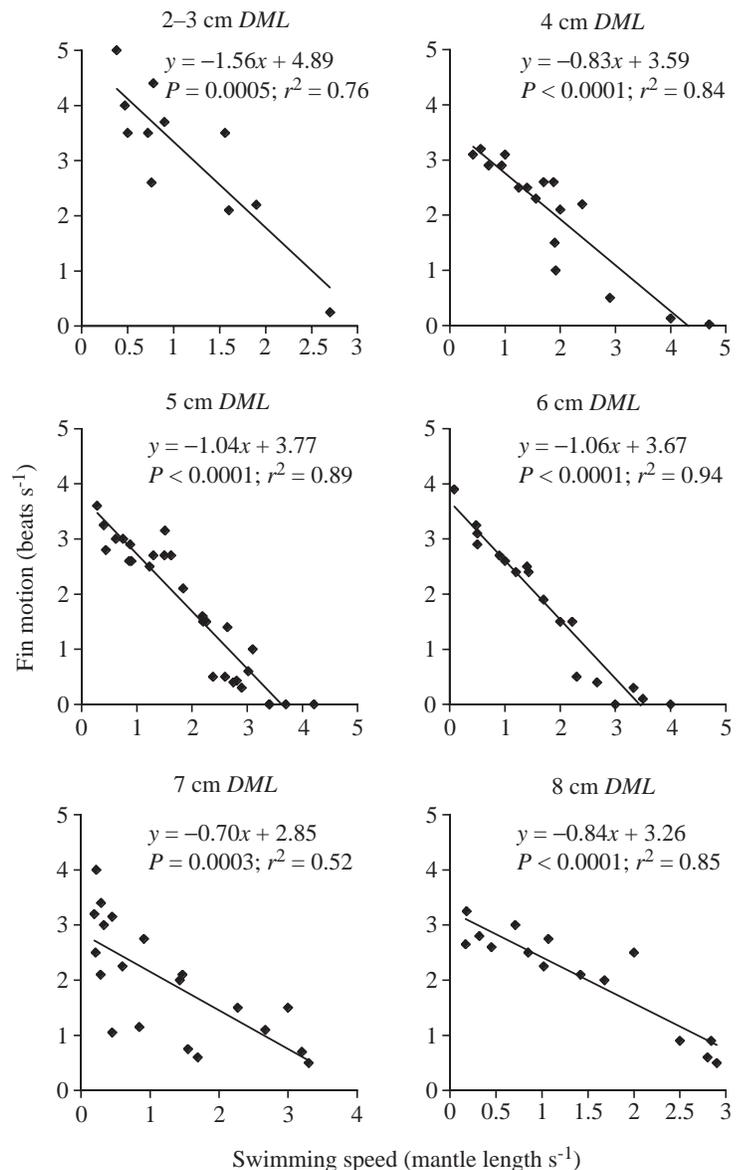


Fig. 2. Linear regressions of mean rate of fin beating (beats $s^{-1}$) *versus* swimming speed (mantle lengths $s^{-1}$) for six size classes of *Lolliguncula brevis*: 2.9–3.9, 4.0–4.9, 5.0–5.9, 6.0–6.9, 7.0–7.9 and 8.0–8.9 cm dorsal mantle length, *DML*. Regression equations, *P*-values and $r^2$ values are included for each size class.
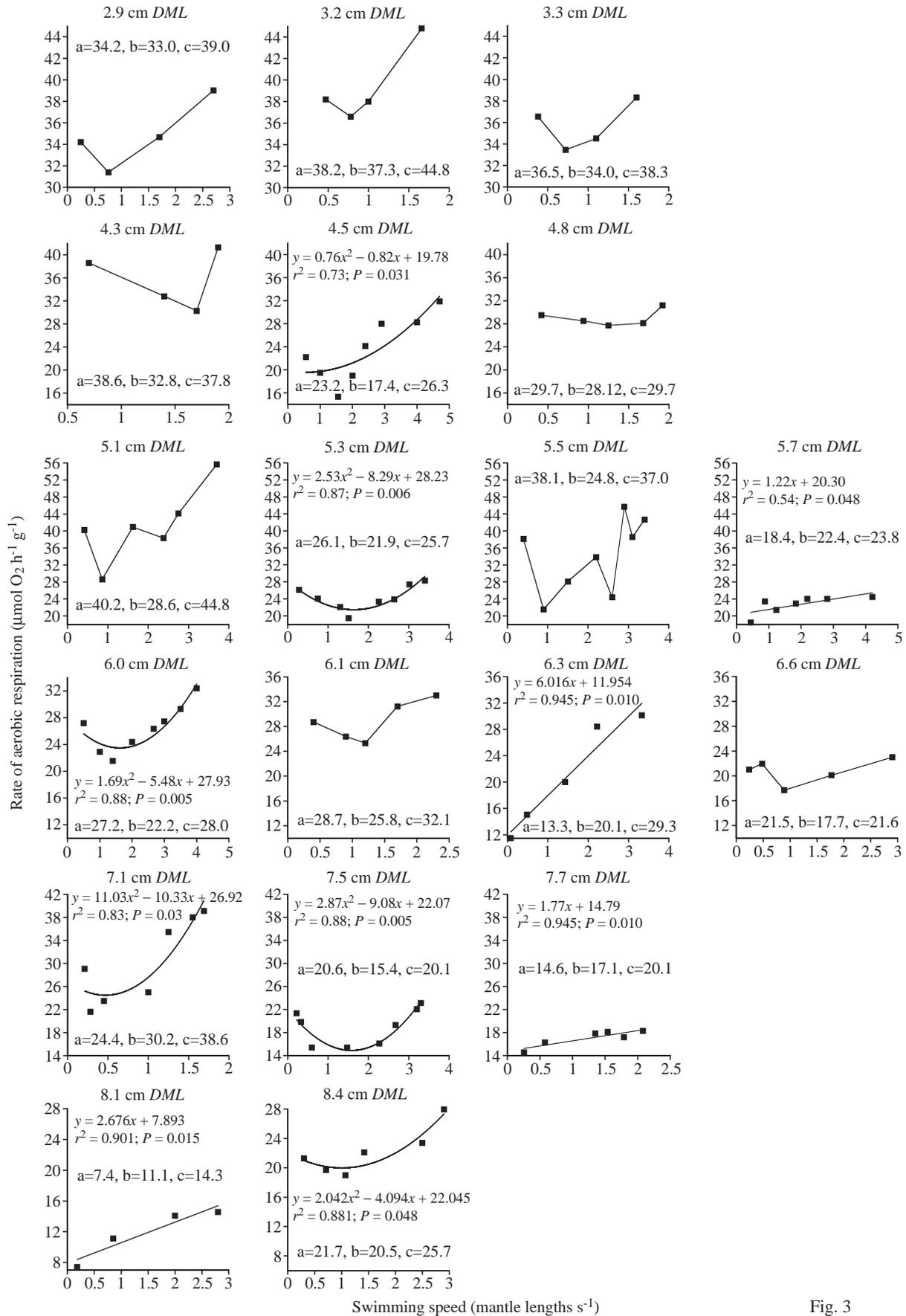
**2.9 cm *DML***
a=34.2, b=33.0, c=39.0

**3.2 cm *DML***
a=38.2, b=37.3, c=44.8

**3.3 cm *DML***
a=36.5, b=34.0, c=38.3

**4.3 cm *DML***
a=38.6, b=32.8, c=37.8

**4.5 cm *DML***
$y = 0.76x^2 - 0.82x + 19.78$
$r^2 = 0.73; P = 0.031$
a=23.2, b=17.4, c=26.3

**4.8 cm *DML***
a=29.7, b=28.12, c=29.7

**5.1 cm *DML***
a=40.2, b=28.6, c=44.8

**5.3 cm *DML***
$y = 2.53x^2 - 8.29x + 28.23$
$r^2 = 0.87; P = 0.006$
a=26.1, b=21.9, c=25.7

**5.5 cm *DML***
a=38.1, b=24.8, c=37.0

**5.7 cm *DML***
$y = 1.22x + 20.30$
$r^2 = 0.54; P = 0.048$
a=18.4, b=22.4, c=23.8

**6.0 cm *DML***
$y = 1.69x^2 - 5.48x + 27.93$
$r^2 = 0.88; P = 0.005$
a=27.2, b=22.2, c=28.0

**6.1 cm *DML***
a=28.7, b=25.8, c=32.1

**6.3 cm *DML***
$y = 6.016x + 11.954$
$r^2 = 0.945; P = 0.010$
a=13.3, b=20.1, c=29.3

**6.6 cm *DML***
a=21.5, b=17.7, c=21.6

**7.1 cm *DML***
$y = 11.03x^2 - 10.33x + 26.92$
$r^2 = 0.83; P = 0.03$
a=24.4, b=30.2, c=38.6

**7.5 cm *DML***
$y = 2.87x^2 - 9.08x + 22.07$
$r^2 = 0.88; P = 0.005$
a=20.6, b=15.4, c=20.1

**7.7 cm *DML***
$y = 1.77x + 14.79$
$r^2 = 0.945; P = 0.010$
a=14.6, b=17.1, c=20.1

**8.1 cm *DML***
$y = 2.676x + 7.893$
$r^2 = 0.901; P = 0.015$
a=7.4, b=11.1, c=14.3

**8.4 cm *DML***
$y = 2.042x^2 - 4.094x + 22.045$
$r^2 = 0.881; P = 0.048$
a=21.7, b=20.5, c=25.7

Rate of aerobic respiration ($\mu$mol O$_2$ h$^{-1}$ g$^{-1}$)

Swimming speed (mantle lengths s$^{-1}$)

Fig. 3

Fig. 3. $O_2$ consumption rates ($\mu$mol $O_2$ h$^{-1}$ g$^{-1}$) of 19 *Lolliguncula brevis* (2.9–8.4 cm dorsal mantle length, *DML*) plotted as a function of swimming speed (mantle lengths s$^{-1}$). Each data point is derived from the slope of percentage $O_2$ saturation *versus* time curves recorded in the final 10 min interval of each speed trial. Linear or polynomial regression equations, $r^2$ values and *P*-values are included in plots when a significant relationship was detected. As a result of limited data, linear or curvilinear relationships were not detected in some squid and, in these cases, data points were simply connected with lines. Mean rates of $O_2$ consumption ($\mu$mol $O_2$ h$^{-1}$ g$^{-1}$) for the three speed ranges are included for each squid (a, <0.5 *DML* s$^{-1}$; b, 0.5–1.5 *DML* s$^{-1}$; c, >1.5 *DML* s$^{-1}$).

0.5 *DML* s$^{-1}$ and, in one case, speeds above 1.5 *DML* s$^{-1}$. Because one objective of this study was to characterize the nature of the $O_2$ consumption rate *versus* speed relationship over the entire range of sustained swimming velocities, these squid, which ranged in size from 4.7 to 8.8 cm in *DML*, were eliminated. When all speed trials were considered for these squid with questionable performance, even those trials in which squid remained on the bottom, pushed off with their arms and pressed against the side of the respirometer, linear relationships between speed and $O_2$ consumption rate were observed in six of the eight squid (linear regressions: $P<0.05$, $r^2>0.72$).

### Rates of $O_2$ consumption

Partial (J-shaped) or full (U-shaped) parabolic patterns of $O_2$ consumption rate as a function of speed were observed for many squid with measurements from all three speed ranges (<0.5 *DML* s$^{-1}$, 0.5–1.5 *DML* s$^{-1}$, >1.5 *DML* s$^{-1}$) (Fig. 3). Mean $O_2$ consumption rates for the three speed ranges (a, b and c, respectively) for each of the cooperative squid tested are included in Fig. 3. A randomized-block ANOVA performed on these mean data indicated that there was a significant difference among the three speed ranges (Table 1). Subsequent Newman–Keuls multiple-comparison tests revealed that $O_2$

Table 1. *Randomized-block ANOVA (upper table) and Newman–Keuls multiple-comparison tests (lower table) of mean rates of $O_2$ consumption for three speed ranges*

| Source of variation | d.f. | SS | MS | F | P |
|---|---|---|---|---|---|
| Speed | 2 | 365.99 | 183.00 | 17.16 | <0.0001 |
| Blocks (squid) | 18 | 3549.89 | 197.22 | 18.50 | <0.0001 |
| Error | 36 | 383.82 | 10.66 | | |
| Total | 56 | 4299.70 | | | |

| Comparison of speed ranges | Difference in means | S.E.M. | q | P | $q_{0.05}$, 36, P | Significance |
|---|---|---|---|---|---|---|
| c *versus* b | 6.15 | 0.75 | 8.20 | 3 | 3.46 | Yes |
| c *versus* a | 3.84 | 0.75 | 5.12 | 2 | 2.86 | Yes |
| b *versus* a | 2.21 | 0.75 | 2.95 | 2 | 2.86 | Yes |

The 19 *Lolliguncula brevis* considered in the experiment were treated as blocks.

Rates of $O_2$ consumption for all three speed ranges differed significantly, with values being lowest in the 0.5–1.5 *DML* s$^{-1}$ speed range (range b).

Mean a=26.43; mean b=24.22; mean c=30.37.

*DML*, dorsal mantle length; d.f., degrees of freedom; SS, sum of squares; MS, mean square.

Speed ranges: a, <0.5 *DML* s$^{-1}$; b, 0.5–1.5 *DML* s$^{-1}$; c, >1.5 *DML* s$^{-1}$.

consumption rates were lowest at intermediate speeds (0.5–1.5 *DML* s$^{-1}$, b) and highest at the highest speeds (>1.5 *DML* s$^{-1}$, c).

Data pooled by size class are depicted in Table 2. Despite high variation among individuals, mean $O_2$ consumption rates for the intermediate speed range (0.5–1.5 *DML* s$^{-1}$) tended to be lower than those for the low (<0.5 *DML* s$^{-1}$) and high (>1.5 *DML* s$^{-1}$) speed ranges for most sizes, which is consistent with the results of the randomized-block ANOVA and

Table 2. *Wet masses, rates of $O_2$ consumption values and aerobic swimming capacities for* Lolliguncula brevis *of three size classes*

| Size class, DML (cm) | Mass (g) | Rate of consumption ($\mu$mol $O_2$ h$^{-1}$g$^{-1}$) | | | Range of $O_2$ consumption rates ($\mu$mol $O_2$ h$^{-1}$g$^{-1}$) | Factorial aerobic scope |
|---|---|---|---|---|---|---|
| | | Velocities <0.5 *DML* s$^{-1}$ | Velocities 0.5–1.5 *DML* s$^{-1}$ | Velocities >1.5 *DML* s$^{-1}$ | | |
| 2.9–3.9 | 2.31±0.59 | 36.31±2.01 | 34.77±2.32 | 40.71±3.56 | 33.80±2.62 to 40.71±3.56 | 1.20 |
| 4.0–4.9 | 7.50±2.21 | 30.42±7.73 | 24.77±7.15 | 29.00±6.45 | 24.45±8.00 to 34.80±5.64 | 1.42 |
| 5.0–5.9 | 12.25±3.59 | 30.71±10.27 | 23.56±3.24 | 33.09±10.18 | 23.47±3.97 to 38.54±14.69 | 1.64 |
| 6.0–6.9 | 15.75±2.27 | 22.68±6.98 | 21.43±3.45 | 27.79±4.05 | 19.02±5.89 to 29.20±4.23 | 1.54 |
| 7.0–7.9 | 27.70±2.98 | 21.49±4.40 | 20.90±7.99 | 23.60±10.68 | 17.20±3.84 to 27.19±10.51 | 1.58 |
| 8.0–8.9 | 41.10±10.11 | 14.41±9.81 | 17.97±4.76 | 20.00±6.82 | 13.20±8.18 to 21.27±9.48 | 1.61 |

Values are means ± S.D. (*N*=3–4).

Factorial aerobic scope is the mean maximum rate of $O_2$ consumption divided by the mean minimum rate of $O_2$ consumption during swimming.
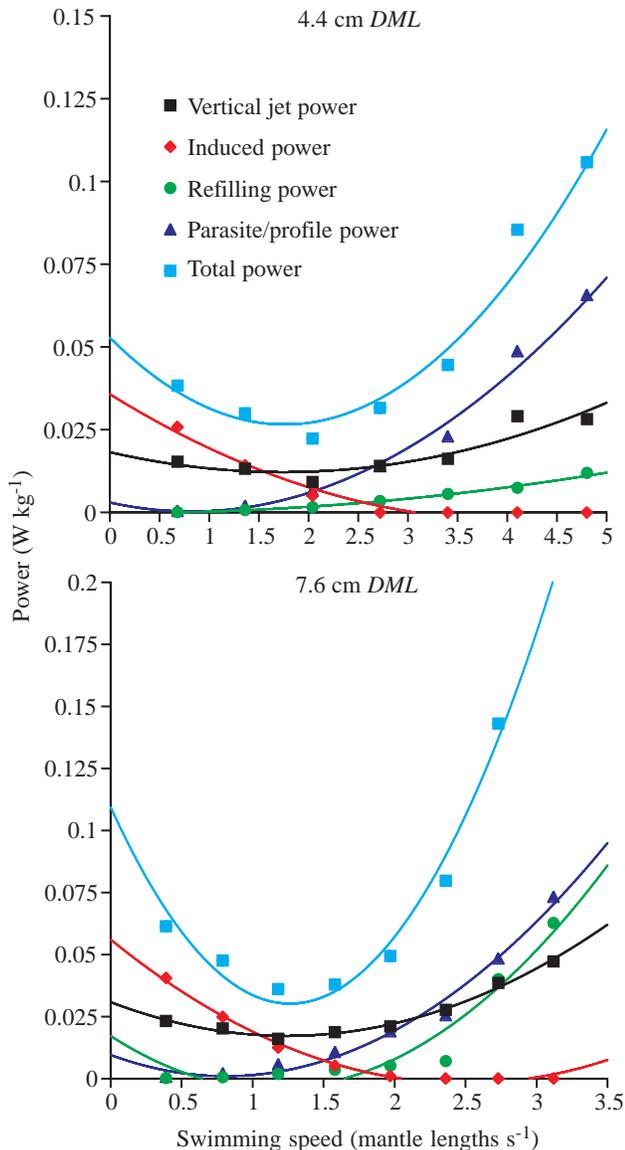
*DML*, dorsal mantle length.

Fig. 4. Vertical jet power, induced power, refilling power, parasite/profile power and total power requirements for a 4.4 cm dorsal mantle length (*DML*) and a 7.6 cm *DML Lolliguncula brevis* swimming over a range of speeds. Vertical jet power is the power required by the jet to keep the squid up in the water column, induced power is the power required by the fins to keep the squid up in the water column, refilling power is the power required to fill the mantle cavity, parasite/profile power is the power required to overcome drag on the body, fins and arms and total power is the sum of all the above power terms.

Newman–Keuls multiple-comparison tests performed on speed range means for individuals. Furthermore, the mean range of O$_2$ consumption rates generally decreased with increasing size, and *L. brevis* had a limited factorial aerobic scope for swimming (i.e. mean maximum O$_2$ consumption rate divided by mean minimum O$_2$ consumption rate) (Table 2). The mass-specific scaling coefficient, *b*, for brief squid was −0.24, and the scaling relationship between mass-specific metabolic rate

and size was: $y=47.29x^{-0.24}$ ($P=0.0001$; $r^2=0.80$), where *y* is the rate of O$_2$ consumption ($\mu$mol O$_2$ h$^{-1}$ g$^{-1}$) and *x* is mass (g).

### *Power and efficiency*

Induced power for a 4.4 and a 7.6 cm *DML* squid was the highest power demand at low speeds, but decreased exponentially with speed (Fig. 4). There was a parabolic relationship between vertical jet power and speed, with power minima between 1.2 and 2.0 *DML* s$^{-1}$. Refilling and parasite/profile power increased exponentially with speed for both squid examined. There was a parabolic relationship between total power, the sum of all power terms, and speed (Fig. 4). The speed at which the rate of total power expenditure was lowest (minimum power speed, $U_{mp}$) was 1.2–1.7 *DML* s$^{-1}$.

Gross COT curves based on aerobic data revealed that the speed of maximum range ($U_{mr}$), the minima of COT curves, was 4.0 and 2.5 *DML* s$^{-1}$ for a 4.5 and 7.5 cm *DML* squid, respectively (Fig. 5A). COT curves based on hydrodynamic data (Fig. 5B) revealed that $U_{mr}$ was 2.5 and 1.5 *DML* s$^{-1}$ for a 4.4 cm *DML* and 7.6 cm *DML* squid, respectively. The speed of maximum aerobic performance ($U_{crit}$) was 5.0 *DML* s$^{-1}$ for a 4.4/4.5 cm *DML* squid and 3.5 *DML* s$^{-1}$ for a 7.5/7.6 cm *DML* squid. Aerobic efficiency ($N_a$) curves for a 4.4/4.5 and a 7.5/7.6 cm *DML* squid are depicted in Fig. 5C. For a $U_{mr}$ of 2.5–4.0 *DML* s$^{-1}$, aerobic efficiency was 1.2–2.7 % for a 4.4/4.5 cm *DML* squid; for a $U_{mr}$ of 1.5–2.5 *DML* s$^{-1}$, aerobic efficiency was 1.8–5.0 % for a 7.5/7.6 cm *DML* squid. At $U_{crit}$, aerobic efficiency was 3.3 % for a 4.4/4.5 cm *DML* squid and 8.8 % for a 7.5/7.6 cm *DML* squid.

### Discussion

#### *Parabolic O$_2$ consumption rate/power curves*

The results of this study indicate that partial (J-shaped) or full (U-shaped) parabolic patterns of rate of O$_2$ consumption/power as a function of swimming speed exist in *Lolliguncula brevis*. Parabolic relationships between power or O$_2$ consumption rate and speed have been observed in helicopters (Bramwell, 1976), birds (Pennycuick, 1968; Pennycuick, 1975; Tucker, 1972; Tucker, 1973; Greenwalt, 1975; Rayner, 1979; Rothe et al., 1987; Dial et al., 1997), bats (Thomas, 1975; Carpenter, 1986; Norberg, 1987) and bees (Ellington et al., 1990). These devices/organisms require considerable power to fly slowly, when lift generation is costly, and fast, when overcoming drag is expensive, but fly more economically at intermediate speeds. Parabolic relationships have been detected in the aquatic realm also for slow-swimming negatively buoyant fish, such as the mandarin fish *Synchiropus picturatus* (Blake, 1979a; Blake, 1979b; Blake, 1981). However, rate of O$_2$ consumption/power increases exponentially with swimming speed for most fish, and parabolic relationships are rare [for a review of fish swimming respiration, see Beamish (Beamish, 1978)]. High metabolic/power costs at low speeds are lacking for most pelagic swimmers in part because they are neutrally buoyant or close to it, and thus generation of lift at low speeds, a considerable energetic expense for negatively buoyant organisms, is not a significant issue.

*Lift generation and stability control at low speeds*

The high rates of $O_2$ consumption of *L. brevis* at low speeds are largely because of induced power and vertical jet power demands. During hovering and at low speeds, little momentum is directed downwards as a result of the forward motion of the squid, and lift forces, which scale with the square of velocity, are low. Consequently, to generate the necessary downward momentum to counteract negative buoyancy (negative buoyancy is approximately 3.4–4.0 % in brief squid), *L. brevis* flaps its fins progressively faster and at higher amplitudes as speed decreases (Bartol et al., 2001b), a phenomenon also observed in birds and fish (Norberg, 1990; Blake, 1979b; Webb, 1974). The downwash of water produced by the fins (of finite length) alters the pressure distribution so that the lift vector increases, but the resultant vector also tilts backwards. The power required to overcome this rearward component of the resultant force vector (induced drag) is costly at low speeds when large downward deflections are necessary (Vogel, 1994; Dickinson, 1996). In *L. brevis*, some of the downward momentum at low speeds is also generated by the jet, which is directed more vertically at such speeds (Bartol et al., 2001b). Directing the jet vertically is energetically costly because water has to be expelled at high velocity both to keep the squid aloft and for it to swim horizontally. The power drains of the fins (induced power) and jet (vertical jet power) were clearly apparent in the power curves. The observed increase in vertical jet power at high speeds was an interesting artifact of a greater dependence on the jet for vertical thrust as fin activity decreased and higher jet velocities at higher speeds.

Profile, parasite and inertial power demands made up a smaller component of the observed low-speed rate of $O_2$ consumption. To generate greater lift, the fins and third (III) arms with heavy keels, which resemble traditional human-made lift-generating airfoils, as well as the mantle, head and remaining arms were positioned at high angles of attack. Both the fins and third (III) arms were extended laterally at low speeds, while the body of the squid was positioned at high angles of attack, forcing water to move faster over their upper surfaces, increasing the pressure differential above and below the biofoils and, consequently, increasing lift. Similarly, negatively buoyant elasmobranchs, tuna and mackerel increase pectoral fin area and/or angle of attack at low speeds to increase lift (Magnuson, 1978; Bone and Marshall, 1982; He and Wardle, 1986). Although the mantle, head and remaining arms (i.e. the body) do not resemble traditional airfoils/biofoils, they too generate lift when positioned at high angles of attack

(Bartol et al., 2001b). Body lift plays a critical role in lift generation in ski jumpers (Ward-Smith and Clements, 1982), honeybees (Nachtigall and Hanauer-Thieser, 1992), birds (Tobalske and Dial, 1996) and negatively buoyant fish (He and Wardle, 1986; Heine, 1992). Positioning various body appendages at high angles of attack increases pressure drag, which results from flow separation from the surface of the animal, and friction drag, which results from viscous shearing stresses in the boundary layer, on the fins and body.

Even with added drag forces from high angles of attack, parasite power, the work required to overcome pressure and friction drag on the body, is small at speeds below $0.5\,DML\,s^{-1}$ because forward swimming speed is so low. Profile power, the work required to overcome pressure and friction drag on the fins, is affected by high fin flapping speed and induced velocity at low speeds and, consequently, contributes more to energetic costs at such speeds. However, relative to induced and vertical jet power, profile power demands are low, as in birds (Pennycuick, 1972). Inertial power, the rate of work needed to accelerate the fins at each stroke, may also add some cost to swimming at low speeds, when stroke amplitudes, stroke twisting and unsteady effects are high (Norberg, 1990). Inertial power was not considered in this study, but was probably considerably lower than induced and vertical jet power at low
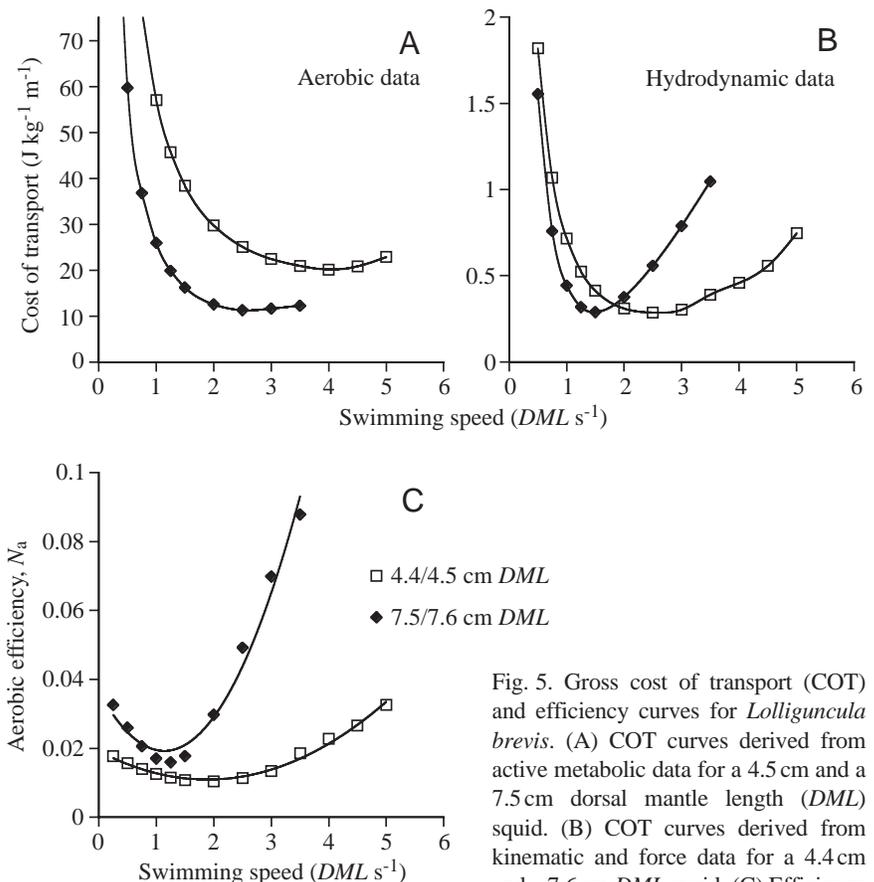


Fig. 5. Gross cost of transport (COT) and efficiency curves for *Lolliguncula brevis*. (A) COT curves derived from active metabolic data for a 4.5 cm and a 7.5 cm dorsal mantle length (*DML*) squid. (B) COT curves derived from kinematic and force data for a 4.4 cm and a 7.6 cm *DML* squid. (C) Efficiency curves, which were determined from ratios of power output (based on kinematic and force data from the 4.4 and 7.6 cm *DML* squid) to power input (based on active metabolic rates from the 4.5 and 7.5 cm *DML* squid). See text for details of calculations.

speeds given that Norberg (Norberg, 1976) found inertial power to be approximately 2 % of total aerodynamic power at low speeds in bats.

In addition to high power costs, high fin activity and amplitude and high angles of attack at low speeds, further evidence that lift generation is a critical and energetically costly component of low-speed $O_2$ consumption may be found in the respiratory costs of 'uncooperative' squid. Squid that remained on the bottom or that consistently pushed off the bottom generally did not have high costs at low speeds like free-swimming squid. These organisms had linear rather than parabolic $O_2$ consumption curves.

Positioning the body and appendages at high angles of attack and actively moving the fins are critical not only for lift generation at low speeds but also for stability control. High angles of attack increase drag, requiring the propulsors (i.e. the fins) to beat more rapidly to provide greater thrust. This increased thrust is better matched to body inertia, a force that can provide significant resistance to the return of aquatic organisms to desired paths at low speeds and, thus, provides greater stability control (Webb, 1993; Webb, 2000). High body/arm angles of attack coupled with active fins at low speeds for purposes of stability control have also been observed in neutrally buoyant fishes, such as trout and bluegill (Webb, 1993).

### Drag costs at high speeds

Drag forces scale approximately with the square of velocity just like lift, which explains the observed exponential increase in profile and parasite power as speed increased. In squid, the power required to refill the mantle also increases exponentially with speed, as it becomes necessary to accelerate greater volumes of water at higher speeds to fill the mantle. Therefore, exponential increases in rates of $O_2$ consumption with speed were expected, as have been widely reported in fish (Brett, 1965; Webb, 1973; Blake, 1983; Dewar and Graham, 1994) and squid (O'Dor, 1982; Webber and O'Dor, 1986). In the present study, exponential increases in rates of $O_2$ consumption were not always apparent, even at speeds above $0.5\,DML\,s^{-1}$. Anaerobic metabolism, which may begin as early as $1.5$–$2.0\,DML\,s^{-1}$ and account for 14.4 and 21.9 % of the energy required for swimming at 2.5 and $3.5\,DML\,s^{-1}$, respectively (Finke et al., 1996), may be responsible for the lack of exponential relationships. Even with anaerobic recruitment, sizable lift generation costs at low speeds and considerable drag costs at high speeds allowed for the development of $O_2$ consumption minima at speeds between 0.5 and $1.5\,DML\,s^{-1}$.

### $O_2$ consumption minima and behaviors that reduce costs of locomotion

A minimum $O_2$ consumption speed range ($U_{min}$) of $0.5$–$1.5\,DML\,s^{-1}$ and a minimum power speed range ($U_{mp}$) of $1.2$–$1.7\,DML\,s^{-1}$ are strong evidence that squid can swim the longest on a given amount of fuel at intermediate speeds. The slight discrepancy in values is not surprising given that $O_2$ consumption rates did not incorporate anaerobic costs and power estimates did not account for unsteady lift and propulsive mechanisms (Bartol et al., 2001b). Oxygen and power minima at intermediate speeds are reasonable given the lift, stability and drag demands described above. At intermediate speeds, less of a downward deflection of fluid is required to balance the buoyant weight because the fins, body and arms come in contact with more water per unit time, and thrust forces are better matched to body inertia than at low speeds. Therefore, the fins and jet can be used more for forward propulsion and less for lift generation and stability control, thus reducing swimming costs. Furthermore, because swimming speed and concomitant drag are not high at intermediate speeds, profile/parasite drag costs are not expensive compared with high speeds.

Given that swimming costs are lowest at intermediate speeds, negatively buoyant squid such as *L. brevis* should spend more time swimming at intermediate speeds than hovering. Observations of negatively buoyant *Loligo forbesi* in nature reveal that it seeks out current speeds close to the optimal speeds detected in this study and holds position against the current while swimming (O'Dor et al., 2001). In flow-through tanks in the laboratory, many brief squid tended to congregate near tank intakes in areas of low/moderate flow or swam continuously, which is also consistent with the prediction above. However, squid were also frequently observed away from intakes hovering arms-first with their arms oriented in front of the body at low angles of attack (often in a conical arrangement), while their mantles were positioned near the tank floor at high angles of attack. In this posture, fin flapping was often employed. This behavior is of interest because several squid that did not demonstrate parabolic $O_2$ consumption curves swam near the bottom in a similar manner at low speeds. Blake (Blake, 1979a) determined that negatively buoyant fish reduce induced power costs from 30 to 60 % by positioning themselves near the bottom and exploiting ground effects. Thus, brief squid positioned near the bottom in this arms-first posture may have been taking advantage of similar effects to lower overall low-speed metabolic costs. In nature, negatively buoyant *Loligo forbesi* and *Sepioteuthis australis* appear to use climb and glide behaviors and upwelling regions to reduce the large metabolic costs associated with counteracting negative buoyancy (O'Dor et al., 1994; Webber et al., 2000).

### Metabolic allometry

The relationship between organism mass ($M$) and metabolic rate ($R$) is frequently described by a power-law function $R=aM^b$, where $a$ is the mass coefficient and $b$ is the mass exponent (Schmidt-Nielsen, 1997). This relationship is not well understood in most cephalopods, and the scaling data that are available are quite variable. The mass-specific exponent (i.e. $b$ when metabolic rates are expressed per unit mass) for *L. brevis* in this study was −0.24, which is within the range of that measured in other aquatic invertebrates and algae [mass-specific $b$ ranges from −0.53 to +0.28 (Patterson, 1992)]. This mass-specific exponent is also consistent with that reported by

O'Dor and Webber (O'Dor and Webber, 1986) for *Illex illecebrosus* ($b$=−0.25 to −0.27) and by Seibel et al. (Seibel et al., 1997) for *Vampyroteuthis infernalis* ($b$=−0.30), *Japatella diaphana* ($b$=−0.27) and *Histioteuthis heteropsis* ($b$=−0.20). However, less concordance has been found in other metabolic studies on cephalopods. Manginnis and Wells (Manginnis and Wells, 1969) determined that mass-specific $b$ was −0.17 for *Octopus cyanea*; Johansen et al. (Johansen et al., 1982) reported a mass-specific $b$ between −0.23 and −0.01 for *Sepia officinalis*; Macy (Macy, 1980) found $b$ to be between −0.56 and +0.28 for *Loligo pealei*; and Segawa and Hanlon (Segawa and Hanlon, 1988) determined a mass-specific $b$ of −0.10 for *Octopus maya*, −0.09 for *Lolliguncula brevis* and −0.15 for *Loligo forbesi*. The wide range of mass-specific exponents among the various cephalopods is probably a product of inter- and intra-species behavioral variation during experimentation, which was frequently reported.

The $O_2$ consumption rates recorded in this study are in reasonable agreement with those reported previously for *L. brevis*. Segawa and Hanlon (Segawa and Hanlon, 1988) placed *L. brevis* in 2–4 l bottles for 0.3–1.3 h, and determined that $O_2$ consumption rates of brief squid hovering in the middle or near/on the bottom of bottles ranged from 24.4 $\mu$mol h$^{-1}$ g$^{-1}$ for a 39.98 g squid to 28.4 $\mu$mol h$^{-1}$ g$^{-1}$ for a 2.00 g squid. Wells et al. (Wells et al., 1988) measured $O_2$ uptake of *L. brevis* hovering in 2 l jars over a wide range of temperatures, and reported that mean $O_2$ consumption rates of brief squid (mean mass 9.21–10.78 g) varied from 24.3 $\mu$mol h$^{-1}$ g$^{-1}$ at 20 °C to 34.1 $\mu$mol h$^{-1}$ g$^{-1}$ at 27–30 °C ($Q_{10}$=1.47).

Wells et al. (Wells et al., 1988) and Finke et al. (Finke et al., 1996) provided limited data on $O_2$ consumption rates of *L. brevis* during swimming. Wells et al. (Wells et al., 1988) measured $O_2$ extraction by five *L. brevis* at two swimming speeds, 9.5 and 16 cm s$^{-1}$. Unfortunately, only extraction percentages were presented and, without knowledge of the tunnel dimensions and trial duration, swimming $O_2$ consumption rates could not be calculated in $\mu$mol $O_2$ h$^{-1}$ g$^{-1}$ for comparative purposes. Finke et al. (Finke et al., 1996) measured $O_2$ consumption rates of four *L. brevis* (11.9–15.1 g) during swimming that increased from 21 $\mu$mol $O_2$ h$^{-1}$ g$^{-1}$ at 0.5 $DML s^{-1}$ to 36 $\mu$mol $O_2$ h$^{-1}$ g$^{-1}$ at 2.9 $DML s^{-1}$. These values, which were measured at 20–22 °C, are similar to those recorded in the present study for squid of similar size at 24 °C (see Table 2). No parabolic relationship was detected by Finke et al. (Finke et al., 1996), but no speeds lower than 0.5 $DML s^{-1}$, speeds at which lift generation is especially costly, were considered. Interestingly, Finke et al. (Finke et al., 1996) discovered that the pressure of mantle contractions actually falls in some brief squid between speeds of 0.5 and 1.1 $DML s^{-1}$ and attributed this to a reduction in lift requirements.

### Anaerobic metabolism

In the present study, *L. brevis* was capable of sustained speeds as high as 27 cm s$^{-1}$ for 15 min, which is slightly higher than the upper aerobic limit (22.3 cm s$^{-1}$) measured by Finke

et al. (Finke et al., 1996) for *L. brevis* (11.9–15.1 g), but anaerobic metabolism may be used at much lower speeds. Finke et al. (Finke et al., 1996) determined that anaerobic metabolism contributes to energy production in *L. brevis* beginning at speeds of 1.5–2.0 $DML s^{-1}$ by measuring α-glycerophosphate, succinate and octopine accumulation in the mantle tissue. This finding, coupled with the small factorial scope of aerobic metabolism recorded in this study (1.20–1.64), suggests that brief squid are adapted for low-speed swimming. Consequently, it is possible that anaerobic metabolism during the 10 min training period, when speeds briefly approached 18–21 cm s$^{-1}$, may have produced an $O_2$ debt that elevated $O_2$ consumption rates during low-speed trials. This is unlikely, however. *L. brevis* does not accumulate large $O_2$ debts, recovers quickly from anaerobic metabolism and returns to pretrial respiratory rates even after extreme exhaustion within 20 min, the length of the recovery period after training in the present study (O'Dor, 1982; O'Dor and Webber, 1986; Pörtner et al., 1993). Moreover, squid that had significantly higher low-speed $O_2$ consumption rates at the beginning compared with the middle of the trials (during 'checks') were not considered in this experiment. Therefore, $O_2$ consumption rates measured above 1.5–2 $DML s^{-1}$ in the present study may not reflect the total metabolic costs for swimming, but $O_2$ consumption rates at speeds of 0.5–1.5 $DML s^{-1}$, when costs are lowest, and at speeds below 0.5 $DML s^{-1}$, when costs are high, are probably qualitatively representative.

### Aerobic efficiency

As mentioned above, there is some inherent error in aerobic-based power estimates (i.e. anaerobic contributions are not considered) and hydrodynamic-based power estimates (i.e. unsteady mechanisms are not considered). Consequently, it is not surprising that aerobic estimates of the speed of maximum range ($U_{mr}$) were 1.0–1.5 $DML s^{-1}$ higher than hydrodynamic estimates. Although hydrodynamic-based estimates of $U_{mr}$ are not available for other cephalopods, aerobic-based estimates for at least one squid are similar to aerobic-based estimates for *L. brevis* of similar size. On the basis of $O_2$ consumption data at 17.5 °C (O'Dor, 1982), a 41 g *Loligo opalescens* has a $U_{mr}$ of approximately 3 $DML s^{-1}$ (40 cm s$^{-1}$) and a $U_{crit}$ of approximately 3.4 $DML s^{-1}$ (45 cm s$^{-1}$). In this study, aerobic-based estimates of $U_{mr}$ and $U_{crit}$ for a 32 g *L. brevis* tested at 24 °C were 2.5 $DML s^{-1}$ (19 cm s$^{-1}$) and 3.5 $DML s^{-1}$ (26 cm s$^{-1}$), respectively.

The aerobic efficiencies for *L. brevis* reported in the present study appear to be low relative to efficiencies reported for other cephalopods, but there are some key differences in how efficiencies were calculated in the different studies. O'Dor and Webber (O'Dor and Webber, 1991) reported aerobic efficiencies of 6.1 % for *Nautilis pompilius*, 2.8 % for *Sepia officinalis*, 5.9 % for *Loligo pealei* and 13 % for *Illex illecebrosus* at $U_{mr}$. With the exception of *Sepia officinalis*, all these cephalopods have higher efficiencies than the 4.4/4.5 cm $DML$ and 7.5/7.6 cm $DML$ *L. brevis* in this study, which had

aerobic efficiencies of 1.2–2.7% and 1.8–5.0%, respectively, at $U_{mr}$. O'Dor and Webber (O'Dor and Webber, 1991) reported aerobic efficiencies of 8% for *Nautilis pompilius*, 7% for *Sepia officinalis*, 15% for *Loligo pealei* and 18% for *Illex illecebrosus* at $U_{crit}$. On the basis of these estimates, *Loligo pealei* and *Illex illecebrosus* have higher efficiencies than the 4.4/4.5 and 7.5/7.6 cm *DML L. brevis* in this study, which had efficiencies of 3.3% and 8.8%, respectively, at $U_{crit}$. However, direct comparisons between efficiencies are misleading because O'Dor and Webber's (O'Dor and Webber, 1991) estimates were based on cephalopods 600 g in mass, while efficiency estimates in this study were based on squid weighing less than 35 g. Because of lower mass-specific $O_2$ consumption rates, larger cephalopods will have higher aerobic efficiencies. This was observed in the present study and can be seen when a 500 g *Illex illecebrosus*, which has aerobic efficiencies of 8.4% and 14% at $U_{mr}$ and $U_{crit}$, respectively (O'Dor, 1988b), is compared with efficiencies for the 600 g *Illex illecebrosus* described above. Efficiencies for a 600 g *L. brevis* were not computed for comparison because a 600 g *L. brevis* has little physiological relevance [*L. brevis* does not reach sizes above 60 g (Hixon, 1980)], and there is insufficient data for scaling power output to such sizes.

Although power input was calculated in a similar manner for both studies, power output was calculated from jet pressures and funnel area by O'Dor and Webber (O'Dor and Webber, 1991), while power output was calculated from kinematic data and force measurements in the present study. These differences also may lead to disparate estimates of efficiency. Aerobic efficiencies for *Loligo opalescens* that are more directly comparable with efficiencies in this study may be calculated using power output estimates from hydrodynamic/kinematic data from O'Dor (O'Dor, 1988a) and power input estimates from metabolic data given by O'Dor (O'Dor, 1982). On the basis of these data, aerobic efficiency at 2.5 $DML\,s^{-1}$ for a 30–40 g *Loligo opalescens* is 3.2%, which is lower than an aerobic efficiency of 5% for a 32 g *L. brevis* in the present study.

### Energetic comparisons with cephalopods

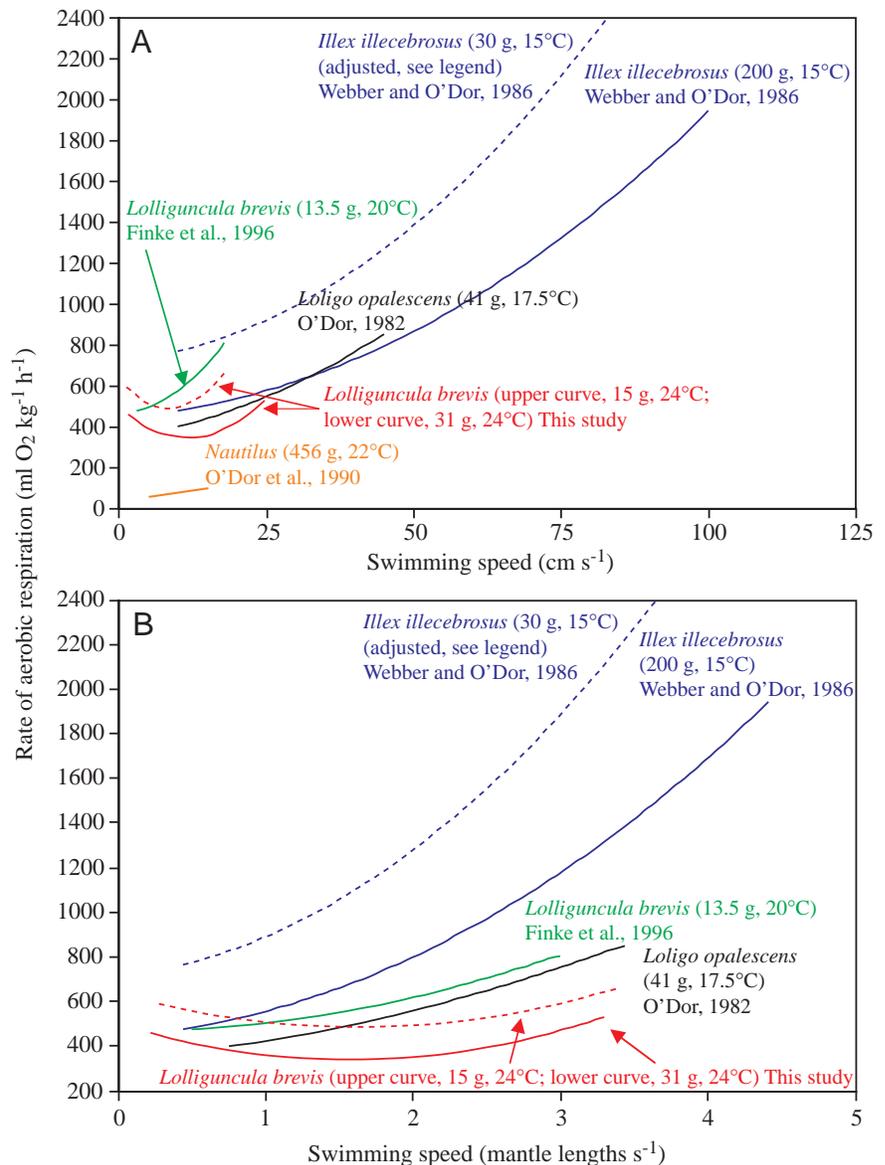*L. brevis* rarely swam faster than 24 $cm\,s^{-1}$ for sustained



Fig. 6. $O_2$ consumption rates ($ml\,O_2\,kg^{-1}\,h^{-1}$) of various cephalopods plotted against swimming speed. Swimming speeds are expressed in (A) $cm\,s^{-1}$ and (B) mantle lengths $s^{-1}$. The 15 and 31 g *Lolliguncula brevis* in the figure correspond to the 5.3 and 7.5 cm dorsal mantle length (*DML*) squid, respectively, depicted in Fig. 3. These squid were selected as representative of this study because they were particularly cooperative and their $O_2$ consumption rates were close to the mean $O_2$ consumption rates for their respective size classes. Since *Illex illecebrosus* was considerably larger than *L. brevis*, its mass was adjusted to 30 g using the metabolic scaling equation: $R=aM^b$, where $R$ is metabolic rate ($ml\,O_2\,kg^{-1}\,h^{-1}$), $M$ is organism mass (kg), $a$ is the mass coefficient and $b$ is the mass exponent (−0.25) (O'Dor and Webber, 1986). For comparative purposes, $O_2$ consumption rates for *I. illecebrosus* were extrapolated to slightly lower speeds than those studied. The mass of each organism and the temperature of the water within the respirometers are included in parentheses. Sources of the data are listed in the figure.

periods, whereas *Loligo opalescens* and *Illex illecebrosus* swim up to 45 and 100 $cm\,s^{-1}$, respectively, for sustained periods (O'Dor, 1982; Webber and O'Dor, 1986) (Fig. 6A). When velocities are converted to $DML\,s^{-1}$, however, *L. brevis*

is more competitive, reaching speeds of approximately $3.5\,DML\,s^{-1}$, which is similar to those achieved by *Loligo opalescens* (Fig. 6B). Oxygen consumption rates during swimming for a typical *L. brevis* (31 g, 24 °C) recorded in this study are lower than those of *Illex illecebrosus* [30 g (adjusted), 200 g (unadjusted), 15 °C] recorded by Webber and O'Dor (Webber and O'Dor, 1986) and *Loligo opalescens* (41 g, 18 °C) measured by O'Dor (O'Dor, 1982). *Loligo opalescens* and *Illex illecebrosus* are negatively buoyant, yet parabolic metabolic relationships have not been reported. This is surprising given that O'Dor (O'Dor, 1988a) determined that 66–92 % of the total force required for *Illex illecebrosus* to swim at $10\,cm\,s^{-1}$ is associated with maintenance of vertical position and counteracting negative buoyancy. The absence of parabolic oxygen consumption patterns may be because speeds below $10\,cm\,s^{-1}$ $(0.75\,DML\,s^{-1})$ and below $28\,cm\,s^{-1}$ $(1.2\,DML\,s^{-1})$ were not considered in respiratory trials of *Loligo opalescens* or *Illex illecebrosus*, respectively. As observed in the present study, high lift generation costs occur at speeds below $0.5\,DML\,s^{-1}$.

### Energetic comparisons with fishes

Squid are thought to consume 5–7 times more $O_2$ per unit mass per unit time than fish during swimming (O'Dor, 1982; Webber and O'Dor, 1986; O'Dor and Webber, 1986), but comparisons between *L. brevis* and ecologically comparable fishes reveal that the $O_2$ consumption differences are less dramatic. In Fig. 7, brief squid $O_2$ consumption rates are compared with those of mullet, flounder, menhaden and striped bass. When swimming velocities are expressed in $cm\,s^{-1}$ and comparisons are made between organisms of similar mass, brief squid have $O_2$ consumption rates 2.7–3.5 times higher than those of mullet, 1–2.25 times higher than those of striped bass and 1.3–1.75 times higher than those of flounder (Fig. 7A). When swimming velocities are expressed in body lengths $s^{-1}$ and comparisons are made between organisms of similar mass, brief squid actually have lower $O_2$ consumption rates at certain speeds than those of striped bass, flounder and menhaden (Fig. 7B). These comparisons suggest that brief squid are not as ill-equipped to compete with fish as once thought, but rather may be quite competitive with certain fish found in similar habitats.
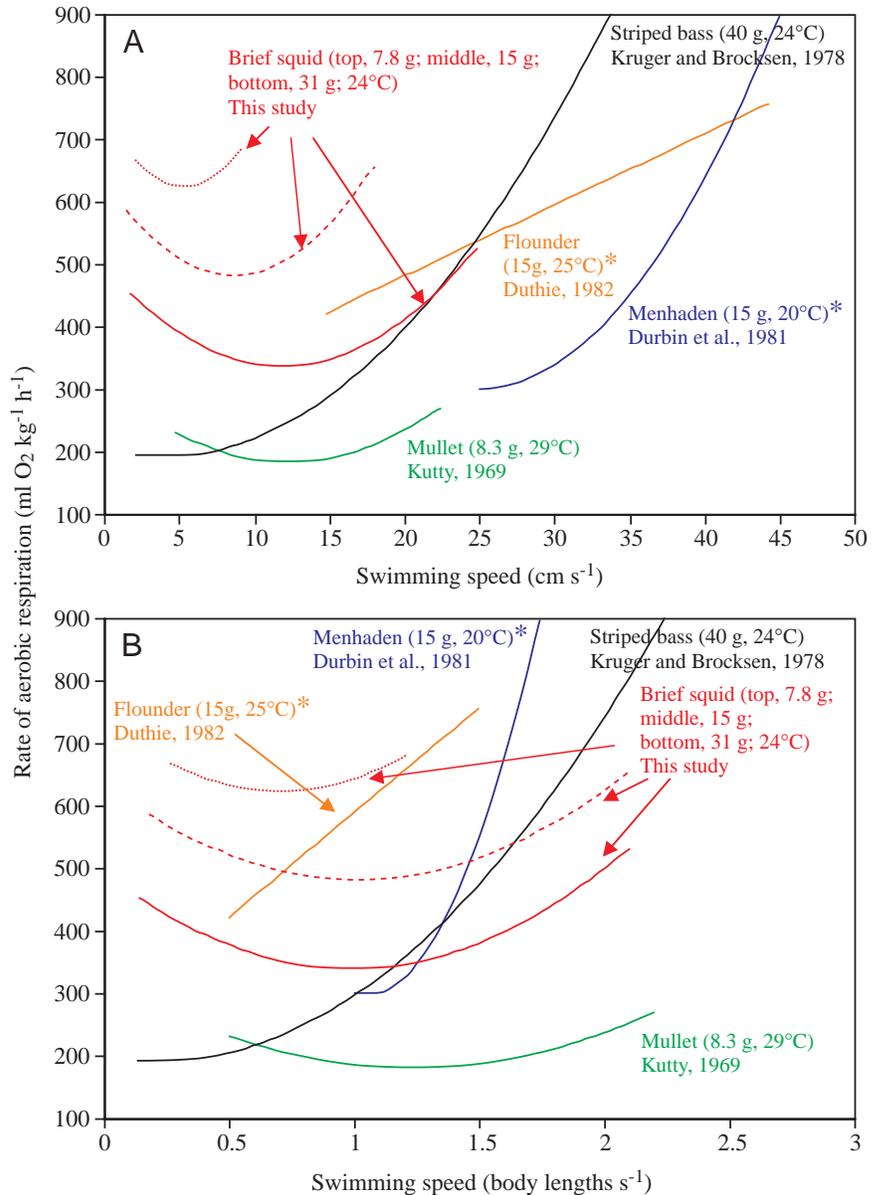


Fig. 7. $O_2$ consumption rates ($ml\,O_2\,kg^{-1}\,h^{-1}$) of *Lolliguncula brevis* and various fishes plotted against swimming speed. Swimming speeds are expressed in (A) $cm\,s^{-1}$ and (B) body lengths $s^{-1}$. The 7.8, 15 and 31 g *L. brevis* in the figure correspond to the 4.8, 5.3 and 7.5 cm dorsal mantle length (*DML*) squid, respectively, depicted in Fig. 3. These squid were selected as representative of this study because they were particularly cooperative and their $O_2$ consumption rates were close to the mean $O_2$ consumption rates for their respective size classes. Squid mantle lengths (*ML*) were converted to body lengths (*BL*) using the equation $BL=1.6ML$ derived from morphological measurements of *L. brevis*. The masses of menhaden and flounder (denoted with asterisks) were adjusted to 15 g using the equation: $R=aM^b$, where $R$ is metabolic rate ($ml\,O_2\,kg^{-1}\,h^{-1}$), $M$ is organism mass (kg), $a$ is the mass coefficient and $b$ is the mass exponent (−0.25) (O'Dor and Webber, 1986). Moreover, flounder oxygen consumption rate was converted to 25 °C using data on the effects of temperature on the active metabolic rate of flounder (Duthie, 1982). Sources of the data are listed in the figure.

O'Dor and Webber (O'Dor and Webber, 1991) and Wells (Wells, 1994) suggest that, in environments where food density is low, jet-propelled cephalopods must maximize speed and

power density to compete effectively. In environments such as the Chesapeake Bay and inshore, complex ecosystems where prey are abundant, the requirements may differ. *Lolliguncula brevis* swims slowly, uses considerable fin activity and is competitive metabolically with ecologically comparable fish, despite the inherent inefficiencies of jet propulsion. Fin flapping used by *L. brevis* helps to lower metabolic costs because large volumes of water are driven backwards with each fin movement, allowing for a more economical generation of thrust than with the jet alone. Since the energy required for jet propulsion increases exponentially with swimming velocity, simply swimming at low speeds may also minimize the inefficiencies of jet propulsion and lower cost. As a result of negative buoyancy, there is a lower limit to swimming speed before energetic efficiency is compromised. Many mid- and deepwater cephalopods have eliminated the problems associated with negative buoyancy by incorporating tissue with many fluid-filled spaces containing ammonium chloride (ammoniacal tissue) throughout much of their bodies and reducing muscle density (Wells, 1994; Hanlon and Messenger, 1996). These organisms frequently rely less on the jet and more on fin motion for propulsion, and consequently their metabolic rates are low (Seibel et al., 1997). *Lolliguncula brevis* has probably not reduced muscle and incorporated ammoniacal tissue to achieve neutral buoyancy because sudden, powerful jet thrusts directed in various orientations *via* its maneuverable funnel are highly advantageous in highly populated environments, both for avoiding predators and for ambushing prey.

### Concluding remarks

There are surprisingly few reports on parabolic O2 consumption rate/power curves as a function of swimming speed among negatively buoyant fishes and squid. This is presumably because low speeds are often omitted from energetic/hydrodynamic studies because the organism demonstrates inconsistent behavior at such speeds. In this study, some variation in low-speed swimming behavior was also observed, but this variation was interpreted to be integrally linked to costs associated with keeping position in the water column. This is not an unrealistic assumption given that power predictions based on hydrodynamic data also indicate high costs at low speeds and that recent research (Webber et al., 2000; O'Dor et al., 2001) suggests that cephalopods expend considerable energy counteracting negative buoyancy in nature. The absence of low-speed energetic/hydrodynamic data for many nekton has left a void in our understanding of the costs of low-speed swimming, which may be high even among neutrally buoyant fish because of power requirements for stability (Webb, 1993; Webb, 2000). With the development of digital particle image velocimetry (DPIV) and three-dimensional defocusing digital particle image velocimetry (DDPIV) (Pereira et al., 2000), which provide quantitative data on momentum transfer over short time scales, it is now possible to assess swimming costs effectively at low speed when movements are highly unsteady. Future particle image velocimetry studies should provide valuable insight into the dynamics and mechanics of low-speed swimming.

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