SWIMMING METABOLISM OF YEARLING AND ADULT HARBOR SEALS PHOCA VITULINA[1]

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The swimming metabolism of yearling and adult harbor seals was measured by indirect calorimetry in a flow channel at speeds ranging from 0.5 to 1.4 $m \cdot s^{-1}$. Minimum resting metabolic rates in still water were 5.1 and 4.6 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ for the two yearling seals (body mass [M_b] = 33 kg) and one adult seal (M_b = 63 kg), respectively. Minimum resting metabolic rates were about 1.1 × the predicted standard metabolic rate for mammals of equivalent size. During steady-state swimming, metabolism increased curvilinearly with speed and was best described by the equation $\dot{V}O_2$ (ml $O_2 \cdot min^{-1} \cdot kg^{-1}$) = 5.1 + 6.25 velocity $(m \cdot s^{-1})^{1.42}$ for the yearling seals and $\dot{V}O_2$ = 4.6 + 3.1 velocity$^{1.42}$ for the adult seal. Stroke frequency increased linearly as a function of swimming speed. Cost of transport decreased asymptotically with swim velocity, approaching a minimum at 1.0–1.4 $m \cdot s^{-1}$ of 3.6 $J \cdot m^{-1} \cdot kg^{-1}$ for yearling and 2.3 $J \cdot m^{-1} \cdot kg^{-1}$ for adult seals. The minimum cost of transport was less than for other semiaquatic birds and mammals but 3–4 × the predicted value for salmonid fish of equivalent size at 25 C.

INTRODUCTION

Most studies of swimming energetics have concentrated on fish, especially those species that use a subcarangiform mode of propulsion. These studies have demonstrated that fish have the lowest cost of transport of any aquatic or terrestrial vertebrate (Schmidt-Nielsen 1972). Transport costs for endothermic animals during swimming are comparatively high. Semiaquatic birds and mammals such as the paddling duck (*Anus platyrhynchos*), mink (*Mustela vison*), muskrat (*Ondatra zibethicus*), and humans exhibit transport costs during swimming 10–20 × higher than the predicted value for fish of equivalent size (Prange and Schmidt-Nielsen 1970; Holmer 1972; Nadel et al. 1974; Fish 1982; Williams 1983). The higher transport costs for these animals result from increased drag during surface swimming, inefficient modes of propulsion, and the higher maintenance metabolic rate of endothermic birds and mammals.

The few published values for the swimming energetics of primarily aquatic endotherms are restricted to measurements of seals. Metabolic rates based on hydrodynamic models or incidental measurements of oxygen consumption while the seals swam around a circular tank at a single velocity are 2–3 × the predicted value for salmonid fish (Craig and Pasche 1980; Lavigne et al. 1982). There are no published data on swimming metabolism or the cost of transport at different velocities. The purpose of this study was to measure the metabolic rate of yearling and adult seals in water at rest and during steady-state swimming at different velocities. These data were used to compare the cost of transport for seals of different size with salmonid fish and other aquatic en-

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dotherms. We found that metabolism increased curvilinearly with speed, that the lowest cost of transport occurred between 1.0 and 1.4 $m \cdot s^{-1}$, and that the total cost of transport for the seals was 3–4 × the extrapolated prediction for a salmon of similar size.

MATERIAL AND METHODS

ANIMALS

Two yearling (one male and one female) and one adult, female harbor seal (*Phoca vitulina*) were held in large concrete pools continuously supplied with filtered seawater from September 1982 to June 1983. They were fed twice per day on a diet of herring and mackerel supplemented with vitamins.

EXPERIMENTAL DESIGN

Swimming metabolism was measured in a flow channel located at the Hydraulics Laboratory at Scripps Institution of Oceanography. The channel is 1.1 m square and 16 m long, of which the central 12 m are glass on both sides. Closed loop variable flow is generated by two 60-cm diameter bronze propeller pumps. Flow velocities can be varied from zero to 1.4 $m \cdot s^{-1}$. Water velocity was measured with an electromagnetic flowmeter with the sensor positioned 30 cm above the floor of the flume. This position for the sensor was chosen because the seals usually swam at this depth in the flow channel. However, the flow channel was designed to produce homogeneous flow. Profiles of water flow through the test section showed that variation in water velocity was less than 0.1 $m \cdot s^{-1}$ between the surface and bottom. Water temperature in the flow channel ranged from 15 to 18 C.

Seals swam in a test section 2.5 m long that was partitioned with grills of welded steel ribs 15 mm wide and 2 mm thick. The thin edge of the ribs faced the flow of water and created little wake.

A metabolic hood consisting of an oblong Plexiglas dome (1.1 m long, 0.6 m wide, 0.3 m high) mounted in a wooden frame was suspended 10 cm below the surface of the water in the test section. Air was pumped through intake and exhaust ports mounted in the dome. When water was flowing in the flume, the seals determined their own breathing rate. Four or five practice sessions in the flow channel beginning several weeks before an experiment were usually sufficient to train a seal to swim steadily for 30–60 min at water velocities up to 1.4 $m \cdot s^{-1}$. We considered that the seals were trained when we were able to obtain reproducible values for oxygen consumption at each speed.

During a swimming session, a seal that had been fasted overnight was placed in the flow channel and allowed to accommodate for 30 min. Resting metabolism was measured in still water if the seal remained inactive for 30–60 min. During measurements of swimming metabolism, the first 10 min were allowed for the seal to achieve steady-state metabolism. Metabolic rate was then determined during 30 min of steady-state swimming at different water velocities. During each session, a seal swam at three speeds of increasing velocity ranging from 0.5 to 1.4 $m \cdot s^{-1}$. The seal was allowed to rest for 20 min while the analyzers were recalibrated between measurements at each speed.

O_2 CONSUMPTION AND CO_2 PRODUCTION

The metabolic hood in the flow channel served as an open-circuit system for measuring O_2 consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$). Air was drawn through the chamber with a vacuum pump, and the flow rate was measured with a calibrated dry gas meter (American Meter Division) accurate to within 1%. A flow of 60 liters $\cdot$ min^{-1} kept the fraction of O_2 in the dome above 19.5% and the fraction of CO_2 below 1.3% at maximum swimming speeds. Applied Electrochemistry O_2 and CO_2 analyzers continuously sampled gas in the exhaust line from the dome. Moisture and CO_2 were removed from gas entering the O_2 analyzer with Drierite and Baralyme, respectively. Gas entering the CO_2 analyzer was dried only. $\dot{V}O_2$ and $\dot{V}CO_2$ were calculated according to the equations of Depocas and Hart (1957). The O_2 analyzer was calibrated with dry room air (20.94%) and the CO_2 analyzer with room air (0.03%) and a gas mixture

of 0.5% CO_2 in nitrogen calibrated on a Scholander 0.5-c[3] gas analyzer (Scholander 1947). The analog output of the O_2 and CO_2 analyzers was connected to an Apple II computer with an analog-to-digital interface board. The output from each analyzer was monitored every 2 s and averaged each minute to compute $\dot{V}O_2$, $\dot{V}CO_2$, and respiratory quotient (RQ).

The entire system was calibrated with and without water flowing through the flume using a gas dilution method. For the O_2 calibration, 100% N_2 supplied at 2 liters·min^{-1} through a calibrated flowmeter was mixed with the total flow of air entering the dome. The theoretical fraction of O_2 (FO_2) in the gas leaving the dome was calculated using equation (1) and compared with the measured value from the O_2 analyzer.

$$FO_2 = \frac{(\dot{V}_{STPD} - \dot{V}N_2) \times 0.2094}{\dot{V}_{STPD}}, \quad (1)$$

where $\dot{V}_{STPD}$ is the total flow corrected to STPD, $\dot{V}N_2$ is the flow of 100% N_2, and 0.2094 is the fraction of O_2 in dry, ambient air. For the CO_2 calibration, 16% CO_2 in N_2 flowing at 2 liters·min^{-1} was mixed with the total flow entering the dome. This concentration of CO_2 and flow rate gave a mean concentration of CO_2 in the exhaust gas within the range normally produced when a seal was breathing inside the dome. The theoretical fraction of CO_2 (FCO_2) in the gas leaving the dome was calculated using equation (2) and compared with the measured value from the CO_2 analyzer.

$$FCO_2 = [(\dot{V}CO_2)(0.16) + (\dot{V}_{STPD} - \dot{V}CO_2)(0.0003)]/\dot{V}_{STPD}, \quad (2)$$

where $\dot{V}_{STPD}$ is the total flow corrected to STPD, $\dot{V}CO_2$ is the flow of calibrated CO_2 gas, 0.16 is the fraction of CO_2 in the calibrated gas, and 0.0003 is the fraction of CO_2 in dry, ambient air.

The system was calibrated at water velocities of 0, 0.5, 1.0, and 1.4 m·s^{-1}. The measured FCO_2 was less than the theoretical value at velocities greater than 0.5 m·s^{-1}, presumably because of the absorbance of CO_2 in the flowing water. The correction factor for the fraction of CO_2 was 1.06 for a water flow of 1.0 m·s^{-1} and 1.15 for a flow of 1.4 m·s^{-1}. The theoretical and measured FO_2 in the exhaust gas agreed to within 0.01% at all water velocities.

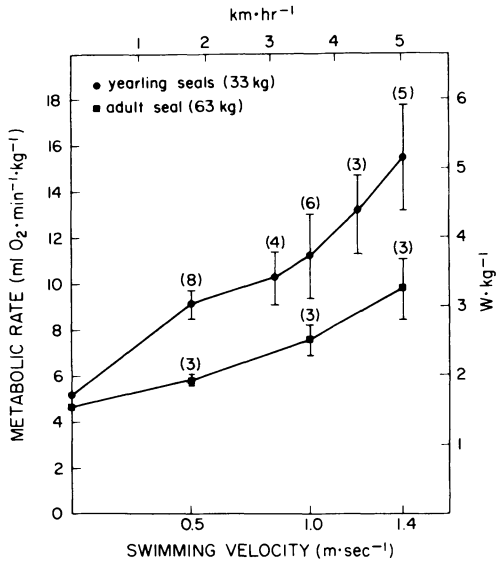

FIG. 1.—Metabolic rate plotted as a function of swimming velocity for one adult and two yearling harbor seals. Plotted are the mean values ± SD. The number of swimming sessions at each speed is shown in parentheses. Metabolic rates at zero swimming velocity are minimum values for seals resting in water.

RESULTS

Minimum resting metabolic rates in still water during a 20–30-min interval were 5.1 and 4.6 ml O_2·min^{-1}·kg^{-1} for the yearling and adult seals, respectively. Apneustic pauses lasted 1–5 min.

During steady-state swimming, metabolism increased curvilinearly with speed (fig. 1) to a maximum velocity for the flow channel of 1.4 m·s^{-1}. It was difficult to get the yearling seals to swim consistently at 0.5 m·s^{-1}. At this low velocity, they would ignore the flow of water and swim back and forth within the test section. This swimming pattern effectively increased the swimming velocity of the seal above the water velocity. As a result, the

apparent metabolic rate at 0.5 $m \cdot s^{-1}$ actually reflects a higher, undetermined swimming velocity. At water velocities greater than 0.5 $m \cdot s^{-1}$, this behavior did not occur and the seals swam steadily against the flow of water. The adult seal swam consistently at all water velocities.

A power curve regression for metabolic rate versus swimming velocity was calculated for yearling and adult seals. Because the yearling seals swam inconsistently at 0.5 $m \cdot s^{-1}$, data were omitted at this speed. The data for the yearling seals are best described by the curvilinear function,

$$\dot{V}O_2 = 5.1 + 6.25(\text{velocity})^{1.42},$$

where $\dot{V}O_2$ is in ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ and velocity is in $m \cdot s^{-1}$. For the adult seal, the data are best described by the curvilinear function,

$$\dot{V}O_2 = 4.6 + 3.1(\text{velocity})^{1.42}.$$

The metabolic rate while swimming at 1.4 $m \cdot s^{-1}$ was 3.0 × the resting rate for the yearling seals and 2.1 × the resting rate for the adult seal. The resting RQ ranged from 0.71 to 0.76 for all seals and did not change significantly during swimming.

Stroke frequency increased linearly with swimming velocity and was best described by the equation $y = 47.0x + 42.4$ ($r = .998$) for the yearling seals and $y = 32.2x + 29.5$ ($r = .997$) for the adult seal (fig. 2). For both yearling and adult seals, stroke frequency increased 1.6 × over the range of swimming velocities from 0.5 to 1.4 $m \cdot s^{-1}$.

When resting in still water, apneusis varied from less than 30 s to 4.5 min. The average dive duration during swimming at 0.5–1.4 $m \cdot s^{-1}$ was 52 ± 20 s for yearling and 73 ± 11 s for the adult seal. The average surface time was 11 ± 3 s for both yearling and adult seals. The fraction of total time spent breath-holding underwater during swimming averaged 82% for yearling seals and 88% for the adult seal. However, swimming speeds of 0.5–1.4 $m \cdot s^{-1}$ are at the low end of the range for adult and yearling harbor seals (Williams and Kooyman 1985). During high-speed swimming, dive and surface durations may change.

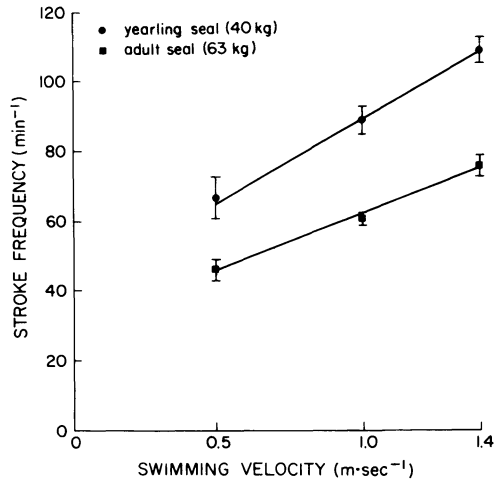

FIG. 2.—Stroke frequency plotted as a function of swimming velocity. Plotted are the mean values ± SD.

DISCUSSION

The standard metabolic rate of pinnipeds measured in captivity, usually from restrained animals, is often higher than for terrestrial mammals of similar size (for a review, see Lavigne et al. 1982). However, the metabolic rate of unrestrained harp seals resting quietly in water approaches the predicted value for terrestrial mammals (Øritsland and Ronald 1975; Gallivan and Ronald 1979). Similar to those of the harp seal, the resting values for harbor seals measured in this study were 1.1 × the predicted standard metabolic rate ($\dot{V}O_2$ [ml · min^{-1}] = 11.27 M_b [kg]$^{0.75}$; Schmidt-Nielsen [1979]). When resting in water, seals will often breath-hold underwater for several minutes. The resting apnea of harbor seals in this study varied from 0.5 to 5 min. Whether the low metabolic rates of seals resting in water are the result of a low level of activity or a reduction in metabolism caused by prolonged apnea during submergence remains uncertain.

The metabolic rate of terrestrial birds and mammals running on a treadmill characteristically increases linearly with speed (Taylor, Hegland, and Maloiy 1982).

Although a linear increase in metabolic rate with swimming speed has been reported for muskrats (Fish 1982) and marine iguanas (Gleeson 1979), a curvilinear increase in metabolic rate has been observed in fish (Brett 1964; Webb 1975; Gordon, Loretz, and Chow 1979), sea turtles (Prange 1976), ducks (Prange and Schmidt-Nielsen 1970), minks (Williams 1983), humans (Holmer 1972; Nadel et al. 1974), and seals (fig. 1). The increase in swimming metabolism correlates with the curvilinear increase in drag as a function of speed. However, Williams and Kooyman (1985) show that drag is proportional to (velocity)$^{1.4}$ in harbor seals for speeds ranging from 0.7 to 3.5 m·s^{-1}. This means that the power to overcome drag (drag power = drag × velocity) should scale to a factor of 2.4. This is greater than the scaling factor of 1.4 for metabolic power versus speed measured for yearling and adult harbor seals. The low scaling factor for metabolic power may be caused by the limited range of swimming speeds that were measured in this study. The scaling factor for metabolic rate versus speed may change when measurements are extended to include high-speed swimming.

In fish, swimming speed (V) is proportional to body length (L), the stroke frequency (f), and the stroke amplitude (A). Bainbridge (1958) showed that for fish f is proportional to V when the specific amplitude (A/L) is constant and f is greater than 5 s^{-1}. In this study, f was linearly proportional to V from 0.5 to 1.4 m·s^{-1}, which indicates that A/L may be constant if the propulsive wavelength is constant. This is similar to the results obtained for mackerel in which A/L was constant and speed was modulated by f. At low swimming speeds in trout in which f was less than 5 s^{-1}, Webb (1971) observed that only the product of fA/L was linearly proportional to V. The relationship between f and V may therefore diverge from linearity for seals at low speeds (e.g., less than 0.5 m·s^{-1}), but we were unable to make reliable measurements in this range.

Another way of expressing the energy requirements of locomotion is the cost of transport, which is obtained by dividing the oxygen consumption (ml O_2·min^{-1}·kg^{-1}) by the velocity (m·min^{-1}). The cost of swimming at 0.5 m·s^{-1} was 1.7 × greater than at 1.4 m·s^{-1} for all seals. The cost of swimming decreased curvilinearly, with velocity reaching a minimum value that was not significantly different ($P < .05$) between 0.85 and 1.4 m·s^{-1} for yearling seals and 1.0–1.4 m·s^{-1} for the adult seal (fig. 3). Animals that swim and fly characteristically show a U-shaped relationship with a minimum cost of transport at intermediate speeds (Prange and Schmidt-Nielsen 1970; Webb 1975; Prange 1976; Fish 1982). However, a U-shaped curve was not aparent for yearling or adult seals in this study because the maximum measured velocity was too low.

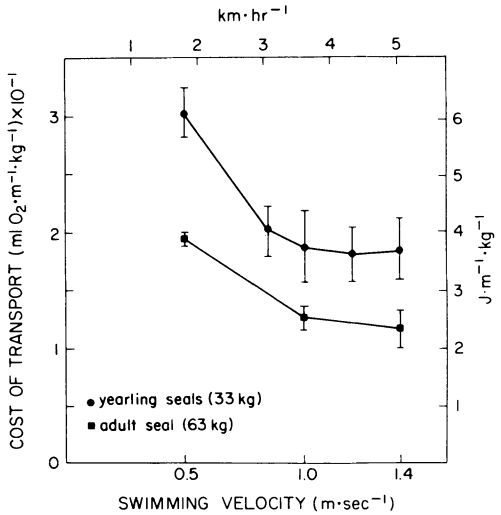

FIG. 3.—Cost of transport plotted as a function of swimming velocity. Plotted are mean values ± SD. The cost of transport values do not differ significantly between 0.85 and 1.4 m·s^{-1} for the yearling and between 1.0 and 1.4 m·s^{-1} for the adult seal.

The minimum cost of transport is a useful way to compare animals of different size because it is independent of speed and a constant for each animal. In comparison with salmon extrapolated to the size of seals using the equation $y = 2.15 M_b^{-0.25}$, which is the lowest cost of transport of any vertebrate (Schmidt-Nielsen 1972; Tucker 1975), the total cost of swimming was 3–4 × higher for the yearling and adult harbor seals (fig. 4). Comparable

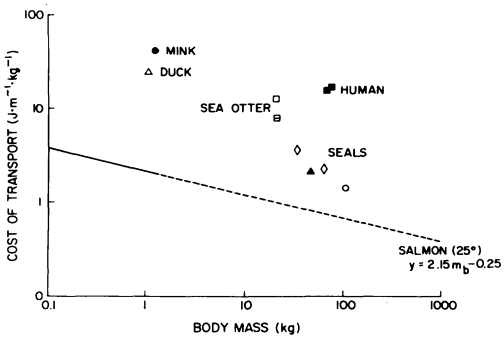

FIG. 4.—The log of the cost of transport plotted as a function of log body weight for several aquatic and semiaquatic vertebrates. Symbols: duck (△), Prange and Schmidt-Nielsen 1970; mink (●), Williams 1983; humans (■), Holmer 1972; Nadel et al. 1974; sea otter surface (□) and submerged (⊟), Williams and Kooyman 1983; harbor seal (▲), Craig and Pasche 1980; harp seal (○), Lavigne et al. 1982; harbor seals (◇), this study.

values were obtained for harbor seals by Craig and Pasche (1980) and harp seals by Lavigne et al. (1982). However, compared to other aquatic and semiaquatic mammals and birds, seals have a much lower cost of swimming. The mink, duck, and human are surface swimmers that use a stroke-recovery mode of locomotion and exhibit a considerably higher cost of transport. The transport costs of sea otters are intermediate between semiaquatic mustelids and harbor seals (Williams and Kooyman 1983). Factors contributing to the lower cost of swimming in seals are enhanced body streamlining and primarily subsurface swimming to reduce drag.

Low RQs ranging from 0.71 to 0.76 during steady-state swimming indicate that fat was the principal metabolic fuel. In addition, venous blood samples taken from a yearling seal during one swimming session showed no increase in the lactic acid concentration over normal resting levels (e.g., 0.4 mM) at speeds up to 1.4 $m \cdot s^{-1}$. This indicates that oxygen stores were sufficient to maintain aerobic metabolism and prevent the accumulation of lactic acid at these work levels. Although the seals were breath-holding during swimming, the average dive duration of 52 s for yearlings and 73 s for adult seals appears to be within their aerobic dive limit at speeds of 1.4 $m \cdot s^{-1}$. Because the seals experience less hydrodynamic drag during submerged swimming as compared with surface swimming (Williams and Kooyman 1985), energetic costs are less if the seal remains submerged as much as possible. By keeping the dive duration within the aerobic dive limit, the seals can maintain steady-state, aerobic metabolism while swimming submerged 80%–90% of the time.

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