Can Versatile Propulsive Systems be Energetically Efficient? The Role of Specialization in Marine and Semi-Aquatic Mammals

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ABSTRACT

Due to reliance on limited on board energy stores during submergence, marine mammals can provide valuable information regarding mechanisms for efficient underwater locomotion. Among marine mammals, the use of oscillating hydrofoils is a common feature that appears to facilitate cost efficient thrust production, stability, maneuverability and speed. Previous studies have focused on the operation of aquatic propellers that are located caudally on the animal, as exemplified by the bottlenose dolphin (*Tursiops truncatus*). In this study, we determine effects of hydrofoil placement on energetics and mechanics by comparing locomotor performance in a variety of marine mammal species that differ in mode and location of propulsion. By comparing the results from these marine mammals to those of semi-aquatic and terrestrial mammals, we also evaluate the role of locomotor specialization on performance. This study indicates a marked similarity in transport costs, routine performance, and distance moved per stroke (transport distance) among cetaceans, phocids and otariids. Specialization for one form of locomotion appears to be an important feature leading to these similarities. The cost of generating force whether against gravity or drag depends primarily upon the level of specialization rather than the type of locomotion in mammals. Consequently, engineers basing AUV design on aquatic mammals may focus on affiliated performance characteristics (i.e. maneuverability, stability, versatility) afforded by specific propeller placement rather than concern for energetic efficiency *per se*.

INTRODUCTION

Key performance features required for autonomous underwater vehicles (AUVs) are speed, maneuverability, stability and propulsive efficiency. These same features are characteristic of many marine mammal species, animals that have had over 50 million years to solve the problem of cost efficient aquatic propulsion (Repenning, 1976; Thewissen *et al*., 1994). Like the batteries of an AUV, the oxygen stores of marine mammals must be periodically recharged by surfacing to breathe (Kooyman, 1989; Butler and Jones, 1997). The duration of a dive and level of underwater performance are constrained by the balance between propulsive costs and fuel reserves (Castellini *et al.*, 1985). Short duration dives permit greater flexibility in speed and swimming mode as the demand on total oxygen reserves is lower. Longer dives in which oxygen reserves become limiting result in the expression of energy conserving strategies. Thus, behavioral and physiological mechanisms used by marine mammals to prolong the period between breaths have provided clues about propulsive efficiency and maximizing the duration of underwater performance when energy stores are limited (Williams *et al*., 1993, 1999; 2000).

The mammalian body required considerable morphological and physiological modifications to change from efficient terrestrial to aquatic locomotion as occurred during the evolution of marine mammals. Rather than a single mode of swimming, different lineages of marine mammal solved the problem of aquatic locomotion in a variety of ways. In most cases the appendages have been enlarged and modified in shape to serve as an oscillating hydrofoil (Fish, 1993). Cetaceans, including the dolphins, porpoises and whales, use dorso-ventral undulation of caudal flukes to generate thrust during swimming and diving (Fig. 1). In otariids such as the California sea lion the hydrofoil is in the form of paired foreflippers and is located near the center of mass of the body (Feldkamp, 1987). Phocid seals use alternate sweeps of the hind flippers in the lateral plane to generate thrust (Fish *et al*., 1988). Even sea otters during submerged swimming use the hind flippers and body as a dorso-ventral oscillating hydrofoil (Williams, 1989). A common feature of these modes of aquatic propulsion is the absence of a prolonged recovery period during the stroke cycle. As a result, thrust can potentially be created throughout the entire cycle. This differs from paddlers or rowers exemplified by semi-aquatic mammals that often use thrust-recovery forms of propulsion (Fish, 1996).

To understand the advantages or disadvantages associated with these different styles of swimming, we compared the efficiency and performance limitations of oscillating hydrofoils used by marine mammals. Biomechanics and locomotor performance were measured for two species of marine mammal, the bottlenose dolphin and California sea lion. The results for these animals were compared to other marine mammal species using different modes of propulsion. The effect of specialization was also assessed by comparing the energetics and performance capabilities of obligate marine mammals and semi-aquatic mammals. Based on this study, we find a marked similarity in energetic cost, routine performance, and distance moved per stroke among cetaceans, phocids and otariids. Specialization for one form of locomotion appears to be an important feature leading to these similarities. In view of this, engineers interested in designing energy efficient AUVs may focus on accompanying performance

characteristics (i.e. maneuverability, stability, movement on land or in water) afforded by propulsor placement rather than concern for efficiency *per se*.

METHODS

Animals. Laboratory and field tests were conducted on four adult male bottlenose dolphins (*Tursiops truncatus*, body mass = 208 ± 27 kg) and three, adult female California sea lions (*Zalophus californianus*, body mass = 86.6 ± 7.6 kg). All animals were housed in salt water enclosures and fed a diet of fish supplemented with vitamins. Data for other species and all energetic measurements were compiled from previous studies conducted in our laboratory.

Kinematics and Performance Characteristics. The kinematics (gait type, stroke frequency, stroke length) and performance characteristics (routine speed range) were examined for sea lions and dolphins trained to swim in a horizontal path between submerged targets. Tests were conducted in salt water pools at Long Marine Laboratory (University of California at Santa Cruz) and in open water off the coast of the Grand Bahama Island. Distance between targets ranged from 10 to 25 m at a depth of 2 – 20 m. Kinematics of the swimming animals were recorded continuously during the tests with a Hi-8 video camera (Sony CCD TR400) mounted in an underwater housing held by a SCUBA diver. The camera was positioned perpendicular to swimming path of the animals. Unexpected camera movements were accounted for by subtracting movement vectors of stationary objects placed in the field of view from those of the swimming animals (Skrovan *et al*., 1999).

Video recordings were subsequently transferred to VHS tape for digital analysis. Video images were manually digitized at 60 fields per sec using a motion analysis system (Peak Performance Technologies, Inc., Englewood, CO). Kinematic parameters were correlated to swimming speed and distance traveled per stroke (transport distance). Transport distance was determined according to Kram and Taylor (1990) with modifications for swimming (Williams *et al.*, submitted). To correlate our results to previously published values for terrestrial species, we analyzed the distance traveled for one phase of the power stroke. For dolphins, this was equivalent to the downstroke (Williams *et al*., submitted). For sea lions, this period was equivalent to the power phase of the stroke cycle (Feldkamp, 1987). Lengths used in the determination of speed and transport distance were calibrated against the measured length of the animals in the video sequence. Timing of the video system was calibrated against a digital clock placed in the field of view.

RESULTS AND DISCUSSION

Energetic Cost and Aquatic Propulsion in Marine Mammals

Despite different modes of propulsion, both the energetic cost and routine performance capabilities of many groups of marine mammals are similar (Fig. 2, Table 1). For example, routine swimming speeds for bottlenose dolphins, harbor seals and

California sea lions range from 1.3 – 3.6 $m.s^{-1}$ (Williams and Worthy, in press) and average 2.0 $m.s^{-1}$. This occurs regardless of differences in location or type of propulsion and over a wide range of body masses (from 30 kg fur seals to 145,000 kg blue whales). Transport distance, defined as the horizontal distance traveled per power phase of a stroke, is identical for dolphins and sea lions at these routine speeds (Table 1).

Interestingly, the stroke frequency required to achieve identical routine speeds and transport distances varies between these species. Sea lions using paired foreflipper propulsion take less than half the number of strokes taken by bottlenose dolphins using a caudal fluke to move at the same speed. In comparison, phocid seals maintain a higher stroke frequency than both of these species when traveling at 2.0 $m.s^{-1}$.

The associated energetic cost of transport for swimming dolphins, seals and sea lions changes predictably with body mass despite different modes of propulsion (Fig. 2). According to Schmidt-Nielsen (1972) the cost of transport describes the amount of energy expended to move the body a unit distance; it is calculated by dividing the fuel consumption rate of the animal by swimming speed. Regardless of swimming mode we find that a single allometric regression describes the cost of transport for marine mammal specialists including sea lions, phocid seals, dolphins and whales. Non-specialists such semi-aquatic mammals and human athletes show comparatively higher transport costs that may reach 2 - 5 times those if marine mammal specialists (Williams, 1999). These elevated transport costs have been attributed to both the inefficiency of a thrust-recovery mode of swimming and to a surface swimming position of non-specialists (Williams and Worthy, in press).

Specialization of the animal for one mode of locomotion also plays a role in the cost per stroke or step and in the cost of overcoming drag or gravity. The amount of energy an animal expends to generate force with each step (Taylor and Kram, 1990) or stroke (Williams *et al*., submitted) dictates the cost of transport and is termed the cost coefficient. For the animals examined in this study we find that the cost coefficient is identical for both aquatic and terrestrial specialists (Fig. 3). Non-specialists show a range of cost coefficients depending on the design of the body. For example, humans are designed primarily for movement on land and maintain a cost coefficient of 0.262 $J.N^{-1}$ for walking and running (Roberts *et al*., 1998). Conversely, when humans swim the cost coefficient increases 6 fold (Williams *et al*., submitted). The cost of generating force whether against gravity or drag depends primarily upon the level of specialization rather than the type of locomotion in mammals.

Implications for AUV design

Because of the high cost of developing, testing and deploying autonomous vehicles, there is considerable interest in creating machines that are inherently versatile in performance. Are features such as speed, maneuverability, fuel efficiency and stealth mutually exclusive for aquatic vehicles? Based on our results for marine mammals, it appears that engineers may be able to take advantage of the similarity in energetic costs for different modes of propulsion to create versatile vehicles.

In nature morphological features associated with high level locomotor performance often appear to be mutually exclusive. High speed terrestrial mammals such as cheetahs maintain lankier appendages and smaller plantar surface areas than animals such as bears designed for stability on the ground. On land, body design requirements

for maneuverability are the opposite of those needed for stability during performance (Hildebrand, 1985). Analogous examples can be found for aquatic animals. Among fishes body design and propulsive surfaces differ markedly and predictably with performance characteristics (Webb, 1984). Consequently, cruising specialists approximate the morphological characteristics of tuna, accelerating specialists are represented by the elongate pike, and the maneuvering specialist is exemplified by the plate-like butterfly fish. Specific body shapes and fin structures are required for each of these types of high level performance.

Marine mammals also show variations in body and fin shape that are associated with performance characteristics (F. Fish, pers. comm.). However, this variation may not necessarily translate into energetic differences. Because the cost of generating force, minimum cost of transport, transport distance, and routine speeds are similar for a wide variety of marine mammals it appears that factors other than locomotor efficiency during routine performance may be considered when designing AUVs. For example, foreflipper propulsion based on sea lion biomechanics offers the same energetic and routine performance benefits as dorso-ventral propulsion by the dolphin fluke (Table 1). However, placement of the otariid hydrofoil by the center of mass also permits increased maneuverability and stability at low swimming speeds. Furthermore if material strength is a concern then the low frequency oscillations of the sea lion foreflipper offers a different operational limit than the comparatively high stroke frequency of the dolphins.

In conclusion, these findings suggest that the propulsive systems of marine mammals serve as useful models for cost efficient, versatile underwater autonomous vehicles. Several different modes of propulsion offer similar advantages in terms of fuel economy during submergence. In view of this, affiliated performance characteristics of the propeller can be considered in vehicle design, and thereby increase the vehicle's operational versatility.

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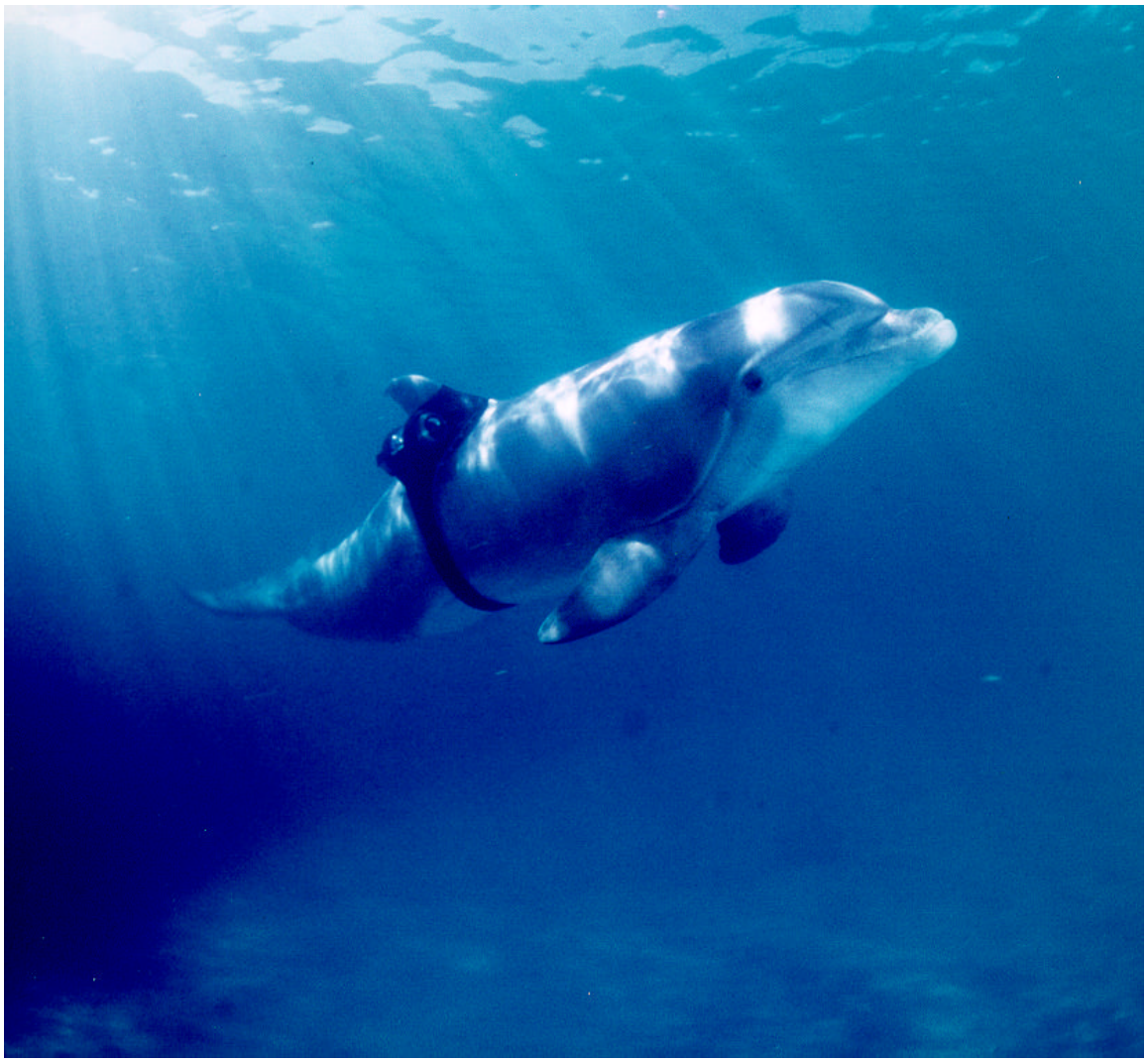

Figure 1. Bottlenose dolphin wearing a submersible camera pack. Such instrument packs were used to monitor locomotor movements of the flukes as animals performed dives to depths exceeding 200m (Williams *et al*., 2000). (Photo courtesy of K. McDonnell.)

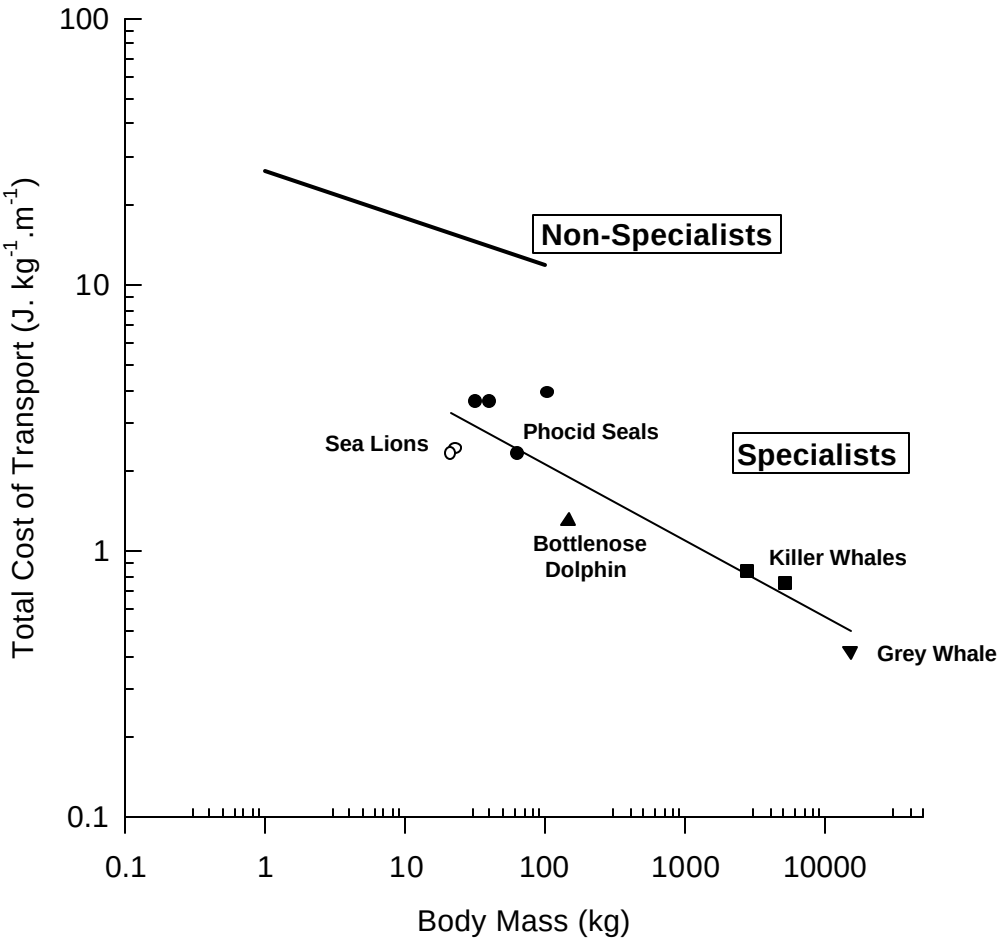

Figure 2. Total cost of transport in relation to body mass for swimming specialists and non-specialists. Symbols denote average values for individual species of marine mammal; all are considered specialists for swimming. Solid lines are the least squares regressions as described by: $y = 26.81x^{-0.18}$ for non-specialists and $y = 7.79x^{-0.29}$ for marine mammal specialists. Data and regressions are from Williams (1999).

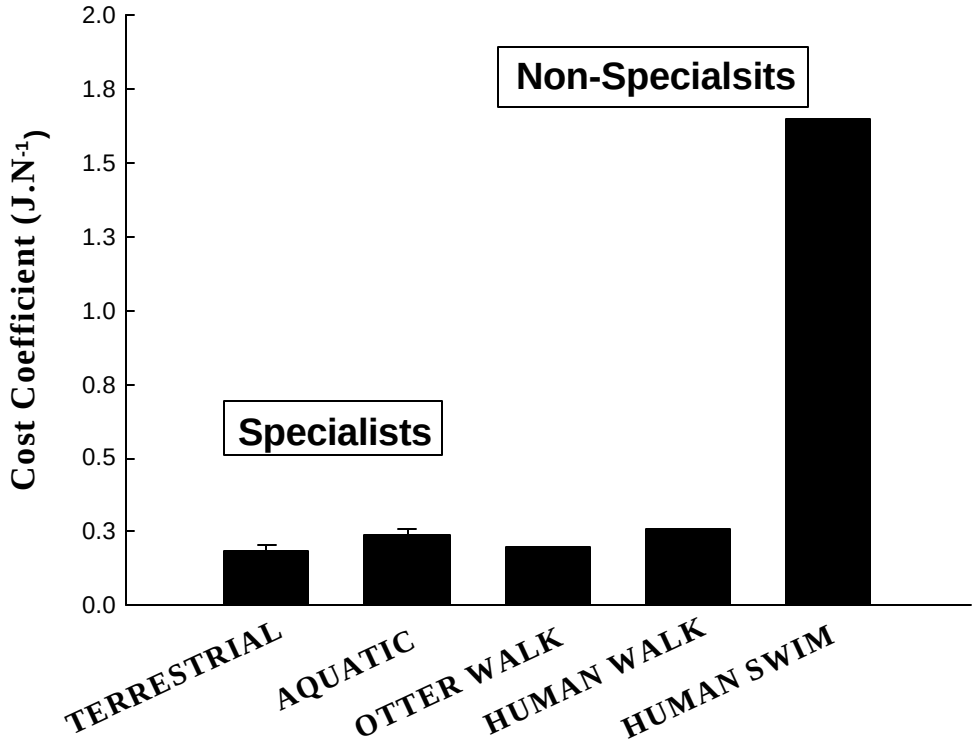

Figure 3. Cost coefficient for locomotor specialists and non-specialists. Height of the bars and lines represent means + 1 S.E.M. for each group. Data for terrestrial specialists are from Kram and Taylor (1990) and include kangaroo rats, ground squirrels, spring hares, dogs and ponies. Aquatic specialists include swimming dolphins, killer whales and gray whales from Williams *et al*. (submitted). Values for non-specialists include walking humans (Roberts *et al*., 1998), and swimming humans and walking river otters (Williams *et al*., submitted).

Table 1. Comparison of performance and energetic characteristics for different marine mammal propulsion systems. Marine mammal specialists include the dolphin, seal and sea lion. Data for the surface swimming and submerged swimming sea otter are provide for comparison with a non-specialist. All values are for animals moving at the minimum cost of transport speed. Transport distances were measured for dolphins and sea lions in this study, and calculated from stroke frequency and speed for sea otters. Data for transport distance was not available for harbor seals.

	Cetacean	**Phocid**	**Otariid**	**Mustelid**	
	Bottlenose Dolphin (208 kg)	Harbor Seal (63 kg)	California Sea Lion (23 kg, 87 kg)	Sea Otter submerged (20 kg)	Sea Otter surface (20 kg)
Hydrofoil Type	Dorso-ventral	Lateral	Paired foreflipper	Dorso-ventral	Paddle/Row
Hydrofoil Position	Caudal	Caudal	Center of Mass	Caudal	Caudal
Routine Speed ($m.s^{-1}$)	2.0	2.0	2.0	1.0	0.6
Stroke Frequency ($st.min^{-1}$)	51.6	68.1	24.1	55.7	72.4
Transport Cost ($J.kg^{-1}.m^{-1}$)	1.29	2.4	2.7	7.4	12.6
Transport Distance (m)	0.59	----	0.59	0.43	0.33
Stroke Cost ($mlO_2.kg^{-1}.st^{-1}$)	0.156	0.129	0.680	0.315	0.409