

Intermittent Swimming by Mammals: A Strategy for Increasing Energetic Efficiency During Diving¹

TERRIE M. WILLIAMS²

Department of Biology, EMS A316, University of California at Santa Cruz, Santa Cruz, CA 95064

SYNOPSIS. The evolutionary history of marine mammals involved marked physiological and morphological modifications to change from terrestrial to aquatic locomotion. A consequence of this ancestry is that swimming is energetically expensive for mammals in comparison to fish. This study examined the use of behavioral strategies by marine mammals to circumvent these elevated locomotor costs during horizontal swimming and vertical diving. Intermittent forms of locomotion, including wave-riding and porpoising when near the water surface, and prolonged gliding and a stroke and glide mode of propulsion when diving, enabled marine mammals to increase the efficiency of aquatic locomotion. Video instrumentation packs (8-mm camera, video recorder and time-depth microprocessor) deployed on deep diving bottlenose dolphins (*Tursiops truncatus*), northern elephant seals (*Mirounga angustirostris*), and Weddell seals (*Leptonychotes weddellii*) revealed exceptionally long periods of gliding during descent to depth. Glide duration depended on depth and represented nearly 80% of the descent for dives exceeding 200 m. Transitions in locomotor mode during diving were attributed to buoyancy changes with compression of the lungs at depth, and were associated with a 9–60% reduction in the energetic cost of dives for the species examined. By changing to intermittent locomotor patterns, marine mammals are able to increase travelling speed for little additional energetic cost when surface swimming, and to extend the duration of submergence despite limitations in oxygen stores when diving.

INTRODUCTION

The morphological, physiological and behavioral traits required for efficient aquatic locomotion by mammals evolved from terrestrial building blocks as ancestral mammals made the transition from land to sea. Fossil evidence indicates that the evolutionary pathway of marine mammals included transitions from terrestrial specialists adapted for running, to intermediate forms that moved on land and water, and finally to aquatic specialists adapted for activity at sea (Repenning, 1976; Berta *et al.*, 1989; Thewissen *et al.*, 1994). As a result of this evolutionary history, marine mammals have had to meet the challenge of aquatic locomotion by modifying structures originally designed for movement on land.

Physical forces encountered by swimming mammals differ markedly from those of running mammals (Dejours, 1987). These undoubtedly influenced many of the morphological modifications that occurred during the transition from terrestrial to aquatic locomotion. On land, gravitational forces dictate the energetic cost of moving the center of mass and limbs during locomotion in terrestrial specialists (Cavagna *et al.*, 1977; Taylor *et al.*, 1980). Except under extreme environmental conditions, body drag and atmospheric pressure have little effect on energetic costs during terrestrial locomotion (Pugh, 1971; Brooks *et al.*, 1996). Conversely, the primary forces influencing locomotor movements and energetic costs in swimming mammals are body drag, buoyancy and hydrostatic pressure. Drag forces resist both forward progression and limb movements of the swimmer. Buoyant forces act in a vertical direction in the water column and result from the weight, volume and compressibility of the tissues and air spaces of the animal's body. Hydrostatic

¹ From the Symposium *Intermittent Locomotion: Integrating the Physiology, Biomechanics and Behavior of Repeated Activity* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 4–8 January 2000, at Atlanta, Georgia.

² E-mail: williams@biology.ucsc.edu

pressure results from the weight of the water column above the swimmer (Heine, 1995).

The magnitude of body drag, buoyant forces and hydrostatic pressure on a swimming mammal will depend on where in the water column activity takes place. For example, drag forces may be 4–5 times higher if the animal remains at or near the water surface than if the animal submerges during swimming. When the animal descends to depths in excess of three body diameters (approximately 3 m for a bottlenose dolphin or Weddell seal) surface wave drag and consequently total body drag is significantly reduced (Hertel, 1966). However, as the animal descends further in the water column hydrostatic pressure progressively increases. For each 10.1 m increase in depth hydrostatic pressure in seawater increases by 1 ATM (Heine, 1995) which will have a profound effect on compressible spaces or tissues, and hence buoyancy of the animal. A consequence of the interrelationships between depth, body drag, hydrostatic pressure and buoyancy is that the physical forces influencing the animal swimming near the water surface are very different from those encountered by the diving animal.

An additional factor affecting aquatic performance in marine mammals that results from its terrestrial ancestry is the necessity to surface periodically to breathe. These surface intervals are usually short in comparison to the duration of submergence during both swimming and diving. To extend the period of submergence, diving mammals balance the metabolic cost of locomotion against oxygen reserves in the lungs, blood and muscle (Kooyman, 1989). Increased locomotor efficiency provides an important advantage for conserving these limited reserves when the mammal is moving underwater.

In this paper, we examine how mammalian physiology and the physical characteristics of the aquatic environment dictate locomotor patterns and behavior in marine mammals. Locomotor mechanics and energetics for a variety of species swimming in a relatively horizontal path are compared to those of submerged mammals moving in a vertical path through water (termed div-

ing). Two cases of horizontal swimming are examined, mammals moving horizontally on the water surface (surface swimming) or moving horizontally below the water surface (submerged swimming). For each type of aquatic activity we examine unique behaviors or styles of locomotion that may contribute to a decrease in energetic costs. Particular attention is paid to physiological requirements that may constrain locomotor activity. In general, we find that marine mammals employ different styles of locomotion, including intermittent propulsion, to reduce the energetic cost of swimming and diving. The energetic benefit afforded by these different locomotor styles depends on the ability of the animal to take advantage of the distinct physical forces encountered near the water surface or in the water column.

DISCUSSION

Horizontal swimming

During the past 20 years a large number of studies have examined the biomechanics and energetics of swimming in mammals. Often the animals were placed in water flumes and required to swim continuously against a current generated by a pump (see Williams, 1999 for a review). The addition of a metabolic chamber on the water surface provided the test animals with a place to breathe and permitted the collection of expired gases for respirometry. Alternative methods have examined small mammals such as beavers swimming submerged between metabolic test chambers (Allers and Culik, 1997). Assessing the swimming energetics of large, fast marine mammals such as dolphins or whales presents a unique challenge and has required novel experimental approaches. These have included training dolphins to match their speed with that of a moving boat in open water (Williams *et al.*, 1993a) or to swim to metabolic stations (Ridgway *et al.*, 1969; Yazdi *et al.*, 1999). Swimming costs have also been estimated from field respiratory rates of killer whales (Kriete, 1995) and gray whales (Sumich, 1983).

By combining the results for a wide variety of swimming mammals we find that

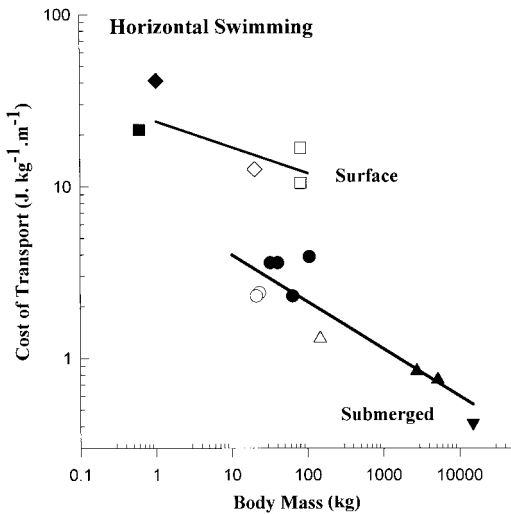


FIG. 1. Total cost of transport (COT) in relation to body mass for surface and submerged swimming mammals moving in a horizontal path. Solid lines represent the least squares regressions through the data points and are presented in the text. Data points represent individual studies and species: surface swimmers include muskrat (closed square; Fish, 1982), mink (closed diamond; Williams, 1983), sea otter (open diamond; Williams, 1989) and humans (open squares; Homer, 1972); submerged swimmers include phocid seals (closed circles; Fedak, 1986; Davis *et al.*, 1985; Williams *et al.*, 1991), sea lions (open circles; Feldkamp, 1987; Williams *et al.*, 1991), bottlenose dolphins (open triangle; Williams *et al.*, 1993a), killer whales (closed triangles; Kriete, 1995) and gray whales (inverted closed triangle; Sumich, 1983).

the energetic cost of swimming may be described by two separate allometric regressions (Fig. 1). The total cost of transport (COT) for semi-aquatic species that swim horizontally on the water surface such as muskrats, mink and humans is described by

$$\text{COT} = 26.81\text{mass}^{-0.18} \quad (n = 4 \text{ species})$$

where COT is in $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ and body mass is in kg (Williams, 1989). Marine adapted species that swim in a horizontal path while submerged may be described by the relationship

$$\text{COT} = 7.79\text{mass}^{-0.29} \quad (n = 6 \text{ species})$$

where COT is in $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ and body mass is in kg (Williams, 1999). This relationship includes values for phocid seals, otariids, and odontocete and mysticete whales.

Based on these allometric regressions, it appears that the total cost of transport for many swimming mammals is significantly higher than predicted for fish of comparable body mass (Brett, 1964). For example, the cost of transport for swimming in the North American mink is 19 times that of salmonid fish (Williams, 1983); human swimmers have transport costs that are 15 to 23 times the predictions (Holmer, 1972). Despite specialization for aquatic locomotion, marine mammals also demonstrate elevated transport costs in comparison to fish. The energetic costs for swimming in marine mammals range from 2 to 4 times the predicted values for comparably sized fish (Williams, 1999).

Several factors appear to contribute to the comparatively high energetic cost of horizontal swimming in mammals. First, under the conditions of these tests, stroking is more or less continuous, where stroking is defined as the movement of a propulsive surface to produce thrust that results in forward motion of the swimmer. Whether in a flume or chasing a boat, continuous stroking was often necessary for the animal to maintain prolonged periods of constant speed in a horizontal plane regardless of position on the water surface or submerged. Second, as mentioned above, drag forces are considerably higher if the swimmer remains at or near the water surface than if it submerges during swimming. The addition of wave drag during surface swimming has been shown to increase the energetic cost of swimming in some mammals by two-fold (Williams, 1989). A third factor contributing to elevated swimming energetic costs, particularly in semi-aquatic mammals, is the efficiency of the propulsor (Fish, 1993). Drag-based propulsion characteristic of many semi-aquatic mammals is less efficient in terms of thrust generation and energetic cost than lift-based propulsion typical of marine mammals and fish. Lastly, the ability to retain endogenous heat, that is the cost of endothermy, explains in part the difference in total energetic cost of swimming between marine mammals and fish (Williams, 1999).

In view of the high energetic cost of swimming in mammals, it is not surprising that

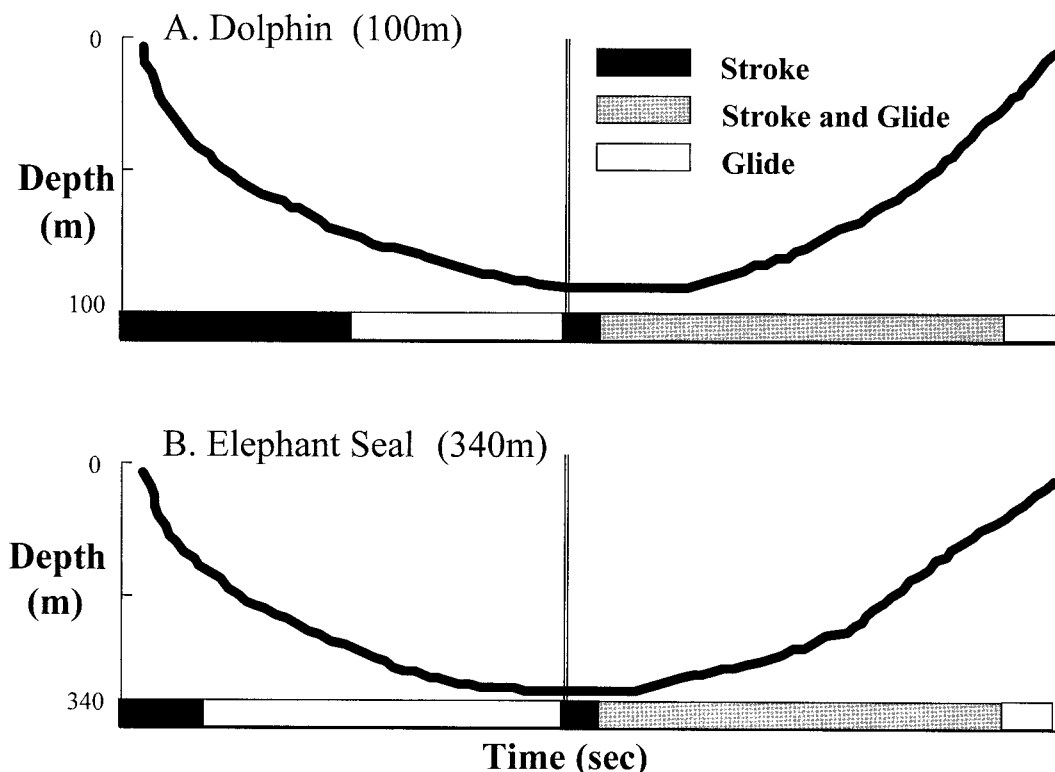


FIG. 2. Representative dive profiles and locomotor modes for an adult bottlenose dolphin performing a 100 m dive (A) and a juvenile northern elephant seal during a 340 m dive. Dark curves denote the change in depth with time during the dive. Horizontal boxes along each dive indicate the preferred locomotor mode during descent and ascent. Black boxes indicate periods of continuous stroking, open boxes denote gliding, and gray boxes show stroke and glide propulsion. Vertical lines denote the change from descent to ascent segments of the dives. The time scale for the dives has been normalized for comparative purposes.

marine adapted species have developed a number of behavioral strategies that enable them to avoid the work of continuous stroking. Porpoising is a behavioral strategy used by small cetaceans and pinnipeds moving at high speed near the water surface. Theoretically, this behavior allows the swimmer to avoid the high costs associated with swimming continuously near the water surface by interrupting locomotion and leaping into the air (Au and Weihs, 1980; Blake, 1983). Wave riding is another strategy that enables the swimmer to avoid continuous stroking. In a study involving bottlenose dolphins trained to swim freely or wave-ride next to a moving boat, we demonstrated a reduction in heart rate, respiration rate and calculated energetic costs for animals riding the bow wave of a boat at $3.8 \text{ m}\cdot\text{sec}^{-1}$. This behavior enabled

bottlenose dolphins to nearly double their forward travelling speed with only a 13% increase in energetic cost (Williams *et al.*, 1992).

Although energetically advantageous when swimming near the water surface, both wave-riding and porpoising have been described for only a limited number of marine mammal species moving at high speeds. These locomotor strategies are not possible during slow transit, in large marine mammals such as elephant seals and whales, or in polar regions where ice covers the water surface. Instead, transit swimming is often accomplished by a sawtooth series of sequential dives that allows the animals to remain submerged except for brief surface intervals to breathe (Crocker *et al.*, 1994; Slip *et al.*, 1994; Davis *et al.*, 2001).

Vertical diving

With data readily available for the cost of swimming in mammals, it seems reasonable to presume that the cost of diving can be calculated. Data from time depth recorders and velocity meters deployed on free ranging marine mammals provide information about the duration, distance and speed of the diver. When combined with the relationships for oxygen consumption and speed from swimming experiments, a theoretical diving cost can be determined. Because marine mammals rely on stored oxygen to maintain aerobic processes during a dive, maximum dive durations supported by these reserves (termed the aerobic dive limit, ADL; Kooyman, 1989) can be calculated by dividing the oxygen store by swimming metabolic rates. This calculation provides an upper limit for the energetic cost of an aerobic dive. Dives exceeding the ADL require a switch to anaerobic metabolism with the consequent detrimental effects associated with increased plasma lactate (see Butler and Jones, 1997 for a review).

Such calculations for diving bottlenose dolphins resulted in a paradox. Descent and ascent durations, and swimming speed were measured with time-depth/velocity recorders carried by dolphins trained to dive in a straight line path to submerged targets (Williams *et al.*, 1999). On a relatively short dive to 57 m we calculated that dolphins used 34% ($11.1 \text{ mlO}_2 \cdot \text{kg}^{-1}$) of the total oxygen store in the blood, muscles and lungs. On deep dives to 206 m metabolic calculations indicated that the oxygen reserves were exhausted after only three quarters of the dive had been completed. Yet, there was little increase in post-dive plasma lactate to indicate a change to anaerobic metabolism (Williams *et al.*, 1993b, 1999).

The discrepancy was resolved by recording the locomotor behavior of the dolphins during the complete dive. Video cameras placed on the diving dolphins revealed the use of several different swimming gaits rather than continuous stroking (Fig. 2). During descent the dolphins switched from active stroking to prolonged gliding. Ascents began with active stroking followed

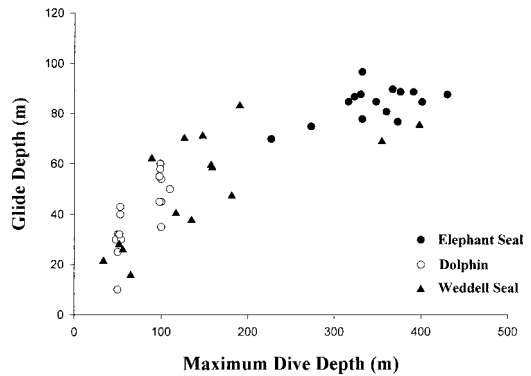


FIG. 3. Depth at the start of the gliding during descent in relation to maximum depth of the dive. Each point represents a single dive for northern elephant seals (closed circle), bottlenose dolphins (open circle) and Weddell seals (closed triangle).

by stroke and glide swimming, and ended with a short glide to the surface (Skrovan *et al.*, 1999). Similar experiments with elephant seals (Davis *et al.*, 2001; Fig. 2), Weddell seals and even blue whales (Williams *et al.*, 2000) reveal identical changes in locomotor patterns during diving. Dive descents for these marine mammals typically begin with a period of active stroking followed by gliding to depth. Ascent is characterized by large amplitude, continuous strokes followed by stroke and glide swimming. Depending on the species, the animal may change to a short final glide to the surface.

The absolute duration of gliding during the descent depends on the maximum depth of the dive. For dolphins, phocid seals and the blue whale, the percentage of time gliding increased significantly with depth of the dive. Nearly 80% of the descent was spent gliding for dives exceeding 200 m (Williams *et al.*, 2000). Interestingly, the depth at which gliding began was similar for the marine mammals examined (Fig. 3). Glide initiation depth increased from 20 m to 70 m as maximum depth of the dive increased to 200 m. A plateau in the glide initiation depth was reached at approximately 80 m for dives exceeding 200 m. The similarity in pattern for these glide depths suggests the influence of physical factors on the diver.

MAMMALIAN LUNGS AT DEPTH

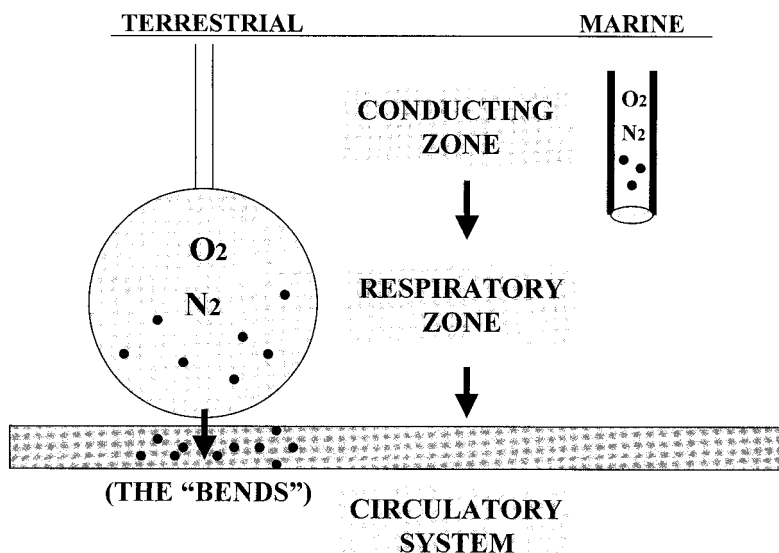


FIG. 4. Changes in the mammalian lung with increases in hydrostatic pressure with depth. The alveoli (gray circle) of terrestrial mammals trap air due to the collapse of connecting airways. Trapped gases remain in the alveolar respiratory zone and may be absorbed into the circulatory system resulting in nitrogen narcosis or decompression illness (the "bends") on ascent. In marine adapted species, the alveoli collapse in response to pressure which moves gases into cartilaginous, reinforced conducting areas.

The mammalian lung at depth

To understand how marine mammals accomplish these prolonged gliding periods we need to examine the structural and functional characteristics of the mammalian lung at depth. Because the lung capacities of many marine mammals are large in comparison to those of terrestrial mammals on a lean weight basis, Kooyman (1973) proposed that the lungs play a role in buoyancy control at sea. Relatively small changes in lung volume depending on whether the animal inhales or exhales could tip the balance between positive or negative buoyancy, and whether an animal floats or sinks when resting on the water surface.

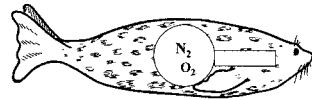
When diving, rapid changes in hydrostatic pressure will also alter lung volume with consequent changes in buoyancy. The magnitude of these changes appears to be associated with morphological modifications coincident with adaptations for a marine lifestyle (Fig. 4). A unique feature of the lungs of marine adapted mammals is cartilaginous reinforcement of the small air-

ways (Scholander, 1940; Denison and Kooyman, 1973). Such reinforcement provides a rigid system to the level of the alveoli that permits the progressive collapse of the airways in response to increases in pressure. As a result, compliant alveoli will compress rapidly at depth emptying gas into the reinforced airways. The structural and functional effects of airway reinforcement have been tested both in the laboratory and at sea. While the alveoli of terrestrial mammals such as dogs trap air during simulated dives, those of sea lions show a progressive collapse from the alveoli to the reinforced airways with increases in pressure (Denison *et al.*, 1971). Pressure chamber tests on Weddell seals and northern elephant seals (Kooyman *et al.*, 1970), and on the excised lungs of bottlenose dolphins (Ridgway *et al.*, 1969) show similar patterns of progressive collapse of the airways with exposure to increased pressure. Differences in the oxygen and carbon dioxide content of expired air of dolphins trained to dive or station at depth (Ridgway *et al.*,

1969) have demonstrated that alveolar collapse is complete once the animals reach 70 m in depth (Ridgway and Howard, 1979). Alveolar volume is considerably reduced at depths of less than 30 m in Weddell seals and elephant seals (Kooyman *et al.*, 1970). Likewise, the lungs of large whales including fin whales and sei whales (Scholander, 1940) and pilot whales (Olsen *et al.*, 1969) show evidence of progressive alveolar collapse in response to increased hydrostatic pressure.

The structural and functional changes that occur at depth in the marine mammal lung appear to serve many roles. First, the movement of alveolar contents away from gas exchange surfaces and into the conducting airways of the lungs enables marine mammals to avoid the deleterious effects of nitrogen narcosis and decompression sickness (Scholander, 1940). Second, strengthening of the peripheral airways permits exceptionally rapid tidal ventilation and respiratory gas exchange when marine mammals surface to breathe (Kooyman and Sinnott, 1979). Furthermore, these same changes in lung volume enable marine mammals to take advantage of the increase in hydrostatic pressure to facilitate prolonged periods of passive gliding during descent (Fig. 5). Skrovan *et al.*, (1999) described the interrelationships between lung volume, dive depth and buoyancy for the bottlenose dolphin. As air spaces compress with depth the volume of the dolphin decreases without an accompanying reduction in mass, and the animal becomes less buoyant. The theoretical buoyant forces associated with this collapse range from 24.3 N when the dolphin is near the water surface and the lungs are fully inflated, to a negative buoyancy of -25.7 N when the lungs are deflated at 67.5 m in depth. Measured deceleration rates of gliding dolphins correlated directly with the calculated changes in buoyant forces coincident with lung compression (Skrovan *et al.*, 1999). Thus, the progressive increase in hydrostatic pressure and subsequent lung collapse with depth led to a progressive increase in the ability of dolphins to glide during descent until maximum lung compression occurred at approximately 70 m. A similar interre-

A. Swimming



B. Diving

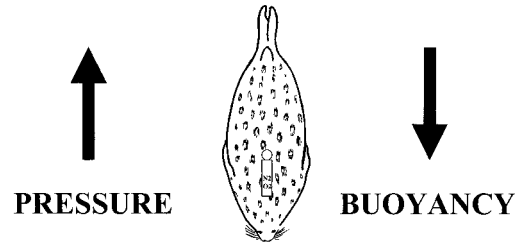


FIG. 5. Relative differences in lung volume of a Weddell seal during horizontal swimming near the water surface (A) and vertical diving (B). Increases in hydrostatic pressure during descent result in compression and a decrease in volume of the lungs. Buoyancy decreases concomitantly. Circle = respiratory zone and rectangle = conducting zone as described in Figure 4. Note the change in location of respiratory gases with changes in hydrostatic pressure. The relative size of the gas volume in the lungs is based on measurements of Weddell seals resting at sea level and during a simulated dive to 306 m in depth from Kooyman *et al.* (1970).

relationship between hydrostatic pressure, lung volume and buoyancy likely occurs in seals. Although phocid seals exhale prior to submergence, even the small changes in volume that occur as the alveoli compress will alter buoyancy during the course of a dive (Webb *et al.*, 1998).

These physical and anatomical changes with depth influence the locomotor behavior of diving marine mammals (Fig. 3). During shallow (<100 m) dives, seals and dolphins initiate short glides early during descent. Deep divers such as the elephant seal (Davis *et al.*, 2001) and Weddell seal begin prolonged gliding at 60–86 m for dives exceeding 200 m in depth. Even the largest diver in the ocean, the blue whale, appears to follow this pattern and begins gliding at approximately 18 m when performing dives to 36–88 m in depth (Williams *et al.*, 2000). The depth at which gliding begins undoubtedly depends on many

TABLE 1. *Energetic costs for theoretical 200 m dives by a phocid seal and dolphin.**

	Energetic Cost (ml O ₂ ·kg ⁻¹)					
	Descent		Ascent		Total Cost	% Total O ₂ Store
	Stroke Period	Glide Period	Stroke Period	Glide Period		
<i>Dolphin</i>						
Intermittent Locomotion	8.9	5.1	19.4	0.4	33.8	102%
Continuous Locomotion	17.2	—	20.6	—	37.8	114
<i>Phocid Seal</i>						
Intermittent Locomotion	2.8	6.7	19.2	0.8	29.5	49
Continuous Locomotion	21.5	—	21.5	—	43.0	72

* Dives completed by intermittent locomotion according to the gait patterns in Fig. 2 or by continuous stroking are compared. For these calculations we assume that the metabolic cost of gliding is equivalent to resting rates as described in the text. Swimming costs were based on Davis *et al.* (1985) for harbor seals swimming at 2.0 m·s⁻¹ and Williams *et al.* (1992) for dolphins swimming at 2.1 m·s⁻¹. These represent the optimal range speeds for low cost swimming for these species (Yadzi *et al.*, 1999; Davis *et al.*, 1985).

factors including body composition and buoyancy characteristics of the species, initial lung volume, and the type of dive (*i.e.*, transit, exploratory, foraging). Short, shallow dives in which oxygen reserves are not limiting permit greater flexibility in locomotor behavior compared to dives approaching physiological limits (Williams *et al.*, 1993*b*). On prolonged dives when the balance between speed and energetic efficiency is critical marine mammals incorporate extended glide periods that often begin when lung compression is near complete (Fig. 3).

Energetic benefits of intermittent locomotion at depth

Because the contraction of skeletal muscle expends energy, behaviors such as gliding that reduce overall locomotor effort should be manifest as a decrease in energetic cost. This view is supported in simple calculations for the cost of diving by phocid seals and dolphins (Table 1). In this exam-

ple the rate of oxygen consumption for harbor seals is 4.6 mlO₂·kg⁻¹·min⁻¹ during rest and 12.9 mlO₂·kg⁻¹·min⁻¹ during swimming at approximately 2.0 m·sec⁻¹ (Davis *et al.*, 1985). Rates of oxygen consumption determined for bottlenose dolphins are 4.6 mlO₂·kg⁻¹·min⁻¹ during rest and 8.1 mlO₂·kg⁻¹·min⁻¹ during swimming at 2.1 m·sec⁻¹ (Williams *et al.*, 1992). Assuming that oxygen consumption during passive gliding approximates resting levels, then a theoretical dive to 200 m by an adult harbor seal will require 43 mlO₂·kg⁻¹ if the animal continuously strokes during descent and ascent. A dive incorporating prolonged periods of gliding as in Figure 2 will need only 29.5 mlO₂·kg⁻¹. For dolphins, a stroking dive to 200 m in depth will use 37.8 mlO₂·kg⁻¹ compared to 33.8 mlO₂·kg⁻¹ for a gliding dive of similar depth.

The benefit of these energetic savings becomes apparent when the size of the oxygen reserve available during submergence is considered. The total oxygen store for an adult, 145 kg bottlenose dolphin is 33.0 mlO₂·kg⁻¹ (Williams *et al.*, 1993*b*), and 65.0 mlO₂·kg⁻¹ for a 24 kg harbor seal (Kooyman, 1989). In terms of the total oxygen reserve available, the gliding seal performing a 200 m dive realizes a 23% savings and the dolphin a 12% savings. Initially, these savings may appear trivial. However, a 12% savings in the oxygen store for the diving dolphin translates into an additional 1.0 min of gliding or 0.5 min of swimming at 2.0 m·sec⁻¹ assuming the metabolic rates described above. For the phocid seal, a 23% saving in the oxygen store represents 3.0 additional minutes of gliding or 1.1 min of swimming at 2.0 m·sec⁻¹.

Many additional factors not accounted for in these simple calculations will also affect the actual cost of diving in marine mammals. Metabolic depression during submergence, dive depth, gliding duration, angles of descent and ascent, velocity, the use of stroke and glide locomotion, and the interactive effects of drag and buoyant forces during a dive will influence total energetic requirements. For example, metabolic depression during diving (Hochachka, 1992) would have an additional conserving

effect on oxygen reserves. Several studies have also demonstrated that stroke and glide locomotion can reduce the energetic cost of swimming by 15–50% in fish (Weihs, 1974; Fish *et al.*, 1991). Stroke and glide propulsion is the preferred mode of locomotion for many species of marine mammal during the ascent portion of a dive (Williams *et al.*, 2000). Consequently, the energetic savings described in these calculations probably represent a conservative estimate depending on the type of dive and gaits selected by the animal. Certainly, the use of interrupted forms of swimming to complete a dive appears to provide an energetic advantage when compared to continuous swimming for the same dive (Table 1).

Recent measurements of the post-dive oxygen consumption of Weddell seals provide direct evidence of the energetic benefits of gliding (Williams *et al.*, 2000). In these studies instrumented adult seals were placed in an isolated ice hole located on the Antarctic sea ice. The hole was covered with a metabolic hood for the collection of respiratory gases and subsequent determination of post-dive oxygen consumption. The seals were free to dive in surrounding waters that exceeded 500 m in depth. Strategic placement of the hole required that the animals return to the metabolic hood to breathe following each dive (Kooyman *et al.*, 1980). By combining measurements of the underwater locomotor behavior of the seals (Davis *et al.*, 1999) with post-dive metabolic rate we found that interrupted swimming during a dive resulted in a 9.2–59.6% energetic savings for the Weddell seals (Williams *et al.*, 2000). Figure 6 demonstrates the difference in energetic costs for dives with and without interrupted swimming periods. Two groups of dives by Weddell seals covering equal distances (1,750–1,850 m) but varying in swimming pattern and depth were compared. Deep dives (231 ± 27 SEM m, $n = 12$) that facilitated gliding due to changes in pressure with depth resulted in a significant (at $P = 0.043$) 35% reduction in recovery oxygen consumption compared to shallow dives (55 ± 7 SEM m, $n = 4$) covering the same distance with nearly continuous stroking.

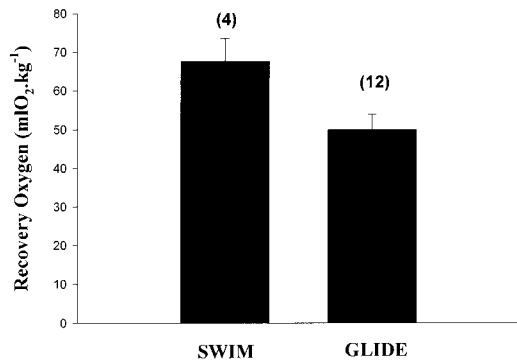


FIG. 6. Post-dive oxygen consumption of Weddell seals travelling 1,750–1,850 m beneath the Antarctic sea ice. Dives incorporating prolonged glide sequences (Glide) are compared to dives completed by continuous or stroke and glide swimming (Swim). Height of the bars and vertical lines denote mean values + 1 SEM. Numbers in parentheses show the number of dives in each category. Differences between the means of the dive categories were significant ($t = 2.227$, $P = 0.043$).

From these results, the incorporation of interrupted forms of locomotion during diving appears to provide an energetic advantage for the diving Weddell seal. Further studies will be needed to determine if this is a general phenomenon for other marine mammal species.

In summary, the evolutionary history of marine mammals has resulted in physiological and morphological characteristics that contribute to elevated costs during swimming. Interrupted forms of locomotion, including wave-riding and porpoising when near the water surface or gliding when descending on a dive, enables marine mammals to mitigate some of these costs. By increasing overall energetic efficiency, these locomotor behaviors allow marine mammals to increase travelling speed for little additional energetic input when swimming, and to prolong the duration of a dive by conserving limited oxygen stores when submerged.

ACKNOWLEDGMENTS

This study was supported by an Office of Naval Research (ONR) grant #N00014-95-1-1023 and NSF Division of Polar Programs grant #OPP-9618384 to T. M. Williams. The author is especially grateful to

the many people involved with the original diving studies including R. W. Davis, L. A. Fuiman, M. Horning, W. Hagey, R. Skrovan, and B. J. Le Boeuf. All animal studies were according to NIH guidelines and were approved by the UCSC Chancellor's Animal Research Committee.

REFERENCES

- Allers, D. A. and B. M. Culik. 1997. Energy requirements of beavers (*Castor canadensis*) swimming underwater. *Physiol. Zool.* 70:456–463.
- Au, D. and D. Weihs. 1980. At high speeds dolphins save energy by leaping. *Nature* 284:548–550.
- Berta, A., C. E. Ray, and A. R. Wyss. 1989. Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science* 244:60–62.
- Blake, R. W. 1983. Energetics of leaping in dolphins and other aquatic animals. *J. Mar. Biol. Assoc. U.K.* 63:61–70.
- Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* 21:1183–1226.
- Brooks, G. A., T. D. Fahey, and T. P. White. 1996. *Exercise physiology: Human bioenergetics and its applications*. Mayfield Publishing Company, Mountain View, CA.
- Butler, P. J. and D. R. Jones. 1997. Physiology of diving of birds and mammals. *Physiol. Rev.* 77(3): 837–899.
- Cavagna, G. A., N. C. Heglund, and C. R. Taylor. 1977. Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233(5):R243–261.
- Crocker, D. E., B. J. Le Boeuf, Y. Naito, T. Asaga, and D. P. Costa. 1994. Swim speed and dive function in a female Northern elephant seal. In B. J. Le Boeuf and R. M. Laws (eds.), *Elephant seals: Population ecology, behavior, and physiology*, pp. 328–342. University of California Press, Berkeley.
- Davis, R. W., L. A. Fuiman, T. M. Williams, S. O. Collier, W. P. Hagey, S. B. Kanatous, S. Kohin, and M. Horning. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–996.
- Davis, R. W., L. A. Fuiman, T. M. Williams, and B. J. Le Boeuf. 2001. Three dimensional movements and swimming of a female northern elephant seal. *Comp. Biochem. Physiol.* (In press)
- Davis, R. W., T. M. Williams, and G. L. Kooyman. 1985. Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiol. Zool.* 58(5):590–596.
- Dejours, P. 1987. Water and air physical characteristics and their physiological consequences. In P. Dejours, L. Bolis, C. R. Taylor, and E. R. Weibel (eds.), *Comparative physiology: Life in water and on land*, pp. 3–11. Fidia Research Series, Springer-Verlag, New York.
- Denison, D. M. and G. L. Kooyman. 1973. The structure and function of the small airways in pinniped and sea otter lungs. *Resp. Physiol.* 17:1–10.
- Denison, D. M., D. A. Warrell, and J. B. West. 1971. Airway structure and alveolar emptying in the lungs of sea lions and dogs. *Resp. Physiol.* 13: 253–260.
- Fedak, M. A. 1986. Diving and exercise in seals: A benthic perspective. In A. Brubakk, J. W. Kanwisher, and G. Sundnes (eds.), *Diving in animals and man*, pp. 11–32. Kongsvold Symposium, Royal Norwegian Society of Sciences and Letters, Tapir, Trondheim.
- Feldkamp, S. 1987. Swimming in the California sea lion: Morphometrics, drag and energetics. *J. Exp. Biol.* 131:117–135.
- Fish, F. E. 1982. Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.* 55:180–189.
- Fish, F. E. 1993. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Austral. J. Zool.* 42:79–101.
- Fish, F. E., J. F. Fegely, and C. J. Xanthopoulos. 1991. Burst-and-coast swimming in schooling fish (*Nothemion cryssoleucas*) with implications for energy economy. *Comp. Biochem. Physiol.* 100(3): 633–637.
- Heine, J. N. 1995. *Mastering advance diving: Technology and techniques*. Mosby Lifeline, St. Louis.
- Hertel, H. 1966. *Structure, form, movement*. Reinhold Publishing Corporation, New York.
- Hochachka, P. 1992. Metabolic biochemistry and the making of a mesopelagic mammal. *Experimentia* 48:570–575.
- Holmer, I. 1972. Oxygen uptake during swimming in man. *J. Appl. Physiol.* 33:502–509.
- Kooyman, G. L. 1973. Respiration adaptations in marine mammals. *Amer. Zool.* 13:457–468.
- Kooyman, G. L. 1989. *Diverse divers: Physiology and behavior*. Springer-Verlag, Berlin.
- Kooyman, G. L., D. D. Hammond, and J. P. Schroeder. 1970. Bronchograms and tracheograms of seals under pressure. *Science* 169:82–84.
- Kooyman, G. L. and E. E. Sinnett. 1979. Mechanical properties of the harbor porpoise lung, *Phocoena phocoena*. *Resp. Physiol.* 36:287–300.
- Kooyman, G. L., E. A. Wahrenbrock, M. A. Castellini, R. W. Davis, and E. E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* 138:335–346.
- Kriete, B. 1995. Bioenergetics of the killer whale, *Orcinus orca*. Ph.D. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.
- Olsen, C. R., F. C. Hale, and R. Elsner. 1969. Mechanics of ventilation in the pilot whale. *Resp. Physiol.* 7:137–149.
- Pugh, L. G. C. E. 1971. The influence of wind resistance in running and walking and the mechanical efficiency of work against horizontal or vertical forces. *J. Physiol., Lond.* 213:255–276.
- Repenning, C. A. 1976. Adaptive evolution of sea lions and walruses. *Syst. Zool.* 25:375–390.
- Ridgway, S. H. and R. Howard. 1979. Dolphin lung collapse and intramuscular circulation during free

- diving: Evidence from nitrogen washout. *Science* 206:1182–1183.
- Ridgway, S. H., B. L. Scronce, and J. Kanwisher. 1969. Respiration and deep diving in the bottlenose porpoise. *Science* 166:1651–1654.
- Scholander, P. F. 1940. Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* 22, Oslo. 1–131.
- Skrovan, R. C., T. M. Williams, P. S. Berry, P. W. Moore, and R. W. Davis. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*) II. Biomechanics and changes in buoyancy at depth. *Journal of Exp. Biol.* 202:2749–2761.
- Slip, D. J., M. A. Hindell, and H. R. Burton. 1994. Diving behavior of Southern elephant seals from Macquarie Island. In B. J. Le Boeuf and R. M. Laws (eds.), *Elephant seals: Population ecology, behavior, and physiology*, pp. 253–270. University of California Press, Berkeley.
- Sumich, J. L. 1983. Swimming velocities, breathing patterns and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Can. J. Zool.* 61:647–652.
- Taylor, C. R., N. C. Heglund, T. A. McMahon, and T. R. Looney. 1980. Energetic cost of generating muscular force during running: A comparison of large and small animals. *J. Exp. Biol.* 86:9–18.
- Thewissen, J. G. M., S. T. Hussain, and M. Arif. 1994. Fossil evidence for the origin of aquatic locomotion in archaeocete whales. *Nature* 263:210–212.
- Webb, P., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* 201:2349–2358.
- Weihhs, D. 1974. Energetic advantages of burst swimming of fish. *J. Theor. Biol.* 48:215–229.
- Williams, T. M. 1983. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. Exp. Biol.* 103:155–168.
- Williams, T. M. 1989. Swimming by sea otters: Adaptations for low energetic cost locomotion. *J. Comp. Physiol. A* 164:815–824.
- Williams, T. M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Phil. Trans. R. Soc. Lond. B* 354:193–201.
- Williams, T. M., R. W. Davis, L. A. Fuiman, J. Francis, B. J. Le Boeuf, M. Horning, J. Calambokidis, and D. A. Croll. 2000. Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science* 288:133–136.
- Williams, T. M., W. A. Friedl, M. L. Fong, R. M. Yamada, P. Sedivy, and J. E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* 355:821–823.
- Williams, T. M., W. A. Friedl, and J. E. Haun. 1993a. The physiology of bottlenose dolphins (*Tursiops truncatus*): Heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* 179:31–46.
- Williams, T. M., W. A. Friedl, J. E. Haun, and N. K. Chun. 1993b. Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). *Symp. Zool. Soc. Lond.* 66:383–394.
- Williams, T. M., J. E. Haun, and W. A. Friedl. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). I. Balancing the demands of exercise for energy conservation at depth. *J. Exp. Biol.* 202:2739–2748.
- Williams, T. M., G. L. Kooyman, and D. A. Croll. 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. Comp. Physiol. B* 160:637–644.
- Yazdi, P., A. Kilian, and B. M. Culik. 1999. Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). *Mar. Biol.* 134(4):601–607.