Swimming by sea otters: adaptations for low energetic cost locomotion

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Summary. The energetics and hydrodynamics of surface and submerged swimming were compared in the sea otter (*Enhydra lutris*).

1. Sea otters used two distinct speed ranges that varied with swimming mode. Sustained surface swimming was limited to speeds less than 0.80 m/s, while sustained submerged swimming occurred over the range of 0.60 to 1.39 m/s.

2. Rates of oxygen consumption ($\dot{V}O_2$) at the transition speed (0.80 m/s) were 41% lower for submerged swimming by sea otters in comparison to surface swimming.

3. Total cost of transport for surface swimming sea otters, 12.56 joules/kg·m, was more than 12 times the predicted value for a similarly-sized salmonid fish. Transport costs for submerged swimming at the same speed was only 7.33 times the predicted value.

4. The allometric relationship for minimum cost of transport in surface swimming birds and mammals was $y = 23.87x^{-0.15}$ where y = cost of transport in joules/kg·m and x = body mass in kg. This regression loosely parallels the relationship for salmonid fish.

5. Correlations between aquatic behavior, morphological specialization, and swimming energetics indicate that the development of swimming in mustelids involved transitions from fore-paw to hind-paw propulsion, and from surface to submerged swimming.

Introduction

The sea otter (*Enhydra lutris*) is an aquatic mammal that shares locomotor characteristics of smaller semi-aquatic mustelids and larger exclu-

sively marine species. Although sea otters are capable of terrestrial locomotion, albeit awkward, they spend their lives at sea, foraging on marine organisms in nearshore marine communities (Estes 1980). Consequently, swimming is its primary means of locomotion. Like other marine mammals, sea otters demonstrate many adaptations that are known to enhance swimming performance and reduce transport costs while in the water. These include, (1) body streamlining (Lang 1974; Williams and Kooyman 1985; Feldkamp 1987), (2) large, specialized plantar surfaces for propulsion, and (3) the ability to remain submerged for extended periods (Williams et al. 1987). In comparison, these features are not characteristic of primarily terrestrial species such as humans. Mink, the smallest aquatic mustelid, demonstrate only the first of these three adaptations, whereas all three adaptations are found in marine mammals that lack the ability to locomote on land.

The ability to swim submerged is most pronounced in highly specialized marine mammals. Because it influences the hydrodynamics and physiology of the swimmer, body position relative to the water surface is an important determinant of swimming transport costs. Wave drag associated with surface swimming increases the relative forces on a moving body by as much as five times the value for a submerged position (Hertel 1966). This has been demonstrated for both seals (Williams and Kooyman 1985) and humans (Miyashita and Tsunoda 1977; Williams and Kooyman 1985). In some mammals, submergence also triggers a set of physiological changes known as the diving response. Many investigators have suggested that hypometabolism associated with this response in actively diving seals will reduce the energy requirements of the animal to 25–50% below resting levels (Guppy et al. 1986; Hochachka 1986).

The purpose of this study was to compare the hydrodynamics, mechanics, and energetics of surface and submerged swimming. Sea otters provided a unique mammalian model for this study because they routinely use both forms of swimming. To determine if there is an energetic advantage with submergence we compared the costs of transport for surface and submerged swimming in sea otters and compared them to values reported for other swimmers. From these comparisons, we developed allometric relationships for animals that use surface and submerged modes of swimming. In addition, we examined morphological, mechanical, and behavioral characteristics that could facilitate low cost swimming. By noting the presence or absence of these characteristics in terrestrial, semi-aquatic and marine mustelids we speculate about the development of swimming in this group of mammals.

Materials and methods

Body morphology. Morphological dimensions were measured on 5 healthy subadult male sea otters, and 3 adult female carcasses. The males were captured and measured in Prince William Sound, Alaska from July to September, 1986. Female carcasses were collected by the California Department of Fish and Game in northern California. Plantar surface areas of the sea otter hind-paw were determined by digitizing outline tracings. Tracings were made with the hind-paws compressed in a natural conformation and fully expanded. The tracings were digitized (Hipad, Inc.) on a personal computer (Apple II Plus) that had been calibrated with tracings of known surface area. The accuracy of the digitizing system was also tested by comparing digitized values to surface areas determined by gravimetric methods.

Swimming mode, preferred speed, and stroke frequency. Swimming mode and routine speeds were determined by videotaping 6 captive, adult female California sea otters (Sea World, San Diego). The animals swam freely in a salt water pool that was 12 m in diameter, and 2.5 m at its maximum depth. A video camera (Sony BetaMax) was secured on a tripod that was stationed on a platform overlooking the entire swimming area. Taping took place at irregular intervals from 0800 to 1900. Following one session, the otters were transferred to a holding tank while the exhibit pool was drained. A grid marked in 1 m increments was mapped at the water level of the pool and videotaped. During analysis the videotaped grid was played back and transferred onto an acetate sheet that covered the monitor screen. The calibrated grid was then superimposed on the image of the swimming otters during videotape replay. This method of analysis compensated for parallax problems resulting from camera placement and from use of a single camera system (van Sciver 1972).

Swimming speed and mode were recorded simultaneously for the otters. We restricted our analysis to consistent performances occurring over a distance of three body lengths in a straight line course. Swimming speed was determined by counting the number of videotape frames that cycled as the sea otters traversed known distance. To avoid underestimation of the distance travelled, swimming bouts involving changes in depth

were omitted from the analysis. Cycling rate of the videotape (13 frames/s) was calibrated against internal and external clocks. We classified performance as submerged or surface swimming, and subdivided surface swimming into ventral up, ventral down, and rolling patterns. Because the 6 animals tended to congregate and follow similar routines, no attempt was made to separate the swimming speeds or patterns of individual animals. However, colored flipper tags enabled us to identify each otter and avoid repetitive measurements of a single animal.

Stroke frequency was determined from frame-by-frame videotype analysis and direct observations of swimming sea otters. For both methods we established the relationships between the frequency of hind-paw stroking, swimming mode, and speed. Sustained and burst swimming performances were analyzed. Simultaneous and asynchronous hind-paw stroking patterns were also noted.

Metabolic measurements. We measured oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$), and respiratory quotient (RQ) of two adult female sea otters (body weight = 19.5, 20.4 kg). The animals were housed in concrete pools (12 m diameter × 2.5 m deep) supplied with filtered sea water, and were fed twice daily on a mixed diet of crab, shrimp, and clams supplemented with vitamins.

Metabolic measurements were obtained from sea otters resting, grooming, or swimming in a $1.0 \times 1.0 \times 3.0$ m test chamber that was partially submerged in a 6.1 m diameter pool. The chamber was constructed of wood and plexiglass along its length, and of 2.5 cm^2 mesh fibre-grating on each end. The mesh did not obstruct water flow. The chamber was braced against the wall of the pool in 1.3 m of sea water. To create a flume, water was circulated around the perimeter of the pool by a 5 hp electric motor connected to a brass impeller. Water was continuously drawn into 20 cm diameter hosing, reaccelerated, and pumped into the pool. Steady state flows were reached within 5 min of starting the pump. By placing the inlet and outlet hosing along the tank perimeter, we could obtain flows of up to 1 m/s through the metabolic chamber. Fibre-grating and a series of baffles mounted on the front of the chamber directed and straightened the water flow into the chamber. Cross-sectional flow profiles of the current in the test chamber were made using a propeller flowmeter (General Oceanics) that had been calibrated from 0.22 to 0.92 m/s in a tow tank (Hydraulics Laboratory, Scripps Institution of Oceanography). Water flows presented in this paper represent the mean velocity through the chamber as calculated from the profiles. Flow velocities varied by less than 11% along the entire length of the test section.

Two months before experimentation the otters were allowed periodic access to the test chamber in still and in moving water. Once accustomed to the chamber the animals were trained to swim against a current. No data were collected until each animal swam consistently. To avoid the effects of specific dynamic action the animals were fasted more than 6 h before metabolic experiments (Morrison et al. 1974; Costa and Kooyman 1984). During each experimental session the sea otter was introduced to the partially submerged metabolic chamber. $\dot{V}O_2$ and $\dot{V}CO_2$ of resting or grooming animals were recorded for a minimum of 13 to 20 min before each swimming session. Variable or inconsistent behavioral periods were deleted. Following resting measurements the water pump was turned on to the desired speed. $\dot{V}O_2$ and $\dot{V}CO_2$ of animals swimming continuously in one mode (surface or submerged) for 12 to 32 min were measured. All metabolic measurements were made using an open-flow respirometry system (Williams 1987) at $T_{ambient} = 22$ °C and $T_{water} = 18$ °C. Ambient air was pulled

at a rate of 65.0 l/min into a plexiglass skylight dome (1.1 × 0.6 × 0.3 cm) that formed the roof of the test section of the metabolic chamber. An airtight seal around the edges of the dome was formed by submerging the chamber up to the bottom of the plexiglass dome. Because the dome provided the only air space for breathing, it served as a metabolic hood. The space was large enough to accommodate the entire otter resting on the water surface. High flow rates of air kept the fraction of O_2 in the dome above 20.0% during the experimental sessions, and were monitored continuously by a calibrated dry gas meter (American Meter) placed in line at the inlet port. Air samples from the effluent line were dried and scrubbed of CO_2 by passage through Drierite and Baralyme columns, respectively. O_2 content of the sampled gas was determined with an Applied Electrochemistry S3-A oxygen analyzer. CO_2 content was measured simultaneously (Applied Electrochemistry CD-3A) from a second sampling line that passed through a Drierite column exclusively. Outputs from both analyzers were monitored every 2 s by a computer (Apple II Plus) with an analog-to-digital interface board. Gas contents were converted to oxygen consumption and carbon dioxide production using the equations of Withers (1977) and Depocas and Hart (1957). All results were converted to STPD and are presented as ±1 S.D.

The entire respirometry system was calibrated daily prior to the experiments using techniques modified from Fedak et al. (1981) and Williams (1987). N_2 (100%) and analyzed CO_2 (10.05% in N_2) gases were bled into the dome at rates equivalent to the displacement of ambient air by the experimental animal. The theoretical fractions of O_2 and CO_2 leaving the dome were calculated from equations presented in Davis et al. (1985) and were compared to the actual response of the analyzers. Calibration checks with ambient air were made throughout the course of the measurements. To account for potential losses of O_2 and CO_2 through absorption of gases into water, calibrations were performed with still water and with water flowing through the chamber at 0.8 m/s. No significant losses in CO_2 and O_2 occurred in either situation. The theoretical and measured fractional concentrations of both gases agreed to within 0.01% in still and moving water.

Cost of transport. Total cost of transport was calculated by dividing the metabolic rate (W/kg) of swimming animals by locomotor speed (m/s) (Schmidt-Nielsen 1972). To assess the relative contribution of active and resting metabolic rates on the cost of transport, total costs were subdivided into locomotor and maintenance costs, respectively. The latter was determined from the metabolic rate of sea otters resting in water. The difference between the total cost of transport and maintenance costs has been termed locomotor cost. This represents the additional energy expended by the animals during swimming and is equivalent to the net cost of transport presented for runners by Schmidt-Nielsen (1972).

Body drag. Total body drag was determined by towing an adult female sea otter carcass (body weight = 16.7 kg) in a water channel. The carcass was frozen in a natural, ventral down swimming position. Over the range of test speeds (0.17 to 0.95 m/s) the carcass floated horizontally with the head and scapular region above the water line. General body form, fur characteristics, and relative swimming position of live sea otters were closely approximated in these experiments. A non-stretchable line was fastened just above the water line of the carcass' neck; its other end was threaded through a pulley suspended at the water level and attached to a load cell (Western Scale, Inc). Load cell signals resulting from forces on the towing carcass were amplified (UFI Instruments) and recorded on a Brush 220

strip chart recorder. The load cell was calibrated with known weights and zeroed prior to each measurement. Drag measurements were conducted in a stratified flow channel located at the Hydraulics Laboratory, Scripps Institution of Oceanography. Because the sea otter carcass was unsteady when submerged, total body drag during submergence was calculated from the conventional formula:

$$\text{Drag} = 0.5\,\rho\;SV^2 Cd$$

where ρ = water density, S = a characteristic surface area (wetted surface area = 0.653 m^2; from Costa and Kooyman 1982), V = water speed, and Cd = drag coefficient (estimated from the sea otter's fineness ratio to be 0.006; from Hoerner 1965). These calculated values represent the lower limit of drag for an otter shaped body.

Results

Body morphology

Physical dimensions for the sea otters are presented in Table 1. Because of the small sizes, data for subadult males and adult females are combined. Plantar surface area of the compressed hind-paw was 115.5 ± 23.9 cm^2, which increased by 36.6% with expansion of the interdigital webbing. Maximum propulsive surface area provided by both hind-paws was 329.6 cm^2.

Swimming modes, preferred speeds, and stroke frequency

Three primary modes of swimming whose locomotory patterns have been described elsewhere (Kenyon 1969; Tarasoff et al. 1972) were observed for

Table 1. Physical dimensions of the sea otter

	n		Mean ± 1 SD	
	Male	Female		
Mass (kg)	2	2	19.85	3.04
Length (cm)	4	3	128.4	15.3
Max. diameter (cm)	4	3	22.5	2.8
Fineness ratio	4	3	5.8	1.2
Plantar surface area (cm^2)				
Hind paw (expanded)	5	3	164.8	36.5
(compressed)	4	3	115.5	23.9
% Surface increase with expansion	4	3	36.6	7.2

Mean values represent the combined data for male and female otters. Fineness ratios were calculated from body length/maximum body diameter

the sea otters. When on the water surface an animal could swim while floating on its back (ventral surface up) or on its belly (ventral surface down). Ventral up swimming was used during periods of food manipulation and ingestion, and in the initial stages of an escape response as the startled otter backed away from a disturbance. In this position, the animal's body was partially submerged with the head and chest held above the water surface. The fore-paws were folded close to the chest above the water line, while the hind-paws provided propulsion. Both alternate and simultaneous strokes of the hind-paws were observed. Occasionally the otters would maneuver slowly by making lateral undulations of the tail while the hind-paws were raised above the water surface.

During ventral down swimming the head and scapular region of the back remained above the water surface. Propulsion was provided by either alternate or simultaneous strokes of the hind-paws. The fore-paws were held against the submerged chest. Neither the fore-paws nor the tail appeared to play a role in propulsion. This position was often used during intermediate speed travel between areas and prior to a dive and high speed submerged swimming.

We also observed an intermediate form of surface swimming that was associated with grooming behavior. Rather than maintain a fixed position, the animals alternately swam with their ventral surface up and down. Such rolling along the long axis of the body was superimposed on the forward progression. As with the other forms of surface swimming, the hind-paws provided the propulsion.

In contrast to the rigid posture of the trunk during surface swimming, dorsoventral undulations of the caudal half of the body contributed to thrust production during submerged swimming. When moving at high speed, the tail and hind-paws were held straight back and trailed the undulatory movements of the trunk. At lower submerged swimming speeds hind-paw strokes that were independent of body undulations also provided thrust. Submerged swimming was performed during foraging dives to the pool floor, as well as during high speed travel.

The sea otters had two distinct speed ranges that varied with swimming mode (Fig. 1). Sustained surface swimming, including ventral surface up, ventral surface down, and rolling body positions, occurred at speeds less than 0.80 m/s ($n = 68$ observations). Generally, ventral up swimming was used at the lower range of preferred speeds (0.10 to 0.50 m/s). With increases in surface swimming speed, this position was replaced by ventral surface
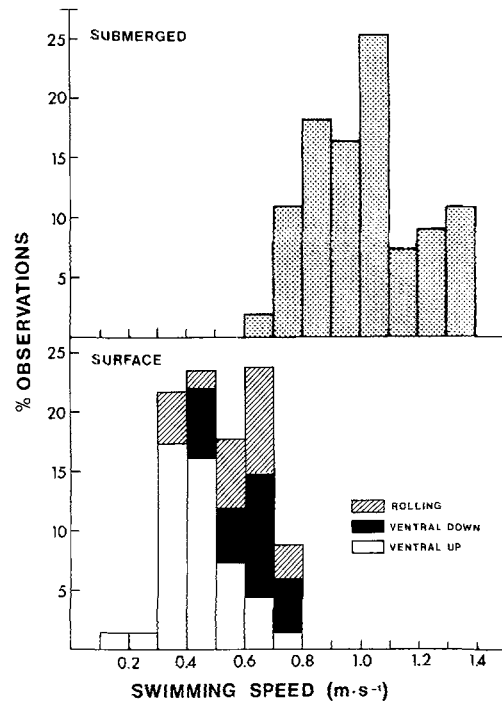

Fig. 1. Routine speeds for sustained surface and submerged swimming by 6 captive sea otters. The percentage of 68 observations for surface swimming and 55 observations for submerged performances are presented for each speed. The mean crossover speed between these two modes of swimming is 0.70 m/s. Note that surface swimming includes 3 different body positions
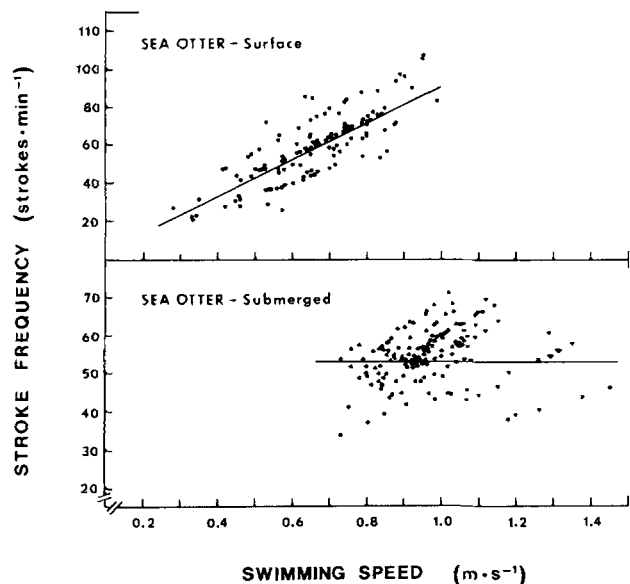

Fig. 2. Stroke frequency in relation to swimming speed for 6 sea otters. Each point represents the average frequency for a single swimming episode. Solid lines denote the least squares linear regression for surface swimming, ($n = 143$, corr $= 0.81$) and the mean stroke frequency for submerged swimming ($n = 174$). Sustained and burst swimming performances are shown

down and rolling positions. Often ventral down swimming preceded submerged swimming; consequently, submerged swimming occurred over a higher range of speeds. Steady swimming by submerged sea otters ranged from 0.60 to 1.39 m/s ($n = 55$ observations). Based on these results, crossover speeds between surface and submerged swimming ranged from 0.60 to 0.80 m/s.

The relationship between stroke frequency and speed demonstrated two different functions that varied with swimming mode (Fig. 2). Over the range of 0.28 to 0.99 m/s, stroke frequency for surface swimming sea otters increased from 27.3 to 82.8 strokes/min. The least squares linear regression was:

stroke frequency (stroke/min)
$= 99.1$ velocity (m/s) $- 6.84$
($n = 143$, corr $= 0.81$)

and included both ventral surface up and ventral surface down positions. In contrast, stroke frequency for submerged sea otters swimming from 0.72 to 1.45 m/s averaged 55.7 ± 9.4 strokes/min ($n = 174$) regardless of speed. At the mean crossover speed for sustained swimming (0.70 m/s) stroke frequency when on the water surface (61.4 ± 4.71 strokes/min) was not significantly different (at $P < 0.01$) from the mean stroke frequency for submerged swimming. Thus, there is little change in the stroke frequency of sea otters with either surface or submerged swimming at this crossover speed.

Oxygen consumption, carbon dioxide production, respiratory quotient

The mean metabolic rate of two female sea otters resting in water at 20 °C was 13.50 ± 1.81 mlO$_2$/kg·min (4.58 ± 0.61 W/kg) (Fig. 3) and was similar to rates reported by Costa and Kooyman (1982) and Morrison et al. (1974). $\dot{V}CO_2$ for otters resting in water was 12.05 ± 0.13 mlCO$_2$/kg·min. Resting RQ was 0.85 ± 0.02. Grooming involved a repertoire of behaviors (e.g. fur pleating and rubbing, rolling, and somersaulting) that varied in intensity. This activity was energetically costly and resulted in a 64% increase in $\dot{V}O_2$ and a 55% increase in $\dot{V}CO_2$ over resting values. In one experiment, $\dot{V}O_2$ was measured within 2 h of food ingestion by the otter. The results show a 34% increase in $\dot{V}O_2$ during grooming over post absorptive animals, and suggest that assimilation costs and grooming costs are additive.

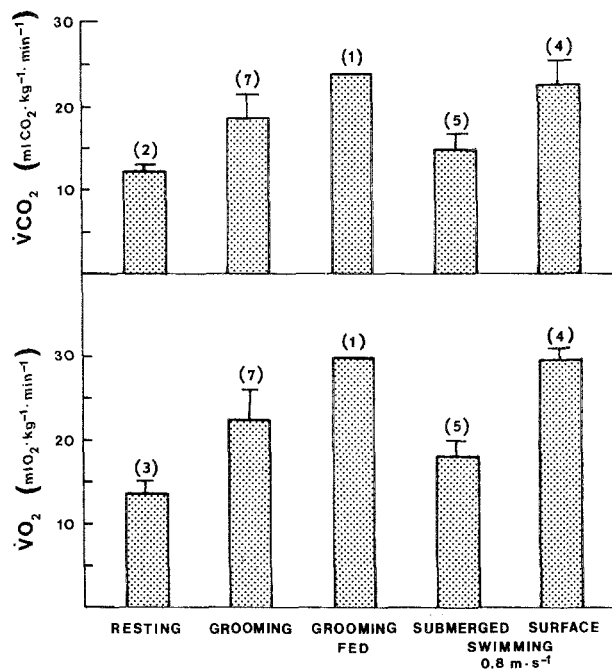During flume swimming the sea otters remained approximately 0.5–0.7 m (2–3 times maxi-

Fig. 3. Oxygen consumption and carbon dioxide production during rest and activity in the sea otter. Filled bars: mean for each behavioral condition. Vertical lines: $+1$ SD. Numbers in parentheses: number of tests for each experimental condition. Note that metabolic rates for surface and submerged swimming were measured at identical speeds. Respiratory quotients corresponding to these data are provided in the text

mum body diameter) below the water surface or swam in a ventral down position on the water. The $\dot{V}O_2$ and $\dot{V}CO_2$ of submerged swimming sea otters was significantly lower (at $P \ll 0.001$) than measured for surface swimming at the identical speed. Mean metabolic rate during submerged swimming at 0.80 m/s was 17.55 ± 1.70 mlO$_2$/kg·min (5.95 ± 0.58 W/kg). In comparison, $\dot{V}O_2$ for sea otters swimming on the water surface at this speed was 29.61 ± 1.60 mlO$_2$/kg·min (10.04 ± 0.54 W/kg). This represents a 41% decrease associated with the change from surface to submerged swimming at 0.80 m/s.

RQ was not significantly different (Kruskal-Wallis ANOVA $H_{0.05, 2, 4, 5, 7} = 3.630$) for resting, grooming, and swimming behaviors. Measured RQ was 0.77 ± 0.10 for surface swimming, 0.80 ± 0.07 for submerged swimming, and 0.86 ± 0.12 for grooming.

Cost of transport

The cost of transport for sea otters was dependent on swimming mode at 0.80 m/s (Fig. 4). Total cost for surface swimming, 12.56 joules/kg·m, was 69% greater than the cost for submerged swimming at
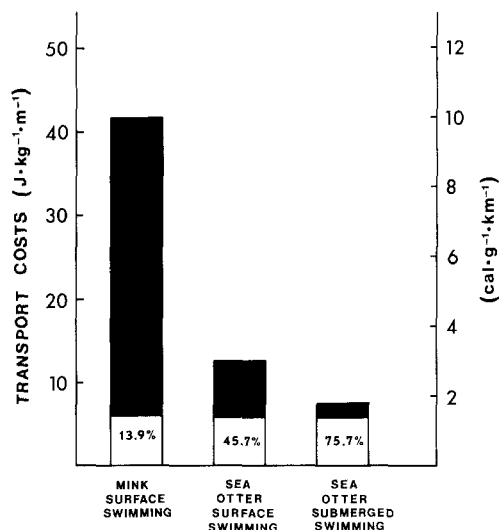
Fig. 4. Total cost of transport (bar height), maintenance costs (open box), and locomotor costs (shaded box) for mink and sea otters. Two modes of swimming by sea otters compared to surface swimming by mink. Data for mink from Williams (1983)

Fig. 5. Body drag of surface (•) and submerged (o) sea otters. Surface values obtained by towing a frozen carcass. Submerged values calculated (see text). Solid lines: least squares regressions. Dashed line: form drag encountered by a sea otter based on its routine surface and submerged swimming speeds. These values represent form drag only and do not account for active drag associated with swimming movements

this speed. The cost index (CI), defined as the ratio of measured transport costs to the value predicted for a similarly sized salmonid fish (from Brett 1964), was 12.24 for surface swimming and 7.33 for submerged swimming sea otters.

Breakdown of total transport costs into maintenance and locomotor components demonstrated a two-fold greater locomotor cost for surface swimming in comparison to submerged swimming (Fig. 4). Assuming that maintenance metabolism does not change with submergence in sea otters (see Discussion), only 24% of the total cost of submerged swimming was accounted for by locomotor costs. In contrast, the total cost of transport for surface swimming at 0.80 m/s was divided almost equally between maintenance and locomotor requirements.

Body drag. Total body drag of a sea otter towed on the water surface increased curvilinearly with speed over the range of 0.17 to 0.95 m/s (Fig. 5). The best fit least squares regression for the relationship between body drag and velocity was:

$$\text{Drag} = 5.58 \text{ velocity}^{1.27}$$
$$(n = 10, r = 0.98)$$

where drag is in newtons and velocity is in m/s. Calculated drag for a submerged body with the same surface area and fineness ratio as the sea otter was less than surface drag at all similar speeds. The difference in drag between the surface and submerged positons increased with speed. At
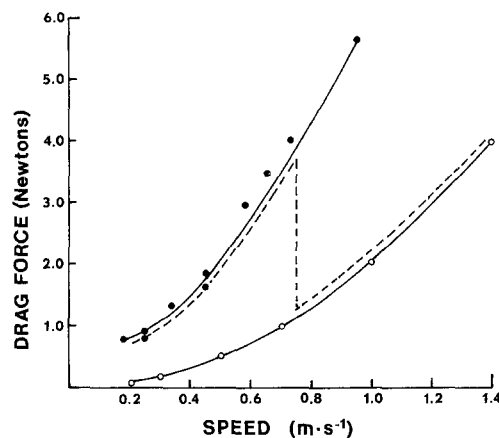
0.8 m/s, body drag for a sea otter on the water surface was approximately 3.5 times that calculated for a submerged animal.

Discussion

The energetic cost of swimming in mammals is dependent on a combination of hydrodynamic, physiological, and morphological factors. Secondarily aquatic mammals such as mink (Williams 1983), muskrats (Fish 1984), and humans (Nadel et al. 1974; di Prampero et al. 1974) are relatively inefficient swimmers; that is, limited power output for propulsion is gained from a considerable metabolic power input. Because the morphological requirements for high speed running are not compatible with those for swimming (Williams 1983), animals that attempt both forms of locomotion often lack the propulsive mechanisms and body streamlining that are necessary for economical swimming. Thus, these animals have high swimming transport costs. In comparison, swimming specialists are limited to a single mode of locomotion and incur lower transport costs than secondarily aquatic mammals (Fig. 6). If aquatic specialization were considered a continuum then sea otters would represent an intermediate species between semi-aquatic and marine mammals (Taylor 1914). Indeed, their swimming transport costs are intermediate to those two groups.

Minimum transport costs are conventionally used to compare the locomotor energetics of differ-
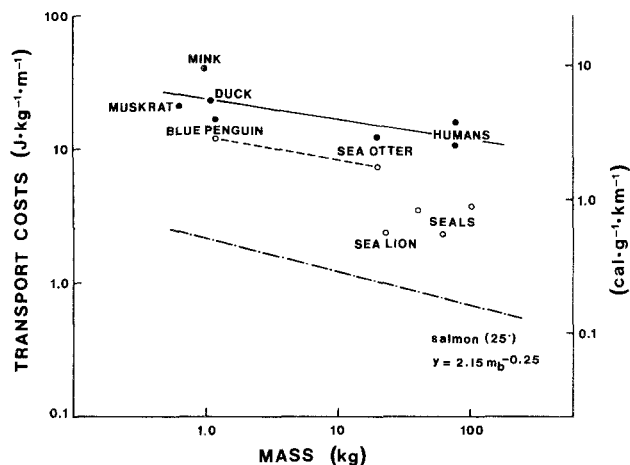
Fig. 6. Log cost of transport plotted as a function of log body mass for several aquatic and semi-aquatic vertebrates. Closed symbols: surface swimming; open symbols: submerged swimming. Data from Williams 1983 (mink); Fish 1982 (muskrat); Baudinette and Gill 1985 (duck, blue penguin); present study (sea otter); Holmer 1972 (human); Davis et al. 1985 (harbor seal); Feldkamp 1987 (sea lion); and Fedak 1986 (grey seal). Solid line: allometric relationship for primarily surface swimmers including blue penguins and sea otters. A second, parallel relationship (dashed line) is described for submerged swimming by animals that perform more than one mode of swimming. Stippled line: predicted cost of transport based on the regression for salmonid fish (Brett 1964)

ent groups of swimmers. Often the lowest costs occur at the mid-range of routine speeds used by an animal and are within a trough of a U-shaped curve that relates transport cost to swimming speed (Williams 1987). Because we were not able to generate such a curve for sea otters, we will assume that it follows the pattern for other swimmers using surface and submerged modes (see Baudinette and Gill 1985). Based on this, transport costs calculated for the crossover speed of 0.8 m/s approximate the minimum costs for the swimming sea otter.

In comparing different swimmers we find that a single allometric regression describes the minimum cost of transport for surface swimming animals (Fig. 6). This relationship

$$y = 23.87 x^{-0.15}$$
$$(n = 7, \text{corr} = 0.73)$$

where y = minimum cost of transport in joules/kg·m and x = body mass in kg, loosely parallels the relationship for salmonids. Interestingly, the transport costs of paddling ducks and muskrats, rowing sea otters, penguins using pectoral wing propulsion, and humans performing the front crawl and breast stroke are within the 95% confidence limits of this regression. Similar observations for fish led Beamish (1978) and Bennett (1985) to conclude that minimum transport costs do not vary greatly with

swimming style for anguillids, sparids, and salmonids. An analogous conclusion has been reported for bipedal and quadrupedal runners (Taylor and Rowntree 1973; Taylor 1980).

Such broad comparisons obscure the energetic advantages associated with different swimming modes or morphological specializations. To assess the effect of specific adaptations a detailed analysis of the factors that contribute to the total cost of transport of the individual animal is required. For example, morphological specialization, including body streamlining and limb modification, reduce transport costs in sea otters. The characteristic mustelid body shape, an elongated tapered trunk and small frontal area, results in a fineness ratio for sea otters (Table 1) that approximates values for a variety of fast swimmers including tuna, porpoises, and seals (Hertel 1966; Webb 1975; Williams and Kooyman 1985). By minimizing drag, streamlining reduces the amount of thrust required to propel the animal and, consequently, the energy demands of swimming.

The energy expended for propulsion is also reduced by modifying the shape of the propulsor and its orientation to forward movement (Webb 1988). Drag-based oscillating appendages (e.g., the propulsors of paddlers and rowers) provide maximum thrust by entraining a large volume of water during the stroke. The most efficient paddle has the least streamlined shape and a large surface area (Miller 1975; Robinson 1975; Barthels 1979), avoids drag interference with the body (Blake 1981), and is triangular in shape (Webb 1988). Examples include the appendages of river otters (Tarasoff et al. 1972), muskrats (Fish 1984), and sea otters (Table 1). In these animals propulsive surface area of the paws can exceed 5% of the total surface area of the swimmer. In comparison, the mink's propulsive surface area is only 1% of its total surface area (unpublished data).

We can demonstrate the interrelationship between locomotor cost and propulsive area by comparing the relative contribution of locomotor and maintenance costs to the total cost of transport of mink and sea otters (Fig. 4). The maintenance costs of both mustelids when immersed are 2.0–2.4 times the values predicted for terrestrial mammals (Costa and Kooyman 1982; Williams 1983), and represent 13.9% to 75.7% of the total swimming costs depending on the species and swimming mode. Locomotor costs account for approximately 86% of the mink's total cost of transport. In comparison, locomotor costs comprise less than 55% of the sea otter's total costs when surface swimming and less than 25% when submerged.

The ability to swim submerged for sustained periods is one of the most important adaptations for aquatic locomotion in mammals. By submerging, the swimmer experiences less drag, particularly in the form of surface wave action (Hertel 1966). Total body drag of humans (Miyashita and Tsunoda 1977), harbor seals (Williams and Kooyman 1985), and sea otters (Fig. 5) towed on the water surface may reach four times the value for towing submerged at the same speed. This position-related difference in drag has a significant effect on cost of transport. At 0.8 m/s the oxygen consumption of sea otters swimming submerged is 41% lower than for the surface swimming (Fig. 3). Similarly, little blue penguins reduce oxygen consumption by approximately 40% in changing from surface to subsurface swimming (Baudinette and Gill 1985). It follows that during subsurface swimming, transport costs are reduced for these animals. In sea otters the cost of transport for surface swimming was more than 12 times the predicted value for a salmonid fish, whereas the value was almost halved for submerged swimming at the same speed.

Besides providing a hydrodynamic advantage, submergence can trigger a set of physiological responses that reduce oxygen consumption and the cost of transport. Although these responses are known to occur during prolonged diving in some highly specialized marine mammals, their role in the submerged swimming animal remains speculative (see Guppy et al. 1986; Hochachka 1986). Because the lungs serve as the primary oxygen depot in sea otters (Lenfant et al. 1970; Kooyman 1973) this animal must maintain circulatory and metabolic integrity during short periods of submergence rather than initiate a diving response. Thus, it is unlikely that hypometabolism contributes to the reduction in oxygen consumption observed for submerged swimming sea otters. Further studies are needed before we can attribute the relatively low cost index of pinnipeds (CI = 2.5–4.0) to metabolic suppression during submergence.

Analogous to a gait change in terrestrial animals, switching to submerged swimming allows sea otters to extend their range of swimming speeds. Sustained surface swimming is restricted to speeds less than 0.8 m/s (Fig. 1) and to a maximum form (pressure) drag of 4.2 N (Fig. 5). Changing to a submerged mode of swimming at the transition speed results in a 3.5 fold decrease in form drag and a 41% decrease in the total cost of transport. As suggested for ducks (Prange and Schmidt-Nielsen 1970) and penguins (Baudinette and Gill 1985) hydromechanical rather than metabolic limitations seem to dictate maximum surface swimming speeds

in sea otters. At the transition speed, the metabolic rate of surface swimming otters was only 2.3 times resting values. This is considerably lower than the typical aerobic scope of 10 observed by Taylor et al. (1982) for terrestrial locomotion by mammals. The calculated form drag for the highest sustained submerged speed of 1.4 m/s approximated 4.0 N and was within 5% of the maximum value for surface swimming. Although we cannot account for the drag associated with locomotor movements, these results suggest a specific limit for form drag tolerated by sea otters during sustained swimming bouts. This limit is the same regardless of a surface or submerged body position.

Few aquatic mammals other than sea otters routinely use more than one mode of swimming. The energetics of both swimming styles combined with behavioral and metabolic information on weasels, mink, and river otters demonstrate the importance of specialization for reducing transport costs. By drawing appropriate parallels this also allows us to speculate about evolutionary events that permitted the transition from a terrestrial to an aquatic lifestyle in mustelids. The elongated body shape of ancestral mustelidae facilitated terrestrial foraging that included the pursuit of prey through burrows (Gambaryan 1974). Despite its origin this body shape provides an energetic and hydrodynamic advantage during swimming. With increased aquatic behavior by mustelids, the size, shape, and location of the propulsive appendages change. The primary propulsor is enlarged and moved from the fore-paws to the hind-paws. As a result, the swimmer avoids disruption of the boundary layer by propulsive movements. In addition, modifications of the shape and size of the propulsive surface influences locomotor costs.

Spinal flexibility, another mustelid characteristic that permitted maneuverability and speed on land (Gambaryan 1974), facilitated the change from paraxial (paddling, rowing) to axial (undulatory) swimming in early marine mammals (Aleyev 1977). Unlike terrestrial mustelids, river otters (Tarasoff et al. 1972) and sea otters (Kenyon 1969) use dorso-ventral undulations of the body and tail to provide propulsion during subsurface swimming. Rather than provide an energetic advantage per se, this change in swimming mode improves the specific performance (e.g. speed, acceleration, and maneuverability) of the mammalian swimmer.

Coincident with the development of an aquatic lifestyle is the transition from surface to subsurface swimming. The effect of such a transition, as observed for sea otters, is increased performance as well as a significant reduction in swimming trans-

port costs. The ability to remain submerged while swimming is well developed in highly specialized marine mammals. It remains to be established whether the physiological mechanisms permitting prolonged submergence in these mammals contribute to transport costs that are comparatively less than determined for the submerged swimming sea otter.

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