

SWIMMING IN THE CALIFORNIA SEA LION: MORPHOMETRICS, DRAG AND ENERGETICS

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SUMMARY

During swimming, the California sea lion, *Zalophus californianus* (Lesson), generates thrust forces solely by means of its pectoral flippers. This study examines the drag, energetic cost and efficiency associated with this method of locomotion. Sea lions are highly streamlined, with a fineness ratio of 5.5 and maximum girth at 40 % of body length. This profile leads to reduced drag and swimming power requirements. Films of gliding animals showed the drag coefficient (based on wetted surface area) to be 0.0042 at a Reynolds number of 2.0×10^6 . This value is comparable to that found for other aquatic vertebrates and suggests that the sea lion's morphology helps to delay turbulent separation and maintain laminar flow over the forward portion of its body.

Swimming metabolism was measured in a water flume at velocities up to 1.3 m s^{-1} . Effective swimming speeds up to 2.7 m s^{-1} were attained by increasing each animal's drag. Oxygen consumption rose exponentially with velocity and for two animals was best described as $\dot{V}_{\text{O}_2} = 6.27e^{0.48U}$, where \dot{V}_{O_2} is in $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ and U is in m s^{-1} . Minimum cost of transport for these animals was $0.12 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ at a relative speed of 1.4 body lengths s^{-1} . This is 2.5 times that predicted for a fish of similar size. Swimming efficiencies were determined from these results using power output values calculated from the measured drag coefficient and standard hydrodynamic equations. At the highest velocity, aerobic efficiency reached a maximum of 15 % while mechanical efficiency of the foreflippers was 80 %. The results demonstrate that foreflipper propulsion is a highly efficient and comparatively inexpensive method of locomotion in aquatic mammals.

INTRODUCTION

Within the order Pinnipedia, two distinct swimming styles have evolved. The Phocidae, or true seals, undulate their bodies and rear flippers in a manner analogous to the subcarangiform mode of locomotion in fish (Lighthill, 1969). Sea lions and fur seals of the family Otariidae use their foreflippers, a style which resembles that of penguins and sea turtles (Robinson, 1975). These contrasting methods of propulsion suggest functionally separate approaches to the problems of aquatic foraging.

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Previous studies on fish demonstrate that the mechanical performances of caudal and pectoral fin propulsion are quite different (Webb, 1975a, 1984; Blake, 1983a). These differences are often reflected in the foraging patterns and choice of habitat among species (Webb, 1984). An ecological separation based upon functional performance may also occur in pinnipeds.

Few studies have investigated the hydrodynamic characteristics, drag and cost of swimming in aquatic mammals. With the exception of several papers on cetaceans (Lang & Daybell, 1963; Lang, 1966) and one on seals (Williams & Kooyman, 1985), most hydrodynamic work has been conducted on models or carcasses (Hertel, 1966; Mordvinov, 1972; Mordvinov & Kurbatov, 1973; Alejev, 1977). Data on the energetic requirements of locomotion are also scarce and, for seals and sea lions, are only available for a single velocity or over a narrow range of velocities (Kooyman, Kerem, Campbell & Wright, 1973; Costello & Whittow, 1975; Oritsland & Ronald, 1975; Craig & Pasche, 1980; Lavigne, Barchard, Innes & Oritsland, 1982). Only Kruse (1975) and Davis, Williams & Kooyman (1985) have addressed the question of how this cost varies with speed. No one has determined the efficiency of marine mammal propulsion.

The purpose of this study was to examine the hydrodynamics and locomotory energetics of foreflipper propulsion in the California sea lion (*Zalophus californianus*), a representative otariid. Body shape was quantified and compared with other swimming animals to assess their streamlined design. Drag coefficients were determined and permit an estimate of the power output requirements necessary for swimming. The energetic cost of locomotion was also measured. Coupled with the drag measurements, this provided a means of determining metabolic efficiency and the mechanical efficiency of the foreflippers at generating thrust.

MATERIALS AND METHODS

Animals

Four sea lions (SL1–SL4) used in these experiments were held in seawater tanks at Scripps Institution of Oceanography and fed a diet of mackerel supplemented with vitamins. Animals were weighed weekly and body mass was maintained at $\pm 3\%$ throughout the study.

Direct measurements were made of body and flipper lengths in all animals. Girth at various locations along the body was determined both by direct measurement and from photographs. Surface areas and volumes were calculated by considering each animal as a series of truncated cones based upon the length and girth measurements. Rear flippers were estimated as triangles. Projected area of the foreflippers was determined by tracing their outline on a digitizing pad. Total surface area was calculated as twice the projected area.

Glide-drag measurements

Drag coefficients were determined using procedures described previously (Clark & Bemis, 1979; Williams & Kooyman, 1985). In brief, sea lions SL1–SL3 were

videotaped as they glided past two reference marks fixed to the tank wall and set 2 m apart. Video cameras were placed perpendicular to the glide path and opposite the reference marks. Cameras were connected to an RCA image splitter that was coupled to a GYYR video recorder. Only glides parallel to the reference lines and in which no strokes occurred were analysed. Velocity at each reference mark was calculated as the animal's length divided by the time required for it to pass the mark. Time to travel from one mark to the next was also determined. Deceleration (A) could be calculated as:

$$A = (U_1 - U_2)/t, \quad (1)$$

where U_1 and U_2 are velocities at the first and second reference marks, respectively, and t is the time required for travel from one mark to the next. Total body drag (D) is then given by:

$$D = (M_b + M_a)A, \quad (2)$$

where M_b is mass of the animal and M_a is the added or virtual mass (Webb, 1975a; Vogel, 1981; Alexander, 1983). Because the length:diameter ratio of the sea lions was 5.5:1 (Table 1), virtual mass was estimated as $0.05 \times$ body mass (Landweber, 1961; Lang, 1966; Blake, 1983b).

Animals appeared to decelerate uniformly between the two reference marks. The average velocity during this deceleration (U_a) was computed as the geometric mean of U_1 and U_2 . Since drag is a power function, the arithmetic mean slightly underestimates the average speed for which the drag measurement is made. This value, the measured drag (D) and a knowledge of the animal's wetted surface area (S_w), enables a calculation of the drag coefficient (C_d):

$$C_d = \frac{2D}{\rho \times S_w \times U_a^2}, \quad (3)$$

where ρ is water density (Hoerner, 1958).

Oxygen consumption measurements

Three juvenile sea lions, two females (SL2, SL3) and one male (SL4) were used in these experiments. SL2 and SL3 both maintained a body mass of 22.5 ± 1.0 kg (± 2 S.E.) over the study period from August to September. Water temperature (T_w) was $26 \pm 0.9^\circ\text{C}$. SL4 was studied on two separate occasions. During the first, from April to May, T_w averaged $19 \pm 0.7^\circ\text{C}$ and the animal weighed 18.0 ± 0.5 kg. The second set of experiments was conducted during August. SL4 had increased in mass to 27 kg and T_w had risen to $25 \pm 0.5^\circ\text{C}$.

Rates of oxygen consumption (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}) were measured as animals swam against a water current generated inside a variable-speed flow channel, 1.1 m in cross-sectional area and 16 m in length. Two 0.6-m diameter propellers generated flow up to a maximum velocity of 1.3 m s^{-1} . Water velocity was calibrated prior to the experiments with an electromagnetic flow probe and correlated with pump speed.

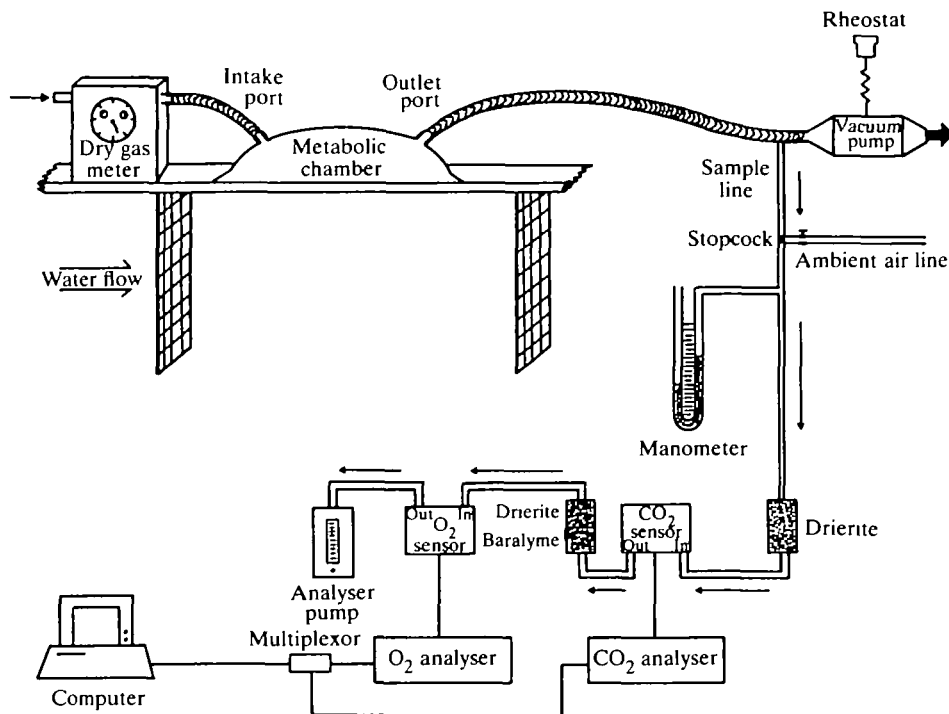


Fig. 1. Schematic diagram of the equipment used to measure oxygen consumption. Sea lions were confined to a test section in the water flume and could only surface to breathe inside the metabolic dome. Air flow entering the dome was measured with a dry gas meter. Expired gas was continuously sampled from the outlet flow and analysed for percentage O₂ and CO₂ content.

A test section was created by partitioning the flume with two grids, 2.5 m apart. These were constructed of 15 mm × 3 mm steel strips welded together to form 13 cm square openings. Strips were oriented 'edge on' to the flow to reduce turbulence. No measurable drop in water velocity was detected at any depth inside the test section.

A Plexiglas dome (1.1 m × 0.6 m × 0.3 m) was set into the forward portion of a plywood frame that covered the test section. Animals could only surface to breathe inside the dome which served as an open-circuit metabolic chamber. Ambient air was pulled through the chamber with a vacuum pump. A dry gas meter connected to the inlet port measured air flow (Fig. 1). Samples of expired gas were continuously removed and dried with Drierite before entering the Applied Electrochemistry (AEI) CO₂ analyser. CO₂ was then removed with Baralyme and the gas redried upon entering the AEI O₂ analyser. An online Apple II+ computer sampled the voltage output of each analyser and provided 1-min averages of the percentage gas concentration. \dot{V}_{O_2} and \dot{V}_{CO_2} were computed using the equations of Depocas & Hart (1957). All values were corrected to STPD.

The system was calibrated daily with dry ambient air and checked for leaks by bleeding 100% N₂ at a known rate into the air entering the dome. The O₂ fraction in the outlet flow was calculated and compared to the analyser reading (Davis *et al.*

1985). Values agreed to within $\pm 0.01\%$ prior to the start of each experiment. No difference was detected between the measured and theoretical O_2 fraction at any water velocity.

The CO_2 analyser was calibrated by bleeding a mixture of 10% CO_2 in N_2 into the total flow. This produced CO_2 levels similar to those of the sea lions. Calibrations were conducted with and without water flowing through the test section. At zero water flow, the theoretical and measured CO_2 values agreed to within $\pm 0.01\%$. At higher speeds, however, the measured value was slightly lower, indicating that CO_2 was dissolving into the water. Factors were determined for each velocity and used to correct these readings. Adjusted values agreed with those calculated to within $\pm 0.01\%$ at all flume speeds.

Practice sessions were undertaken for several weeks prior to the actual measurements. Training was considered complete when reproducible values for \dot{V}_{O_2} were obtained. Animals were fasted for 12–16 h before each swimming session. At each velocity increment, 10 min was allowed for the animals to reach steady state. Recordings were then made for 10–20 min of continuous swimming. 10-min averages of \dot{V}_{O_2} and \dot{V}_{CO_2} provided single data points at each velocity. Only those measurements where the animal swam steadily were used. Flume speeds were varied randomly to avoid systematic errors, and sea lions rested for several minutes between each velocity increment.

Increasing swimming effort

Although sea lions showed an elevated \dot{V}_{O_2} at 1.3 m s^{-1} , this was well below their top swimming speed. To simulate higher swimming velocities, each animal's drag was increased. Two nylon cups (12 cm \times 12 cm \times 5 cm) were attached with cyanoacrylic glue to the midline of their ventral surfaces at 40 and 60% of the body length. No interference was observed between the cups and the foreflippers.

Effective swimming speeds were measured by determining each animal's drag, both with and without drag cups, over the range of experimental velocities. This was accomplished by towing the sea lions underwater behind an electrically powered cart (Williams & Kooyman, 1985). The cart travelled around a circular 'ring' tank which had inner and outer diameters of 14.5 and 21 m, respectively. Towing velocities ranged from 0.9 to 3.8 m s^{-1} . Water depth was 3.5 m.

Animals were trained to bite a soft neoprene mouthpiece that fitted inside their mouths and conformed to the jaw profile. The mouthpiece was attached to a 6.4 mm nylon line that was secured to a force transducer mounted on the cart. From the transducer, the towing line passed vertically down through a streamlined hydrofoil strut, 90 cm in length, mounted underneath the cart in an orientation that minimized turbulence. At the bottom of the strut a pulley, encased in a streamlined fibreglass housing, turned the line 90°. The depth of the pulley was 1 m. The animal was towed approximately 1 m behind the strut to avoid effects of turbulence.

Before each session, the transducer was calibrated with a hand-held dynamometer previously calibrated against a series of weights. Cart velocity was monitored with a magnetic tachometer attached to one of the outer wheels. Outputs from the

transducer and tachometer were simultaneously recorded on a Gould strip chart recorder. During towing, an observer ensured that animals remained motionless with both flippers held against the body in a gliding position. Runs lasted up to 30 s at a constant velocity. Only those which produced a steady trace for a minimum of 5 s and where no movement was observed were analysed.

Animals were towed both with and without drag cups attached. Each served as its own control and appeared to maintain the same towing posture during all experimental trials. For each condition, drag was best fitted by a geometric equation of the form:

$$D = aU^B, \quad (4)$$

where a is a proportionality constant, B is the slope and U is velocity. The effective swimming speed of an animal with drag cups attached was then determined by setting the equations for each condition equal to one another and solving for velocity:

$$\log(U_{w0}) = \frac{(\log a_2 - \log a_1) + (B_2 \log U_w)}{B_1}, \quad (5)$$

where U_{w0} , a_1 and B_1 are parameters of the drag equation obtained without cups, and U_w , a_2 and B_2 represent those with the added resistance (Fig. 2).

Resting measurements

The resting metabolic rates of SL2 and SL3 were measured in a tank, 1.05 m \times 1.5 m in cross-section, 2 m in length, and filled to a depth of 1 m with sea water. Water temperature was 26°C. Sea lions fasted for 24 h prior to these

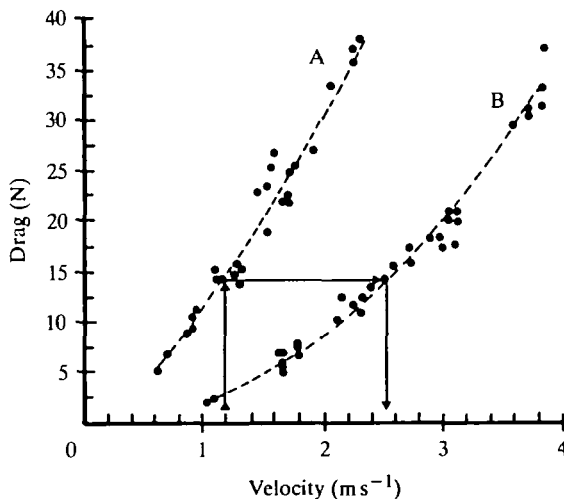


Fig. 2. Example of the method used to determine the relative swimming speed of animals with drag cups. Curve A was obtained by towing SL3 with cups attached. Curve B is from the same animal without added resistance. Both curves were best fitted by an equation of the form: $\text{drag} = aU^B$. In this example, SL3 swimming at 1.2 ms^{-1} with cups experienced the same drag as at 2.5 ms^{-1} without any additional resistance.

measurements. A metabolic dome served as an open-circuit chamber and \dot{V}_{O_2} was measured as described above. Animals were periodically active while in the chamber, but often remained quiet for short (10–30 min) intervals. The lowest 10-min average of \dot{V}_{O_2} was taken to represent the resting metabolic rate.

RESULTS

Morphometrics

Morphometric data for the sea lions are presented in Table 1. The aspect ratio, which averaged 7.9, was determined as span of the flippers divided by their chord. Flipper chord was taken to be the width of the flippers at the wrist. Based on volume estimates, body density was computed to be, on average, $1.02 \times 10^3 \text{ kg m}^{-3}$, nearly equal to sea water ($1.025 \times 10^3 \text{ kg m}^{-3}$ at 15°C ; Vogel, 1981).

Body drag

Drag coefficients, determined from the gliding animals and based on total surface area (C_{d_s}), averaged 0.0039 ± 0.0001 ($\pm 2 \text{ s.e.}$) for SL1 ($N = 13$), 0.0042 ± 0.0002 for SL2 ($N = 31$) and 0.0041 ± 0.0004 for SL3 ($N = 17$). There were no significant differences among the three animals. Reynolds numbers associated with these glides were 2.87×10^6 , 2.03×10^6 and 2.13×10^6 for SL1, SL2 and SL3, respectively (Table 2).

Metabolism and swimming speed

The resting metabolic rate of SL2 and SL3 averaged 6.6 ± 0.33 ($\pm 2 \text{ s.e.}$) and $6.5 \pm 0.17 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, respectively. This rate is 1.4 times that predicted by the Kleiber (1961) relationship of $M = 3.4W^{0.75}$ (M is in watts, W is body mass).

For all sea lions, \dot{V}_{O_2} and \dot{V}_{CO_2} increased curvilinearly with swimming velocity (Fig. 3). There was no significant difference between SL2 and SL3 and their results were pooled. For these two animals, \dot{V}_{O_2} was best described by:

$$\dot{V}_{O_2} = 6.27e^{0.48U} \quad (N = 66; r^2 = 0.90; \text{s.e.e.} = 0.096), \quad (6)$$

where \dot{V}_{O_2} is in $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. Respiratory quotients (RQ) showed no correlation with velocity and averaged 0.75 ± 0.025 ($\pm 2 \text{ s.e.}$; $N = 33$) and 0.76 ± 0.023 ($N = 34$) for SL2 and SL3, respectively. Total power input (P_i , in watts) was also calculated by assuming a calorific equivalent of $20.1 \text{ J ml O}_2^{-1}$. P_i increased exponentially according to the relationship:

$$P_i = 46.63e^{0.49U} \quad (N = 66; r^2 = 0.92; \text{s.e.e.} = 0.093). \quad (7)$$

A detailed study of SL4 was only possible at a T_w of 19°C . At this temperature, \dot{V}_{O_2} was significantly higher (t -test of regression intercept, $P < 0.005$; Zar, 1984) than that of the other animals:

$$\dot{V}_{O_2} = 15.26e^{0.27U} \quad (N = 34; r^2 = 0.89; \text{s.e.e.} = 0.06). \quad (8)$$

Total power input was also greater:

$$P_i = 92.25e^{0.27U} \quad (N = 34; r^2 = 0.88; \text{s.e.e.} = 0.06). \quad (9)$$

Table 1. *Morphometric data for sea lions in this study*

	SL1	SL2	SL3	SL4	Average \pm s.d.
Mass (kg)	37.5	23.3	22.1	19.0	
Total length (m)*	1.46	1.30	1.32	1.23	
Total foreflipper surface area (cm ²)	1 422	1 164	1 126	1 005	
Total body surface area (cm ²)†	9 048	7 006	7 008	6 049	
Frontal area (cm ²)	755	415	417	346	
Total body volume (cm ³)	36 000	23 000	23 000	18 300	
Calculated density (kg m ⁻³ $\times 10^3$)	1.04	1.01	1.00	1.04	1.02 \pm 0.021
Finess ratio (L/d)	4.75	5.65	5.64	5.84	5.47 \pm 0.49
Position of maximum diameter (C/L)	0.40	0.41	0.40	—	0.40 \pm 0.006
Foreflipper span (cm)	95.0	86.6	81.0	78.4	
Foreflipper chord at wrist (cm)	12.5	10.2	10.8	10.0	
Aspect ratio	7.6	8.5	7.5	7.8	7.85 \pm 0.45

* Nose to rear flipper end.

† Includes pectoral flippers.

L, body length; d, maximum body diameter; see Fig. 5 for a definition of C.

Table 2. Drag coefficients and velocities (± 2 S.E.) determined from glide experiments

	SL1	SL2	SL3
N	13	31	17
$Re \times 10^6$	2.87 ± 0.052	2.03 ± 0.021	2.13 ± 0.041
Cd_s	0.0039 ± 0.0001	0.0042 ± 0.0002	0.0041 ± 0.0004
Cd_f	0.046 ± 0.0015	0.070 ± 0.0037	0.069 ± 0.0065
U_a ($m s^{-1}$)	2.36 ± 0.043	2.01 ± 0.021	2.06 ± 0.040
U_a ($L s^{-1}$)	1.62 ± 0.029	1.55 ± 0.016	1.56 ± 0.030

Re , Reynolds number; Cd_s and Cd_f , drag coefficients based on wetted surface area and frontal area, respectively; U_a , average velocity; L , body length.

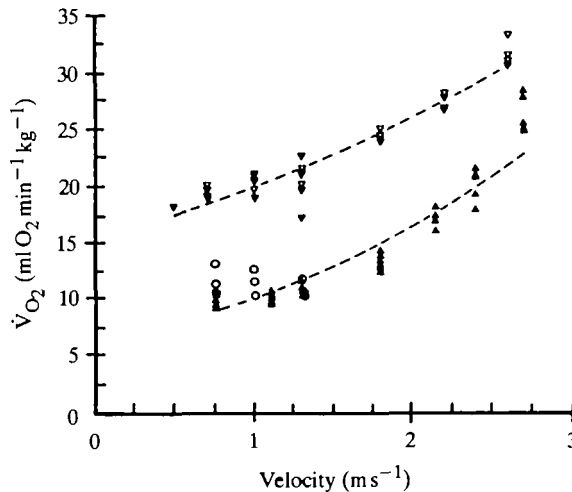


Fig. 3. Mass-specific metabolic rate of three sea lions as a function of swimming speed. The lower curve (\blacktriangle) is from measurements of SL2 and SL3 (22.5 kg) at a water temperature (T_w) of 26°C. The upper curve (∇) is from SL4 (18 kg) at a T_w of 19°C. Open circles (\circ) on the lower curve are results from SL4 (27 kg) when T_w was 25°C.

RQ values remained constant with speed and averaged 0.76 ± 0.027 ($N = 34$), not significantly different from SL2 and SL3.

To determine whether this metabolic elevation was due to a low T_w , an abbreviated study was undertaken several months later at a T_w of 25°C, when SL4 weighed 27 kg. There was no significant difference between the \dot{V}_{O_2} of SL4 and that of SL2 and SL3 up to $1.3 m s^{-1}$ (Fig. 3).

Cost of transport

For SL2 and SL3, the cost of transport (CT), defined as the amount of energy required to move a unit of mass a given distance (Schmidt-Nielsen, 1972; Tucker, 1975), reached a minimum at $1.8 m s^{-1}$, corresponding to a relative speed of

$1.4 \text{ body lengths s}^{-1}$ (L s^{-1}) (Fig. 4). At this velocity, CT averaged 0.12 ± 0.005 ($\pm 2 \text{ s.e.}$) $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$. For SL4, when T_w averaged 19°C , CT continued to decline as velocity increased and showed no distinct minimum. At the highest speed of 2.6 m s^{-1} (2.1 L s^{-1}), CT averaged $0.20 \pm 0.007 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$. At a T_w of 25°C , SL4 showed costs similar to those of SL2 and SL3 at comparable speeds up to 1.3 m s^{-1} (Fig. 4).

DISCUSSION

Morphometrics and drag

Body shape is perhaps the most important variable affecting an animal's swimming performance. Sea lions swim at speeds where fluid flow around their body is characterized by high Reynolds numbers. The Reynolds number (Re), defined as the product of an animal's length and velocity divided by the fluid's kinematic viscosity, is a measure of the relative importance of inertial to viscous forces in this flow (Vogel, 1981). At higher Re values, inertial forces dominate, and flow in the boundary layer changes from laminar to turbulent. As Re increases, the boundary layer begins to separate from the animal, leading to a turbulent wake (Webb, 1975a; Vogel, 1981). This increases the rate of transfer of momentum to the water, removing kinetic energy and slowing the animal's forward progress. Reducing wake size by delaying boundary layer separation is, therefore, of primary importance in minimizing the rate of energy loss during swimming.

At high Re values, streamlining is the most effective way to delay this separation (Webb, 1975a). The ability of an object to reduce drag depends on two factors, its fineness ratio (FR) (length divided by maximum diameter) and the position of maximum diameter along its body (Webb, 1975a; Alejev, 1977). Direct length and girth measurements show that sea lions are highly streamlined (Fig. 5). Their FRs averaged 5.5 (Table 1), not substantially different from the optimum of 4.5 which gives minimal drag for maximal body volume (Webb, 1975a). Moreover, their shoulder is at 40% of body length. This position is sufficiently far back to ensure laminar flow over the forward portion of the animal and to delay the point at which separation occurs (Hoerner, 1958; Alejev, 1977). As a result, disturbance to flow is reduced, a smaller wake is formed, and resistive forces are diminished.

This combination of features has resulted in a morphology that closely resembles a technical body of revolution (Fig. 5). The advantage of this streamlined design is shown by examining the drag coefficient. For objects of similar size travelling at comparable speeds, a lower C_d denotes a reduction in total drag and hence in the power required for steady forward movement (Webb, 1975a). Sea lions have drag coefficients based on wetted surface area (C_{d_s}) of $0.0042\text{--}0.0039$ at Re values of $2.03\text{--}2.87 \times 10^6$ (Table 2). These values are comparable to those found for other large aquatic animals including penguins ($C_{d_s} = 0.002\text{--}0.0044$ at $Re = 10^6$) (Clark & Bemis, 1979; Bilo & Nachtigall, 1980), the white-sided dolphin *Lagenorhynchus obliquidens* ($C_{d_s} = 0.0034$ at $Re = 9.1 \times 10^6$) (Lang & Daybell, 1963) and harbor seals ($C_{d_s} = 0.004\text{--}0.007$ at $Re = 1.6 \times 10^6$) (Williams & Kooyman, 1985). In contrast, the

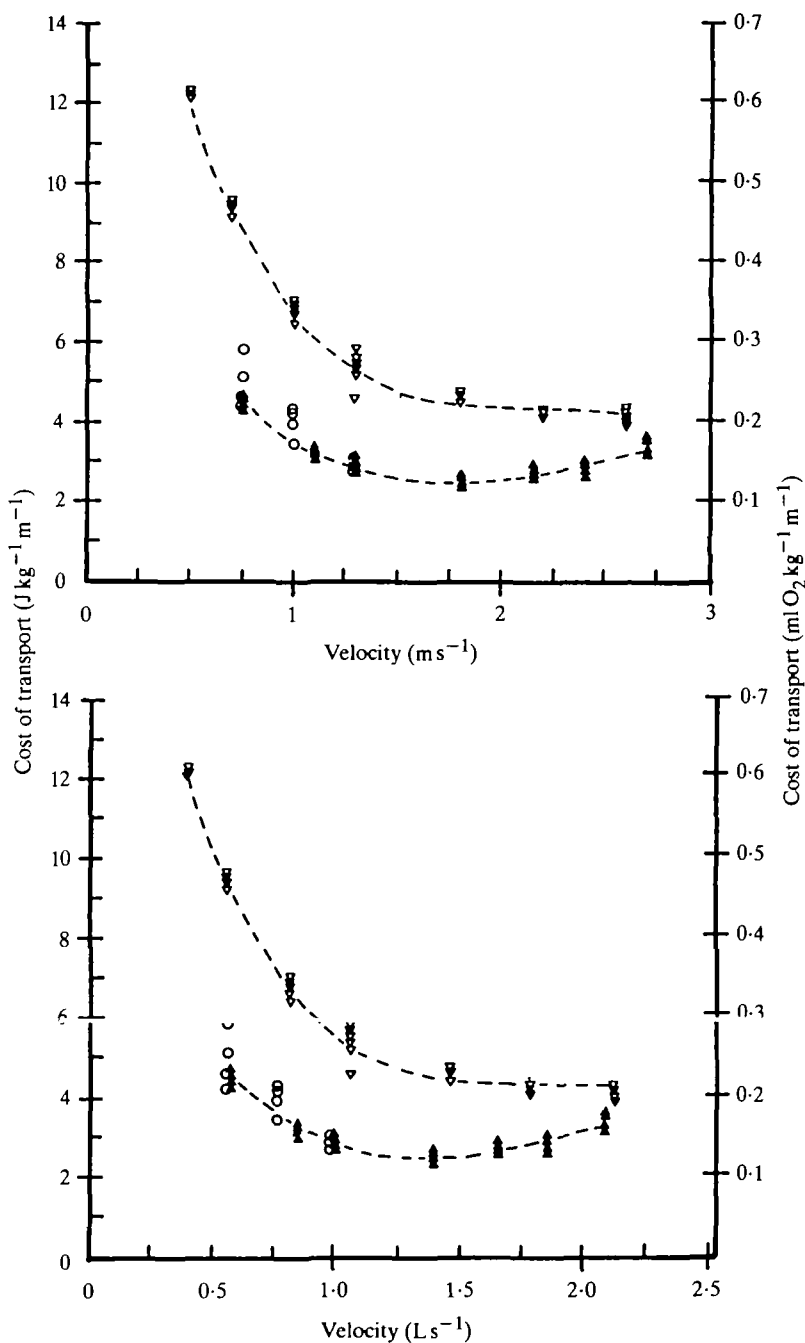


Fig. 4. Cost of transport (CT) plotted for all animals against swimming speed. (A) Speed expressed in m s^{-1} . (B) Speed normalized to body length (L s^{-1}). For SL2 and SL3 (\blacktriangle), CT reached a minimum at 1.8 m s^{-1} (1.4 L s^{-1}). For SL4 (∇), CT showed no distinct minimum but declined throughout the range of speeds examined. Open circles on the lower curves (O) represent measurements of SL4 when water temperature was 25°C .

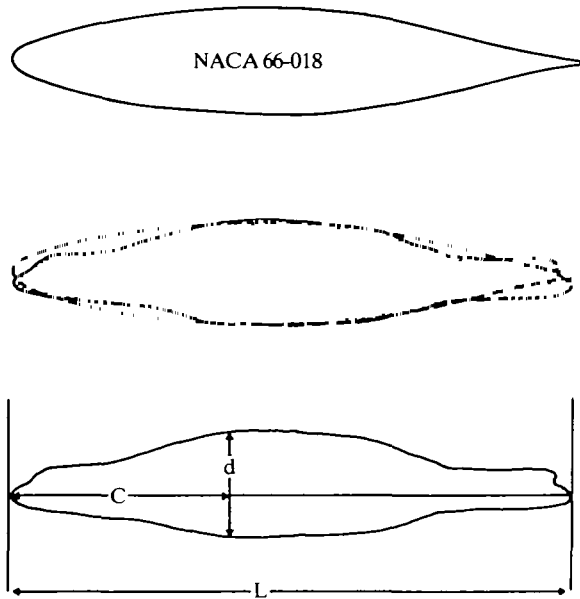


Fig. 5. An illustration of sea lion SL2's streamlined body form compared to a similarly shaped technical body of revolution. The sea lion's outline was drawn from an underwater photograph. The NACA 66-018 streamlined spindle was redrawn from Hertel (1966). Like the sea lion, it has a fineness ratio (L/d) of 5.5 and its maximum diameter (C/L) is at 40 % of body length.

Cd_s values of a streamlined spindle with an FR of 5.5 and a fully turbulent boundary layer were calculated to be 0.0046 and 0.0043 at Re values of 2.0 and 2.9×10^6 , respectively (Hoerner, 1958; Webb, 1975a). The lower values for sea lions demonstrate that they maintain a portion of laminar flow over the forward surface at these speeds.

Thrust forces that are required for swimming at a constant velocity will be equal to drag forces encountered by the animal. Thrust requirements over a range of speeds can be calculated by incorporating the values obtained for Cd into equation 3 where:

$$\text{thrust} = \text{drag} = 1/2 \rho S U^2 C_d, \quad (10)$$

(Hoerner, 1958; Webb, 1975a). The primary assumption in this calculation is that flow around the sea lion's body is equivalent to that of any other geometrically and dynamically similar streamlined object. As shown above, measurements of Cd substantiate this assumption. Additionally, unlike fish, phocid seals and cetaceans, which generate propulsive forces through lateral or vertical oscillations of their caudal appendages (Lighthill, 1969), the sea lion's foreflipper propulsor is relatively independent of the body. When swimming, its body is held stretched straight, parallel to the incident flow, with the rear flippers trailing passively behind. Foreflippers generate all thrust forces with no contribution from the rear flippers or posterior surface (English, 1976). The body's streamlined profile is, therefore, not distorted during stroking. As a result, these calculated forces should closely approximate those acting on the sea lion (Webb, 1975a; Blake, 1983a).

The power requirements for swimming can be obtained in a similar manner. The mean rate of energy expenditure in overcoming fluid resistance will be the product of body drag and average swimming velocity (Webb, 1975a; Yates, 1983). Using the measured value for C_d , the required power output (P_o , in watts) is then given by:

$$P_o = 1/2\rho S U^3 C_d \quad (11)$$

(Webb, 1975a; Yates, 1983).

These calculations describe the drag forces acting on sea lions and reflect the power requirements necessary for overcoming this resistance. When the sea lion is actively stroking, however, total drag will be slightly greater due to resistive forces acting on the foreflippers. These include frictional and pressure drag components as well as interference drag that arises through an interaction between an appendicular propulsor and the body (Blake, 1981). Because foreflippers generate propulsive forces that can be resolved into horizontal thrust and vertical lift components (English, 1976; Feldkamp, 1985), an induced drag component associated with lift formation will also be present (Lighthill, 1975). However, since these forces arise only when the flippers are extended, they are likely to be small in comparison to total body drag (Webb, 1975a; Blake, 1983a). In other animals that swim using pectoral fins, such as the surf perch (*Cymatogaster aggregata*) and the Humboldt penguin (*Spheniscus humboldti*), drag during stroking is elevated by an estimated 20–35 % (Webb, 1975b; Hui, 1983). Sea lions do not stroke continuously but modulate swimming speed by gliding between flipper beats (Feldkamp, 1985). Because of these factors, it is difficult to estimate the contributions of propulsor drag and values reported here should be viewed as a lower boundary to the drag forces encountered.

Cost of swimming

Like other swimmers, including fish (Brett, 1965; Webb, 1971, 1975a,b), turtles (Prange, 1976; Butler, Milsom & Woakes, 1984), ducks (Prange & Schmidt-Nielsen, 1970), mink (Williams, 1983), seals (Davis *et al.* 1985) and humans (Holmer, 1972; Nadel *et al.* 1974), sea lions exhibit a curvilinear rise in metabolic rate with increasing swimming speed. This is primarily due to the hydrodynamic constraints of the medium. As speed and drag increase, power required for propulsion rises at a rate proportional to U^3 . Unlike terrestrial animals, which encounter little aerodynamic resistance during running, swimmers must meet these power requirements through an exponential rise in energy consumption.

Despite this, sea lions use less energy for locomotion than terrestrial mammals of similar size. Taylor, Heglund & Maloiy (1982) developed an empirical formula describing the relationship between metabolism and speed for a variety of running animals. When compared to this, SL2 and SL3 expended less energy than a running mammal at all speeds examined. For SL4, swimming was less costly above 1 m s^{-1} (Fig. 6).

These reduced costs can be attributed to several factors. Sea lions are neutrally buoyant in sea water (Table 1). Thus, energy is not expended to support the body

during swimming. The importance of this is demonstrated by extrapolating the curve of \dot{V}_{O_2} vs swimming speed (equation 6) to zero velocity. The intercept of this curve accurately predicts the sea lion's resting metabolic rate. In terrestrial runners the y-intercept consistently overestimates the resting rate, a fact attributed to the cost of maintaining posture. This cost is independent of speed and is an important energetic component at all running velocities (Taylor, 1977). Sea lions, in contrast, rely on the water for support, thereby eliminating this postural component.

Terrestrial runners must also raise and lower their centre of mass during each stride (Heglund, Cavagna & Taylor, 1982). As the centre of mass falls, muscles already under tension are used to slow its progress. This stretches active muscles that, as a result, consume energy but do no positive work (Tucker, 1975; Heglund *et al.* 1982). In this respect, sea lions again benefit from the support afforded by the medium. It is unlikely that propulsive muscles are stretched while exerting tension during a stroke. Virtually all work performed by the swimming musculature, therefore, contributes directly to the animal's forward progress and none to raising and lowering the centre of mass.

The minimum cost of transport (CT) is a useful measure for comparing the locomotory system of sea lions with that of other animals, because it depends on the efficiency of the transport process (Schmidt-Nielsen, 1972; Tucker, 1975). For

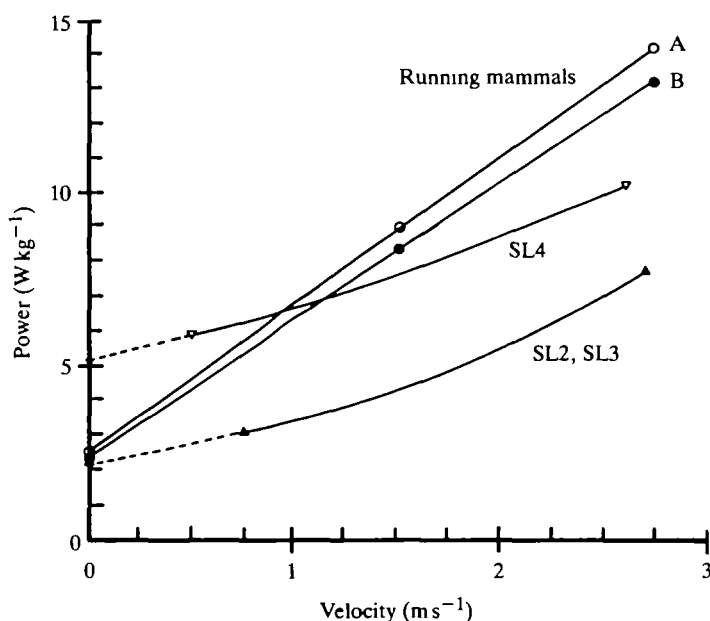


Fig. 6. Mass-specific power requirements determined for sea lions compared with running animals of similar size. Lines for runners were computed as $E/M = 10.7M_b^{-0.316} \times \text{velocity} + 6.03M_b^{-0.303}$ where E/M is in W kg^{-1} and M_b is body mass (Taylor, Heglund & Maloiy, 1982). A, line computed for an 18-kg runner; B, for a 22.5-kg runner.

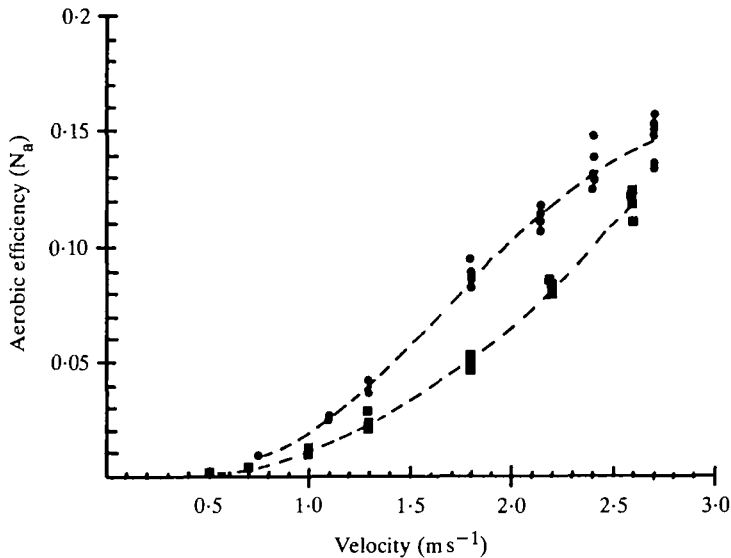


Fig. 7. Aerobic efficiency (N_a) as a function of swimming speed. N_a was computed as power output divided by the total power input (in W). The upper curve (●) is from SL2 and SL3 and reaches a maximum of 15 % at 2.7 m s^{-1} . The lower curve (■) is from SL4; maximum efficiency was 12 % at 2.6 m s^{-1} .

aquatic vertebrates, the minimum CT reflects the importance of swimming and the extent of an animal's adaptive compromise with other forms of locomotion (Vleck, Gleeson & Bartholomew, 1981). For example, salmonid fish have the lowest CT yet measured (Brett, 1965; Schmidt-Nielsen, 1972). Submerged swimming, poikilothermy, neutral buoyancy and an efficient caudal propellor all contribute to this low cost. Swimming reptiles, including turtles (Prange, 1976) and iguanas (Vleck *et al.* 1981), have costs 1.5–2 times that of similarly sized fish. Surface-swimming ducks (Prange & Schmidt-Nielsen, 1970), mink (Williams, 1983) and muskrats (Fish, 1982) have costs 11–20 times greater. The minimum CT measured for SL2 and SL3 ($2.4 \text{ J kg}^{-1} \text{ m}^{-1}$) is also 2.5 times that predicted for fish, suggesting that for sea lions swimming is an efficient means of transport. Moreover, SL2 and SL3 have costs equivalent to those reported for phocid seals (Craig & Pasche, 1980; Lavigne *et al.* 1982; Davis *et al.* 1985). It seems, therefore, that in pinnipeds foreflipper and rear-flipper propulsion are comparable in efficiency.

The aerobic efficiency (N_a) and mechanical efficiency (N_p) of foreflipper locomotion can be calculated using results from the hydrodynamic and metabolic studies. N_a , defined as power output (P_o) divided by the metabolic power input (Webb, 1975a), rose with speed for SL2 and SL3, reaching a maximum of 15 % at 2.7 m s^{-1} . The maximum for SL4 was 12 % at 2.6 m s^{-1} (Fig. 7). The efficiency of the foreflippers in converting muscle power to thrust power can be determined in a similar fashion. By subtracting resting metabolic rates from power input values, net power available to the swimming musculature ($P_{i,\text{net}}$) can be calculated. Power

available to the foreflippers will be that supplied by the locomotory muscles. Propellor efficiency can then be calculated as:

$$N_p = \frac{P_o}{P_{i,net} N_m}, \quad (12)$$

(Webb, 1975*a*), where N_m is the muscular efficiency. Cavagna, Saibene & Margaria (1964) present evidence that, at optimal contraction speed, N_m is 25 %. Calculated in this way, N_p rose with speed and for all sea lions reached a plateau of 80 % at the highest velocities (Fig. 8).

This approach assumes that energy used by the cardiovascular and respiratory support systems remains constant during exercise. Although a small increase in organ energy consumption undoubtedly occurs at higher work levels, estimates of efficiency based on this assumption will err on the conservative side. It is also assumed that a reduction in efficiency and the effects of a lower propulsor drag are negligible at the higher work rates but lower absolute swimming speeds created by the addition of drag cups. Because foreflippers create thrust independently of the body, the estimate of equivalent speeds with extra drag should be accurate given this assumption.

These efficiencies are relatively high, compared with those of other swimmers. The semi-aquatic mink has an N_a of only 1.8 % (Williams, 1983). Similarly, the muskrat has an N_a of 4.6 % with an N_p of 33 % (Fish, 1984). Prange (1976) has shown that the N_a for green sea turtles is of the order of 0.09, while the surf perch *Cymatogaster*, which uses its pectoral fin for swimming, has an N_a of 0.12–0.13 with an N_p of 0.60–0.65 (Webb, 1975*b*). Fish that swim in the carangiform mode have the

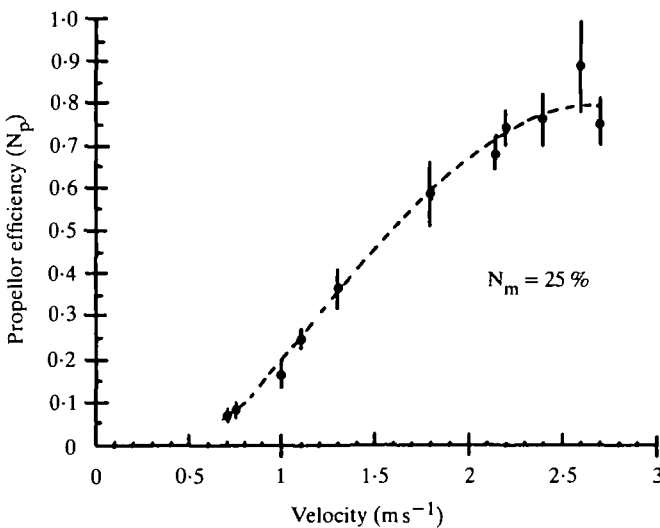


Fig. 8. Propellor efficiency (N_p) as a function of velocity. Points were computed based on an assumed muscular efficiency of 25 %. N_p was determined as P_o (drag \times velocity) divided by net power input and the muscular efficiency. Vertical lines show ± 2 S.E. Maximum N_p was 80 % at the highest speeds.

highest efficiencies reported. The mechanical efficiencies of rainbow trout and sockeye salmon are 0.7 and 0.9 with N_a values of 0.15 and 0.22, respectively (Webb, 1975b).

The shape of the propulsive appendages and the kinematics of thrust generation determine, in large part, these efficiencies (Webb, 1975a,b; Blake, 1983a; Fish, 1984). Mink and muskrats swim by paddling. Thrust is generated during the power phase of the stroke, but recovery introduces substantial drag as the appendages are brought forward to their initial position (Williams, 1983; Fish, 1984). Like sea turtles (Walker, 1971) and the surf perch (Webb, 1975b), sea lions use a lift-based method of propulsion. Thrust is generated in both the power and recovery phases of the stroke cycle (English, 1976; Feldkamp, 1985; Godfrey, 1985). The sea lion's mechanical efficiency is undoubtedly improved by this style of swimming. It is further improved by the design of the foreflippers. They are dorsoventrally compressed and hydrofoil-shaped, with an FR that ranges from 5.4 at the tip to 3.2 at the base (Feldkamp, 1985). This shape reduces pressure drag and improves lift. In addition, they have a comparatively high aspect ratio of 7.9 (Table 1). A long, narrow hydrofoil will diminish induced drag as lift is created during a stroke (Vogel, 1981; Alexander, 1983). It can, therefore, produce forwardly directed lift more efficiently because it imparts a small degree of downward momentum to a relatively large mass of water (Vogel, 1981).

In conclusion, swimming is a comparatively inexpensive means of transport in the California sea lion. Its overall shape approximates to an ideally streamlined object with a noticeable absence of any surface projections that would tend to increase drag and elevate the power requirements for movement. During swimming, the body is supported by the water, negating the postural costs associated with terrestrial locomotion and reducing the amount of negative work performed by the swimming musculature. The foreflippers' hydrodynamic shape, high aspect ratio and continuous generation of propulsive forces all contribute to the high mechanical efficiency of these appendages. As demonstrated by the low transport costs, adaptations for swimming have not been seriously compromised by the need for mobility on land, and enable sea lions efficiently to exploit the marine environment.

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