COST OF TRANSPORT IN STELLER SEA LIONS, *EUMETOPIAS JUBATUS*

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ABSTRACT

The cost of swimming is a key component in the energy budgets of marine mammals. Unfortunately, data to derive predictive allometric equations are limited, and estimates exist for only one other species of otariid. Our study measured the oxygen consumption of three juvenile Steller sea lions (*Eumetopias jubatus*) swimming in a flume tank at velocities up to 2.2 m sec^{-1}. Minimum measured cost of transport ranged from 3.5–5.3 J kg^{-1} m^{-1}, and was reached at swimming speeds of 1.7–2.1 m s^{-1}. These cost-of-transport values are higher than those reported for other marine mammals. However, once differences in stationary metabolic rate were accounted for, the locomotor costs (LC) for the Steller sea lions were commensurate with those of other marine mammals. Locomotor costs (LC in J m^{-1}) appeared to be directly proportional to body màss (M in kg) such that LC $= 1.651 M^{1.01}$. These estimates for the cost of locomotion can be incorporated into bioenergetic models and used to determine the energetic consequences of observed swimming behavior in wild marine mammals.

Key words: cost of transport, swimming metabolism, Steller sea lion, *Eumetopias jubatus*.

The cost of moving is a critical component of an animal's energy budget. Steller sea lions (*Eumetopias jubatus*) spend the majority of their time swimming, although this changes with season, sex, and age class (Higgins *et al.* 1988; Milette 1999; Trites and Porter, in press). Hence, accurate estimates of the cost of locomotion are essential to quantify the energetic consequences of differences or changes in behavior.

The cost of locomotion for an individual is not constant, with total metabolic output generally increasing with velocity. The cost of locomotion for a number of marine mammals has been measured experimentally as the rate of oxygen consumption while the animal is swimming in a flume or, rarely, while

freely swimming in the ocean (see table 1 in Williams 1999). Extrapolation to untested species or age groups is hampered by inconsistent terms used to express this cost. While some allometric equations have been developed to describe the cost of swimming in aquatic mammals across broad taxonomic categories (Culik and Wilson 1991, Williams 1999, Fish 2000), data are insufficient to provide reliable predictions, particularly within underrepresented groups.

Despite the importance of estimates of swimming costs in marine mammals, only a single otariid species has been studied, the California sea lion, *Zalophus californianus* (Feldkamp 1987, Ponganis *et al.* 1991, Williams *et al.* 1991). This paucity of data is largely due to the myriad of logistical hurdles in measuring energy expenditure in a large, periodically breathing, aquatic mammal. There are no estimates of the energetic costs of swimming for Steller sea lions. However, drastic declines in the population of Steller sea lions (Trites and Larkin 1996) have highlighted the need for estimates of swimming costs to understand the consequences of ecosystem changes on sea lion survival. Recent computer modeling has confirmed the need for accurate estimates of individual bioenergetic parameters (Winship 2000).

We measured the oxygen consumption rates of three Steller sea lions swimming in a flume tank across a range of water speeds. Our goals were to determine the specific swimming costs of juvenile Steller sea lions, derive allometric relationships that can be used to estimate costs in other Steller sea lions, and compare swimming costs with other marine mammals.

METHODS

Three subadult sea lions aged 2.5–3.5 yr were tested in a swim flume, similar in design to that described by Åstrand and Englesson (1972). The flume had an active swimming area of 106 × 325 × 83 cm. Water flow was generated by two turbines and flow rates were controlled by individual rheostats. Actual water speed (measured at the position of the respirometry dome, 50 cm below the water surface) was determined through calibration with a low-flow water velocity meter (Probe #FP101, Global Water, Gold River, CA). Changes in water speed across the vertical plane were <10% (except for larger edge effects). Testing water speeds were limited to ≤ 2.2 m sec^{-1} as turbulence interfered with measures of oxygen consumption above that velocity.

The swim flume was equipped with a 120-liter lexan respirometry dome. Metabolism was measured using open circuit (gas) respirometry. Details of the equipment are given in Rosen and Trites (1999). Briefly, air was drawn through the dome at a constant rate, using a modified vacuum pump. Air flow was controlled by a flow meter (7500 series, King Instruments, Garden Grove, CA), maintained at 150–170 liters min^{-1} (depending on animal size), measured between the chamber and the pump. This flow was sufficient to prevent extreme changes in gas concentrations. Oxygen and carbon dioxide concentrations within a continuously sampled, desiccated subsample of expired air were determined by a S-3A/I solid oxide (stabilized zirconia) cell analyzer

(Ametek Inc., Pittsburgh, PN) and an AR-60 infrared gas analyzer (Anarad Inc., Santa Barbara, CA), respectively. A Sable data acquisition system (Sable Systems, Henderson, NV) recorded an average gas concentration from the analyzers every second. Flow rate was corrected to STPD through concurrent barometric pressure and temperature readings at the flow meter.

The experimental apparatus precluded removing carbon dioxide from the sampled air stream. Given that an unknown portion of the CO_2 was absorbed in the water, recorded carbon dioxide concentrations were used only to numerically correct for oxygen concentration readings and not to calculate respiratory quotient values (assumed RQ = 0.70) or energy consumption estimates. Corrected oxygen consumption rates were converted to energy utilization using the equation 1 liter O_2 = 20.0 kJ. Gas concentration readings were baselined against ambient air concentrations before and after each trial, and the entire system was recalibrated through the course of the experiments using gases of known concentrations and a standard nitrogen dilution technique (Fedak *et al.* 1981).

The sea lions had previous exposure to the testing flume, and all tests were performed in the morning, at least 16 h postprandial. Air temperature was variable (17°–24°C) but water temperature was less variable at 8°–10°C. The sea lions were trained to remain calm and stationary within the respirometry dome for a 10–15-min period to obtain a measure of resting (stationary) oxygen consumption. The animals then swam against a pre-selected water current for 10–15 min (swimming oxygen consumption). The animals held their position against a target submerged 50 cm below the surface. As submergence times were less than a minute, oxygen consumption values reported here more closely reflect "transit swimming" costs rather than those for prolonged dives. Only trials where the animals performed satisfactorily for measurements of both stationary and swimming oxygen consumption are presented. The mass of the animals was determined prior to each trial by having them hold stationary on a platform scale (±0.2 kg).

Oxygen consumption rates were expressed in relation to swimming velocity. Total cost of transport (COT_{TOT}), the energy needed to move 1 kg of body mass over a distance of 1 m (Schmidt-Nielsen 1972), was also calculated from the oxygen consumption *vs.* swimming velocity data for each sea lion. The minimum cost of transport (COT_{MIN}) is the minimum rate of energy expenditure per distance, reached at some optimal velocity (U_{opt}; Tucker 1975). It is the value most commonly used in comparative studies (Videler 1993). COT_{MIN} was estimated from a visual examination of the minimum values of COT_{TOT}. In some studies (*e.g.*, Williams 1999) the COT_{TOT} has been partitioned into the maintenance costs of the animal (MC) and locomotor costs (LC) incurred due to physical activity (what Schmidt-Nielsen 1972 termed the net cost of transport, COT_{NET}). LC was calculated as COT_{MIN} − MC, where steady state oxygen consumption during the stationary phase was assumed to reflect MC.

Results

Adequate measures of both stationary and swimming oxygen consumption were obtained from 15 to 21 sessions for each sea lion. Trials were completed

Table 1. Individual costs of swimming for three juvenile Steller sea lions. Body mass during trials presented as mean ± 1 SD. Linear regression for total cost of swimming describes the relationship between oxygen consumption (P in ml O_2 min^{-1}) and swimming speed (U in m sec^{-1}). Locomotor costs (LC) presented for experimental data obtained at velocities of $\sim$2.0 m sec^{-1}, and values extrapolated for swimming speeds of 3.4 m sec^{-1}.

Sea lion	Age (yr)	Mass (kg)	Cost of swimming (ml O_2 min^{-1})	COT_{MIN} (J kg^{-1} m^{-1})	LC (2.0) (J kg^{-1} m^{-1})	LC (3.4) (J kg^{-1} m^{-1})
Male1 (M93TA)	3.5	138.7 ± 4.8	$P = 1879 + 631U$ ($r^2 = 0.80, n = 21$)	3.5	2.8	2.4
Female1 (F94SA)	2.5	110.3 ± 5.6	$P = 2634 + 450U$ ($r^2 = 0.85, n = 15$)	5.3	4.3	3.1
Female2 (F93SU)	3.5	116.5 ± 2.3	$P = 1478 + 713U$ ($r^2 = 0.84, n = 18$)	4.3	3.4	2.8

for each animal within 45 d, during which time body mass remained relatively constant (Table 1).

Rates of oxygen consumption were collected across water speeds of 0.2–2.2 m sec^{-1} (Table 1). Metabolic output (P) was predicted to increase with swimming velocity (U) at a rate approaching $P = aU^3$, which reflects the increasing cost of drag with higher swimming velocities (see Hind and Gurney 1997). However, we found that linear regressions were a more appropriate fit, given the range of the testing speeds in our study. The data are presented as absolute oxygen consumption rates (Table 1). For comparison to other studies, the data are also transformed on a mass-specific basis (Fig. 1), although this convention has little physiological basis (Packard and Boardman 1988, Hayes and Shonkwiler 1996).

Metabolism while holding stationary in the water (MC) ranged from 20.3 to 20.8 MJ d^{-1}. For comparison, this translates into 1.76–2.03 times the resting metabolic rate predicted by Kleiber (1975) for adult terrestrial mammals. These values are similar to resting metabolic rates of the same animals obtained during the same period in a dry metabolic chamber (Rosen and Trites, unpublished data).

The COT_{TOT} (expressed in J kg^{-1} m^{-1}) decreased with increasing water speed (Fig. 2). The initial decrease in COT_{TOT} with increasing speed is typical as animals approach their optimal swimming speed (U_{opt}), but the testing speeds did not reach high enough velocities to clearly demonstrate the expected increase in COT_{TOT} beyond U_{opt}. However, using the minimum observed values, the minimum cost of transport (COT_{MIN}) ranged from 3.5 to 5.3 J kg^{-1} m^{-1} (Table 1), and was reached at 1.7–2.1 m sec^{-1}. The resulting allometric equation across an array of marine mammal species was $COT_{MIN} = 9.54M^{-0.29}$ ($r^2 = 0.67, n = 14, P < 0.001$) (Fig. 3). This equation is not statistically different from that developed by Williams (1999; $7.79M^{-0.29}$).
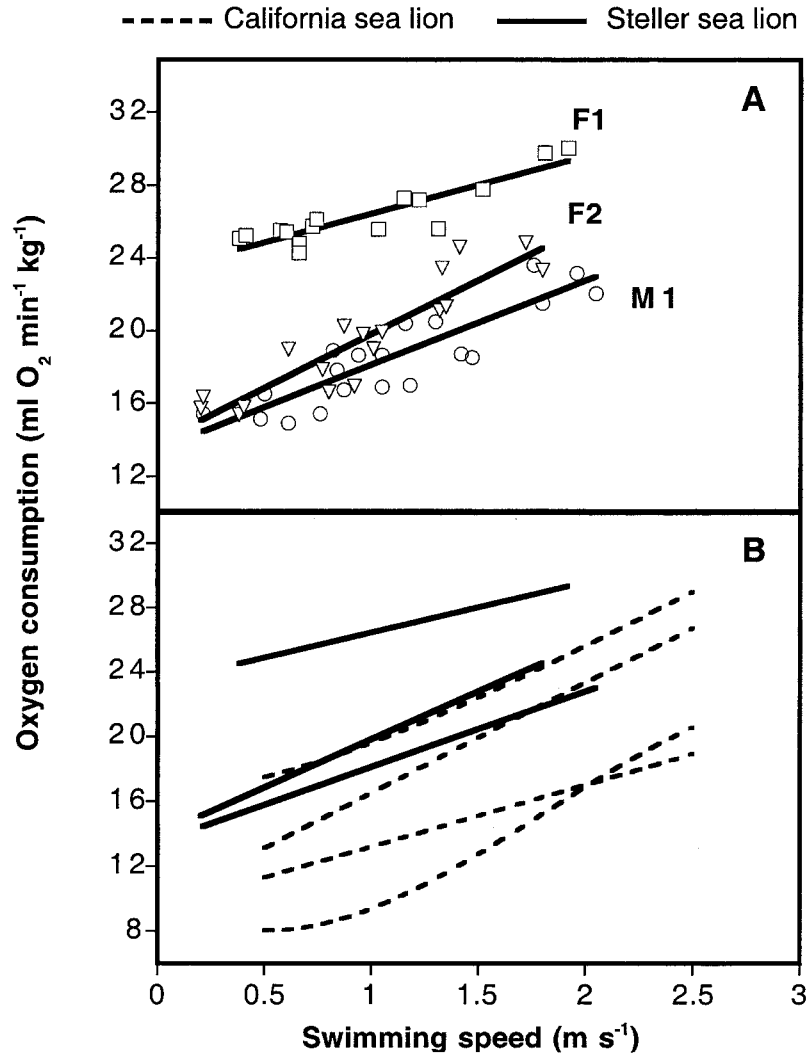
Figure 1. Change in mass-specific oxygen consumption with swimming speed for three Steller sea lions (A). Regressions also presented with data for California sea lions in (B) (broken lines = data from Feldkamp 1987, Ponganis *et al.* 1991).

Williams (1999) suggested that locomotor costs ($LC = COT_{MIN} - MC$), by removing differences in resting metabolism, would provide a more accurate comparative measure of the added metabolic cost due solely to locomotion. For the Steller sea lions in our study, LC at speeds of 1.7–2.1 m sec^{-1} were 2.8–4.3 J kg^{-1} m^{-1}. By these estimates, LC represents 78%–80% of COT_{MIN}.

DISCUSSION

Studies of comparative bioenergetics can be used to determine intra- and interspecific allometries. These, in turn, can be used to highlight fundamental differences (*i.e.,* deviation from the allometry) for further investigation and to formulate predictions for species for which no data are available. A number of studies have reviewed the cost of locomotion, and several have focused on the cost of swimming in marine mammals (*e.g.,* Williams 1999, Fish 2000). Even

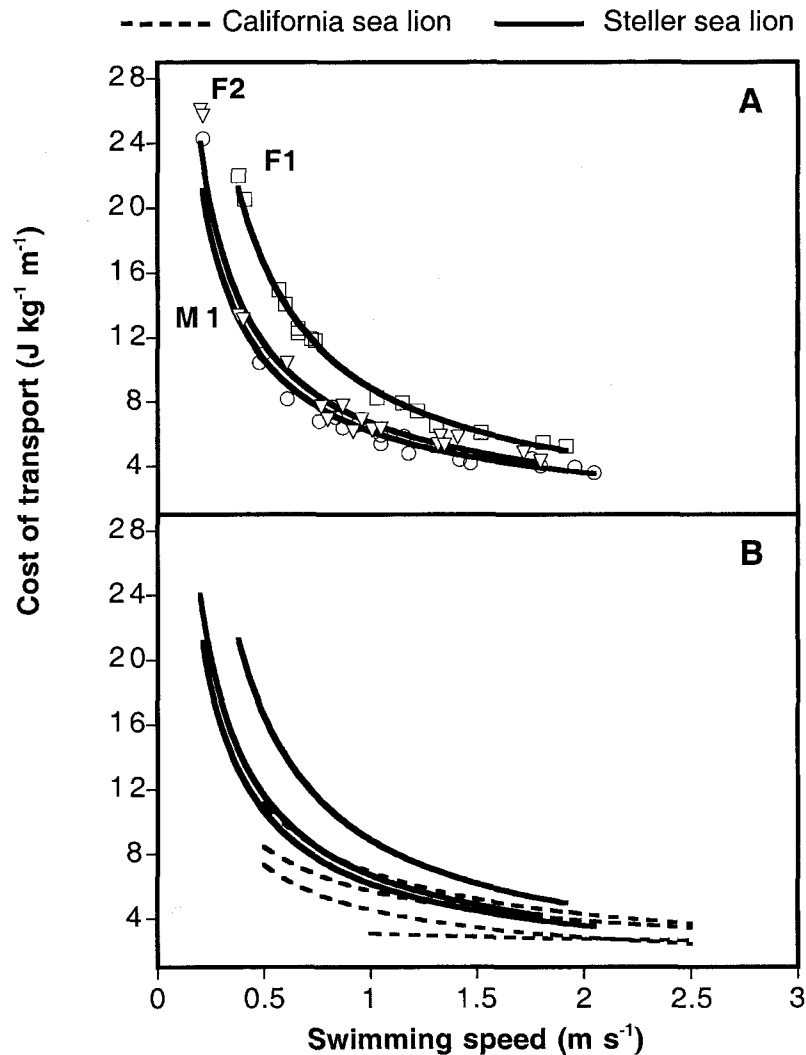- - - - California sea lion ———— Steller sea lion

Figure 2. Change in total cost of transport with swimming speed for Steller sea lions (A). Regressions are compared to similar data from California sea lions (B) (broken lines = data from Feldkamp 1987, Ponganis *et al.* 1991). Power functions fitted to data for illustrative purposes.

within this narrow group, the energy cost of swimming can be affected by a number of factors, such as the mode of propulsion and body size.

Marine mammals utilize a variety of propulsive modes (see Fish 2000); therefore, care must be taken when comparing across taxa. Unlike other marine mammals, otariids use foreflipper oscillation for propulsion. However, to date, data on the cost of swimming within this group have been limited to a single species, the California sea lion. Additionally, the body size of species classified as marine mammals ranges across four orders of magnitude. Traditionally, differences in body mass have been partially controlled for by expressing the energy cost of locomotion as the cost of transport (COT_{TOT}; J kg^{-1} m^{-1}).

The COT_{TOT} of the sea lions in our study was higher than that reported for California sea lions (Fig. 2), particularly at lower swimming speeds. However, the minimum cost of transport (COT_{MIN}) is generally accepted to provide
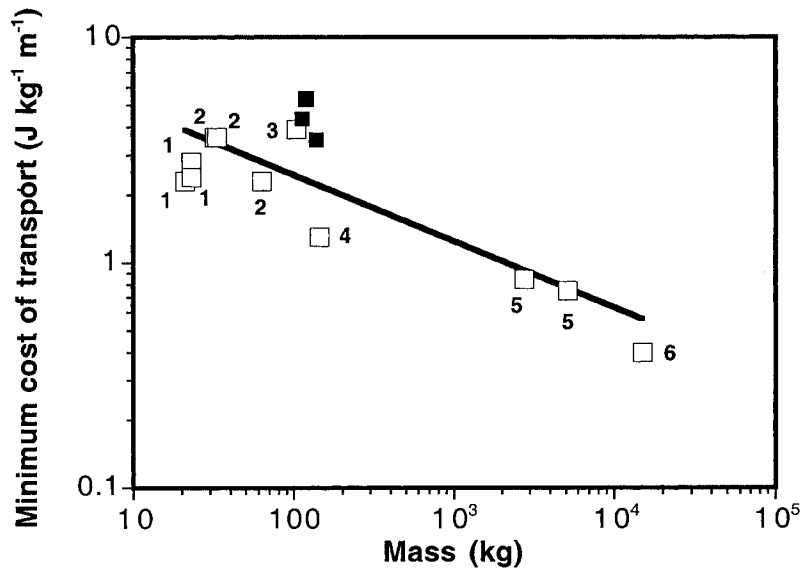
Figure 3. Minimum measured cost of transport for three Steller sea lions (solid symbols) compared to other marine mammals (open symbols, summarized in Williams 1999). The resulting regression was $COT_{MIN} = 9.54M^{-0.29}$. Species are: 1. California sea lion, 2. harbor seal, 3. gray seal, 4. bottlenose dolphin, 5. killer whale, and 6. gray whale.

a more equitable comparison of locomotor energetics between animals (Videler 1993, Fish 2000).

COT_{TOT} for an individual decreases with increasing velocity (due to increasing propulsive efficiency) until some minimum value (COT_{MIN}) is reached at some optimal velocity (U_{opt}). Thereafter, COT_{TOT} increases because of increasing drag forces and decreasing efficiency. COT_{MIN}, by definition, occurs at a speed where an animal can cover the greatest distance for the least cost and is presumed to represent an animal's "preferred" swimming speed. COT_{MIN}, therefore, is often used to estimate the energy expenditure of free-swimming animals.

The lowest COT values recorded from the sea lions in our study were 3.5–5.3 J kg^{-1} m^{-1}. These were $\sim$1.8 times greater than those reported for California sea lions (Feldkamp 1987, Ponganis *et al.* 1991) (Fig. 3). This difference is contrary to the interspecific trend of decreasing COT_{MIN} with increasing body mass (Schmidt-Nielsen 1972). This discrepancy may have occurred because of (1) experimental design, (2) limitations in testing speeds, or (3) the effect of differences in resting metabolism.

Animals tested in swim flumes may not be operating at peak efficiency. Stroke kinematics may be curtailed due to size constraints, decreased mechanical efficiency, and increased total locomotory costs. The depth of the animal may be insufficient to eliminate surface drag effects, which will theoretically increase swimming costs unless the animal is submerged about three body diameters below the surface (Hertel 1966). Therefore, the cost of transport values that we present in this paper should probably be regarded as maximum estimates.

Second, the sea lions in our study may not have reached their optimal swimming speed. In general, U_{opt} increases with increasing body mass (Videler and Nolet 1990). Robbins (1993) suggested that the most efficient speeds for submerged swimming scaled to body mass (M in kg) such that: speed (m sec^{-1}) = $0.57M^{0.21}$. However, this formula probably underestimates U_{opt} for otariids. It predicts that the Steller sea lions in our study should have displayed COT_{MIN} at swimming speeds between 1.53 and 1.60 m sec^{-1}, which is lower than the 1.7–2.1 m sec^{-1} observed in our study. Similarly, studies of California sea lions reported COT_{MIN} at swimming speeds of 1.8–2.6 m sec^{-1} (Williams et al. 1991), and one study found no clear minimal point below 2.5 m sec^{-1} (Feldkamp 1987), both of which are higher than would be predicted from Robbins' interspecific equation.

Alternatively, Videler and Nolet (1990) suggested that U_{opt} for swimmers was best calculated from Reynolds numbers (Re), such that U_{opt} = $0.002Re^{0.48}$. Stelle et al. (2000) calculated that Re was 5.5×10^6 for the same sea lions that were used in our study. This value results in a calculated U_{opt} of 3.4 m sec^{-1}, which also corresponded to the animals' observed preferred swimming speed. If we were to extrapolate from the regressions presented in Figure 1, COT at 3.4 m sec^{-1} is predicted to be 2.9–3.7 J kg^{-1} m^{-1}, which is still greater than that predicted from interspecific comparisons (Fig. 3).

Finally, and most importantly from a comparative perspective, the higher metabolic rates from younger Steller sea lions undoubtedly contributed to the higher than predicted COT_{MIN}. This result emphasizes the importance of making equitable comparisons and of understanding the relationship between COT and its components, LC and MC.

Usually, the total cost of transport for animals that swim has been reported to be less than that for animals that fly or run (Schmidt-Nielsen 1972). However, the sea lions in our study had COT_{MIN} ~5.6–8.8 times that traditionally predicted for swimmers. Peters (1983) suggested that the discrepancy between swimmers and marine mammals was attributable to the lower maintenance costs of ectothermic species that have been primarily used to date in comparative analyses to represent swimmers, versus the higher maintenance costs of endothermic marine mammals. Indeed, in an analysis using mammalian examples, COT_{MIN} for marine mammals while swimming was identical to that for terrestrial runners (see fig. 3b in Williams 1999).

Still, the sea lions in our study had COT_{MIN} ~1.9–2.7 times that predicted by the equation that Williams (1999) produced specifically for marine mammals (Fig. 3). However, much of this difference is due to the higher MC of these juvenile animals. Williams emphasized the importance of accounting for differences in resting metabolic rates of marine mammals before they could be used to compare the locomotory costs of mammalian runners and swimmers. Similarly, this operation would also control for the higher mass-specific metabolic rates of younger animals.

Once MC is removed from COT_{MIN}, the locomotor costs (LC, expressed in J kg^{-1} m^{-1}) for Steller sea lions are similar to those of other marine mammals. LC was 2.8–4.3 J kg^{-1} m^{-1} at the measured swimming speeds of 1.8–2.1 m
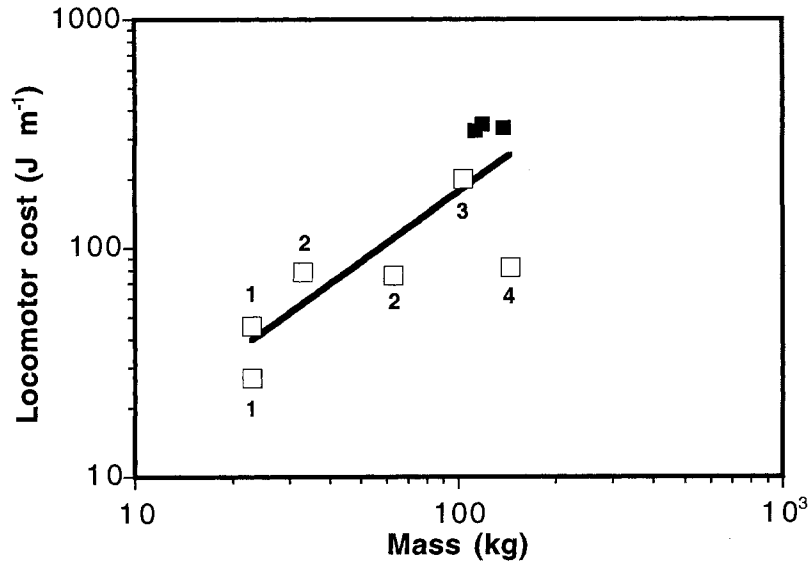
Figure 4. Estimated locomotor costs (LC) for three Steller sea lions swimming at 3.4 m sec^{-1} (solid symbols) compared with other marine mammals (open symbols). Resulting regression was LC $=$ 1.651 M$^{1.01}$. Comparative data derived from Williams (1999). Species designations as for Figure 3.

sec^{-1}. The extrapolated LC at a swimming speed of 3.4 m sec^{-1} was 2.4–3.1 J kg^{-1} m^{-1} (Table 1). By these estimates, LC comprised about 80% of COT. Interestingly, the five-fold relationship between MC and COT$_{MIN}$ is similar to the standard multiplier between MC and swimming costs used in many bioenergetic models (*e.g.*, Ashwell-Erickson and Elsner 1981, Doidge and Croxall 1985, Olesiuk 1993, Winship 2000).

Contrary to expectations, there appeared to be no significant allometric relationship between LC and body mass. However, this is likely due to the manner in which LC is expressed. Use of a mass-specific conversion (*i.e.*, J kg^{-1} m^{-1}) may aid in interspecific comparisons, but they are of questionable physiological basis (Packard and Boardman 1988, Hayes and Shonkwiler 1996). When expressed as a rate of absolute energy consumption (J m^{-1}), a strong relationship emerges: LC $=$ 1.651M$^{1.01}$ $r = 0.71, P = 0.004$) (Fig. 4). It is interesting to note that the exponent of this equation implies that the cost to an animal for moving through the water is directly proportional to body mass. This conforms to the basic laws of physics—it takes twice as much energy to move twice as much mass the same distance. However, care must be taken in interpreting these equations, given the narrow range of body masses for which data are available. Similarly, while the allometric relationship predicting COT$_{MIN}$ from body mass may appear quite strong (Fig. 3), the relationship is heavily influenced by a single data point for a gray whale whose metabolism was estimated from breathing rates (Sumich 1983). There is clearly a need for further studies on larger (>200 kg) marine mammals.

Still, understanding and defining the relative roles of locomotor and maintenance costs allows predictions of swimming costs across a range of taxa, age, and size classes. Specifically, the total energy costs of swimming can be par-

titioned into metabolic and locomotor costs, both of which are scaleable to body mass. The implication is that these parameters can be estimated for species for which data are unavailable. These bioenergetic estimates can be incorporated into models and used to determine the energy consequences of observed swimming behavior in wild animals.

For example, it has been suggested that changes in prey distribution may be adversely impacting the Steller sea lion population through increased foraging costs. Using the derived allometric functions it is possible to estimate the total swimming costs associated with changing the foraging location of a 150-kg "typical" marine mammal from 10 km to 20 km away. For a 150-kg marine mammal the estimated cost of travelling an additional 20 km (an extra 10 km each way) at an optimal speed is 6,700 kJ ($= 9.54 \text{ M}^{-0.29} \times 20,000$ m $\times$ 150 kg).

To put this into further ecological context, this value represents the energy from consuming about 1.2 kg of herring or 1.9 kg of pollock (given respective net energy values of 5.5 and 3.5 kJ g^{-1}, Rosen and Trites 2000). However, a portion of this total cost is the metabolic costs of merely being in the water (*i.e.,* MC), a value that can vary greatly with the age of the individual. The additional predicted cost of swimming the required distance (removing the incurred cost of stationary metabolism by using the equation for predicting LC) is 5,210 kJ ($= 1.651 \text{ M}^{1.01} \times 20,000$ m).

Again, it is important to note that neither of these calculations factor in the energy differences between MC in the water and metabolism on land, or the energy cost of diving or additional foraging. However, the differences in these two estimates highlight the effect that variation in stationary metabolism (due to age, thermoregulation, *etc.*) can have on estimates of the additional costs associated with swimming, and how these factors can be accounted for in bioenergetic calculations. They also highlight the capacity of allometric equations derived from comparative bioenergetic studies to provide valuable estimates when empirical data are lacking.

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