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6. AUTHOR(S)

Williams, Terrie, M.

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

Department of EE Biology, COH-Long Lab
100 Shaffer Road, UCSC
Santa Cruz, CA 95064

8. PERFORMING ORGANIZATION REPORT NUMBER

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14. This study determined the efficiency and per. ance limitations of oscillating hydrofoils used in nature. Specific studies compared the kinematics and energetics associated with the transition from terrestrial to aquatic performance by semi-aquatic mammals, and evaluated cost saving strategies of obligate marine mammals using dorso-ventral or lateral undulatory propulsion. Key factors for low cost performance on land included the incorporation of aerial phases and elastic energy storage, particularly during high-speed transits. Likewise, the use of elastic energy storage and prolonged gliding associated with changes in hydrostatic pressure and buoyancy reduced locomotor costs by nearly 64% for some divers. These findings provide new insights for improving the propulsive efficiency of large aquatic and semi-aquatic vehicles.

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FINAL REPORT

GRANT #: N00014-00-1-0761

PRINCIPAL INVESTIGATOR: Terrie M. Williams

INSTITUTION: University of California at Santa Cruz

GRANT TITLE: Marine Mammals as Models for Cost Efficient AUVs: Specifications of Oscillating Hydrofoils

AWARD PERIOD: 10 May 2000 - 30 April 2003

OBJECTIVE: To determine key factors leading to cost-efficient locomotion in aquatic and semi-aquatic animals using oscillating hydrofoils for propulsion; to compare performance capabilities of locomotor specialists and generalists.

APPROACH: Three approaches were used in this study. A laboratory component was conducted with bottlenose dolphins (*Tursiops truncatus*), California sea lions (*Zalophus californianus*), river otters (*Lontra canadensis*) and sea otters (*Enhydra lutris*) to assess the mechanical operation and energetic cost of oscillating hydrofoils performing in controlled environments. The second component used field tests on freely swimming and diving dolphins, phocid seals and sea otters to evaluate the performance limitations of hydrofoils under open water conditions. Routine locomotor speeds, preferred swimming gaits, and stroking mechanics were measured. In the third component, we combined the results of our tests with data for terrestrial, semi-aquatic, and other marine mammals to provide a comparative synthesis of oscillating hydrofoil performance.

ACCOMPLISHMENTS: We completed studies on the biomechanics and energetics of hydrofoils in bottlenose dolphins (dorso-ventral fluke oscillation), phocid seals (lateral hind flipper oscillation), and sea lions (fore-flipper oscillation). From these studies we were able to, 1) define the effects of body size on stroke costs (Williams *et al.*, 2004, 2) compare stroke and stride costs for aquatic and terrestrial specialists (Williams *et al.*, 2002), 3)

determine the effects of load on stroke costs and resultant elastic energy storage during dorso-ventral propulsion by dolphins (Williams, 2000), and 4) assess the impact of aquatic specialization on terrestrial and aquatic performance in mammals (Williams, 2001; Williams *et al.*, 2002). Comparative studies on running river otters and dogs were also completed to determine the importance of axial flexion on reducing locomotor costs and enabling energetic efficiency both on land and in water. We found that the ability to incorporate a period of suspension during high-speed running resulted in a 34-46% decrease in the cost of running in mammals depending on speed.

Lastly, three-dimensional tracking of free-ranging elephant seals and Weddell seals was used to test theories concerning the relationships between locomotor speed, buoyancy, energetic cost and efficiency, power limitations, and stroke mechanics (Williams *et al.*, 2000; Davis *et al.*, 2001; Williams *et al.*, 2004). We demonstrated that the duration of underwater performance can be predicted from the total number of strokes required to complete a specific task (ascent, descent, cruising, turning, stationing). As a result, ``turning the motor off'' by gliding resulted in a 10 -60% cost savings depending on the depth of the dive. Gliding was facilitated by the animal taking advantage of changes in buoyancy and hydrostatic pressure with depth. These studies have begun to define the performance specifications and duty factors leading to optimum energy utilization by different types of undulating hydrofoils.

CONCLUSIONS: Based on our results for stroking energetics in marine mammals, it appears that the duty factor rather than the mode of oscillation is a key factor in dictating propulsive costs and resultant power requirements. For large seals using lateral undulation, the cost per stroke was 1.61 $J.kg^{-1}.stroke^{-1}$ - 2.87 $J.kg^{-1}.stroke^{-1}$. This compares with 5.0 $J.kg^{-1}.stride^{-1}$ for running mammals ranging in body mass over four orders of magnitude. The difference in stroke and stride costs for animals suggest that autonomous vehicle designs based on biological systems should focus on strategies used by aquatic animals if energy efficiency is to be optimized. One mechanism for increasing efficiency is the ability to take advantage of changes in physical forces in the environment during locomotion. The type of propulsion system (fore-flipper oscillating hydrofoil, lateral hind flipper propulsion, dorso-ventral oscillating hydrofoils) does not appear to affect overall energetic cost, enabling engineers to use different modes of aquatic propulsion to create versatile vehicles. Similarities in the cost of generating force, minimum cost of transport, transport distance, and routine speeds for marine mammals suggest that factors other than locomotor efficiency during

routine performance may be considered when designing AUVs. This is not the case for semi-aqueous vehicle design.

SIGNIFICANCE: Our studies have provided information concerning the relationship between body design, biomechanics, and power consumption in a wide variety of aquatic organisms. These results have been applied to, 1) the design of aquatic gliders, 2) engineering models for undulatory propulsion, and 3) models for assessing performance limitations in free-ranging marine mammals.

PATENT INFORMATION: N/A

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Sink or Swim: Strategies for Cost-Efficient Diving by Marine Mammals

Terrie M. Williams,[1*] R. W. Davis,[2] L. A. Fuiman,[3] J. Francis,[4] B. J. Le Boeuf,[1] M. Horning,[2] J. Calambokidis,[5] and D. A. Croll[6]

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Sink or Swim: Strategies for Cost-Efficient Diving by Marine Mammals

Terrie M. Williams,[1*] R. W. Davis,[2] L. A. Fuiman,[3] J. Francis,[4] B. J. Le Boeuf,[1] M. Horning,[2] J. Calambokidis,[5] D. A. Croll[6]

Locomotor activity by diving marine mammals is accomplished while breath-holding and often exceeds predicted aerobic capacities. Video sequences of freely diving seals and whales wearing submersible cameras reveal a behavioral strategy that improves energetic efficiency in these animals. Prolonged gliding (greater than 78% descent duration) occurred during dives exceeding 80 meters in depth. Gliding was attributed to buoyancy changes with lung compression at depth. By modifying locomotor patterns to take advantage of these physical changes, Weddell seals realized a 9.2 to 59.6% reduction in diving energetic costs. This energy-conserving strategy allows marine mammals to increase aerobic dive duration and achieve remarkable depths despite limited oxygen availability when submerged.

Swimming is energetically expensive for mammals and results in transport costs that are 2 to 23 times the levels predicted for fish (*1, 2*). To reduce these costs, marine mammals have developed a wide variety of energy-conserving swimming behaviors. Adherence to a narrow range of routine transit speeds (*3, 4*), wave-riding (*5*), and porpoising (*6*) decrease the amount of energy expended when pinnipeds and cetaceans move near the water surface. Although these energy-conserving strategies are especially beneficial during underwater activity, when access to ambient oxygen is limited, two of the behaviors, porpoising and wave-riding, cannot be used when the animal is submerged. In view of this, it has been assumed that marine mammals swim constantly at cost-efficient routine speeds during diving (*3, 4*). Indeed, the routine speeds of many freely diving marine mammals fall within a relatively narrow range (*7, 8*). A paradox arises when

[1]Department of Biology, EMS-A316, University of California, Santa Cruz, CA 95064, USA. [2]Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77553, USA. [3]Department of Marine Science, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX 78373, USA. [4]Committee for Research and Exploration, National Geographic Society, 1145 17th Street NW, Washington, DC 20036, USA. [5]Cascadia Research, 218½ West Fourth Avenue, Olympia, WA 98501, USA. [6]Institute of Marine Science, EMS-A316, University of California, Santa Cruz, CA 95064, USA.

*To whom correspondence should be addressed. E-mail: williams@darwin.ucsc.edu

metabolic rates are assigned to these swimming speeds. Calculations based on measured speeds during diving and metabolic rates for bottlenose dolphins swimming near the water surface predict that the animals would be unable to complete a 200-m-deep dive using aerobic metabolic pathways. Yet, dolphins perform these dives with only small changes in postdive plasma lactate concentrations, where elevated levels would indicate a transition to anaerobic metabolism (*9*). Similar discrepancies between predicted aerobic capabilities and diving performance have been reported for a wide variety of marine birds and mammals (*10, 11*). The mechanisms by which these divers resolve the apparent conflict between the energetic demands of swimming and the conservation of limited oxygen stores during submergence are not understood (*12, 13*). Metabolic depression (*14*) and regional heterothermy (*15*) associated with cardiovascular changes during diving have been suggested, although the influence of activity level has not been assessed. This has been due in part to the difficulty of observing and monitoring diving animals at depth.

Here, we monitored locomotor behavior during diving with video cameras carried by free-ranging cetaceans and pinnipeds. Unlike other instruments placed on marine mammals in which behavior has been inferred from time-depth records or velocity profiles (*16*), video images permit direct observation of swimming periods, stroke frequency, and glide sequences. Coupled with time-depth recorders, these new tools allowed us to assess the locomotor strategies used by marine mammals throughout their dives.

Subjects for this study included three adult Weddell seals (*Leptonychotes weddellii*, body mass = 393 ± 2 kg) diving from an isolated ice hole in McMurdo Sound, Antarctica (*17*), a juvenile northern elephant seal (*Mirounga angustirostris*, 263 kg) freely diving in Monterey Bay, California (*17*), an adult bottlenose dolphin (*Tursiops truncatus*, 177 kg) trained to dive to submerged targets offshore of San Diego, California (*18*), and an adult blue whale (*Balaenoptera musculus*, estimated mass = 100 tons) traveling offshore of northern California along Cordell Bank (*19*). Each animal carried a submersible video system with a camera facing either forward to record movements of the head or backward to record propulsive movements of the flukes or hind flippers. Data loggers simultaneously monitored duration and depth of dives.

Instrumented animals were free to perform sequential dives in open water or, in the case of the Weddell seals, below the frozen sea ice. The video system and instrumentation were retrieved when the animals hauled out (Weddell seals, elephant seal) or returned to a trainer (dolphin), or the package was detached by a release mechanism (blue whale). Swimming mode, relative stroke amplitude, stroke frequency, and gliding periods were determined for each video sequence, using a motion analysis system (Peak Performance, Englewood, Colorado). These data were then matched to duration and depth of the associated dive (*20*). To assess the effect of changes in locomotor pattern on energetic costs, we measured postdive oxygen consumption of instrumented Weddell seals breathing into a metabolic hood (*21, 22*).

Despite independent evolution of swimming in cetaceans and pinnipeds, and differences in body size and propulsive mechanisms, we found a similar sequence of locomotor gaits during diving for the four species examined (Fig. 1). Diving descents began with 30 to 200 s of continuous stroking that was followed by a marked, prolonged period of gliding to maximum depth. Gliding began at similar depths (86 ± 10 m, n = 3 species) and continued to the bottom of the dive for the seals and dolphin, although maximum dive depths ranged from 115 to 385 m. The blue whale began gliding at comparatively shallower depths (18 ± 1 m, n = 3 dives) during dives of 36 to 88 m in depth. Descent rate during the glide varied little among the three smaller species (1.1 ± 0.1 m s^{-1}, n = 3 species), whereas the blue whale descended considerably slower at 0.3 to 0.4 m s^{-1}. The absolute duration of stroking or gliding sequences depended on maximum depth and dive duration. Deep divers (the phocid seals) showed the longest absolute glide periods. Maximum glide duration was 6.0 min for the juvenile elephant seal descending to nearly 400 m and 6.2 min for an adult Weddell seal descending to 540 m.

Initial ascent of each dive was characterized by sequential, large-amplitude strokes. The range of frequencies during steady stroking on initial ascent was 60 to 110 strokes min^{-1} (1.0 to 1.8 Hz) for the three smaller species (dolphin, elephant seal, Weddell seal). In comparison, the range of stroke frequencies was one-tenth of this range (6 to 10 strokes min^{-1}; 0.1 to 0.2 Hz) for the massive blue whale. Ascent rate during the period of constant stroking was 1.0 ± 0.2 m s^{-1} for all four species examined.

Following the period of continuous stroking, the animals switched to stroke-and-glide swimming for the remainder of the ascent except for a short (<100 s) glide to the surface. Only the Weddell seals did not glide the final 10 m to the surface, a behavior that was undoubtedly influenced by the presence of the sea ice and the maneuvering required to reach the isolated ice hole.

The similarity in locomotor behaviors for these four species is striking given the ranges of body sizes and propulsive mechanisms. Both cetaceans use dorsoventral undulations of a lunate tail for propulsion (*23*). The two pinniped species swim with alternate lateral sweeps of paired hind flippers in which the posterior half of the body may flex (*24*).

Passive gliding by the seals and dolphin began at nearly identical depths, suggesting that changes in hydrostatic pressure and buoyant forces prompted the incorporation of prolonged glide sequences during descent. Previous stud-

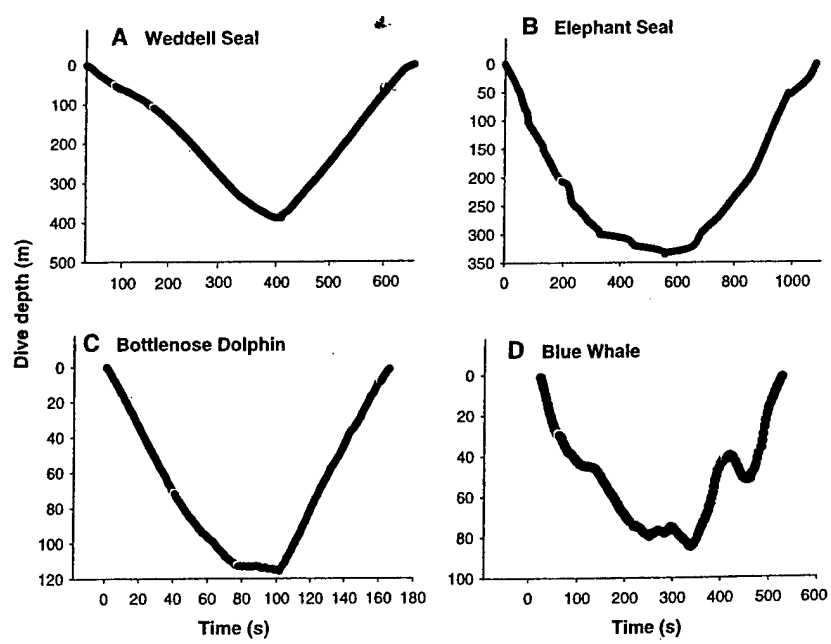

Fig. 1. Locomotor activity of four species of diving marine mammal. Representative deep dives are presented for the (**A**) Weddell seal (maximum depth = 385 m), (**B**) northern elephant seal (333 m), (**C**) bottlenose dolphin (115 m), and (**D**) blue whale (84 m). Each curve represents dive depth in relation to time elapsed during the dive. Color of the line corresponds to stroking (black) and gliding (red) periods. Stroking periods include both continuous stroking and stroke-and-glide activities. Note the prolonged gliding period during descent for each species.

ies have shown that bottlenose dolphins (*25*) and elephant seals (*26*) modify ascent and descent rates during deep dives in response to changes in buoyancy. In dolphins diving to 100 m, the magnitude of the buoyant force changes from positive (+24.3 N) near the water surface to negative (–25.7 N) at depths exceeding 67 m (*25*). These changes are attributed to the gradual collapse of the lungs and a decrease in lung volume that occur with increasing hydrostatic pressure during descent. Complete collapse of the alveoli occurs once dolphins have reached pressures equivalent to 65 to 70 m in depth (*27, 28*). Likewise, the morphological structure of the respiratory system of elephant seals and Weddell seals indicates the capacity for collapse that may affect buoyancy during the course of a dive (*29, 30*). Because compression of the air spaces decreases the volume of the animal without a change in mass, buoyancy decreases on descent. When the downward force of negative buoyancy exceeds drag forces, the animal may glide passively during descent, thereby avoiding the energetic costs associated with active stroking.

As might be expected, dive depth, and therefore distance traveled, affects the percentage of time available for gliding. The percentage of time spent gliding during descent increased significantly ($n = 53$, $r^2 = 0.70$, $P < 0.001$) and nonlinearly with increasing dive depth (Fig. 2). This percentage ranged from 10 to 63% for shallow dives of less than 100 m and reached a plateau of 82 ± 2% ($n = 21$) for deep dives exceeding 200 m. All deep dives were by the phocid seals. Blue whales also showed extended gliding sequences that exceeded 78% of the descent period for dives to 88 m.

A reduction in locomotor effort afforded by gliding should be manifested as a decrease in energetic cost. This has been reported for short-duration glides associated with intermittent (stroke-and-glide) locomotion in fish (*31*) and diving birds (*32, 33*). We found a similar result for Weddell seals that incorporated prolonged glides during diving (Fig. 3). Oxygen consumption during the recovery periods of individual dives was measured for three adult, free-ranging seals wearing video instrumentation (*21, 22*). Two groups of dives covering similar distances but differing in gliding and swimming behaviors were compared (*34*). Dives incorporating gliding during descent resulted in a 9.2 to 59.6% (mean = 27.8 ± 5.5%, $n = 10$) reduction in recovery oxygen consumption compared with dives using stroke-and-glide or continuous swimming. In general, greater savings occurred with deep dives, which is consistent with the increase in the proportion of time gliding with depth (Fig. 2). In view of these results, there appears to be a significant energetic advantage to gliding rather than swimming on descent by marine mammals.

The value of the energetic savings is demonstrated by examining the effect on the oxygen reserves of the diving seal. A 400-kg Weddell seal stores 87 ml of O_2 per kg of body weight (ml O_2 kg^{-1}) in its lungs, blood and muscle to support aerobic metabolism while submerged (*10, 11*). An average energetic savings of 27.8% (Fig. 3) due to prolonged gliding represents 24.2 ml O_2 kg^{-1}. The metabolic rate of Weddell seals during rest or low levels of underwater activity was 3.2 ml O_2 kg^{-1} min^{-1}. At this metabolic rate, the oxygen saved by gliding allows the seal to extend its aerobic dive time by 7.5 min (24.2 ml O_2 kg^{-1} divided by 3.2 ml O_2 kg^{-1} min^{-1}) assuming the same level of activity. This additional time represents 38% of the routine 20-min dive duration of free-ranging Weddell seals. The energetic savings could make the difference between completing a dive aerobically or relying on anaerobic metabolism with the coincident disadvantages associated with the accumulation of lactate and prolonged recovery (*10, 11*). For marine mammals that are hunting, these savings may increase the overall efficiency of foraging. During traveling, the energetic savings when submerged may reduce the cost of long-distance migrations.

The ability of marine mammals to take advantage of physical changes at depth permits the conservation of limited oxygen stores during submergence. These results provide insight into the means by which diving marine mammals resolve the conflict between the energetic demands of swimming and the need for energy conservation during submergence. Prolonged gliding behavior by diving marine mammals appears to be a general phenomenon, irrespective of the method of propulsion and size of the animal. Even the largest mammalian diver, the blue whale, displays this behavior.

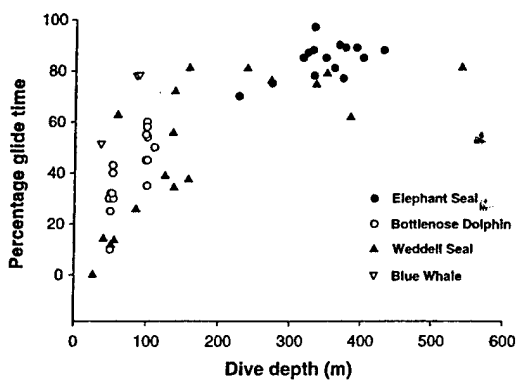

Fig. 2. Percentage glide time during descent in relation to dive depth for four species of marine mammal. Each point represents an individual dive. The data were described by the nonlinear function, percentage glide time =

$$85.9 - \left(\frac{2820.3}{\text{Depth}}\right)$$

($n = 53$, $r^2 = 0.70$, $P < 0.001$). Except for the dolphins, the range of depths was determined by the free-ranging behavior of the instrumented animals.

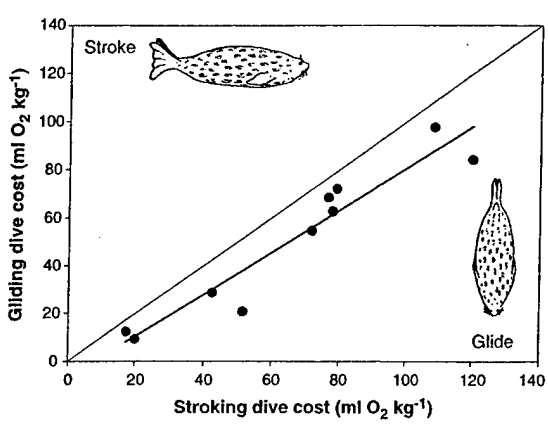

Fig. 3. Recovery oxygen consumption of gliding dives in relation to stroking dives for free-ranging Weddell seals (*34*). Each point represents a gliding dive paired with a stroking dive of equal distance traveled (±60 m) for an individual seal. Total distance traveled ranged from 354 to 3614 m, which resulted in the range of energetic costs. The thin line through the origin represents the line of equality for the cost of gliding dives and stroking dives. The thick solid line denotes the least-squares linear regression through the data points. Dives incorporating prolonged gliding were consistently less costly than stroking dives of similar distance, as described by glide cost = 0.88 stroke cost – 7.30 ($n = 10$, $r^2 = 0.91$, $P < 0.001$). Consequently, all paired dives fell below the line of equality.

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17. The experimental setup and instrumentation for Weddell seals are described in (*35*). Similar instrumentation was deployed on an elephant seal captured at Ano

Nuevo Point, CA, and released offshore in Monterey Bay. After release, the seals returned to instrumentation sites where the data and videos were retrieved.
18. The experimental setup and instrumentation for the dolphin studies are described in (*25*). The instrument pack was neutrally buoyant and weighed 8 kg in air. Twenty experimental dives from 50 to 110 m were conducted in open water.
19. Blue whale studies used CRITTERCAM instrumentation (*36*) attached with a low-profile silicon suction cup (22 cm diameter). The cup released after a predetermined interval through the dissolution of a corrosible magnesium plug. The blue whale (length = 22 to 25 m) had been individually identified photographically during 1990–98 along the California coast. It was considered an adult of at least 10 years in age.
20. Gliding was defined as periods exceeding 3 to 12 s in which no locomotor movements occurred and flippers or flukes were aligned along the body axis. Deployments involving forward-facing cameras on Weddell seals also used a tail-mounted ±2-g, single-axis accelerometer (Ultramarine Instruments, Galveston, TX) to assess stroking activity. Head movements of the blue whale were considered indicative of stroke activity because of counter movements of the head and tail in swimming cetaceans (*25, 37*). Videotapes were reviewed at normal speed, except for the blue whale; cycling rate was increased sevenfold to facilitate analyses of the exceptionally slow movements of the whale.
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30. Because seals exhale before diving, the relative contribution of lung compression to changes in buoyancy during diving is unknown for pinnipeds. The large, incompressible blubber layer of pinnipeds is less dense than seawater and may represent a significant component of the upward buoyant force (*26*).
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Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land?☆

Terrie M. Williams[a,*], M. Ben-David[b], S. Noren[a], M. Rutishauser[a], K. McDonald[a], W. Heyward[a]

[a]*Department of EE Biology, Center for Ocean Health – Long Marine Laboratory, 100 Shaffer Road, University of California, Santa Cruz, CA 95060, USA*

[b]*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA*

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Abstract

Semi-aquatic mammals move between two very different media (air and water), and are subject to a greater range of physical forces (gravity, buoyancy, drag) than obligate swimmers or runners. This versatility is associated with morphological compromises that often lead to elevated locomotor energetic costs when compared to fully aquatic or terrestrial species. To understand the basis of these differences in energy expenditure, this study examined the interrelationships between limb morphology, cost of transport and biomechanics of running in a semi-aquatic mammal, the North American river otter. Oxygen consumption, preferred locomotor speeds, and stride characteristics were measured for river otters (body mass = 11.1 kg, appendicular/axial length = 29%) trained to run on a treadmill. To assess the effects of limb length on performance parameters, kinematic measurements were also made for a terrestrial specialist of comparable stature, the Welsh corgi dog (body mass = 12.0 kg, appendicular/axial length = 37%). The results were compared to predicted values for long legged terrestrial specialists. As found for other semi-aquatic mammals, the net cost of transport of running river otters (6.63 $J\,kg^{-1}\,min^{-1}$ at 1.43 $m\,s^{-1}$) was greater than predicted for primarily terrestrial mammals. The otters also showed a marked reduction in gait transition speed and in the range of preferred running speeds in comparison to short dogs and semi-aquatic mammals. As evident from the corgi dogs, short legs did not necessarily compromise running performance. Rather, the ability to incorporate a period of suspension during high speed running was an important compensatory mechanism for short limbs in the dogs. Such an aerial period was not observed in river otters with the result that energetic costs during running were higher and gait transition speeds slower for this versatile mammal compared to locomotor specialists.
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Keywords: Cost of transport; Stride frequency; Corgi dog; River otter; Limb length; Energetics; Running

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*Corresponding author. Tel.: +1-831-459-5123; fax: +1-831-459-3383.
E-mail address: williams@biology.ucsc.edu (T.M. Williams).

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1. Introduction

As intermediaries between the terrestrial and aquatic environment, semi-aquatic birds and mammals face physiological challenges rarely encountered by specialists. Water is 800 times denser and 60 times more viscous than air, making locomotor movements comparatively more difficult in water. Primary forces that govern aquatic locomotion are drag and buoyancy, and for deep diving animals hydrostatic pressure (Williams, 2001; Denny, 1993). This contrasts markedly with locomotion on land in which gravitational forces acting on the body represent the major physical factor to be overcome. A consequence of the disparate physical properties of air and water are very different forms of locomotion for runners and swimmers (Dejours, 1987). Despite the apparent difficulties associated with accommodating the mechanics of running and swimming, semi-aquatic species routinely engage in both activities.

The energetic costs associated with swimming by semi-aquatic animals can be exceptionally high depending on the degree of aquatic adaptation. As a group, semi-aquatic birds and mammals swimming on the water surface show some of the highest transport costs measured to date. The total cost of transport for swimming by semi-aquatic mammals is 2.4–5.1 times greater than found for swimming marine mammals (Williams, 1999). When compared to transport costs for swimming fish, the differences are even greater, with semi-aquatic birds and mammals showing transport costs that are 10–25 times higher than predicted for comparably sized fish (Schmidt-Nielsen, 1972). These differences in swimming transport costs between semi-aquatic animals and swimming specialists have been attributed to drag associated with a surface or submerged position (Williams, 1989), and to the efficiency of the propulsive mechanism (Fish, 1993, 1996, 2000). Inherent in the latter is the design of the animal for one or more than one form of locomotion. Animals such as Eurasian otters (*Lutra lutra*; Pfeiffer and Culik, 1998), American mink (*Mustela vison*; Williams, 1983), muskrats (*Ondatra zibethicus*; Fish, 1982), water rats (*Hydromys chrysogaster*; Fish and Baudinette, 1999) and penguins (*Eudyptula minor*; Baudinette and Gill, 1985) that move both on land and in water show elevated costs of transport for swimming in comparison to locomotor specialists.

The relationships between morphological specialization, and the biomechanics and energetic costs of running by semi-aquatic animals are less clear. Earlier studies on the American mink reported little difference in stride frequency or stride length at the trot–gallop transition speed between mink and similarly sized terrestrial mammals (Williams, 1983). The resulting cost of transport for running mink was higher than predicted for running specialists (Taylor et al., 1982). Similar results are reported by Fish and Baudinette (1999) for running Australian water rats. The cost of transport for walking by a semi-aquatic bird such as the penguin is even higher than observed for these semi-aquatic mammals, approaching twice that predicted for similarly sized terrestrial mammals (Pinshow et al., 1977). Recently, these elevated costs have been attributed to the comparatively short legs of the birds (Griffin and Kram, 2000).

The general conclusion from these previous studies is that compromises in body morphology to accommodate two forms of locomotion (swimming and running) often lead to elevated energetic costs of transport in semi-aquatic birds and mammals. To understand the basis of these elevated costs when moving on land, we examined the kinematics and energetics of running in the North American river otter (*Lontra canadensis*). This mammal was chosen because of its reported locomotor proficiency on land and in water (Fish, 1994, 2000; Kruuk, 1995). Measurements included oxygen consumption during running, gait characteristics and preferred speeds. The effects of limb length on performance characteristics were assessed by comparing gait transition speeds and maximum running speeds for river otters to a terrestrial specialist of similar size and body structure, the Pembroke Welsh Corgi dog (*Canis familiaris*). Kinematic data for both the river otters and corgi dogs were then compared to predictions for long legged, terrestrial mammals. Lastly, we compared the data on running energetics of the otters to previously reported values for aquatic and terrestrial specialists as well as other semi-aquatic mammals.

2. Materials and methods

2.1. Animals

Morphological characteristics of the animals used in this study are presented in Table 1. Fifteen

Table 1
Morphological characteristics of the river otters and dogs in this study

	Body mass (kg)	Body length (m)	Appendicular/ axial length
River otters			
Male ($n=10$)	11.1±0.7	0.90	0.29
Corgi dogs			
Female ($n=1$)	13.2	0.80	0.35
Male ($n=1$)	12.2	0.75	0.39

Body length was the straight line measurement from the nose to the base of the tail. Height at the shoulders when standing was used as an index of appendicular length. Mean values for adult animals are presented.

North American river otters had been captured from northwestern Prince William Sound, Alaska and flown to the Alaska SeaLife Center (Seward, AK) for a companion study (Ben-David et al., 2000). Locomotor studies on 10 of the captive otters were conducted after a 5-month acclimation period in the facility.

Details of the capture methods, housing, and diet are reported elsewhere (Ben-David et al., 2000). Briefly, river otters were housed as a single group in outdoor pens surrounding one large salt-water pool (4.5 m diameter×3 m deep) and five additional smaller pools (1 fresh water, 4 salt water). Otters were fed daily on a diet of fish supplemented with vitamins. All otters were released at the site of capture following completion of the studies.

To determine if short stature was the primary factor affecting performance in river otters, we also conducted kinematic studies on a similarly sized 'short' dog, the Pembroke Welsh corgi. Two adult Welsh corgis from a local breeder were used in the studies. Dogs were housed in indoor–outdoor kennels and fed daily on a diet of dog chow supplemented with vitamins.

2.2. Oxygen consumption

The rate of oxygen consumption ($\dot{V}O_2$) was determined for river otters at rest and during running on a motorized treadmill. Each animal was trained over several months to run in a Plexiglas chamber (54 cm high×31 cm wide×138 long) mounted over the treadmill surface. Resting measurements were made on sedentary animals prior to the exercise tests. Oxygen consumption was determined using an open flow respirometry system as in Williams (1983) and Ben-David et al. (2000). Air was drawn in along the lower edge of the chamber with a vacuum pump (Sears 2.0 Hp Wet/Dry Vac) at flow rates averaging 61–64 $l\,min^{-1}$. Flow rates were maintained at levels to ensure that oxygen levels in the chamber remained above 20% during the tests, and were monitored continuously with a calibrated dry gas flow meter (American Meter Co., Inc., DTM-325; San Leandro, CA). Expired air was removed through a port located on the top of the metabolic chamber and samples dried (Drierite) and scrubbed of CO_2 (Sodasorb) before entering the oxygen analyzer (AEI Technologies S3-A; Pittsburgh, PA). The percentage of oxygen in the exhaust air was monitored continuously during the experiments, and recorded with a personal computer using Sable Systems Software (Salt Lake City, UT). The output from the oxygen analyzer was monitored every second and averaged for each minute. These values were converted to $\dot{V}O_2$ using equations modified from Fedak et al. (1981) and Withers (1977) assuming a respiratory quotient of 0.77. All values were corrected to standard temperature and pressure, dry. The entire system was calibrated daily with dry ambient air (20.94% O_2) and nitrogen gas (100% N_2) using the nitrogen dilution techniques of Fedak et al. (1981). The theoretical fraction of O_2 leaving the chamber was calculated (Davis et al., 1986) and compared to the measured values from the oxygen analyzer. The flow of calibration gases into the dome was controlled and monitored by an electronic flowmeter (Omega, Model #FMA-772V) that was accurate to within 1%. Calibrations of the flowmeter were conducted with nitrogen gas and a rotameter (Cole-Palmer Instruments) before and after the studies.

All respirometry experiments were conducted outdoors at T_{air}=2.9–9.4 °C, which prevented the exercising otters from becoming overheated. On each experimental day, an otter was placed in the metabolic chamber and allowed to rest for approximately 10–15 min. Following the rest period the treadmill was started and the speed increased until the desired test speed was reached. Percentage oxygen was monitored continuously. Otters maintained a forward position in the front of the chamber during the tests. Each animal ran for 10–20 min and was considered to be in a steady state when $\dot{V}O_2$ varied by less than 4% over at least a 5-min period. Following the run, the otters were

released from the chamber and allowed to join the rest of the group in the enclosure. Only one speed was tested on any experimental day. The range of test speeds was determined by the ability of the otters to maintain a forward position in the front of the chamber and steady gaits. Experiments were terminated if running performance was inconsistent or the otters turned around. All otters were fasted overnight and were post-absorptive at the time of the tests.

2.3. Running kinematics

Running gaits and stride frequency were determined from videotape records of river otters running on a motorized treadmill and corgi dogs running along a 10 m outdoor, gravel test course. Locomotor movements of the running animals were recorded continuously during the tests with a video camera (Sony CCD TR400) mounted on a tripod. The camera was positioned perpendicular to the treadmill or running path of the otters and dogs, respectively. To ensure consistency between methods, a series of treadmill tests were also conducted with the corgi dogs. Stride frequencies determined from treadmill tests and the outdoor course agreed to within 12% over the range of speeds and gaits examined.

Video images were manually digitized at 60 fields per second using a motion analysis system (Peak Performance Technologies, Inc., Englewood, CO). Running gaits of the animals were correlated to speed and stride frequency. For comparative purposes, we assessed stride frequency according to Heglund and Taylor (1988). The timing intervals for sequential cycles of the front right limb were averaged from video sequences of the running animals, and the number of strides taken per second calculated for each gait. These calculated values were compared to stride frequencies determined from digitized video sequences and were found to be accurate to within 10%. Distances used in the determination of speed were calibrated against the measured length of the animals (Table 1) as well as 10-cm markers placed in the background of the test course and treadmill. Timing of the video system was calibrated against a digital clock placed in the field of view.

2.4. Analysis and statistics

Break points in the data for oxygen consumption in relation to running speeds were determined from the intersection of multiple regressions following the approach of Yeager and Ultsch (1989). Allometric regressions for cost of transport in relation to body mass, and relationships for oxygen consumption versus speed were determined using least squares methods (Sigma-Stat, Jandel Scientific Software, 1995). Remaining data are reported as means ± 1 S.E.M. unless otherwise indicated.

3. Results

3.1. Oxygen consumption

The mean rate of oxygen consumption for the otters resting in the metabolic chamber was 9.69 $mlO_2\,kg^{-1}\,min^{-1} \pm 0.91$ ($n=3$ lowest recordings for 10 otters). This value was within 1.5% of the value reported by Kruuk (1995) for the Eurasian river otter and was 34.4% higher than the predicted value for basal metabolic rate in mustelids (Iverson, 1972). Oxygen consumption increased with running speed and showed two different functions depending on gait (Fig. 1). From rest to 1.2 $m\,s^{-1}$ oxygen consumption increased linearly with speed as described by

$$\dot{V}_{O_2} = 14.1 + 23.4\ \text{speed} \quad (n=27\ \text{trials},\ r^2=0.76,\ P<0.001) \qquad (1)$$

where $\dot{V}O_2$ is in $mlO_2\,kg^{-1}\,min^{-1}$ and speed is in $m\,s^{-1}$. Over this range of speeds the river otters used a walking gait. At higher tread speeds the otters switched to a half-bound or bounding gait and showed no relationship between oxygen consumption and bounding speed. Mean $\dot{V}O_2$ during bounding from 1.2 to 1.6 $m\,s^{-1}$ was 38.01 ± 0.74 ($n=18$ trails).

3.2. Running kinematics

As previously described by Tarasoff et al. (1972), river otters used two primary gaits during the treadmill tests, a walk at slow speeds (0.5–1.2 $m\,s^{-1}$) and a bound or half-bound at higher speeds. Because the half-bound was used intermittently and overlapped with the range of bounding speeds, data for both gaits were combined and termed 'bound' for the remainder of the analyses. The transition between walking and bounding gaits occurred at 1.2 $m\,s^{-1}$.

Stride frequency of running river otters showed

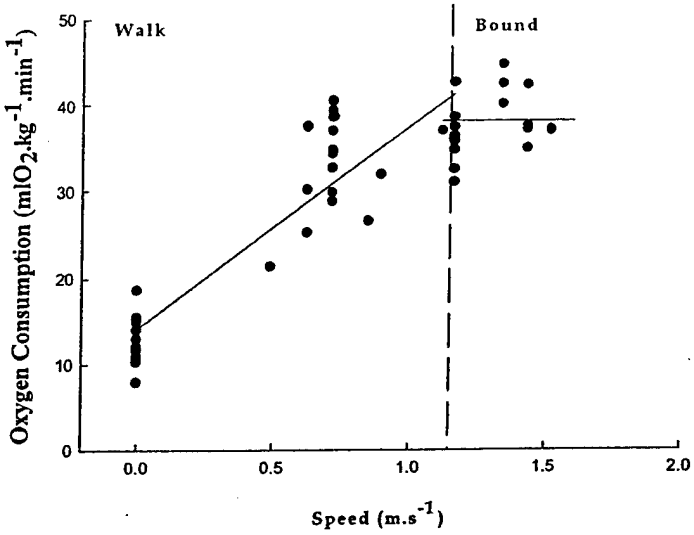

Fig. 1. Oxygen consumption in relation to running speed for river otters. Each point represents a single trial for an individual otter. The solid lines are the least squares linear regression for the walking otters and the mean level for bounding otters, respectively, as described in the text. The vertical dashed line denotes the average gait transition speed for the otters. Data at zero speed is for sedentary otters in the metabolic chamber prior to the exercise session.

two patterns with locomotor speed that depended on gait (Fig. 2a). Over the range of walking speeds stride frequency increased linearly with speed according to the relationship

$$\text{Stride frequency} = 1.06 + 0.68 \text{ speed} \quad (n = 25 \text{ trials}, r^2 = 0.53, P < 0.001) \qquad (2)$$

where stride frequency is in strides s^{-1} and speed is in $m\,s^{-1}$. In contrast, the frequency of high speed bounding showed no pattern with speed. Mean stride frequency for bounding was 2.08 ± 0.03 ($n = 16$ trials) for the river otters.

Unlike the otters, corgi dogs showed the three distinct gaits typical of running quadrupedal mammals (Heglund et al., 1974; Heglund and Taylor, 1988). At speeds less than 1.1 $m\,s^{-1}$ corgis used a walking gait (Fig. 2b). This was followed by a change to trotting, and finally galloping at speeds greater than 2.2 $m\,s^{-1}$. The range of speeds the animals performed also differed between the otters and dogs. Running speeds ranged from 0.6 to 1.6 $m\,s^{-1}$ in the river otters. In comparison, corgi dogs ran over a range of 0.6–7.4 $m\,s^{-1}$.

Stride frequency of the corgi dogs showed two relationships with running speed that depended on the transition between trotting and galloping (Fig. 2b). During walking and trotting stride frequency increased linearly with speed and was described by the equation

$$\text{Stride frequency} = 1.47 + 0.51 \text{ speed} \quad (n = 57 \text{ trials}, r^2 = 0.60, P < 0.001) \qquad (3)$$

where the units are as in Eq. (2). A second linear regression described the relationship between stride frequency and galloping speed:

$$\text{Stride frequency} = 2.28 + 0.30 \text{ speed} \quad (n = 61 \text{ trials}, r^2 = 0.62, P < 0.01) \qquad (4)$$

where the units are as in the previous equations.

4. Discussion

4.1. The effect of body morphology on energetic costs in semi-aquatic mammals

The body morphology of river otters reflects the combined demands of an aquatic and terrestrial lifestyle, and has resulted in river otters being considered 'intermediates' to terrestrial or aquatic specialists (Tarasoff, 1974). As a group, river otters are relatively large (0.5–2.0 m long depending on species) semi-aquatic carnivores that live on land but forage primarily in water. Movements on land can be extensive, with males in particular covering large ranges (Kruuk, 1995). Several morphological adaptations enable river otters to meet these diverse locomotor demands with the most obvious being spinal flexibility and a reduction in the length of the limbs (Fig. 3). The former is

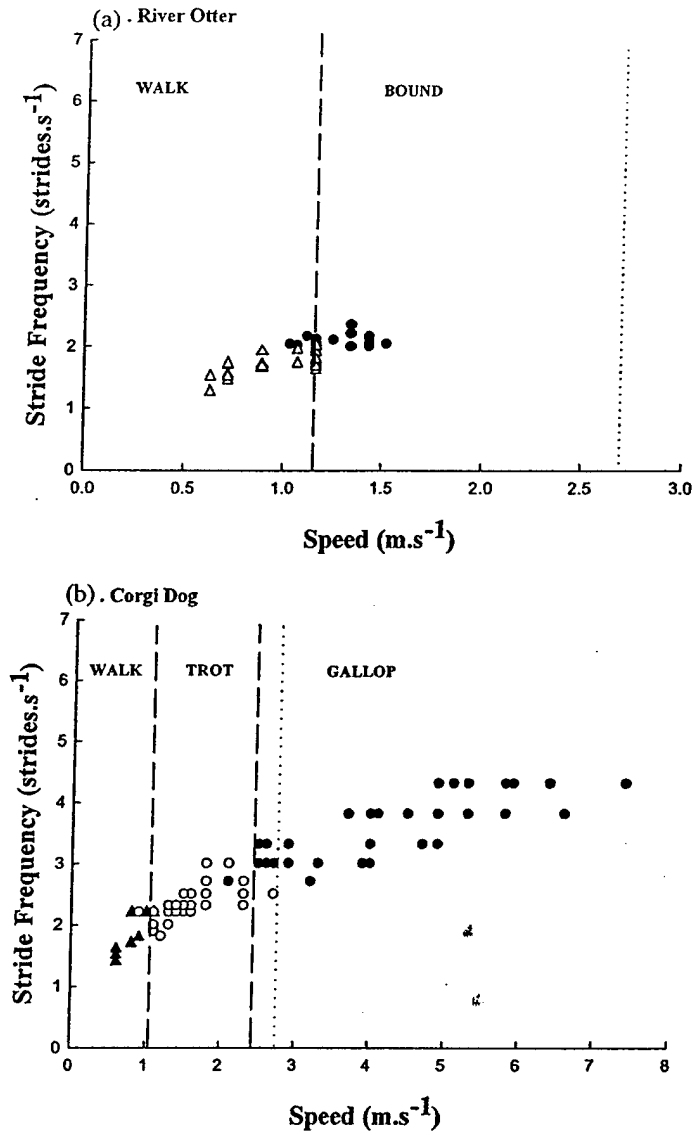

Fig. 2. Stride frequency in relation to running speed for river otters (a); and corgi dogs (b). Each point represents a single exercise trial for an individual animal. Values for walking (open and closed triangles), trotting (open circles), and bounding and galloping (closed circles) are presented. Vertical dashed lines denote the measured transition speed between gaits and vertical dotted lines the predicted trot–gallop speed for quadrupedal mammals (Heglund and Taylor, 1988). Note in particular the difference in the range of locomotor speeds between these similarly sized mammals. Sample size of $n=32$ trials for river otters and 119 trials for dogs.

considered an advantage for dorsoventral bending to power swimming in semi-aquatic (Williams, 1983) and marine (Long et al., 1997) mammals. While long limbs and small plantar (foot) surfaces characterize elite terrestrial runners such as the cheetah, reduced appendicular skeletons and enlarged plantar surfaces are typical of semi-aquatic mammals, the river otter being no exception (Table 1). The appendicular to axial ratio is 0.29 for the North American river otter, 0.37 for a short-legged dog such as the Welsh corgi, and nearly 0.60 for average proportioned dogs such as the border collie. The benefit of such morphological specialization in semi-aquatic mammals is a streamlined body that produces less hydrodynamic drag during swimming (see Fish, 2000 for a

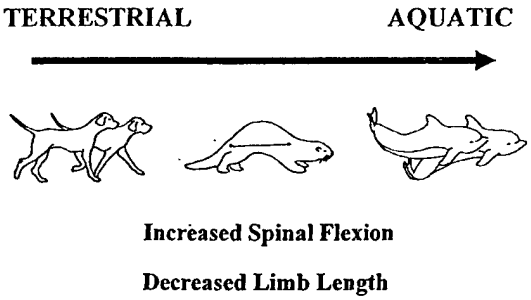

Fig. 3. Relative changes in morphology with the increase in aquatic specialization in mammals. Two major factors affecting terrestrial locomotion in semi-aquatic mammals, an increase in spinal flexion and decrease in limb length, are characteristic of animals designed for an aquatic lifestyle.

review). A potential disadvantage, however, is reduced efficiency when moving on land.

In river otters this disadvantage is manifested as an elevation in the energetic cost of running when compared to the costs of locomotor specialists (Fig. 4). The total cost of transport calculated from the oxygen consumption of bounding river otters (Fig. 1) was 8.90 $J\,kg^{-1}\,m^{-1}$. Using basal metabolic rates predicted for river otters from Iverson (1972) we obtain a net cost of transport of 7.21 $J\,kg^{-1}\,m^{-1}$. This is reduced to 6.63 $J\,kg^{-1}\,m^{-1}$ if the resting metabolic rates obtained in the present study are used in the calculation. The resulting values for net cost of transport are 34–46% greater than predicted for running quadrupedal mammals (Taylor et al., 1982) or swimming marine mammals (Williams, 1999) of similar body mass. Despite the differences in energetic costs between these groups, the elevation in running costs observed for river otters are typical of semi-aquatic mammals. For example, the cost of transport for running North American mink is 25% higher than predicted for terrestrial specialists (Williams, 1983). The Australian water rat demonstrates a minimum cost of running that is 70% higher than predicted values (Fish and Baudinette, 1999).

Fish and Baudinette (1999) have shown that the relative cost of running and swimming for animals correlates with the degree of locomotor specialization. Thus, mammals designed primarily for locomotion on land such as humans have swimming costs that are nearly 4 times that of running (DiPrampero, 1986). At the other extreme of the continuum presented by these investigators is the penguin, an aquatic bird that has exceptionally high walking costs and a relative cost ratio of only 0.55. As might be expected, semi-aquatic mammals are intermediate to the extremes with swimming cost to running cost ratios of 1.25–2.73. Based on the total cost of running in the present study and the cost of submerged swimming of Eurasian otters from Pfeiffer and Culik (1998), the relative cost ratio for river otters is only 0.17. However, the low ratio for river otters calculated here undoubtedly reflects the effects of submergence on body drag and the physiological responses to diving on the energetic cost of swimming (Williams, 1989). The relative cost ratio for river otters is increased to 1.95, the mid range for semi-aquatic mammals, if the predicted cost of surface swimming (Williams, 1999) is used in the calculation.

Initially, it seems reasonable to attribute the elevated running costs of semi-aquatic mammals to the reduced length of the limbs. This presumes that short limbs will result in shorter stride lengths

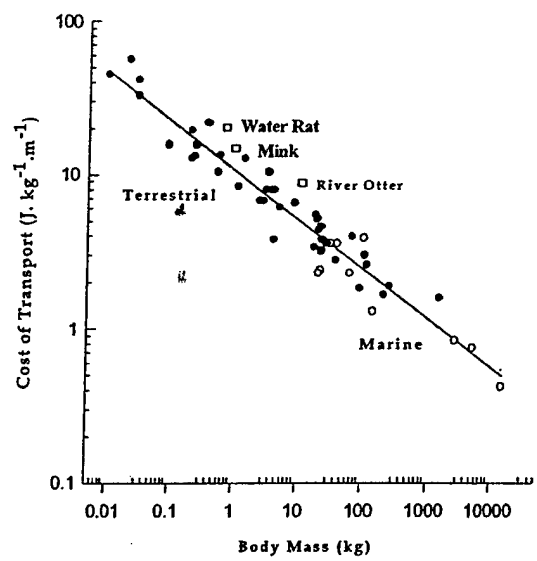

Fig. 4. Cost of transport in relation to body mass for running terrestrial (closed circles), swimming marine (open circles), and running semi-aquatic (open squares) mammals. All animals were considered locomotor specialists except for the water rat, mink, and river otter. The solid line is the least squares regressions through the data points. The data and regression represent 29 species of terrestrial specialist and 6 species of marine mammal (from Williams, 1999). Data for the running water rat and mink are from Fish and Baudinette (1999) and Williams (1983), respectively. Cost of transport for the river otter was calculated from the data in Fig. 1.

and a consequent increase in stride frequency to cover a set distance. To test the relationship between limb length and the energetic cost of running, Steudel and Beattie (1995) conducted a phylogenetic analysis for a wide variety of mammals. Their analysis did not find a significant relationship between these variables beyond a 'mutual correlation with body mass'. Kinematic tests on semi-aquatic mammals including the present study support this conclusion. Rather than a compensatory increase in stride frequency, the river otters showed stride frequencies at gait transition speeds that were lower than those predicted for running specialists from Heglund and Taylor (1988). The mean stride frequency at the trot–bound transition speed for river otters, 1.88 ± 0.05 strides s^{-1} ($n=9$), was 36% lower than predicted for the walk–gallop transition of terrestrial mammals (Fig. 2a). Running North American mink (Williams, 1983) and water rats (Fish and Baudinette, 1999) demonstrated less than a 2% difference between predicted and measured stride frequencies at the gait transition.

These results are somewhat misleading due to several compensatory changes in performance by semi-aquatic mammals during high speed running. For a wide range of running mammals, the trot to gallop transition speed changes predictably with body mass (Heglund et al., 1974; Heglund and Taylor, 1988). Based on regressions from these previous studies, the expected gait transition speed for an 11.1 kg river otter is 2.6 $m\,s^{-1}$. This compares with the observed walk to bound transition speed of 1.2 $m\,s^{-1}$ (Fig. 2a), a speed that is less than half of predicted. Other performance characteristics including the range of running speeds and maximum speed were also reduced in the river otters compared to other runners, long- or short-legged (Fig. 2). The maximum running speed for river otters, 1.6 $m\,s^{-1}$, was only 35% of the preferred galloping speed predicted for terrestrial mammals of similar body mass and 'normal' body proportions (Heglund and Taylor, 1988). The effect of these shifts in the gait transition and maximum speeds is lower stride frequencies than predicted. Thus, the frequency of limb movements in river otters is comparable or lower than expected, but comes at the expense of the speed of performance.

The question remains, is reduced limb length in semi-aquatic mammals the primary cause of the kinematic and energetic differences observed between this group and terrestrial specialists? Data for the running corgis suggest that short stature need not be a mechanical hindrance. This breed of dog, similar in body proportions to the river otter, showed gait patterns, stride frequencies and gait transition speeds typical of other terrestrial mammals (Fig. 2b). Unlike the otters (Fig. 2a), the stride frequency of corgis at the trot–gallop transition, 2.9 ± 0.2 strides s^{-1} ($n=5$), was within 4% of the predicted value for terrestrial specialists (Heglund and Taylor, 1988). The primary difference in biomechanics between the otters and corgis was the incorporation of spinal flexion and a period of suspension during high speed running. Galloping corgis, like many other canids, show little spinal flexion but maintain a period of suspension at high speeds (Brown, 1986). Conversely, river otters show a 20.5% decrease in axial length (measured shoulder to hip) and only rarely incorporate an aerial phase during bounding (Scaramozzino, 2000).

Previous studies have suggested that axial flexion during running provides an advantage for increasing speed (Gambaryan, 1974) particularly for semi-aquatic mammals (Williams, 1983). Rather than axial flexion per se, we find that the ability to incorporate a period of suspension during high speed running provides the locomotor advantage for short-legged runners whether or not it is associated with body flexion. Consequently, there is a general trend among semi-aquatic mammals for higher relative costs in those species without a period of suspension during high speed gaits (i.e. water rats, river otters) compared to those with a pronounced aerial phase (i.e. mink, Fig. 4). Likewise, locomotor performance defined in terms of predicted gait transition speeds and range of speeds for short-legged mustelids (Scaramozzino, 2000) and dogs (Fig. 2) is greater in those species that demonstrate a period of suspension during high speed running.

In summary, morphological adaptations to accommodate more than one form of locomotion allows river otters to take advantage of two different environments when hunting. The price of this locomotor versatility includes higher energetic costs during running, and slower gait transition speeds and maximum speeds in comparison to terrestrial specialists. Thus, for the three semi-aquatic mammals tested to date (water rat, mink, and river otter) the energetic cost of both swimming and running are elevated in comparison to

locomotor specialists. The magnitude of the difference between semi-aquatic and terrestrial mammals depends on the degree of morphological specialization.

In addition to basic information on locomotion in semi-aquatic mammals, these results on extant species provide additional insights regarding the physiological and behavioral challenges that may have been encountered as ancestral mammals made the transition from land to sea (Williams, 1999). As body morphology changed to accommodate two forms of locomotion during the transition, the energetic trend would have been from the comparatively low costs of the terrestrial specialist to the comparatively high costs of the semi-aquatic transitional mammal. With improved streamlining and propulsive efficiency, locomotor energetic costs would have decreased to the low cost level of the swimming specialist (Fig. 4). Based on our results for rivers otters, it is likely that ancestral semi-aquatic mammals faced both energetic and performance 'hurdles' during the transition from an obligate terrestrial to an obligate aquatic lifestyle.

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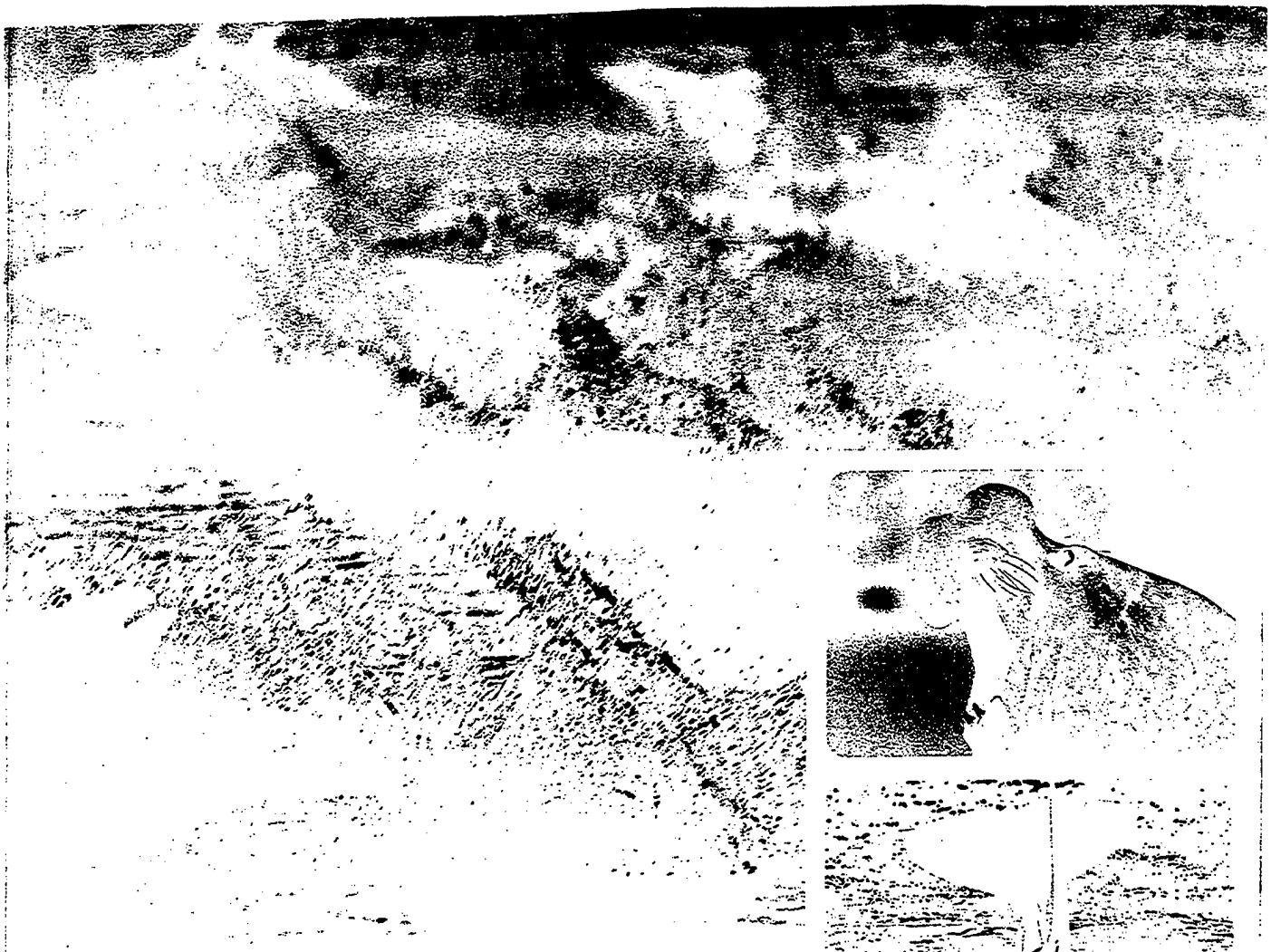

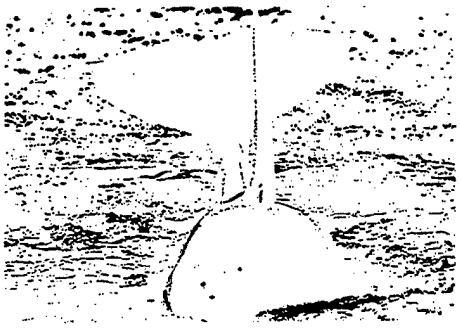

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AN EVOLUTIONARY APPROACH

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CHAPTER 3

Anatomy and Physiology: the Challenge of Aquatic Living

Terrie M. Williams and Graham A. J. Worthy

3.1 INTRODUCTION

Sixty million years ago marine mammals made the transition from terrestrial specialists to intermediate forms capable of moving both in air and water, and from these intermediate forms to aquatic specialists (Repenning 1976; Berta *et al.* 1989; Thewissen *et al.* 1994). Marked anatomical and physiological modifications were necessary during these evolutionary stages to meet the physical demands of living in water instead of air. Water is 800 times denser and 60 times more viscous than air (Dejours 1987) making locomotor movements comparatively more difficult. On land, gravity is the primary physical force to be overcome by the body and limbs during running. In water, buoyancy and drag are the major physical forces challenging the swimmer. Furthermore, changes in hydrostatic pressure as the marine mammal dives will influence locomotion. Differences in the thermal characteristics of air and water also have a profound impact on the physiology and anatomy of mammals. The thermal conductivity of water is 24 times that of air at the same temperature. As a result, aquatic living mammals are exposed to exceptionally high levels of heat transfer; simply keeping warm was undoubtedly a major evolutionary hurdle as mammals moved from land to sea. The high salinity of the marine environment also necessitated modification of the terrestrial kidney to allow marine mammals to maintain osmotic homeostasis (internal water and electrolyte balance) in the absence of fresh water. In sum, the unique physical characteristics of water make the oceans a challenge for mammalian systems that originated on land.

Remarkably, not just one but several major lineages, the pinnipeds, cetaceans and sirenians, made the transition from land to sea. Polar bears and sea otters are also specialized for a marine lifestyle. In this chapter we examine some of the major anatomical and physiological solutions used by these mammalian groups to meet the challenge of aquatic living. We focus on key features that were influenced by the physical characteristics of water. These include: (i) swimming locomotion, (ii) diving, (iii) thermoregulation, and (iv) osmoregulation. Each of these represents a hurdle that required both morphological and physiological modifications for the mammal to change from an efficient terrestrial predator to a marine predator.

3.2 LOCOMOTION: DESIGNING THE MAMMALIAN BODY FOR AQUATIC PERFORMANCE

One of the most obvious differences between marine and terrestrial mammals is the shape of the body and appendages. Lanky limbs and small plantar (foot) surfaces characteristic of elite terrestrial athletes such as the cheetah have been replaced with a markedly reduced appendicular skeleton, streamlined bodies and enlarged propulsive appendages (Fig. 3.1). An example of the evolutionary transition in general body form can be traced in the cetacean lineage as illustrated in Fig. 3.2. The closest relatives of whales, mesonychid condylarths, were terrestrial quadrupeds that shared features of modern ungulates (see Chapter 2 for details on evolution). With increased aquatic specialization we find a gradual reduction in the length of the fore- and hindlimbs and an increase in surface area of the appendages. *Ambulocetus natans* provides fossil evidence of these changes and literally means 'walking whale'. It is likely that *Ambulocetus*

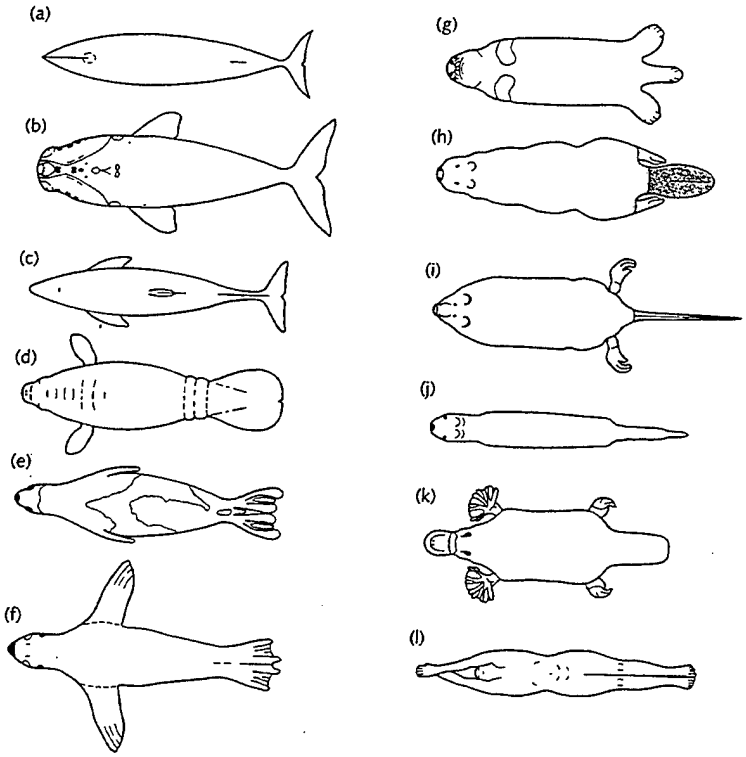


Fig. 3.1 General body shape of mammalian swimmers. Marine mammals are shown in (a)–(g) and display more body streamlining than terrestrial and semiaquatic mammals (h)–(l). (a) Minke whale; (b) right whale; (c) harbour porpoise; (d) Florida manatee; (e) harp seal; (f) California sea lion; (g) sea otter; (h) beaver; (i) muskrat; (j) mink; (k) platypus; (l) human. (From Fish 1993a, with permission.)

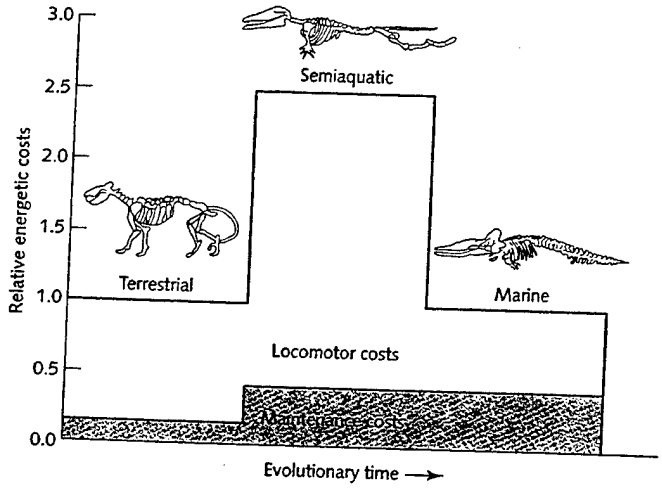


Fig. 3.2 Changes in locomotor costs and basal maintenance costs with the evolution of marine mammals. The evolutionary pathway assumes that ancestral marine mammals included an obligate terrestrial form that was followed by a semiaquatic form (i.e. *Ambulocetus natans*), and finally an obligate marine form. Note the similarity in total energetic costs for terrestrial and marine specialists despite the change in relative contribution of locomotor and maintenance costs. (From Williams 1999, with permission.)

was a marine mammal capable of walking on land as well as swimming in water. The limbs of these transitional marine mammals were more robust than they are in extant species. The shape of the vertebral column indicates that *Ambulocetus* used dorsoventral undulations similar to the swimming movements of extant sea otters (Thewissen *et al.* 1994). Positions of the elbow and femur suggest a sprawling gait on land similar in form to the otariids. In comparison, obligate marine mammals as exemplified by modern cetaceans show vestigial hindlimbs that are not externally visible and forelimbs and elbow joints

rendered functionally obsolete in stiffened pectoral fins. The skeletons of ancestral pinnipeds such as *Potamotherium* (Repenning 1976) and *Enaliarctos mealsi* (Berta *et al.* 1989) indicate both otter-like and seal-like locomotor patterns for archaic pinnipeds.

3.2.1 Hydrodynamics and body shape

The simple explanation for these dramatic morphological changes is the mechanical and energetic advantage afforded by body streamlining. By smoothing body contours, the magnitude of drag forces is reduced during swimming. Four types of drag are encountered by swimming marine mammals: (i) frictional drag, (ii) pressure drag, (iii) induced drag, and (iv) wave drag. The first two are associated with the physical characteristics of water surrounding the body of the swimmer. Consequently, the size and shape of the animal will affect the magnitude of frictional and pressure drag. When swimming submerged, these two types of drag predominate (Fish 1993a). The third type of drag, induced drag, is associated with water flow around the flippers, fins and flukes of marine mammals. Many of these body features act as hydrofoils to create lift and thrust during swimming. A consequence of this design, however, is induced drag which results from the pressure difference between the two surfaces of the hydrofoil and the formation of vortices at its tips (Webb 1975).

As the swimmer moves near or on the water surface they experience an additional type of resistance, wave drag. Energy that could have been directed towards moving the animal forward is wasted in producing waves. Total body drag is 4–5 times higher for a body moving on or near the water surface than for the same body submerged due to wave drag (Hertel 1966). This has been demonstrated for humans and harbour seals (Williams & Kooyman 1985) and sea otters (Williams 1989) by towing the subjects on the water surface and submerged (Box 3.1). Wave drag is reduced considerably by submerging and becomes negligible

BOX 3.1 BODY STREAMLINING AND DRAG REDUCTION

Swimmers are subject to physical forces, termed drag, that resist forward movement in water and are described by the equation:

$$\text{Drag} = 1/2pV^2ACd$$

where p = density of the fluid, V = velocity of the swimmer, A = area of the body (surface area or frontal area, and Cd = drag coefficient, a term that takes into account the flow characteristics of the fluid around the body.

It is obvious from this equation that velocity has a comparatively large impact on body drag. As the animal attempts to move faster through the water, drag forces on the body increase exponentially. This, in turn, affects locomotor effort and the energetic cost to the swimmer.

The sea otter provides a good example of the effects of swimming velocity on drag forces. In Fig. 1, drag forces for surface (closed circles) and submerged (open circles) sea otters moving through the water at different velocities are compared. Note the non-linear increase in drag force with velocity of the animal. The dashed line denotes the drag forces routinely encountered by wild sea otters based on their preferred surface and submerged swimming speeds. These values represent form drag (drag force from the body moving through the water) only and do not account for active drag (drag associated with swimming movements) (Williams 1989).

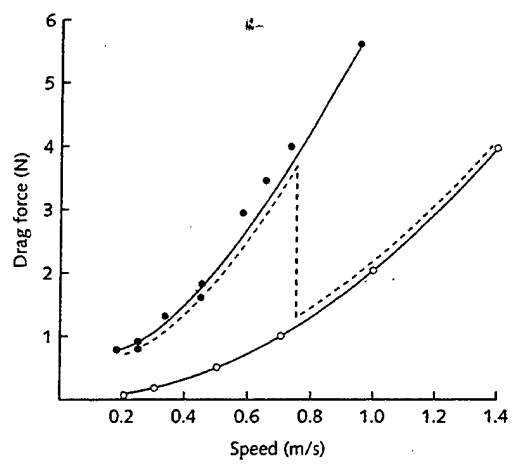


Fig. 1 The effects of swimming speed on drag forces. (Data from Williams 1989.)

once an animal has moved three body diameters down into the water column. The interrelationships between position in the water column, wave drag and subsequent effort have been used effectively by human swimmers. To increase speed during competition in the 1996 Atlanta Olympics, human athletes relied on prolonged periods of submergence and an undulatory dolphin kick following each flip turn off of the pool wall. Sea otters (*Enhydra lutris*) also use this trick of submergence and undulatory swimming to increase speed. Surface swimming by this mammal is relatively slow and usually does not exceed 0.8 m/s. When sea otters want to move fast, they switch to a submerged undulatory style of swimming and can reach speeds of 1.4 m/s.

Another means of minimizing total body drag is to streamline the body and appendages. The morphological modifications required for streamlining are consistent among very different mammalian lineages. Otariids, phocids, odontocetes, and even mysticete whales, have remarkably similar body shapes consisting of rounded leading edges that taper progressively towards the tail (Fig. 3.1). The optimum body shape minimizes drag for a maximum body volume and is described by the fineness ratio (FR) where:

FR = Length of the body/Maximum body diameter

The optimum range of FR for fast swimming vertebrates is 3–7 with an ideal value of 4.5 (Webb 1975). A survey conducted by Fish (1993a) demonstrates that many marine mammals have well streamlined body dimensions within the theoretical optimum FR range. Odontocetes, otariids, phocids, sirenians and the sea otter have body shapes with FRs that range from 3.3 to 8.0. The FRs of mysticetes range from 4.8 to 8.1 for Balaenopteridae and 3.3–8.0 for Balaenidae. Exceptions include the northern right whale dolphin (*Lissodelphis borealis*) and semiaquatic mustelids (mink and river otters) whose body shapes approach snake-like proportions and FRs of 9.0–11.0.

3.2.2 Locomotor movements and the cost of swimming

Body streamlining is not enough to guarantee athletic prowess when moving through water. The mechanism that propels the animal forward must be efficient and powerful enough to counter the effects of drag. Different lineages of marine mammals have solved the problem of aquatic propulsion in a variety of ways. Common features to all are specialized, enlarged propulsive surfaces that oscillate to create thrust. This oscillatory mode of swimming differs considerably in mechanical efficiency, thrust production and energetic cost from terrestrial or semiaquatic mammals that rely on paddling limbs for propulsion (Fish 1996). During paddling, as used by surface-swimming sea otters and polar bears (*Ursus maritimus*), the stroke cycle consists of alternating power and recovery phases. The power phase enables the animal to move forward. The recovery phase is used primarily to reposition the appendage for the following stroke and as such represents a portion of the cycle that does not contribute to the forward movement of the swimmer.

Stroke efficiency is improved in highly derived marine mammals by oscillating the appendages and modifying their shape to serve as hydrofoils (Fish 1993a). Rather than paddling, pinnipeds, cetaceans and sirenians use hydrodynamic lift-based momentum exchange to move through the water (Webb 1984; Fish 1993a). The fore-flippers of otariids, the flukes and pectoral fins of cetaceans, and the paired hind-flippers of phocid seals act as hydrofoils to generate thrust. However, the mechanics of each mode of swimming are very different. Otariids, such as the California sea lion (*Zalophus californianus*), use fore-flipper propulsion (Feldkamp 1987). Walruses (*Odobenus rosmarus*) and phocid seals use alternate lateral sweeps of the hind-flippers in which the posterior half of the body may flex. Cetaceans use dorsoventral movements of the posterior third of the body and fluke to produce thrust. An important feature of the swimming modes of both pinnipeds and cetaceans is the absence of a prolonged recovery phase during the stroke cycle. Thus, thrust can be produced throughout the stroke cycle and mechanical efficiency is increased.

Because marine mammals use so many different modes of swimming, we might expect that cruising speeds would vary according to style. However, this is not what is observed for marine mammals at sea. The range of cruising speeds for marine mammals varies little over a wide range of body sizes and

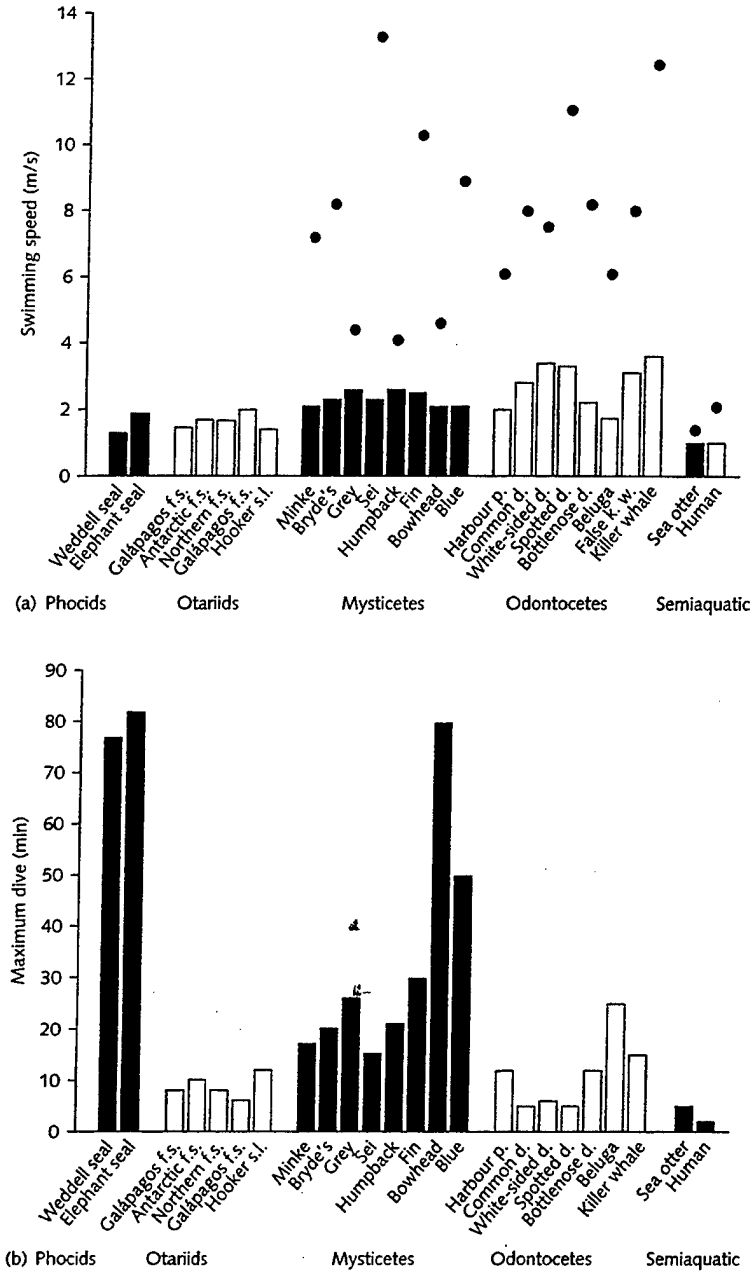


Fig. 3.3 (a) Swimming speeds and (b) maximum dive duration of marine mammals. Phocid seals, otariids, mysticetes, odontocetes and semiaquatic mammals are compared. Bars represent cruising speed while circles represent sprint speeds for the animals in (a). The mass of the animal increases within each taxonomic group.

styles of swimming (Fig. 3.3a). Average swimming speeds for phocid seals using lateral undulation, otariids using fore-flipper propulsion, and mysticetes and odontocetes using dorsoventral undulation range from 1.3 to 3.6 m/s. In comparison with terrestrial mammals, this represents a narrow range of locomotor speeds when the range of body mass (30 kg fur seals to 145 t blue whales) is taken into account.

Sprint speeds of marine mammals are considerably higher and may reach over 10 m/s in odontocetes and mysticetes. Once again body size does not

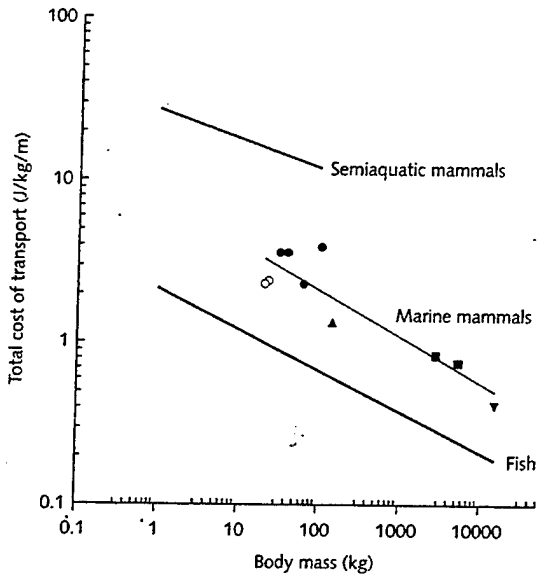


Fig. 3.4 Total cost of transport (COT_{TOT}) in relation to body mass for different classes of swimmers. Individual marine mammals are compared to regressions for semiaquatic mammals and salmonid fish. Marine mammal specialists include phocid seals (closed circles), California sea lions (open circles), bottlenose dolphins (upward triangle), killer whales (squares) and gray whales (downward triangle). The line through the data points for marine mammals is the least squares regression and is described by $COT_{TOT} = 7.87$ $Mass^{-0.29}$. The lower solid line represents the extrapolated regression for salmonid fish where $COT_{TOT} = 2.15$ $Mass^{-0.25}$. The upper solid line shows the regression for swimming semiaquatic mammals where $COT_{TOT} = 26.81$ $Mass^{-0.18}$. (From Williams 1999, with permission.)

necessarily correspond to the fastest swimmers. Sprint speeds for the 120 kg spotted dolphin (*Stenella attenuata*) reach 11.1 m/s and rival the speeds of 5 t killer whales and 68 t fin whales. The slowest sprint speed recorded for a cetacean is 5.1 m/s for the narwhal (*Monodon monoceros*), a comparatively sluggish marine mammal that moves slowly within the Arctic pack ice (Dietz & Heide-Jorgensen 1995). Not surprisingly, the swimming speeds of marine mammals exceed even the best efforts of human athletes. For the sake of comparison, we note that the average human swimmer moves at a cruising speed of 1.0 m/s. The gold medal performance for sprint swimming during the 1996 Olympics in Atlanta was just over 2.0 m/s.

With increased specialization in body morphology for aquatic movements there is a corresponding change in the energetic cost of locomotion (see Chapter 9). The total cost of transport (COT_{TOT}) is defined as the amount of fuel it takes to transport one unit of body mass over a unit distance (Schmidt-Nielsen 1972). COT_{TOT} for swimming mammals falls into two distinct groups based on where the animal swims in the water column and the degree of specialization of the propulsor (Fish 1993a, 1996; Williams 1999). Semiaquatic mammals (minks, muskrats, humans and sea otters swimming on the water surface) have elevated transport costs that are 2–5 times higher than those observed for marine mammals (Fig. 3.4). The lower swimming costs of marine mammals are described by a different regression. Interestingly, this single regression explains the cost of dorsoventral undulation in cetaceans (Fish 1993b, 1998), fore-flipper propulsion in otariids (Feldkamp 1987) and lateral undulation of paired hind-flippers in phocid seals (Fish *et al.* 1988). This may seem unusual in view of the very different mechanics associated with each mode of swimming. However, similar results have been reported for other groups of exercising animals. Transport costs do not vary greatly with the style of swimming in fish (Schmidt-Nielsen 1972, 1984; Bennett 1985) or with bipedal or quadrupedal running in terrestrial mammals (Taylor & Rowntree 1973; Fedak & Seeherman 1979).

Surprisingly, the relationship describing transport costs in swimming marine mammals does not differ from that reported for running terrestrial mammals (Williams 1999). We find that the COT_{TOT} of swimming harbour seals are similar to those of a running goat of equal size; COT_{TOT} for a swimming dolphin approaches that of a running horse. Transport costs of swimming killer whales are similar to those of running elephants. From these relationships it is not hard to imagine the changes in locomotor energetics that may have occurred as ancestral marine mammals made the transition from land to sea (Fig. 3.2). The energetic trend would have been from the comparatively low costs of the terrestrial specialist to the comparatively high costs of the semiaquatic transitional mammal. As body morphology changed to accommodate streamlining and improve propulsive efficiency,

energetic costs were reduced back to the original low cost level of the specialist.

Both hydrodynamics and energetics of swimming indicate that the ability to remain submerged provides a distinct advantage for marine mammals. Yet, this poses an interesting physiological challenge for a mammal. How does an air-breathing animal support metabolic processes while under water? The following section will examine this question for transitional mammals that move between land and water, and for marine mammal specialists that spend over 90% of their lives submerged.

3.3 DIVING PHYSIOLOGY: EVOLUTION OF THE UNDERWATER ATHLETE

An important consequence of the aquatic lifestyle of marine mammals is a marked change in how oxygen is delivered, stored and utilized by the body, especially when compared to terrestrial mammals. In general, the components of the pathway for oxygen in marine mammals are similar to those of terrestrial mammals and reflect the evolutionary connection between the groups. However, the function of the individual components differs between terrestrial and marine mammals due to differences in access to air. Anatomical structures originally intended for use on land must now accommodate the special needs of the diving mammal. Unlike the fixed open system of terrestrial mammals, the oxygen pathway for marine-living mammals performs multiple roles (Fig. 3.5). During activities on land or on the water surface, the pathway is open and can operate as in terrestrial mammals. Oxygen flows from ambient air to the lungs, diffuses across the alveoli into capillaries, and is transported through the cardiovascular system to the skeletal muscles where it is ultimately used in oxidative phosphorylation within the mitochondria (Weibel *et al.* 1987). Dispersed within the tissues of each major anatomical component are oxygen and energy stores that can act as buffers along the oxygen pathway. As discussed below, these oxygen stores play a unique role in supporting prolonged periods of submergence by mammals specialized for a marine lifestyle.

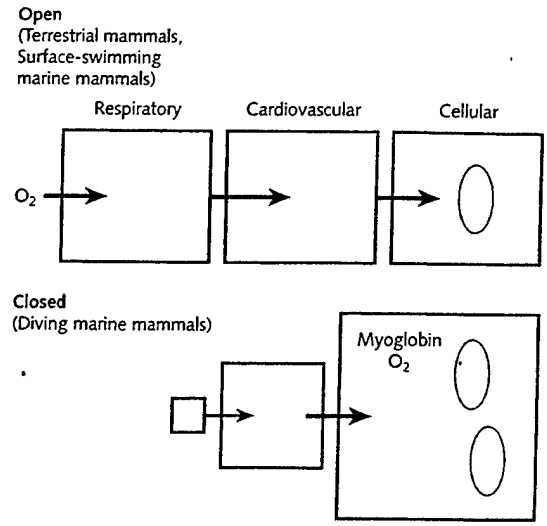


Fig. 3.5 The pathway for oxygen in mammals. Each box represents a major component of the path from ambient air to utilization in the skeletal muscles. The size of the boxes illustrates the relative importance of each component during open and closed states. Note the increased number of mitochondria and myoglobin stores characteristic of the skeletal muscles of marine mammals.

These same pathway components operate as a closed system when the marine mammal performs a dive. Ambient oxygen is no longer available, and the lungs often collapse with increased hydrostatic pressure at depth (Ridgway & Howard 1979; Skrovan *et al.* 1999). Bradycardia (decreased heart rate) associated with the dive response results in a reduction in cardiac output, changes in distribution of the blood, and marked changes in the transport of oxygen to skeletal muscles (see Butler & Jones 1997 for a review). Thus, during the course of a dive, the oxygen pathway of marine mammals is initially open for oxygen loading, closes during submergence when exercise takes place (and oxygen demands are highest), and subsequently reopens after surfacing.

3.3.1 Adapting the lungs for diving

The lungs of marine mammals show several morphological adaptations that support the transition to an aquatic lifestyle. However, the volume of the mammalian lung is dictated more by body size than by preference for a terrestrial or aquatic lifestyle.

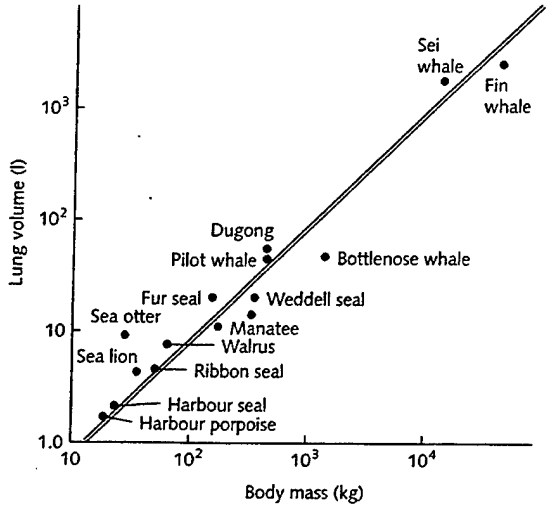


Fig. 3.6 Logarithmic plot of lung volume in relation to body mass for marine mammals. The solid line denotes the regression for all mammals from bats to whales. Note the exceptionally large lungs of the sea otter for its body size. (Redrawn from Kooyman 1973.)

For example, the volume of marine mammal lungs increases with body mass in a manner similar to that of terrestrial mammals (Fig. 3.6). Exceptions include sperm whales (*Physeter catadon*), bottlenose whales (*Hyperoodon* spp.) and fin whales (*Balaenoptera physalus*) whose maximum lung capacities are approximately half that expected for terrestrial mammals (Slijper 1976). Sea otters, dugongs (*Dugong dugon*) and several species of otariid show larger than expected lung volumes.

The size of the lung relative to body mass undoubtedly impacts buoyancy regulation and oxygen storage capacity. The sea otter in particular has an exceptionally large lung volume for its body size. Both lung mass and lung volume are nearly twice that measured for other marine mammals of similar body mass (Kooyman 1973). Such a large lung provides a convenient anatomical float for these animals as they feed on the water surface while using their abdomen as a table.

Although the large lung of the sea otter may also act as an oxygen depot during short dives, it is unlikely that the lungs of deep-diving marine mammals serve a similar role. Morphological evidence suggests that the lungs of many marine mammals collapse at depth, consequently altering buoyancy and the lung's usefulness as an oxygen store during submergence. Experiments comparing the mechanical properties of isolated lungs from dogs and sea lions demonstrated a progressive collapse in the marine mammal lung as hydrostatic pressure increased during simulated dives. The lungs of the dog trapped air rather than collapsed with changes in pressure (Denison *et al.* 1971). Pressure chamber tests on Weddell seals (*Leptonychotes weddelli*) and northern elephant seals (*Mirounga angustirostris*) also demonstrated tracheal collapse to less than half of its original dimension with exposure to increased hydrostatic pressure (Kooyman *et al.* 1970). Similar tests using lungs from bottlenose dolphins (*Tursiops truncatus*) indicate that the bronchi and trachea as well as the alveoli of the cetacean lung are collapsible. Only the bony nares, comprising a volume of 50 ml, are rigid (Ridgway *et al.* 1969). Changes in the oxygen and carbon dioxide content of expired air of a bottlenose dolphin trained to dive, swim and station at depth indicate that alveolar collapse is complete by a depth of 100 m (Ridgway *et al.* 1969). The lungs of larger whales including the pilot whale (*Globicephala melaena*) (Olsen *et al.* 1969), fin whale and sei whale (*Baleanoptera borealis*) (Scholander 1940) also show evidence of lung collapse in response to increased pressure. As discussed below (see 'Oxygen stores'), the unique collapsible lung of marine mammals enables the animals to avoid a deleterious buildup of nitrogen (N_2) and associated nitrogen narcosis, and decompression sickness (the 'bends') during a dive. Prolonged gliding behaviour during ascent and descent have also been attributed to changes in buoyancy that occur with lung collapse in several species of deep-diving marine mammals (Williams *et al.* 2000).

Mechanical differences in the lungs of mammals correspond to variations in the anatomical structure of the airways. A gradation in the architecture of small and large airways occurs in parallel with the degree of aquatic specialization in mammals. The semiaquatic river otter (*Lutra canadensis*) and shallow-diving sea otter have circular trachea with partially calcified rings. Calcification of the tracheal rings results in structural rigidity that may prohibit deep diving by these mammals. In comparison, deep-diving marine mammals such as the harp seal (*Pagaphilus groenlandicus*), Weddell seal, harbour

seal (*Phoca vitulina*) and walrus show decreased calcification of the trachea. This adaptation allows the tracheal rings to bend without breaking during compression at depth (Tarasoff & Kooyman 1973). Among marine mammals the phocid seals have the least modified terminal airway structure compared to terrestrial mammals. In seals a non-cartilaginous portion of bronchiole connects to a respiratory bronchiole and finally the alveoli. Large smooth muscles surround the cartilage-free segments. The otariids and whales represent the other extreme and have cartilaginous reinforced airways leading directly into the alveoli. A series of sphincter muscles are also present in the smaller airways of the cetacean lung (Kooyman 1973). Walrus and sea otter lungs are intermediate to these extremes and show some terminal airways without cartilage and others in which the cartilage extends directly to the alveoli. Whether by muscle or cartilage it is apparent that the airways of marine mammals, especially deep-diving species, are reinforced to ensure patency during lung compression at depth. These adaptations allow a progressive collapse of the lung structures as hydrostatic pressure increases during descent, with initial collapse by the alveoli and subsequently the small and large airways. The pattern then works in reverse as hydrostatic pressure decreases on ascent, and the lungs are able to reinflate in a progressive manner.

3.3.2 Oxygen stores

Despite routine closure of the oxygen pathway, marine mammals can maintain high levels of activity while submerged and preferentially rely on aerobic metabolism to support these activities (Kooyman 1989; Butler & Jones 1997). Maintenance and tight regulation of aerobic metabolism may be more critical in aquatic-adapted species than in terrestrial mammals due to the deleterious effects of anaerobic end-products, particularly on oxygen-sensitive tissues (i.e. brain and heart) during submergence. Unlike terrestrial mammals, sea otters, polar bears, pinnipeds and cetaceans must support the energetic demands of exercise while holding their breath. The ability to balance the conflicting demands for oxygen conservation and utilization during submergence ultimately dictates the diving limitations of the animal (Castellini *et al.* 1985; Hochachka 1986).

Exceptionally large stores of oxygen in the lungs, blood and muscles act as an on-board 'scuba tank' and facilitate aerobic activity by marine mammals during periods of submergence. Total oxygen stores of marine mammals often exceed 2–3 times those of terrestrial species such as dogs and humans. The distribution of these stores varies among the many taxa of marine divers (Fig. 3.7). In dolphins and

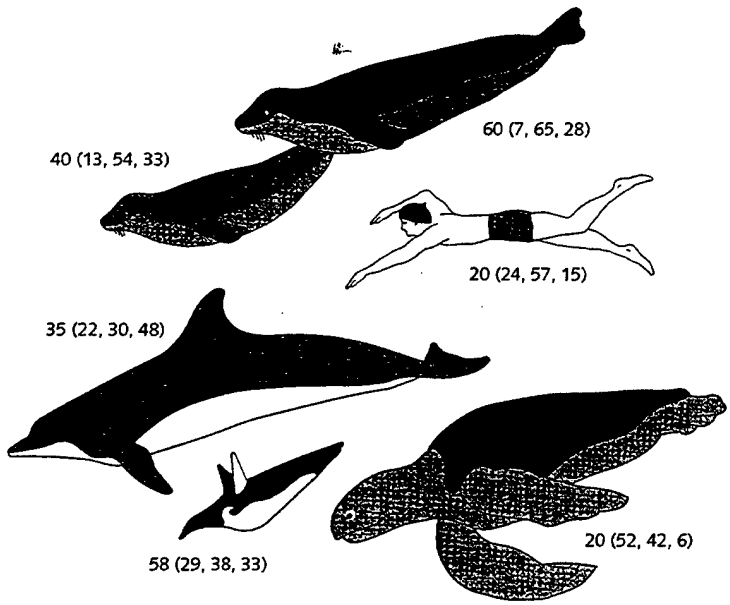


Fig. 3.7 Comparison of oxygen stores for major taxa of diving vertebrates. The numbers outside the parentheses represent the total oxygen store in ml O_2/kg. The numbers in parentheses are the percentage of the total oxygen store located in the lungs, blood and muscles, respectively. (From Kooyman 1989, with permission.)

humans, 22–24% of the total oxygen store is located in the lungs while the remaining 72–78% is sequestered in the blood and skeletal muscles. Only 13% of the total store occurs in the lungs of otariids. This compares to 7% in the lungs of phocid seals. Because nitrogen is stored with oxygen in the lungs, reliance on lung reserves would place the diver at risk of high blood nitrogen tensions at depth. To avoid this, elite divers such as Weddell seals, elephants seals and deep-diving whales have collapsible lungs that move air into the upper airways where it is not in contact with blood. These marine mammals preferentially use the skeletal muscles and blood as the primary oxygen storage sites. Over 87% of the total oxygen reserve of deep divers is distributed between these two tissues (Kooyman 1989).

Myoglobin serves as the primary oxygen carrier in the skeletal muscles of mammals and is exceptionally high in concentration in marine-adapted species. For example, the myoglobin contents of the locomotor muscles of terrestrial mammals often remain below 1.0 g myglobin/100 g wet muscle regardless of whether the animal is an elite sprinter or endurance athlete (Castellini 1981; Williams *et al.* 1997). In comparison, marine mammals show myoglobin contents that are 3–7 times higher. The skeletal muscles of sea otters have a myoglobin content of 3.1 g myglobin/100 g wet muscle (Lenfant *et al.* 1970). Among pinnipeds, the myoglobin content of the locomotor muscles correlates with maximum dive duration. Otariids, which are comparatively short divers, maintain myoglobin contents near 3.0 g myglobin/100 g wet muscle. Phocid seals, the elite divers among pinnipeds, have myoglobin contents that average 4–5 g myglobin/100 g wet muscle (Kooyman 1989). Cetaceans also rely on large oxygen reserves in the muscles to support aerobic metabolism during diving. However, the relationship between dive duration and myoglobin content is less clear for cetaceans and is complicated by the extreme range of body sizes for this group (Noren 1997). Large muscle oxygen reserves in cetaceans are a function of both high myoglobin content and large muscle mass, particularly in the enormous mysticete whales. Among odontocetes, myoglobin concentration in the longissimus dorsi (the primary swimming muscle)

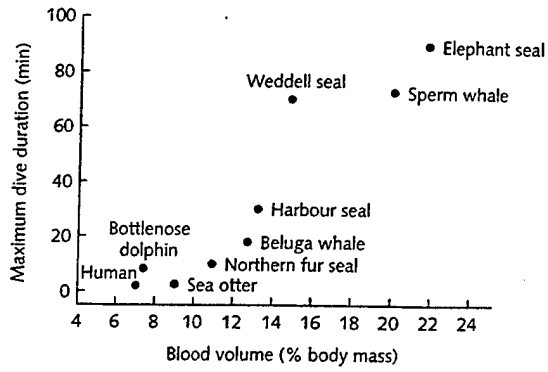


Fig. 3.8 Blood volume of marine mammals as a percentage of body mass in relation to maximum dive duration. (Data from Kooyman 1989.)

ranges from approximately 2.0 g myglobin/100 g wet muscle in the northern right whale dolphin to 8.0 g myglobin/100 g wet muscle in the narwhal (Noren 1997). Myoglobin contents of mysticetes range from 0.9 g myglobin/100 g wet muscle in the sei whale (Tawara 1950) to 3.5 g myglobin/100 g wet muscle in the bowhead whale (*Balaena mysticetus*) (Noren 1997; Noren & Williams 2000).

Oxygen storage capacity in the blood is enhanced in marine mammals by increases in: (i) blood volume, (ii) the number of circulating red blood cells, and (iii) haemoglobin concentration. As illustrated in Fig. 3.8 there is a positive correlation between blood volume and maximum dive duration in mammals. This was demonstrated in a study by Ridgway and Johnston (1966) that compared the oxygen storage characteristics of blood from three species of small cetacean. The species selected varied in diving and swimming capabilities. The investigators reported blood volumes of 143 ml blood/kg body mass for the highly active, deep-diving Dall's porpoise (*Phocoenoides dalli*). Values were 108 ml blood/kg body mass for the intermediately active Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and 71 ml blood/kg body mass for the more sedentary, coastal-dwelling bottlenose dolphin. Haemoglobin concentration, an important component of the oxygen-carrying capacity of blood, also reflected the aquatic

behaviour of each species. The highest haemoglobin concentration was found in the Dall's porpoise and the lowest in bottlenose dolphins. In general, haemoglobin concentrations for mammals are 14–17 g/100 ml blood for shallow to moderate divers such as humans, sea otters, northern fur seals (*Callorhinus ursinus*) and bottlenose dolphins, and 21–25 g/100 ml blood for deeper divers such as harbour seals, elephant seals, Weddell seals, Dall's porpoise and beluga whales (*Delphinopterus leucas*) (Kooyman 1989).

The elite divers among marine mammals, phocid seals, also alter blood oxygen by changing the number of circulating red blood cells during the course of a dive. The most detailed work concerning these changes has been conducted on freely diving Weddell seals in the Antarctic. Haematocrit (the volume of red blood cells per volume of blood) in these superb divers rises as the dive progresses, and declines back to resting levels during the postdive recovery period. The magnitude of these changes in haematocrit depends on the length of the dive. The longer the dive the greater the increase in haematocrit. Because the spleen of the Weddell seal is large (3–4 times larger than terrestrial mammals for its body mass), it can serve as an enormous reservoir of oxygenated red blood cells. During a dive, the spleen of the Weddell seal contracts and injects red blood cells into the circulation (Hurford *et al.* 1996). This results in the characteristic elevation in haematocrit and can induce a 60% increase in haemoglobin concentration within the first 10 min of a dive (Qvist *et al.* 1986). The benefit to the seal is an infusion of circulating oxygen within the red blood cells for the working tissues. Although highly developed in Weddell seals, this physiological mechanism is not unprecedented among mammals and has also been observed in exercising racehorses and dogs. Seals are simply able to take advantage of this physiological mechanism to support aerobic diving. Preliminary evidence suggests that splenic contraction occurs during breath-holding in other species of phocid seals, including the northern elephant seal. It remains to be seen whether the sequestering of red blood cells during rest and their mobilization during submergence provides an advantage for aerobic diving in other semiaquatic or marine mammals.

3.3.3 Physiological responses to submergence

During submergence mammals undergo a suite of physiological changes known as the dive response. Key elements of the response are: (i) breath-holding, which is termed apnoea, (ii) bradycardia, a pronounced reduction in heart rate, and (iii) peripheral vasoconstriction characterized by the selective redistribution of blood to oxygen-sensitive tissues. The level of response is variable and depends on such factors as the degree of aquatic specialization, species, dive duration, behaviour and type of dive. Very different physiological responses occur for voluntary and involuntary dives, with the most extreme diving response displayed during forced submersion.

The physiological response to submergence is a general mammalian phenomenon, although the degree of response differs in terrestrial, semiaquatic and marine mammals. Despite the ubiquitous nature of these physiological events among mammals, they should not be considered part of an invariant reflex. The response is far more complex than that. An unfortunate choice of terminology in earlier studies labelled the physiological changes with submersion as the 'diving reflex'. Later studies involving free-ranging marine mammals, as well as sea lions (Ridgway *et al.* 1975) and bottlenose dolphins (Elsner *et al.* 1966) trained to dive on command, demonstrated a level of conscious control over the intensity of bradycardia developed during submergence. As a result, the term 'diving response' rather than 'diving reflex' is considered more accurate in describing the many physiological changes that occur with submersion (Elsner 1999).

Obviously, the key to successful diving is the ability to breath-hold. In this regard, marine mammals are unrivalled. This is due in part to their large size and to their ability to store oxygen in the lungs, blood and muscles. As found for swimming speed, the duration of breath-hold does not necessarily correlate to body size in marine mammals (Fig. 3.3b). Phocid seals, especially the elephant seals and Weddell seal, tend to show longer dive durations than otariids, odontocetes and even many larger species of mysticetes. Within each of these taxonomic groups, however, body size appears to have an effect on breath-hold ability, and maximum dive

Taxonomic group	*n*	Mass range (kg)	Regression
Phocids	16	80–4000	Max. duration = 3.39 $Mb^{0.42}$
Otariids	13	30–270	Max. duration = 6.22 $Mb^{0.10}$
Odontocetes	22	60–51 700	Max. duration = 0.51 $Mb^{0.51}$
Mysticetes	9	12 700–145 000	Max. duration = 0.04 $Mb^{0.61}$

Table 3.1 Allometric relationships for maximum dive duration in relation to body mass for pinnipeds and cetaceans. Dive duration is in minutes and body mass (Mb) is in kilograms. (Data from Schreer & Kovacs 1997.)

duration increases predictably with body mass for each group (Table 3.1) (Schreer & Kovacs 1997). Maximum dive durations for phocid seals range from 11 min in the 250 kg crabeater seal (*Lobodon carcinophagus*) (Bengtson & Stewart 1992) to 120 min in a 600 kg female southern elephant seal (*Mirounga leonina*) (Hindell *et al.* 1991). Ranges for other marine mammal groups are 6–16 min for otariids, 2–138 min for odontocetes, and 15–50 min for mysticetes. Size ranges for these groups are shown in Table 3.1. Maximum dive duration for the 1.9 t walrus is 13 min (Wiig *et al.* 1993), and for the 1.6 t manatee (*Trichechus* spp.) is 16 min (Irving 1939). The longest dive duration recorded for a mammal is 138 min for the 51.7 t sperm whale (Watkins *et al.* 1985).

One of the hallmarks of the dive response is bradycardia, a marked reduction in heart rate. Nearly all marine mammals measured to date show a rapid and profound decrease in heart rate upon submergence. Bradycardia is maintained throughout the dive and followed by tachycardia, a rapid increase in heart rate, as the animal surfaces. Often an 'anticipatory tachycardia' occurs during the ascent from a dive as the animal prepares the cardiovascular system for oxygen loading (Fig. 3.9). Likewise, changes in heart rate may also occur during the predive period in anticipation of the upcoming dive. For an elite diver such as the elephant seal, typical heart rates for 150–250 kg animals range from 103 to 112 beats/min on the water surface to 20–50 beats/min during 10–17 min dives (Andrews *et al.* 1997). This compares with 197 kg bottlenose dolphins on trained dives ranging from 1 min to 4 min in which predive heart rates averaged 101–111 beats/min and decreased to 30–37 beats/min during submergence (Williams *et al.* 1999a). A 3.7 t male killer whale freely swimming and diving in a net pen demonstrated a range of heart rates from approximately 60 beats/min when on the water surface to 30 beats/min when submerged for longer than 15 s (Spencer *et al.* 1967). Cardiovascular responses of an otariid, the California sea lion, are comparatively slower. Predive surface heart rates of 150–250 beats/min gradually slowed to 20–50 beats/min during 1–3 min trained dives by 25–35 kg sea lions (Ponganis *et al.* 1997). The Amazonian manatee (*Trichechus inunguis*) is an exception to the typical pattern of surface tachycardia and marked bradycardia during submergence in marine mammals.

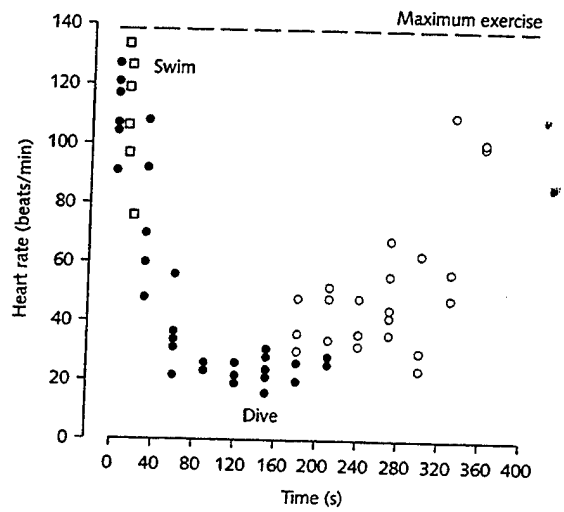


Fig. 3.9 Heart rate in relation to dive duration for bottlenose dolphins freely diving to 210 m. Each point represents the average heart rate for 10 s intervals during the dive. Solid circles are values for heart rate during the descent; open circles are for the ascent phase. Average heart rates for dolphins swimming on the water surface are shown by the squares. The upper dashed line illustrates the maximum heart rates for bottlenose dolphins pushing on a load cell. (From Williams *et al.* 1999a, with permission.)

The average heart rate of these comparatively sedentary herbivores is approximately 50 beats/min when breathing on the water surface and decreases slowly to just 30–40 beats/min on voluntary dives (Gallivan & Best 1986). Although the level of bradycardia in freely diving manatees seems attenuated, this sirenian is capable of marked bradycardia equivalent in magnitude to other marine mammals. When frightened during a dive, manatees can decrease their heart rate to as low as 5–6 beats/min.

The length of a dive influences the level of bradycardia developed by marine mammals. Free-ranging Weddell seals (Kooyman & Campbell 1972; Hill *et al.* 1987), grey seals (*Halichoerus grypus*) (Thompson & Fedak 1993), elephant seals (Andrews *et al.* 1997; Hindell & Lea 1998) and bottlenose dolphins (Williams *et al.* 1999a) demonstrate an inverse relationship between heart rate and the length of the dive. The longer the dive, the more intense the bradycardia, and hence, the lower the heart rate during submergence. One of the more impressive demonstrations of this response is in the grey seal. When resting on the water surface the heart rate of this 200 kg phocid seal averages 119 beats/min. Heart rate drops immediately upon submergence and can remain at only 4 beats/min during dives exceeding 15 min (Thompson & Fedak 1993). This intense bradycardia appears to be part of the normal physiological repertoire of the foraging grey seal. Many species of marine mammal, as illustrated by the manatee, also demonstrate exceptionally low heart rates if forcibly submerged or subjected to a behavioural disturbance during the dive (Kooyman 1989; Butler & Jones 1997). These extreme heart rates can be 2–10 times lower than measured during natural dives.

The decrease in heart rate on submergence is accompanied by a selective redistribution of blood in the diving mammal. As observed for heart rate, the level of vascular response depends on the type of dive. In a detailed study of Weddell seals, injected microspheres were used to determine relative blood flow to tissues during involuntary submersions. Significant declines in blood flow from resting values were recorded for all tissues except the brain during the simulated dive (Zapol *et al.* 1979). Evidence from renal and hepatic tests indicates that blood flow to the kidneys and liver is more variable during voluntary diving by Weddell seals (Davis *et al.* 1983). Normal renal and hepatic function, and hence blood flow to these organs, occurs during natural aerobic dives. During prolonged dives that exceed 23 min, kidney function is reduced but hepatic blood flow may be maintained in Weddell seals.

It seems obvious that circulation to the skeletal muscles involved in powering swimming movements would be beneficial for supporting aerobic activity during the dive. Measured indirectly by changes in temperature (Ponganis *et al.* 1993) and partial pressures of nitrogen (Ridgway & Howard 1979), circulation to the skeletal muscles does appear to remain open in freely diving marine mammals. Extreme vasoconstriction can occur during involuntary or exceptionally long dives, and markedly reduces blood flow to the skeletal muscles. A consequence of this vascular shutdown is a sharp rise in blood lactate during the postdive recovery period once blood flow to the muscles is restored (Scholander 1940).

3.3.4 Exercising under water

In view of the marked physiological responses to diving, how does the marine mammal exercise while submerged? In terrestrial mammals, heart rate typically increases as a function of exercise intensity (Brooks *et al.* 1996). This does not always occur for marine mammals, particularly during submergence. Recent studies using miniaturized heart rate monitors and time depth recorders on free-ranging marine mammals have demonstrated that the duration of submergence rather than the level of exercise *per se* dictates many of the cardiovascular and respiratory responses observed during diving. For example, the changes in heart rate for bottlenose dolphins freely diving to 210 m (Fig. 3.9) are similar to those of sedentary dolphins quietly resting on the bottom of a 2 m deep oceanarium pool (Elsner *et al.* 1966). Many diving pinnipeds, including elephant seals (Andrews *et al.* 1997), grey seals (Thompson & Fedak 1993) and California sea lions (Ponganis *et al.* 1997), maintain steady, reduced heart rates during submergence irrespective of locomotor speed. Based on these studies, the physiological adjustments associated with the dive

response over-rides those typically associated with an exercise response. This over-ride feature appears to be most developed in highly adapted marine mammals. Other diving vertebrates, including many species of sea birds (Butler & Jones 1997) and the hippopotamus (Elsner 1966), show increased variability in heart rate when exercise is superimposed on breath-holding during submergence.

These findings do not imply that the level of effort has no effect on oxygen utilization or energetic cost to the diver. Rather, the timing of oxygen loading for marine mammals differs from that of terrestrial mammals. Except under extreme levels of effort, oxygen loading occurs simultaneously with exercise in terrestrial mammals. In diving and swimming marine mammals there is a requisite temporal delay in oxygen loading relative to when exercise takes place. As a result, the physiological effects of exercise during diving are manifested primarily during the postdive recovery period. Exceptionally high physiological rates may occur in the period immediately after a dive. For example, the postdive heart rate and respiratory rate of bottlenose dolphins reach the highest levels recorded for any activity (Williams *et al.* 1993). Several studies on pinnipeds (Thompson & Fedak 1993; Andrews *et al.* 1997) have suggested that comparatively high physiological rates during these postdive periods benefit the marine mammal by reducing the requisite recovery time and shortening the interdive surface interval.

A recent study that simultaneously examined the postdive oxygen consumption and locomotor behaviour of Weddell seals has demonstrated the effect of exercise on diving costs. Seals were fitted with a miniaturized, submersible camera and released into an isolated ice hole. The animals freely dived and foraged beneath the Antarctic sea ice while flipper stroking was videotaped from the backward-facing camera (Davis *et al.* 1999). Analysis of the tapes revealed several modes of swimming by the seals including constant stroking, prolonged gliding on descent and burst-and-glide locomotion on ascent. The range of swimming speeds averaged 1.5–2.0 m/s regardless of the mode of swimming. However, the energetic costs of each were very different. The more strokes used by the seal, and consequently the greater the number of muscle contractions, the higher the postdive oxygen consumption (Williams *et al.* 2000). Clearly, exercise, even if performed while submerged requires energy for the working muscles and an oxygen payback on surfacing.

Several biochemical and morphological adaptations allow the skeletal muscles of marine mammals to continue working despite the closure of the respiratory pathway (Fig. 3.5). Oxygen storage in myoglobin has already been discussed. Other adaptations include elevated mitochondrial volume density and enhanced aerobic enzyme capacities in the muscles that power swimming movements. The volume density of interfibrillar mitochondria in the locomotor muscles of pinnipids (Steller sea lions, northern fur seals and harbour seals) is 1.7–2.2 times greater than predicted for terrestrial mammals of similar size (Kanatous *et al.* 1999). Whether an adaptation to hypoxia (Kanatous *et al.* 1999) or endurance exercise (Hochachka 1998), such elevated skeletal muscle mitochondrial densities place these marine mammals among the elite mammalian athletes.

3.4 THERMOREGULATION: THE CHALLENGE OF WARM BODIES IN COLD WATER

One of the most difficult challenges faced by mammals making the transition from land to sea was thermoregulation. In retaining the same high body temperatures of terrestrial mammals, these animals often faced large thermal gradients for heat loss, particularly when living in polar regions (but see also Box 3.2). The physical properties of water, including high heat capacity and thermal conductivity, result in heat transfer rates that reach 24 times that of air at similar temperatures (Dejours 1987). Transitional marine mammals, as well as extant pinnipeds, whose life history includes terrestrial and aquatic periods are further challenged by the conflicting responses necessary for coping with the disparate thermal properties of air and water.

Marine mammals deal with the potentially high rate of heat loss during immersion in two ways, physiologically and morphologically. They can elevate heat production by increasing metabolic rates to compensate for high heat losses. Alternatively, they can increase insulation to help retain body heat

BOX 3.2 TOO HOT OR TOO COLD?

We frequently think of thermoregulation in marine mammals as a problem in keeping warm while immersed. However, under certain conditions marine mammals must also be able to dissipate excess heat. This requires the use of 'thermal windows' to circumvent the insulating layer of fur or blubber. Sparsely haired appendages and enlarged peripheral areas such as the dorsal fins and flukes of cetaceans (Pabst *et al.* 1995) facilitate the transfer of excess heat during periods of high heat production or elevated environmental temperatures (Fig. 1).

These poorly insulated areas are serviced by a specialized countercurrent arrangement of blood vessels (Parry 1949; Scholander & Schevill 1955; Hampton & Whittow 1976). Blood flow to the skin surface is increased during periods of high heat production to provide maximum cooling. The increases in heat flow associated with these circulatory changes have been examined in a wide variety of marine mammals including bottlenose dolphins (Williams *et al.* 1999b), harbour porpoises (Kanwisher & Sundnes 1965) and Hawaiian spinner dolphins (Hampton & Whittow 1976). The use of the dorsal fin and flukes as radiators seems especially important in some odontocetes for the regulation of temperature-sensitive organs such as the intra-abdominal testes (Rommel *et al.* 1994; Pabst *et al.* 1995).

Many pinnipeds, particularly those in polar regions, routinely experience high solar radiation and have high densities of arteriovenous anastomoses (AVAs) in their skin. These specialized blood vessels are used to bypass the insulating blubber layer in times of heat stress and carry excess heat to the skin surface for dissipation (Molyneux & Bryden 1978; Bryden 1979). AVAs are also found in the flippers of otariids and may be used for removing excess heat while swimming (Bryden & Molyneux 1978). In addition, sweat glands on the flippers of otariids aid in heat transfer. On hot days

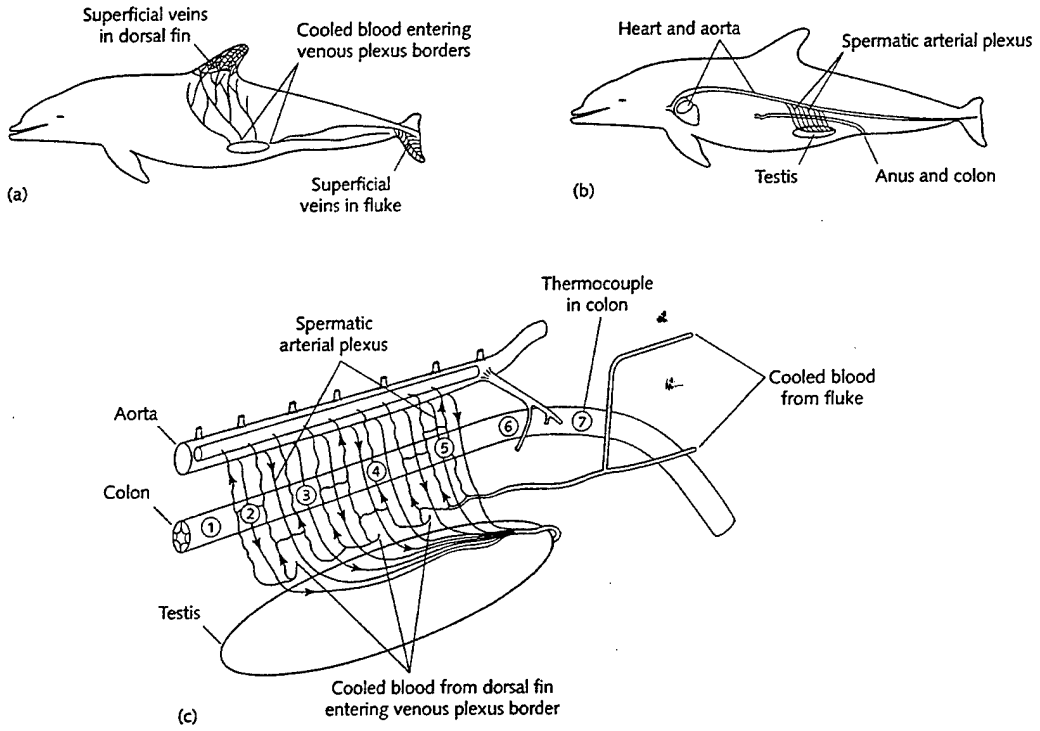


Fig. 1 Countercurrent exchangers in the extremities and the testes of the bottlenose dolphin. (a) Blood in the superficial veins of the dorsal fin and flukes is cooled by exposure to surrounding water. (b, c) This cooled blood is then passed to a countercurrent exchanger in association with the testes. In this way the peripheral structures form a radiator that help to cool the internal organs. Numbers 1–7 represent measurement sites for assessing variation in the temperature of blood leaving and entering the testicular region. (From Pabst *et al.* 1995, with permission.)

(*continued on p. 88*)

BOX 3.2 (*cont'd*)

sea lions and fur seals can often be seen fanning their flippers and increasing evaporative heat loss at these sites (Blix *et al.* 1979). It should be noted that sweat glands are not found in the skin of cetaceans.

Evaporative cooling resulting from both sweating and respiratory losses accounts for less than 20% of heat production in California sea lions studied under experimental conditions (Matsuura & Whittow 1974; South *et al.* 1976). Instead of relying solely on physiological mechanisms, these animals may use behavioural thermoregulation such as simply entering the water as the primary mechanism for dealing with high environmental temperatures (see Odell 1974 for a review). Likewise, many tropical or temperate pinniped species are overinsulated for life on land and rely on behavioural mechanisms to prevent overheating. During extended periods of time ashore, as occurs during breeding and molting, these marine mammals may avoid the sun or move into water to cool down (Gentry 1972; Limberger *et al.* 1986; Frances & Boness 1991). Similarly, some species of phocid seals will spend the warmer periods of the day in the water to avoid excessive heat absorption (Watts 1992).

when immersed. The former response is an excellent short-term solution, but is energetically expensive if maintained for long periods (see Chapter 9). The latter is the most efficient long-term solution for maintaining a high stable core temperature while living in water.

3.4.1 Increasing metabolic rate

Heat production in marine mammals may be increased by a variety of mechanisms including activity, the processing of food, and shivering and non-shivering thermogenesis (see Chapter 9). The sea otter provides an excellent example of a marine mammal that takes advantage of all of these mechanisms to help maintain its body temperature. This small marine mammal has a highly variable core body temperature (Costa 1982; Costa & Kooyman 1982; Davis *et al.* 1988) that rises during periods of activity and slowly falls during rest periods. To compensate for high heat losses in water, sea otters rely on a basal metabolic rate that is 2.4 times the expected value of a terrestrial mammal. In addition, these mammals increase their level of activity as water temperature decreases, and utilize heat produced from the digestion of food to maintain high core temperatures (Costa & Kooyman 1982, 1984).

The relative importance of these various mechanisms for supplementing heat production in other species of marine mammal is not known. For decades it had been widely accepted that the basal metabolic rates of marine mammals are considerably greater than those of terrestrial mammals of similar size (Scholander 1940; Scholander *et al.* 1942; Irving & Hart 1957; Hart & Irving 1959; Kanwisher & Sundnes 1965, 1966; Ridgway & Patton 1971; Ridgway 1972; Snyder 1983). These high rates were thought to result from the perceived need to cope with thermal stresses associated with exposure to the cold aquatic environment. However, recent studies suggest that the basal metabolic rates of marine mammals may depend on the individual species and life history patterns (see Fig. 9.1, Chapter 9). Some species appear to have metabolic rates near those predicted for terrestrial mammals of similar size (Oritsland & Ronald 1975; Parsons 1977; Gallivan & Ronald 1979; Gaskin 1982; Lavigne *et al.* 1982; Yasui & Gaskin 1986; Worthy 1987; Kasting *et al.* 1989). This is consistent with measurements by Worthy *et al.* (1987) on juvenile porpoises, but contrasts with Kanwisher and Sundnes (1966) who suggest that porpoises need to function at six times predicted metabolic levels to survive. Other species such as the sea otter have exceptionally high basal metabolic rates. Still others including manatees and dugongs have relatively low metabolic rates that average 25–30% of values predicted for similarly sized terrestrial mammals (Scholander & Irving 1941; Gallivan & Best 1980, 1986; Gallivan *et al.* 1983; Irvine 1983; Miculka & Worthy 1995). Most probably, the herbivorous feeding habits, sedentary lifestyle and tropical distribution of these sirenians contribute to the low rates of heat production observed.

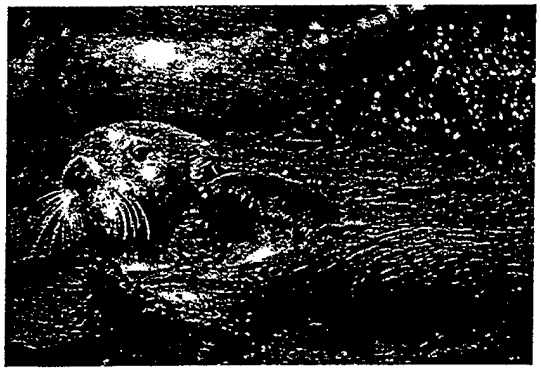
Activity and the processing of food may supplement heat production in many of these species, but

will depend on the mobility of the animal as well as composition of the diet. Parry (1949) inferred from his studies on the insulation of harbour porpoise, that small cetaceans are obliged to remain active to maintain core body temperature. The Atlantic bottlenose dolphin and the Hawaiian spinner dolphin (*Stenella longirostris*) depend on the energy produced by activity and the digestion of food, as well as marked control over peripheral blood flow to maintain thermal balance (Hampton & Whittow 1976).

3.4.2 Increasing insulation

The alternative solution to maintaining core temperature during immersion is to insulate the body. For mammals, the type of insulation varies with the degree of aquatic specialization, and undoubtedly changed during the transition from terrestrial to aquatic living. Semiaquatic mammals such as beavers, muskrats and otters that move between the thermally disparate media of air and water, maintain dense pelage for insulation in water. In some of these species, fur insulation alone is inadequate for retaining body heat during prolonged periods of immersion. Small semiaquatic mammals including the water rat and mink show a progressive decrease in core body temperature when immersed, and must shuttle between cooling periods in water and warming periods on land (Williams 1986). In contrast, sea otters spend most of their lives in water and rely exclusively on fur for insulation (Fig. 3.10a). This is made possible by an exceptional, waterproof fur coat that is the densest of any mammal measured to date with over 150 000 hairs/cm^2 in some anatomical sites (Williams *et al.* 1992). The insulating value of this unique fur is similar to that of blubber but is packaged in a thinner layer. However, relying on dense pelage for insulation while in water comes at an energetic cost to the sea otter. The maintenance of this specialized fur requires that sea otters spend at least 12% of their day grooming to maintain its water repellency and insulating value.

The insulation of choice for obligate marine mammals is blubber. Otariids, particularly the fur seals, combine an external fur layer and an underlying blubber layer to keep warm. Most marine mammals, including phocid seals, sirenians and cetaceans, rely



(a)

(b)

Fig. 3.10 Two types of insulation in marine mammals. (a) Sea otters rely on dense pelage for remaining warm in water while cetaceans (b) and seals utilize a thick layer of blubber. The blubber layer also provides body streamlining and an energy store for marine mammals.

solely on a thick, internal blubber layer to conserve heat (Worthy & Lavigne 1987; Worthy 1991; Watts 1992; Williams *et al.* 1992; Miculka & Worthy 1995). Although blubber acts as the primary insulator for most marine mammals, it also serves several other functions including as an aid for streamlining and buoyancy, and as a major energy store (Fig. 3.10b). Depending on the animal's immediate needs, these roles may conflict and result in regional variations in blubber depth. For example, Ryg *et al.* (1988) reported that some anatomical sites of phocid seals appear to be overinsulated while other sites are underinsulated. Similar results have been found for elephant seals (Gales & Burton 1987) and a variety of cetaceans including beluga whales and narwhals (Doidge 1990), as well as bottlenose dolphins, a

species that shows a high degree of seasonal variability in blubber thickness for different body regions.

A large database established for bottlenose dolphins documents seasonal changes in blubber depth (G.A.J. Worthy *et al.*, unpublished data). These changes correspond to seasonal changes in water temperature. However, the magnitude of change in blubber depth seems relatively minor in comparison to the marked seasonal temperature changes experienced by some dolphins. For example, mean overall blubber depths in Florida bottlenose dolphins range from 12.8 mm when the water temperatures approach 33°C to 17.6 mm in the winter when water temperatures decline to 20°C.

These relatively small changes in thickness may be all that is necessary for retaining body heat due to variability in the quality of insulation provided by blubber. The blubber layer is the most obvious store of body fat for marine mammals. Furthermore, the quantity and type of fat dictates the thermal characteristics of blubber (Parry 1949; Kanwisher & Sundnes 1966; Ryg *et al.* 1993). In some species, blubber may account for virtually all of the body's fat stores (Worthy *et al.* 1992). Worthy and Edwards (1990) reported that harbour porpoise blubber is comprised of 81.6 ± 3.6% lipid, while the blubber of spotted dolphins is only 54.9 ± 2.8% lipid. These differences in lipid content in addition to a thicker blubber layer results in an insulating layer in harbour porpoises that is four times more effective in retaining body heat than the blubber of spotted dolphins (Worthy & Edwards 1990). Comparative studies on other cetaceans indicate that the blubber of Pacific white-sided dolphins and common dolphins (*Delphinis delphis*) is a more effective insulator than that of bottlenose dolphins. The differences have been attributed to both blubber thickness and marked differences in lipid content (Worthy 1991).

The importance of insulation to the survival of marine mammals becomes especially apparent during environmental or anthropogenic events that overwhelm the thermoregulatory capabilities of the animal. This was noted during the 1989 *Exxon Valdez* oil spill in Alaska. The disruption of fur insulation following contamination with crude oil was a factor that contributed to the high mortality of sea otters (Williams & Davis 1995). Unusual water temperatures encountered by wild marine mammals can also be detrimental if insulation is inadequate. This occurred in the winter of 1989–90 when exceptionally cold temperatures froze the coastal waterways of Texas. The thin blubber layer of bottlenose dolphins trapped in frozen bays resulted in high levels of heat loss and led to the deaths of 26 animals.

3.5 OSMOREGULATION: WATER BALANCE WHILE LIVING IN THE OCEAN

A delicate balance between water intake and excretion is required for mammals to maintain the appropriate concentration and volume of internal fluids that bathe the cells. This process, termed osmoregulation, is responsible for maintaining the concentration of water and electrolytes comprising the animal's internal environment. The primary organ responsible for osmoregulation is the kidney. Feeding and water ingestion by an animal alters osmoregulatory balance, which is re-established by the removal of excess fluids and electrolytes through urine, faeces and evaporation.

The high salinity of sea water and the absence of fresh drinking water present major physiological challenges to the osmoregulatory system of marine mammals, and undoubtedly influenced the transition from land to sea in some lineages. As observed for the other organ systems examined in this chapter, both physiological and morphological modifications accompanied the transition from reliance on fresh water to living in sea water.

The size and structure of the kidneys of marine mammals reveal the morphological solution to the problem of water balance when living in highly saline environments. In general, the kidneys of marine mammals are larger than found in terrestrial mammals of similar body mass (Beuchat 1996). The ratio of kidney to body mass ranges from 0.44% in the fin whale to 1.1% in the bottlenose dolphin and white-sided dolphin. This compares with the relatively small kidney to body mass ratio of terrestrial mammals which ranges from 0.3% in elephants to 0.4% in humans, deer and zebras (Slijper 1979). Another difference between marine and terrestrial

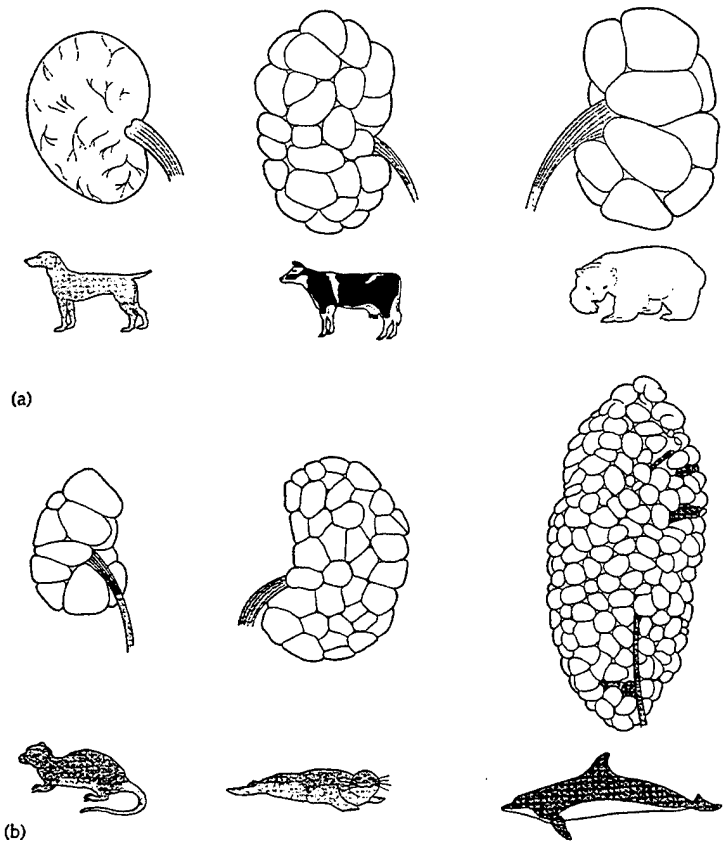


Fig. 3.11 External structure of the mammalian kidney. (a) Terrestrial mammals (dog, cow, bear) are compared to (b) semiaquatic (river otter) and marine (seal, dolphin) mammals. Note the increased number of lobes (reniculi) for the kidneys of marine-living mammals. (Redrawn from Slijper 1979.)

mammals is the number of lobes, termed reniculi, that comprise each kidney. Rather than a single, smooth lobe as found for humans and horses, the kidneys of many species of marine mammal are highly subdivided with each reniculus often serving as a complete miniature kidney with a cortex, medulla, papilla and calyx (Fig. 3.11). The number of reniculi is larger in cetaceans than observed for cattle. Thus, we find over 450 reniculi in the kidney of the bottlenose dolphin, and more than 3000 reniculi in mysticete whales. Elephants, bears, West Indian manatees and otters have 6–8 reniculi in each kidney, while cattle may have 25–30 reniculi. The dugong is an exception. Although this mammal lives in a marine environment, it has a smooth kidney. The number of reniculi in the kidneys of marine mammals corresponds roughly to the salinity of the diet, and, therefore, increased capacity for urine excretion. Whales and seals that feed on saline-enriched crustaceans tend to have a more lobulated kidney than river dolphins or other freshwater animals with a low salt content diet (Slijper 1979).

Not all marine mammals live in a highly saline environment. Amazon River dolphins (*Inia geoffrensis*) and manatees occupy freshwater rivers, and some populations of phocid seals can be found in freshwater lakes. Polar-living phocids such as Weddell seals may chew on ice or snow, and captive seals will drink from a hose or trough (Ridgway 1972). Obviously, fresh water is available for these animals. However, is it absolutely necessary? Do marine mammals need to drink fresh water to maintain internal water and electrolyte balance? The answer to both of these questions is no.

Animals can utilize three basic sources of water for osmoregulation. The most obvious source is free water that the animal drinks. Less obvious, but of great importance to many marine mammals, is preformed and metabolic water in food. Preformed

water is a direct component of food. Because most fish and invertebrates consist of 60–80% water, these prey items supply a considerable amount of free water to an animal without actually drinking. Metabolic water is derived from the metabolism of fat, protein or carbohydrate during the digestion of food. Mammals can derive 1.07 g of water from each gram of fat that is broken down, and 0.4 g of water from each gram of protein. The fattier the fish, the more water that is available to the animal. Interestingly, the same process takes place when the animal breaks down internal fat and protein stores, as occurs when marine mammals fast. Marine mammals can derive both energy and water from the catabolism of its own fat reserves during fasting. The catabolic process is so effective that no adverse effects were reported for a sea lion deprived of fresh water and salt water for 45 days (Pilson 1970). Concomitant with fasting by marine mammals is a decrease in urinary output to conserve water. Fasting elephant seal pups will reduce urine output by 84% after 10 weeks of fasting (Adams & Costa 1993) complementing other water-sparing mechanisms (Huntley *et al.* 1984).

Much of the anatomy and physiology of marine mammals is designed for reducing water loss. The major routes of water loss from the body are through evaporative processes and excretion in urine and faeces. Pinnipeds possess few sweat glands and cetaceans have none. Thus, water loss through surface evaporation is relatively minor in these mammals. Evaporation of water from the respiratory tract is also low due to the presence of countercurrent exchangers that help retain moisture (Huntley *et al.* 1984). These countercurrent mechanisms are similar in function to those of desert species. Water loss associated with urinary output will also vary according to the degree of protein catabolism. Protein breakdown results in the formation of urea that must be removed in the urine. As a result, increased protein catabolism results in increased water losses for marine mammals. The net effect is a loss of water.

Mariposia (seawater drinking) may be beneficial to animals on a high protein diet, since sea water can provide urinary osmotic space for urea (Hui 1981; Costa 1982). Sea otters have one of the highest reported rates of seawater consumption for any marine mammal, averaging 62 ± 27 ml/kg/day, with a range of 0–124 ml/kg/day (Costa 1982). It is unlikely that this rate of saltwater ingestion is incidental to swallowing prey since sea otters consume their prey while floating on their backs. Rather, Costa (1982) suggests that sea otters actively consume sea water to aid in the high rates of urea production associated with the animal's high protein diet.

Seawater ingestion has been reported for a number of other marine mammals. Captive northern fur seals consume 1.8 ml sea water/kg body mass/day, and harbour seals will consume 4.8 ml/kg/day incidental to feeding (Depocas *et al.* 1971). The rate of seawater ingestion is considerably higher for cetaceans. Common dolphins will drink 12–13 ml/kg/day of sea water when not feeding, and take in approximately 73 ml sea water/kg body mass/day across the skin surface (Hui 1981). Similar rates of seawater influx have been reported for harbour porpoises and feeding Atlantic bottlenose dolphins (D.P. Costa & G.A.J. Worthy, unpublished data). The bottlenose dolphins had a water flux of 42.1–71.3 ml/kg/day, 31% of which was from preformed and metabolic water, and 69% of which was from drinking water or water crossing the skin surface. Other species of seals, sea lions and porpoises either actively ingest sea water or are at least capable of it (Pilson 1970; Ridgway 1972; Gentry 1981).

Water balance is especially interesting in the manatee, a freshwater marine mammal. Little is known about the ability of wild manatees to osmoregulate and maintain water balance, but their anatomy suggests an enhanced capacity to concentrate their urine (Maluf 1989). Captive manatees held in saltwater conditions without access to fresh water and fed a diet of sea grass showed significant increases in plasma osmolality and plasma concentrations of sodium and chloride within 9 days (Ortiz *et al.* 1998). The manatees eventually refused to eat sea grasses containing high salt concentrations. These data suggest that wild manatees may require regular access to fresh, or perhaps brackish, water to meet water balance needs. In captive situations, this need is met by drinking fresh water or by eating food that is high in free water (e.g. lettuce at approximately 94% water). Manatees living in fresh water and consuming lettuce show the highest rate of water

intake (145 ± 12 ml/kg/day) compared to manatees in salt water on a diet of lettuce (45 ± 3 ml/kg/day) or manatees exposed to salt water on a diet of sea grass (21 ± 3 ml/kg/day).

3.6 CONCLUSIONS

It is apparent from this chapter that the physiology of mammals underwent considerable modifications that accompanied marked anatomical changes during evolution. Many of the physiological responses can be attributed to the unique physical characteristics of the marine environment in comparison to life on land. Each modification in body form and physiological function undoubtedly came with an energetic consequence. How these modifications affect metabolic rate and contribute to the total energy budget of marine mammals is discussed in Chapter 9.

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Three-dimensional movements and swimming activity of a northern elephant seal ☆

Randall W. Davis[a,*], Lee A. Fuiman[b], Terrie M. Williams[c], Burney J. Le Boeuf[c]

[a]*Department of Marine Biology, Texas A&M University at Galveston, 5007 Avenue U, Galveston, TX 77553, USA*
[b]*Department of Marine Science, University of Texas at Austin, Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA*
[c]*Department of Biology and Institute of Marine Science, University of California, Santa Cruz, CA 95064, USA*

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Abstract

We attached a video system and data recorder to a northern elephant seal to track its three-dimensional movements and observe propulsive strokes of the hind flippers. During 6 h of recording, the seal made 20 dives and spent 90% of the time submerged. Average dive duration, maximum depth and swimming speed were 14.9 min ± 6.1 S.D., 289 m ± 117 S.D. and 1.1 m s^{-1} ± 0.12 S.D., respectively. The distance swum during a dive averaged 925 m ± 339 S.D., and the average descent and ascent angles were 41° ± 18 S.D. and 50° ± 21 S.D., respectively. Dive paths were remarkably straight suggesting that the seal was navigating while submerged. We identified three modes of swimming based on the interval between propulsive strokes: continuous stroking; stroke-and-glide swimming; and prolonged gliding. The seal used continuous stroking from the surface to a mean depth of 20 m followed by stroke-and-glide swimming. Prolonged gliding started at a mean depth of 60 m and continued to the bottom of dives. For dives to depths of 300 m or more, 75% of the descent time was spent in prolonged gliding and 10% in stroke-and-glide swimming, amounting to 5.9–9.6 min of passive descent per dive. Average swimming speed varied little with swimming mode and was not a good indicator of propulsive effort. It appears that the seal can use prolonged gliding to reduce the cost of transport and increase dive duration. Energetically efficient locomotion may help explain the long and deep dives that routinely exceed the theoretical aerobic dive limit in this species. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Elephant seal; Swimming; Diving; Three-dimensional; Navigation; Orientation; Locomotion

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* Corresponding author. Tel.: +1-409-740-4712; fax: +1-409-740-5002.
E-mail address: davisr@tamug.tamu.edu (R.W. Davis).

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1. Introduction

The northern elephant seal (*Mirounga angustirostris*) is a pelagic marine mammal that spends most of the year in the eastern North Pacific Ocean. At Año Nuevo Point (37° 8.0′N Lat., 122° 20.0′W Long.), California, adult females come ashore between mid-December and mid-February to give birth and breed and in April to molt (Le Boeuf et al., 1994). At sea, females migrate long distances (up to 10 800 km round-trip) in a broad expanse of the eastern Pacific as far north as 60° N Lat., and from near the coastline to as far west as 172.5° E Long. (Le Boeuf et al., 1993; Stewart and DeLong, 1993, 1994; Le Boeuf et al., 2000). During the 10-week foraging trip after the breeding season, females older than 2 years dive for an average duration of 20.8 min ± 4.1 S.D. (range = 16–23 min), swim at routine speeds of 0.9–1.7 m s^{-1}, and reach an average maximum depth of 509 m ± 147 S.D. (range = 325–550 m) (Le Boeuf et al., 1992; Crocker et al., 1994; Le Boeuf, 1994). Stewart and DeLong (1994) reported similar results for females breeding on San Miguel Island in southern California. During the 8-month foraging trip to sea after molting, which coincides with gestation, average dive duration of females in the third trimester of pregnancy is 39% longer than in non-pregnant females (Le Boeuf, 1994), possibly due to an increase in blood volume (Danforth, 1977) and total body oxygen stores. For both non-pregnant and pregnant females, intervals at the surface between dives are generally short (approx. 2.1 min ± 0.5 S.D.), and approximately 90% of the total time at sea is spent submerged (Le Boeuf, 1994; Le Boeuf et al., 2000).

Our knowledge of the underwater behavior of elephant seals is based primarily on indirect information provided by dive depth and duration statistics and estimated swim speeds. In an attempt to elucidate the underwater behavior of these animals, these data have been used to identify several dive types that occur during transit, benthic or pelagic foraging, and food processing (Le Boeuf et al., 1988, 1992, 1993; Hindell et al., 1991; Asaga et al., 1994; Crocker et al., 1997). The data supporting these putative dive types are not empirical but circumstantial. To provide a better understanding of elephant seal diving behavior, we attached a small video system and data recorder to a female elephant seal in Monterey Bay, California. We use this new and highly detailed information to describe diving behavior, evaluate potential energy-saving locomotor strategies, and comment on diving physiology and navigation.

2. Methods

2.1. Animal

We used the translocation–homing paradigm to study diving behavior of an elephant seal as it returned to the beach from which it was displaced (Oliver et al., 1998). Most seals return to the capture site in approximately 4 days after being translocated to sea by approximately 50 km. Diving performance in this situation is similar to that of migrating seals (Le Boeuf et al., 1996; Oliver, 1997).

We captured a 27-month-old female northern elephant seal that weighed 263 kg (Identification Number GJ904R; standard length = 201 cm; axillary girth = 165 cm) at Año Nuevo Point, California, on 2 April 1996 and transported it 30 km south to the Long Marine Laboratory at the University of California at Santa Cruz. The seal was immobilized with an intramuscular injection of ketamine hydrochloride (2 mg kg^{-1}). After cleaning the fur in the mid-dorsal area with acetone, a piece of neoprene rubber (0.5-cm thick, 30 cm in diameter) was glued to the fur along the dorsal midline above the shoulders with neoprene rubber cement. The video system was attached with hose clamps to small brass rings sewn to the rubber. The video camera faced rearward so that we could observe the propulsive strokes of the hind flippers during dives. The antenna for a Global Positioning System (GPS) was glued to the fur on the top of the seal's head, and a satellite telemeter (Wildlife Computers, Redmond, WA, USA) and VHF radio (Advanced Telemetry Systems, Bethel, MN, USA) were glued to the neoprene rubber on its back. The seal was allowed to recover from the sedative overnight. It was then transported offshore and released beyond the continental shelf in northern Monterey Bay (36° 46.428′ N Lat., 122° 1.053′W Long.) at 11.45 PST on April 3. Video and data were recorded from 11.38 to 17.38 PST. The seal returned to Año Nuevo Point 1 week later and the instrument was recovered.

2.2. Video system and data recorder

The video system and data recorder were fabricated by Pisces Design (San Diego, CA, USA). The torpedo-shaped, aluminum housing was 30-cm long, 13 cm in diameter and pressure rated to a depth of 2000 m. The instrument weighed 6.2 kg in air and 2.2 kg (less than 1 % of the seal's body mass) in water. The cross-sectional area of the housing was 6% of the maximum cross-sectional area of the seal. The wide angle (80° horizontal, 60° vertical) low-light sensitive (0.3 lux), black and white CCD camera (Chinon GX060, Mountainside, NJ, USA) was encircled by an array of blue light emitting diodes (LEDs) (Ledtronics, Torrance, CA, USA). The blue LEDs provided sufficient illumination for the camera to record objects at a distance of 2 m in complete darkness. When additional ambient light was available, objects were visible at much greater distances. The aluminum housing contained an 8-mm video tape recorder (Sony EVO-220 VTR), lithium batteries, and a microprocessor for programming camera functions and encoding data from transducers. A data encoder received digital signals directly from transducers or from the 14-bit A/D board (Maxim, Sunnyvale, CA, USA) and encoded them into the vertical blanking interval of the videotape. The signal from the hydrophone was recorded on the VTR's audio track. The video system was activated by an external switch on the housing or by a programmable microcontroller. Maximum recording duration was 6 h. Onboard transducers sampled once per second. A pressure transducer (Series-20, Keller-PSI, Hampton, VA, USA) was used to record depth. Swimming speed though the water (water speed) was measured with a miniature, vertical axis impeller transducer (Ultramarine, Galveston, TX, USA) that had excellent linearity and was able to record from 0.3 m s^{-1} (stall speed) to over 3.5 m s^{-1} $\pm$ 0.045 S.D. It was calibrated in situ using the method of Hill (1986) and Blackwell et al. (1999) in which the rate of change in depth (m s^{-1}) was plotted against the output from the speed sensor and a linear equation was fitted to the upper edge of the data. This line represents vertical movements in which depth change and speed are equal. Using computed positions in three spatial dimensions (see Section 2.3, below), there were 140 observations for which the seal was moving at an angle $> 80°$ from horizontal. The flux-gate compass (KVH, Middletown, RI, USA) was fully gimbaled ($\pm 95°$) and had a mean standard deviation for any compass bearing of 0.38°. Rolls or pitches more than $\pm 95°$ exceeded the gimbaling and were recorded as an error to indicate unreliable bearing data. Location at the surface was determined with a GPS (GPS 25, Garmin, Lexena, KS, USA) and 6-cm diameter submersible antenna (Applied Ocean Physics, San Diego, CA, USA). The hydrophone (Pisces Design, San Diego, CA, USA) had a frequency response of 50–16 kHz. The data encoder superimposed time, date, depth (m), swimming speed (m s^{-1}) and compass bearing (0–360°) on the video image during playback.

2.3. Data analysis

Three-dimensional dive paths were computed from depth, compass bearing, and swimming speed using standard 'dead reckoning' methods (Bowditch, 1995). Dead reckoning enabled us to compute the animal's position at any time during a dive from knowledge of a known position (i.e. GPS position prior to diving), time, water speed, and bearing. Initial dive path calculations produce the 'course steered', which reflects the result of only the animal's swimming. Ocean currents and accumulated sensor errors also affect calculation of the animal's position. The direction and speed of these external effects are called 'set' and 'drift,' respectively, and are calculated from the difference between the end of the course steered and the GPS position at the end of each dive. The final dive path, called the 'course made good,' is computed by applying the set and drift equally throughout the dive, thereby assuming uniformity in space and time (Bowditch, 1995). The corrected coordinates of the course made good enable calculation of the speed of the seal relative to a fixed position in space (ground speed). This is different from the speed reported by the onboard flow meter, which reports water speed.

The digitized video image, synchronous three-dimensional dive path, and numerical data (time, depth, water speed and compass bearing) were integrated and displayed simultaneously on a personal computer using software developed at Texas A&M University. This type of analysis enabled us to relate the seal's movements in space with flipper strokes and water speed. Flipper stroke interval was calculated as the time between maximum left and maximum right excursions of the flippers

as seen on the digitized video record. These points were recorded as video frame numbers, giving a resolution of 0.033 s. Stride length is defined as the distance the seal traveled during a single flipper stroke (i.e. left-to-right or right-to-left). It was determined from the onboard flow meter data and not corrected for set and drift because stride calculations pertain to swimming effort and the movement of the seal with respect to the water, rather than with respect to a fixed position on the ground. Straightness of swimming paths and surface GPS positions was quantified using the net-to-gross displacement ratio (NGDR), the net distance between two endpoints divided by the total distance swum between those points. NGDR takes a value of 1.0 when the animal swims in a straight path between the endpoints. Any deviation from a straight path decreases the ratio.

3. Results

During the 6 h of continuous video and data recording, the seal made 20 dives and spent 90% of the time submerged (Table 1). Average dive duration was 14.9 min ± 6.1 S.D. (range = 0.6–22.2 min), and average maximum depth was 289 m ± 117 S.D. (range = 14–430 m). Swimming speed (water speed) while submerged averaged 1.1 m s^{-1} ± 0.12 S.D. The distance swum along the course steered averaged 925 m ± 339 S.D., ranging from 41 to 1273 m ($N = 20$ dives). Surface intervals between dives averaged 1.8 min ± 0.4 (range = 0.4–2.3 min). While at the surface, the seal rested in an upright or prone position, being carried by the current at approximately 0.3–0.4 m s^{-1}. No vocalizations or other distinguishable sounds were heard on the audio recording.

3.1. Three-dimensional movements during dives 1–8

Three-dimensional dive paths (course made good) were calculated for dives 1–8 (Fig. 1). The GPS antenna cable failed after dive 8, so the seal's surface location at the beginning and end of dives 9–20 could not be determined. Although this prevented computation of the course made good for the later dives, depth, speed, bearing, and stroke data were collected for all 20 dives.

Net horizontal displacement based on the first and last GPS positions (point-to-point) for dives 1–8 was 3.3 km along a west–northwesterly heading of 297°. The path through the animal's surface positions was remarkably straight (Fig. 1), with a horizontal net-to-gross displacement ratio (NGDR) of 0.91. The courses steered while sub-

Table 1
Summary statistics for the series of 20 dives by the elephant seal

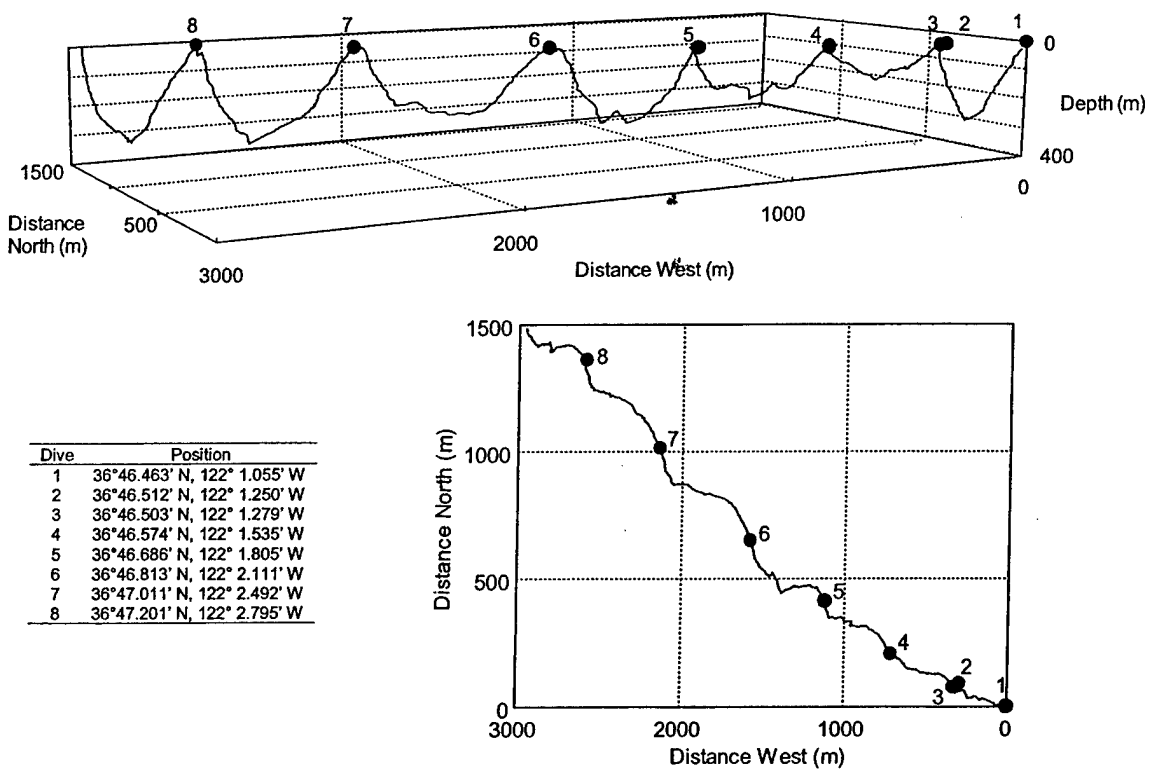
Dive	1	2	3	4	5	6	7	8	9	10
Pre-dive interval (min)	2.23	1.75	1.37	2.02	2.15	1.90	1.65	2.28	1.87	2.00
Duration (min)	9.42	0.63	7.65	10.38	12.78	13.27	15.50	17.85	18.45	15.00
Mean depth (m)	150	8	69	113	163	153	192	221	228	231
Maximum depth (m)	260	14	115	173	247	229	333	325	343	402
Distance steered (m)	708	41	550	777	946	961	1097	1038	996	939
Mean speed (m s^{-1})	1.3	1.0	1.2	1.2	1.2	1.2	1.2	1.0	0.9	1.0
Maximum speed (m s^{-1})	2.2	1.3	1.5	1.7	1.7	1.7	1.7	1.7	1.7	1.5
Total propulsive strokes	531	34	456	602	723	676	723	715	667	656
Time gliding (min)	3.47	0.1	2.28	3.47	4.38	5.33	6.93	9.18	10.9	6.9

Dive	11	12	13	14	15	16	17	18	19	20	Mean
Pre-dive interval (min)	1.87	1.7	2.03	1.37	0.42	1.45	2.02	1.77	2.13	1.98	1.8
Duration (min)	14.97	18.97	19.43	18.72	2.23	21.58	22.23	19.00	19.57	20.38	14.90
Mean depth (m)	205	240	242	223	32	257	258	223	244	259	186
Maximum depth (m)	333	352	361	323	58	384	394	332	374	430	289
Distance steered (m)	940	1004	1133	1049	156	1229	1258	1162	1245	1273	925
Mean speed (m s^{-1})	1.1	0.9	1.0	0.9	1.2	1.0	0.9	1.0	1.1	1.0	1.1
Maximum speed (m s^{-1})	1.6	1.7	1.5	1.6	1.4	1.6	1.7	1.5	1.5	1.5	1.6
Total propulsive strokes	609	655	729	638	101	769	798	725	820	783	621
Time gliding (min)	7.53	11.13	10.38	11.10	1.03	12.07	12.53	10.27	9.68	10.63	7.47

merged in each dive averaged 283° ± 9.0 and were significantly less linear than the GPS path, with an average horizontal NGDR of 0.69 ± 0.12. However, the effect of currents was to straighten the actual dive paths (mean horizontal NGDR for course made good = 0.78 ± 0.08 S.D.).

The seal descended to depths of more than 100 m in all but dive 2, a dive that was very short (38 s) and which will be excluded from further analysis. Dives 3, 4, 5, and 6 included more than one descent and ascent, whereas dives 7 and 8 involved a single descent to the bottom of the dive, followed by an ascent to the surface. Mean total distance traveled over the course made good (906 m ± 179 S.D., 7 dives) was 1.9 (±0.4 S.D.) times the net displacement (476 m ± 101 S.D.) between the surface positions at the start and end of dives. This ratio is a measure of the additional distance that the animal traveled by descending to depth rather than swimming directly between the endpoints at the surface. The mean horizontal transit speed (net displacement per dive divided by elapsed time) was 0.7 m s^{-1} ± 0.18 S.D.

Angles of descent and ascent (dives 1, 3–8) were calculated from the three-dimensional position data and smoothed using an 11-s moving average to reduce the error arising from the 1-m precision of the depth sensor. Mean (smoothed) descent angle was 41° ± 18 S.D. and was not significantly different during the first 60 m of descent (42° ± 17 S.D.) or when the seal was deeper (40° ± 18 S.D.). The mean ascent angle was 50° ± 21 S.D. Ascent angles during the last 60 m were steeper (55° ± 23 S.D.) than they were for deeper portions of ascents (48° ± 20 S.D.). All pairwise differences in these four mean angles (shallow and deep during descent and ascent) were highly significant ($P < 0.001$, Student's t-test) except shallow (≤ 60 m) vs. deep dive angles during descent ($P = 0.049$). Calculating average descent and ascent angles from swim speed, time, and depth data alone, rather than using the



Dive	Position
1	36°46.463' N, 122° 1.055' W
2	36°46.512' N, 122° 1.250' W
3	36°46.503' N, 122° 1.279' W
4	36°46.574' N, 122° 1.535' W
5	36°46.686' N, 122° 1.805' W
6	36°46.813' N, 122° 2.111' W
7	36°47.011' N, 122° 2.492' W
8	36°47.201' N, 122° 2.795' W

Fig. 1. Reconstructed three-dimensional dive path of an elephant seal during the first eight dives of the deployment. Surface GPS positions prior to the beginning of each dive are shown in the figure. Submerged positions are plotted at 1-s intervals computed by dead-reckoning techniques and corrected for the effects of currents. The lower panel (aerial view of the same series of dives) shows the relatively straight path swum by the seal. The depth of water at this location was approximately 1000 m.

three-dimensional position data, yielded lower values. For example, mean (smoothed) descent angle was 34° ± 18 and mean ascent angle was 34° ± 20 S.D.

3.2. Locomotor activity

Analysis of the interval between propulsive strokes of the hind flippers in all 20 dives revealed three modes of swimming: continuous swimming; stroke-and-glide swimming; and prolonged gliding. The division between continuous stroking and stroke-and-glide swimming was at a local minimum (2.5 s) in the frequency distribution for tail beat interval (Fig. 2). The division between stroke-and-glide swimming and prolonged gliding was where the declining trend of stroke-and-glide swimming met the level distribution for prolonged gliding (see inset of Fig. 2). Using these divisions, the mean tail beat interval was 0.76 s (±0.19 S.D.) for continuous stroking, 5.7 s (±2.28 S.D.) for stroke-and-glide swimming, and 51.6 s (±67.8 S.D.) for prolonged gliding. Many episodes of prolonged gliding lasted for 1–2 min and some as long as 6 min.

The occurrence of these swimming modes varied with depth and whether the seal was descending or ascending (Fig. 3). The seal used continuous stroking as it descended from the surface down to a mean depth of 20 m (range = 6–34 m), then began using a stroke-and-glide swimming mode. Prolonged gliding started at a mean depth of 60 m (range = 5–177 m) and continued to the bottom of the dive. For the 13 dives to depths of 300 m or more, 75% of the descent time was spent in prolonged gliding (range = 54–85%) and 10% in stroke-and-glide swimming (range = 2–27%) (Fig. 4). This amounted to 5.9–9.6 min of passive descent (during stroke-and-glide swimming and prolonged gliding) per dive.

Swimming (water) speeds varied slightly with swimming mode and whether the seal was ascending or descending, as exemplified by data for dives 1–8 (Fig. 5). Overall mean speed was 1.2 m s^{-1} (±0.23 S.D.); continuous stroking yielded the fastest speeds and prolonged gliding the slowest. Stride length for continuous stroking averaged 0.8 m (±0.13 S.D.) overall. During descent, stride length for continuous stroking was slightly greater than during ascent (0.9 ± 0.13 S.D. vs. 0.8 ± 0.11 S.D.). Continuous stroking during ascent was vigorous and produced noticeable yaw in the dive

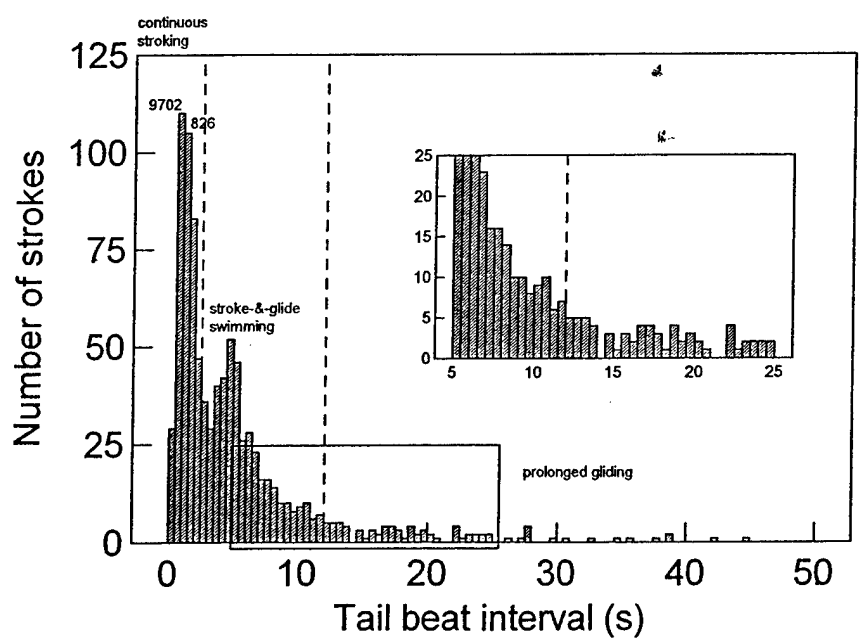


Fig. 2. The frequency distribution for intervals between consecutive propulsive strokes during 20 dives shows three modes of swimming. The limits of these swimming modes are at 2.5 and 12 s (dashed lines). Inset shows area of larger distribution enclosed by the rectangle. Bar width for both plots is 0.5 s. The two highest bars in the larger plot exceed the scale on the *y*-axis; numbers show actual frequencies.

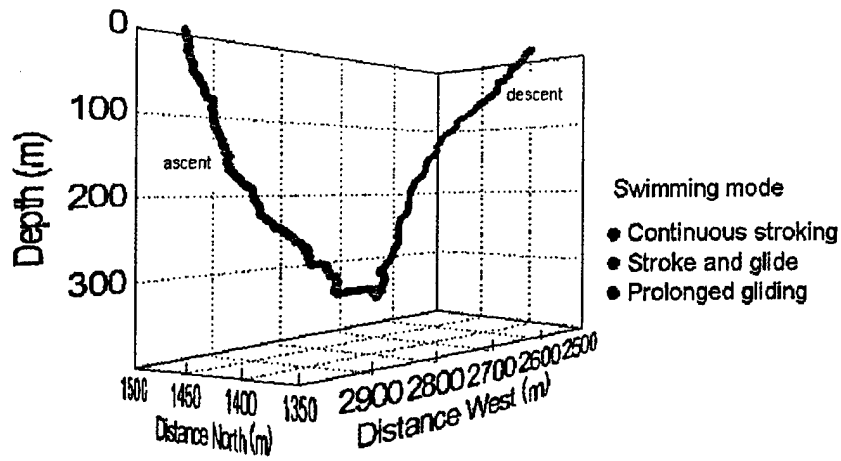


Fig. 3. Reconstructed three-dimensional dive path for dive 8 showing the spatial distribution of swimming modes. Prolonged gliding dominated the descent and continuous stroking was principally used during ascent. Stroke-and-glide swimming was used in horizontal swimming.

path. During ascents, stroke-and-glide swimming and prolonged glides occurred at mean speeds that were 11–13% less than during descent. Lowest mean speeds were recorded during prolonged glides in ascents (1.0 m s^{-1} ± 0.24 S.D.). However, such glides were rare (66 of 1938 s of ascent in dives 1–8), occurring mostly during the final approach to the surface when the animal was positively buoyant. By comparison, prolonged glides during descents averaged 1.1 m s^{-1} (±0.19 S.D).

4. Discussion

4.1. Diving behavior

Dive depth as a function of time has been well described for northern elephant seals based on data obtained from time–depth recorders (Le Boeuf et al., 1986, 1988; Le Boeuf, 1994). Although these time–depth profiles appear to give two-dimensional information, they provide only one spatial dimension (i.e. depth). In one study, depth and swim speed (water speed) were measured simultaneously providing information on two spatial dimensions (depth and horizontal displacement) so that descent and ascent angles could be estimated (Le Boeuf et al., 1992; Crocker et al., 1994). However, because of the absence of data for the third dimension, movements within the horizontal plane were neglected. The NGDR for course steered while submerged (0.69) reflects lateral meanders that contribute to a greater total distance traveled than would be estimated from

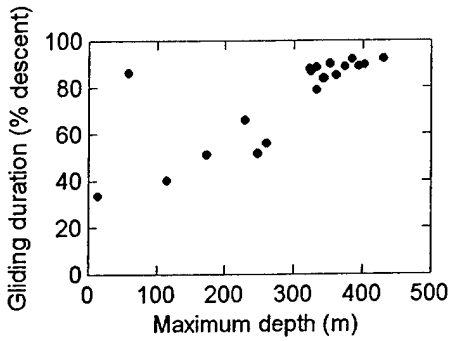


Fig. 4. Proportion of time spent gliding during descent in 20 dives. The seal used progressively more gliding to descend in deeper dives.

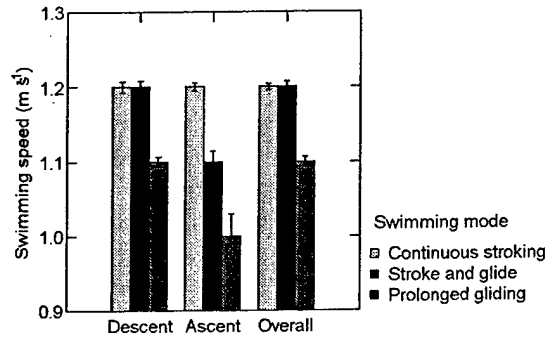


Fig. 5. Swimming speeds (water speeds) for each swimming mode and direction of movement. The seal maintained relatively consistent speeds in all swimming modes, even while passively gliding for prolonged periods.

depth and speed and which would result in an underestimate of computed angles of descent and ascent. In addition, the absence of GPS position at the surface precluded calculation of set and drift values that are necessary to convert water speed into ground speed (i.e. speed relative to a fixed position). As a result, true multi-dimensional spatial analysis of elephant seal dives has not been possible until now.

It was not possible to measure the potential effects of the video system and data recorder on the hydrodynamic drag of the seal in this study. However, the instruments were small relative to the size of the animal, representing less than 1% of the seal's body mass in water and 6% of maximum cross-sectional area. The depth, duration and average swimming speed of dives recorded were consistent with previous studies of female elephant seals using smaller time–depth recorders (Le Boeuf et al., 1996). We therefore consider the results to be comparable to previous studies of elephant seal diving behavior.

Most of the dives had the characteristics of Type A and B transit dives based on time–depth records (Le Boeuf et al., 1992, 1993; Asaga et al., 1994). In the present study, the seal descended at an average angle of 41° and ascended at an average angle 51°. These angles are similar to the those estimated by Le Boeuf et al. (1992) based on measurements of dive depth and swimming speed. However, this latter approach underestimates ascent and descent angle (see Section 3 above) relative to the more accurate, three-dimensional description of the dive path.

4.2. Energy-saving locomotor strategies

Stroke-and-glide swimming and prolonged gliding during descent can reduce the cost of transport in aquatic animals (Weihs, 1974) and, for air-breathing animals, may significantly increase dive duration (Williams et al., 2000). Both stroke-and-glide swimming and prolonged gliding incorporate periods of passive movement made possible as the ambient pressure compresses residual gas in the lungs to make the seal negatively buoyant (Williams et al., 2000). At a depth of 60 m, the negative buoyancy is greater than the seal's hydrodynamic drag when swimming at 1.0 m s^{-1} (Appendix A) and this allows the animal to continue its descent by gliding, without incurring the additional cost of stroking and with no change in swimming speed.

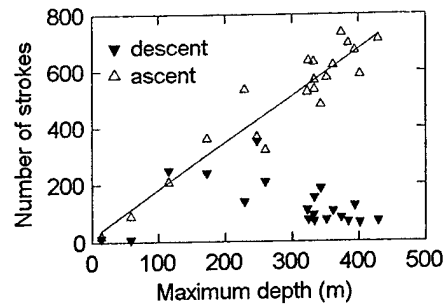


Fig. 6. Number of strokes used during a dive as a function of maximum depth. The number of strokes during ascent was proportional to the maximum depth ($Y = 16.76 + 1.65x$; $R^2 = 0.88$), whereas the number of strokes during descent was independent of dive depth.

Most of the cost of transport (excluding basal metabolism) arises from the propulsive strokes of the hind flippers. Williams et al. (2000) combined measurements of post-dive recovery oxygen consumption and distance swum over the course made good to estimate that Weddell seals can achieve an energy savings of 9–60% by incorporating prolonged gliding into dives. In the absence of recovery oxygen measurements in this study, the total number of propulsive strokes used during each of the dives provides a relative estimate of the energetic costs and possible energy savings incurred by gliding. The number of strokes used during ascents was directly proportional to maximum depth of the dive ($R^2 = 0.86$), whereas the number of strokes used during descents was independent of maximum depth ($R^2 = 0.01$) (Fig. 6). In 13 dives to depths exceeding 300 m, the seal used one-sixth as many strokes on descent as ascent. Indeed, the seal used fewer strokes (less than half as many) to descend to 300 m or deeper than it used in descents to shallower dives (< 250 m). Thus, the seal traveled farther and for a longer time using fewer strokes.

Another way to evaluate energy savings is to use the mean stride length (0.8 m) for continuous stroking to estimate the total number of strokes that would be required to cover the distance swum during a dive and to compare this with the actual number of strokes used. Such a comparison shows that the seal used 32–50% fewer strokes than predicted in the 20 dives. The savings were greatest in the deepest dives (> 300 m), where the seal spared 489–769 strokes, a savings

of 43–50% over continuous stroking throughout. If the number of strokes in a dive is a reasonable index of the cost of transport, these calculations suggest substantial energy savings by gliding.

Energy savings that arise from incorporating the stroke-and-glide and prolonged-gliding modes of locomotion into dives allow elephant seals and other diving mammals and birds to extend the length of time they are submerged. This helps resolve a paradox over the apparent ability of some diving animals to routinely exceed their theoretical aerobic dive limit (ADL) (Ponganis et al., 1992; Boyd and Croxall, 1996; Butler and Jones, 1997). The ADL is defined as the longest dive that an air-breathing animal can make while relying principally on oxygen stored in the lungs, blood and muscles to maintain aerobic metabolism (Kooyman et al., 1980). Most commonly, a theoretical ADL is calculated by dividing an animal's body oxygen stores by an estimate of diving metabolic rate which is assumed to be proportional to swimming speed (Le Boeuf et al., 1988; Ponganis et al., 1992; Butler and Jones, 1997). Based on such calculations, Hindell et al. (1992) observed that southern elephant seals (*Mirounga leonina*) regularly exceed their theoretical ADL and suggested that assumptions about body oxygen stores or diving metabolic rate must be incorrect. Boyd and Croxall (1996) came to a similar conclusion in a general review of routine dive durations for pinnipeds and seabirds.

Estimates of diving metabolic rate ranging from 0.7 to 5 times the mass-specific basal metabolic rate (BMR; Kleiber, 1975) have been used in calculations of the theoretical ADL for various species (Le Boeuf et al., 1988; Ponganis et al., 1992; Boyd and Croxall, 1996; Butler and Jones, 1997). In many cases, a diving metabolic rate greater than 1–2 times BMR results in an ADL that is too low to account for a high percentage of observed dive durations. These longer dive durations would be possible if diving metabolic rate were less than BMR (hypometabolism), which could theoretically result from the combined effects of the dive response (i.e. bradycardia and peripheral vasoconstriction) and hypoxic hypoxia (Butler and Jones, 1997). However, there is no experimental evidence for hypometabolism in pinnipeds during aerobic dives, and most organs and tissues probably receive adequate oxygen to maintain normoxic metabolic rates (Davis and Kanatous, 1999). Another explanation is that a large percentage of dives involves significant anaerobic metabolism (Ponganis et al., 1992). However, the brief surface intervals between dives (Table 1), even following unusually long and deep dives (Le Boeuf et al., 1988), do not allow sufficient recovery time for processing the high concentrations of lactic acid that would result from significant anaerobic metabolism. Our observations and those of Williams et al. (2000) demonstrate that swimming speed overestimates diving metabolism because gliding is less costly than continuous stroking. During gliding periods, muscular activity for propulsion is near zero and the animal does not incur the added active drag resulting from the movements of its flippers, which may be as much as three to five times the passive drag of a gliding animal (Fish et al., 1988; Skrovan et al., 1999). We suggest that gliding during large portions of a dive may lower metabolic rate so that it approaches resting levels without invoking a generalized hypometabolism. Such a low metabolic rate would help reconcile the discrepancy between routine dive durations and theoretical ADL.

4.3. Orientation and navigation

Based on GPS positions at the surface, the elephant seal was able to maintain a consistent mean heading of 297° over a horizontal distance of 3.3 km. This compass heading was parallel to the coast and in the direction (320°) of the capture site at Año Nuevo Point. Oliver et al. (1998) observed that the initial orientation of translocated elephant seals is often in the direction of the rookery where they were captured. Although the seals may head home immediately, they often do not haul out immediately once they reach the rookery. This is consistent with the behavior of the seal in this study.

The capacity of marine mammals to find their way at sea and the cues they use are poorly understood. Although the data from this study are limited, the seal appears to have been using navigation, rather than orientation. Orientation is the skill of recognizing and maintaining a direction. In orientation, an animal displaced laterally continues in its original direction as if it had not been displaced. Navigation requires the identification of the direction for a given point in space (Bowditch, 1995). When displaced laterally, a navigating animal adjusts its direction so that it con-

tinues to move toward a specific point. During prolonged gliding descent, the elephant seal was displaced in the general direction of the average current (i.e. to the northwest, based on set and drift calculations) (Fig. 1). However, the seal made course changes when it began stroking at the bottom of several dives or during ascents, which put it on a more westerly heading. Some of these course changes were gradual while others were as much as 90° over several seconds, suggesting that the seal was correcting for current. These course changes were executed primarily when the seal was propelling itself and not simply gliding. The effect of these 'corrective' changes in course was a consistent mean heading at the surface even though the dive path was less linear.

If this elephant seal was navigating a course, the cues it used are unknown. Possible orientation or navigation cues include water-borne sounds, landmarks visible at the surface, and the geomagnetic field. Evidence weighs against some acoustic and visual cues. Seals have keen directional hearing (Wartzok et al., 1992), but the hydrophone attached to the seal detected no sounds at frequencies between 50 Hz and 16 kHz. The seal could have sighted features on the coastline 19 km to the north, but this does not explain its ability to maintain a relatively straight course while submerged. A geomagnetic sense seems most likely. Use of geomagnetic cues for spatial orientation is widely distributed in vertebrates (Walker et al., 1984; Kirschvink et al., 1985; Walker et al., 1985; Deutschlander et al., 1999; Salmon and Wyneken, 1994; Lohmann and Lohmann, 1996; Walker et al., 1997). There have been no psycho-physical experiments to demonstrate that marine mammals can sense a magnetic field. Magnetic material has been reported in several cetaceans, although it remains uncertain whether it is magnetite (Zoeger et al., 1981; Bauer et al., 1985). If marine mammals can sense direction relative to the earth's geomagnetic field, water speed (Dehnhardt et al., 1998), depth and time, then they have the information needed to navigate. The data in this study suggest interesting possibilities for submerged navigation that will require further research.

5. Conclusions

Our unexpected discovery that elephant seals may spend long periods gliding during descent has important implications for our understanding of diving energetics. Dives to depths of more than 1000 m and migration distances of over 3000 km lasting up to months are energetically demanding. Better knowledge of the relationships among swimming activity, distance traveled, speed, and buoyancy is necessary before we can understand the full impact of gliding on energy budgets. It was equally unexpected that translocated seals would travel such direct return paths while submerged and in the presence of cross-currents. This observation points strongly toward a navigational capability. However, experiments will be necessary to verify this ability.

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Appendix A

The buoyancy of a 263-kg female elephant seal carrying the video system and data logger was estimated using the following equation modified from Webb et al. (1998):

$$B_T = (0.8871 M_T \times A) + (-0.6689 M_T \times L) + [0.027 g \rho M_T/(1 + D/10)] + (-21.6)$$

where B_T is total buoyancy in Newtons (N), M_T is total body mass, A is the percentage of adipose

tissue, L is the percentage of lean tissue, g is the acceleration due to gravity (9.8 m s^{-2}), ρ is the density of seawater (1.02 kg l^{-1}), D is the depth in meters, 0.8871 is the mass-specific buoyancy of adipose tissue (N kg^{-1}), −0.6689 is the mass-specific buoyancy of lean tissue (N kg^{-1}), 0.027 is the diving lung volume (l kg^{-1}; Kooyman et al., 1999), 1 is the atmospheric pressure at the surface, 10 is a factor for converting depth in meters to atmospheres of pressure, and −21.6 is the buoyancy (N) of the video/data recorder. We assumed that the female elephant seal was 36% adipose tissue and 64% lean tissue (Webb et al., 1998). Based on this equation, the instrumented seal was 21.8 N positively buoyant at the beginning of a dive and was neutrally buoyant at a depth of 4 m. At a depth of 20 m, when the seal began stroke-and-glide swimming, it was 26.6 N negatively buoyant. At a depth of 60 m, we assume that the negative buoyancy of the seal (−40.1 N) carrying the video system and data logger was greater than its hydrodynamic drag allowing it to glide passively for the remainder of the descent.

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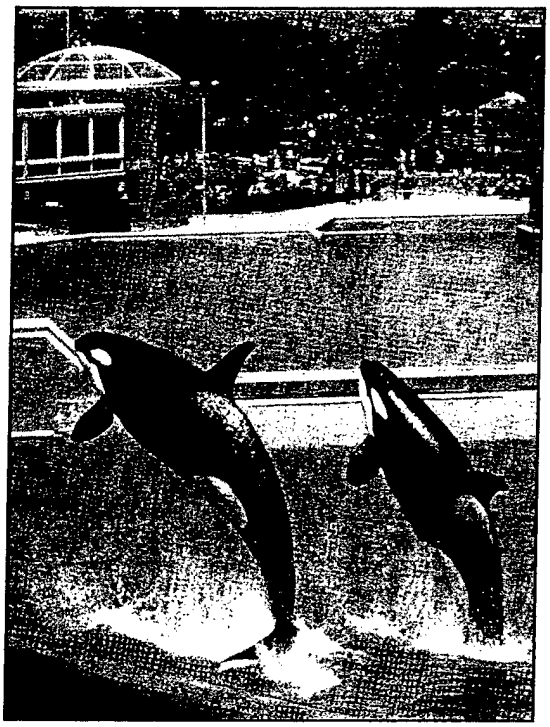

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18.3

Behavioral influences on diving energetics in penguins.

Rory P. Wilson
Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany

Free-living Magellanic Penguins *Spheniscus magellanicus* breeding at Cabo Virgenes, Argentina were equipped with new logging technology to examine factors important in the energetics of foraging. The following parameters were recorded: swim speed, depth, flipper beat frequency and amplitude, prey ingestion and volume of air inhaled immediately prior to diving. During dive descent, flipper beat frequency and amplitude decreased with increasing depth. Bottom phases of dives featured flipper beats with extended gliding phases and ascent typically featured an increasing time spent gliding closer to the surface. Trends in these patterns were more marked in dives to greater depths, this being apparently due to steeper descent and ascent angles and larger volumes of air inhaled prior to diving. This latter attribute serves to maximize oxygen stores while negating the effect of upthrust via compressed air spaces. During prey pursuit, flipper beat frequencies and amplitudes increased dramatically leading to increased energy expenditure and correspondingly shortened dives. Knowledge of the energetics of penguin swimming underwater under varying conditions of inhaled air, hydrostatic pressure, speed etc. enables the benefits of observed strategies to be modelled out. This work was funded by ICSU under the auspices of SCAR.

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18.4

THE EFFECT OF BEHAVIOR ON PHYSIOLOGICAL DIVE CAPACITY IN MARINE MAMMALS: WHAT LIES BENEATH.

Terrie M. Williams[1], L.A. Fuiman[2], M. Horning[3], and R.W. Davis[3], [1]Dept. of EE Biology, Univ. of California, Santa Cruz, CA, 95060; [2]Univ. of Texas, Port Aransas, TX 78373; [3]Texas A&M Univ., Galveston, TX 77553.

Many of the most energetically costly behaviors of marine birds and mammals occur while the animals are submerged. This not only represents a physiological challenge for air breathing vertebrates that must rely on limited oxygen stores, but also represents a logistical challenge to investigators trying to understand how these stores are used by freely diving animals. Advances in animal-borne video technology and instrumentation have provided new insights regarding the relationship between behavior and the energetic cost of diving in mammals. One strategy used by cetaceans and pinnipeds is to incorporate prolonged periods of gliding during a dive by taking advantage of changes in buoyancy at depth. For Weddell seals such "sink or swim" strategies result in a 9 - 60% savings in the energetic cost of a dive. Indeed, the cost of diving by these seals can be estimated from the total number of flipper strokes taken during submergence. By matching hunting behavior to recovery costs following a dive, we find that the energy expended to heat and assimilate prey is superimposed on other diving costs. For elephant seals and Weddell seals these additive costs represent a disadvantage in terms of dive capacity, with the animals balancing the cost of diving for distance or for digestion. For the smallest marine mammal, the sea otter, these digestive costs represent a necessary component of thermal balance, and as such provide a benefit by reducing long-term energetic costs. Supported by NSF- Polar Programs.

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18.5

PHYSIOLOGY AND BEHAVIOR OF FREE-DIVING PENGUINS.

Paul J. Ponganis, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093-0204.

Remarkable progress in elucidation of the diving behavior and physiology of penguins has been made with the use of time depth recorders, satellite transmitters, cameras, and the continued development of sensors and microprocessor-based data loggers. A variety of foraging strategies and swim patterns have been revealed by recent research. Findings include evidence for probable benthic foraging by several species, alterations in swim speeds by different species during the foraging phases of pelagic dives, detection of prey ingestion by esophageal temperature changes, sub-ice foraging by emperor penguins, and prolonged gliding during ascents of king penguins.

Recent physiological research has focused on the respiratory system and temperature regulation. Fluctuations in air sac pressures secondary to wing beats probably contribute to air sac O_2 utilization during swimming. Calculated diving air volumes of king penguins increase with maximum depth of dive, but are reduced on a mass-specific basis in comparison to those of Adelie penguins. Remarkable anterior abdominal temperature decreases have been documented in king and emperor penguins. Although it has been suggested that this may be associated with core hypothermia and decreased O_2 consumption during dives, findings in emperor penguins are more consistent with a preservation of core temperature and cooling of peripheral tissues. Complete understanding of the mechanisms responsible for the deeper- and longer-than-expected dives of penguins awaits further investigation.

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ORIGINAL PAPER

S. R. Noren · V. Cuccurullo · T. M. Williams

The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*)

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Abstract Bradycardia is an important component of the dive response, yet little is known about this response in immature marine mammals. To determine if diving bradycardia improves with age, cardiac patterns from trained immature and mature bottlenose dolphins (*Tursiops truncatus*) were recorded during three conditions (stationary respiration, voluntary breath-hold, and shallow diving). Maximum (mean: 117 ± 1 beats·min^{-1}) and resting (mean: 101 ± 5 beats·min^{-1}) heart rate (HR) at the water surface were similar regardless of age. All dolphins lowered HR in response to apnea; mean steady state breath-hold HR was not correlated with age. However, the ability to reduce HR while diving improved with age. Minimum and mean steady state HR during diving were highest for calves. For example, 1.5–3.5-year-old calves had significantly higher mean steady state diving HR (51 ± 1 beats·min^{-1}) than 3.5–5.5-year-old juveniles (44 ± 1 beats·min^{-1}). As a result, older dolphins demonstrated greater overall reductions in HR during diving. Longitudinal studies concur; the ability to reduce HR improved as individual calves matured. Thus, although newly weaned calves as young as 1.7 years exhibit elements of cardiac control, the capacity to reduce HR while diving improves with maturation up to 3.5 years postpartum. Limited ability for bradycardia may partially explain the short dive durations observed for immature marine mammals.

Keywords Heart rate · Bradycardia · Dive response · Development · Dolphins

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S. R. Noren (✉) · T. M. Williams
Ecology and Evolutionary Biology Department,
Center for Ocean Health, University of California,
Santa Cruz, CA 95060, USA
E-mail: snoren@biology.ucsc.edu
Fax: +1-831-4593383

V. Cuccurullo
The Dolphin Experience, PO Box F42433, Freeport,
Grand Bahamas Island, Bahamas

Abbreviations *ADL* aerobic dive limit · *cADL* calculated aerobic dive limit · *ECG* electrocardiogram · *HR* heart rate · *TDR* time–depth recorder

Introduction

The control of heart rate (HR) by marine mammals is a critical feature of the dive response that facilitates the prolonged breath-holds required for foraging and locomotion (Kooyman 1989). A hallmark of this control is bradycardia, a pronounced lowering of HR in response to submergence. Adult bottlenose dolphins (Irving et al. 1941) and killer whales (*Orcinus orca*; Spencer et al. 1967) exhibit a 50% reduction in HR upon submergence compared to resting on the water surface. Elsner et al. (1966) demonstrated an even more pronounced reduction in HR for an adult Pacific bottlenose dolphin (*Tursiops truncatus gilli*) trained to dive in a pool. In this animal, HR declined from 90–100 beats·min^{-1} while on the water surface to a minimum HR of 20 beats·min^{-1} within 60 s of diving. These studies on cetaceans and previous work on pinnipeds (Harrison and Tomlinson 1960; Irving et al. 1963; Van Critters et al. 1965; Ridgway et al. 1975; Andrews et al. 1997) suggest that bradycardia is a fundamental response to breath-hold by adult marine mammals.

Less is known about the cardiovascular responses of immature marine mammals or the relationship between diving capability and bradycardia during development. Postnatal development of cardiac control has been studied in terrestrial mammals, and to a lesser extent in marine mammals. Several changes in cardiorespiratory patterns characterize postnatal mammalian development. One of the most important is the link between respiratory and cardiac events. For example, cardiorespiratory patterns in human infants are irregular from birth to the sixth month of life (Patzak et al. 1996). The appearance of sinus arrhythmia, in which HR increases during inhalation and decreases during exhalation, is a normal pattern in terrestrial mammalian postnatal

development (Katona et al. 1980; Schubert et al. 1987; Leistner et al. 1990). As in terrestrial mammals, elephant seals (*Mirounga angustirostris* and *Mirounga leonina*) develop many features of cardiac control early in life (Castellini et al. 1994a, 1994b; Falabella et al. 1999). The changes in HR associated with normal sinus arrhythmia, sleep apnea, and diving apnea appear to be similar in seals, suggesting that regulation is by a common homeostatic control mechanism (Castellini et al. 1994b). Thus, attaining cardiac control during apneustic events prior to weaning likely facilitates the transition to sea, and the ability of seal pups to maintain bradycardia during diving. However, the development of diving bradycardia in marine mammals has only been examined in forced submergence studies on seals (Harrison and Tomlinson 1960; Irving et al. 1963; Hammond et al. 1969).

Although postnatal development of cardiac control has been studied in pinnipeds, little is known about changes in cardiac function with development in cetaceans. Unlike seals and sea lions, whales and dolphins are born directly into water and must breath-hold to swim and dive immediately postpartum. Consequently, cetaceans may exhibit evidence of cardiac control earlier in life than pinnipeds. Alternatively, because seals demonstrate a shorter period of maternal dependence and must independently forage sooner in life than dolphins, dolphins may be afforded a longer developmental period. For example, the developmental period required to attain mature oxygen stores that support diving is much shorter in seals than in dolphins (Noren et al. 2001); bottlenose dolphins do not attain mature oxygen stores in the muscle or blood until 3 years postpartum (Noren et al. 2001, 2002).

To determine the changes in cardiac response that occur with development in cetaceans, HR patterns of immature bottlenose dolphins (1.7–5.4 years old) were examined and compared to similar measurements collected from adult dolphins. We investigated instantaneous and average HR during stationary respiration on the water surface, voluntary breath-hold just below the surface, and shallow diving to depths of 4–5 m. Variability in HR throughout the respiratory cycle and the degree of bradycardia were quantified. The results show that although calves demonstrate elements of cardiac control by weaning, the level of bradycardia during diving improves with age until approximately 3.5 years postpartum.

Materials and methods

Animals

Nine dolphins (seven calves and juveniles, two adults) housed at the Dolphin Experience (Freeport, Grand Bahamas Island) were trained for the experiments. All dolphins were maintained in large (15 m×15 m×5 m deep) saltwater enclosures connected to the open ocean and fed a daily diet of capelin and herring supplemented with multi-vitamins (Sea Tabs). Studies were conducted over three field seasons (June–July 1999, May–June 2000, and June 2001). Mean temperatures for water and air were 29.0±0.10 °C and 29.6±0.29 °C, respectively. When possible, immature dolphins were studied longitudinally for all 3 years. The duration of the longitudinal studies for each dolphin depended on the age and level of training of the dolphin at the start of the study. All immature dolphins had been born at the facility and were of known age. Adults were sexually mature and had been maintained at the facility for at least 9 years; exact ages were unknown as they were originally obtained from the wild.

Body mass for each dolphin was calculated using Morphometric Calc pre-release Version 1.4 (Outernet Technologies International 1999, 2000) accessible at: http://www.outernet-tech.com/research/download/ (Messinger and Weissensel 1999). This equation utilizes gender, total body length, maximum girth, and age of the dolphin to estimate body mass. The equation was designed specifically for bottlenose dolphins; data used to formulate the equation were acquired from dolphins at four facilities including The Dolphin Experience. To validate the equation, both an adult and immature dolphin from the present study were weighed on a beaching scale. The measured and calculated body mass differed by only 4% and 9% for the adult and immature dolphin, respectively.

Heart rate

Data collection for HR was limited to calves that were old enough to be trained to wear the experimental equipment and to follow the experimental protocols (see below). Methods and equipment were similar to those used previously for assessing resting and active HRs in adult bottlenose dolphins (Williams et al. 1993b).

Instantaneous HR

To determine the relationship between respiratory events and instantaneous changes in HR, electrocardiogram (ECG) traces were recorded on grid paper for seven dolphins, one adult (age >9 years) and six immature animals (ages: 1.7–5.4 years). Two suction cups (8 cm diameter with a 2.5-cm diameter silver plate electrode) were attached to the dolphin. One cup was placed along the ventral midline directly below the pectoral fin insertions, and the other was placed above the right scapula. The two electrodes were attached by shielded wires to an electrocardiograph (Birtcher Model 365). Beat to beat measurements were recorded on an ECG trace while the dolphins performed two behaviors: (1) stationary respiration, and (2) voluntary breath-hold. For the stationary respiration trials, HR was recorded from breath to breath while the dolphin calmly rested on the water surface. One stationary respiration trial was conducted for each dolphin. The voluntary breath-hold trials were conducted to supplement shallow diving tests because equipment limitations prevented ECG recordings during diving. For these trials, each dolphin was trained to float upside-down on the water surface while ECG was continuously recorded from breath through submergence to the following voluntary breath (which ended the trial) according to Williams et al. (1993b). One voluntary breath-hold trial was conducted for five dolphins (age range: 2.0 years to adult). Throughout the trials, respiratory events of the dolphins were marked onto the ECG traces by an observer. HRs and breath-hold durations were determined from the scored traces (described in Instantaneous HR analysis below).

Average HR

To determine the effects of age on diving bradycardia, average HR was recorded for dolphins trained to dive to 4–5 m in depth. Suction cup electrodes were placed on the dolphins as described above, and attached to an HR monitor that was housed in a strap secured around the dolphin's pectoral fin. Signals from the HR monitor

were received continuously by a time–depth recorder (TDR; Mke 3 Wildlife Computers, Redmond, Wash.) also housed in the pectoral fin strap; average values for HR were recorded for each 10-s interval. HR was monitored while the dolphins performed two behaviors: (1) voluntary breath-hold as described above, and (2) shallow diving to 4–5 m. For the latter trials, the dolphins were trained to dive to a trainer on SCUBA stationed at 4–5 m subsurface. The dolphins were rewarded with fish throughout the dive. Dive trials ended when the dolphin voluntarily swam to the surface and took a breath. Two adults and seven immature dolphins (studied over 1–3 years) were used in these tests, affording an age range for immature dolphins of 1.7–5.4 years. During each session, several voluntary breath-hold or dive trials were performed while HR was continuously measured. An observer recorded the behavior (voluntary breath-hold or dive) and respiratory events of the dolphins throughout each session. The observer's watch was synchronized with the TDR clock prior to each session to correlate cardiac, respiratory, and behavioral events.

Analysis and statistics

Data were used to assess differences throughout maturation in: (1) the rate of onset of bradycardia upon breath-hold, (2) the ability to maintain a stable steady state HR during breath-hold, (3) mean HR during stationary respiration, breath-hold, and diving, (4) maximum HR at the surface, (5) minimum HR while diving, and (6) the percentage change in HR from surface breathing to diving. Statistical analyses were performed using Sigma Stat (Jandel Scientific 1999). Means ± 1SEM are presented and results deemed significant at $P < 0.05$ unless otherwise noted.

Instantaneous HR

Interbeat intervals were derived from the ECG trace (Fig. 1) after visually identifying each QRS complex. HR was calculated from each R-to-R interval visually, as the paper trace consisted of 1-mm square grids and the paper speed was set at 25 $mm \cdot s^{-1}$. Apnea duration during stationary respiration and voluntary breath-hold was determined from the time interval between two adjacent breaths using the observer marks on the ECG strip.

ECG records from stationary respiration trials were used to calculate mean resting HR. ECG records from voluntary breath-hold trials were used to assess mean steady state HR during breath-hold. In order to calculate mean steady state HR during breath-hold, the data were first smoothed by transforming the heartbeats into running means (based on the average of three consecutive heartbeats). The transformed data were then plotted against time into the trial and visually inspected to determine the inflection points that defined the beginning and end of the steady state period during breath-hold (where HR remained at a consistently low rate). The incline sections prior to and after this segment represented transitional HRs associated with breathing. The transformed HR data representing the steady state segment were averaged, and to ensure that all heartbeats associated with the steady state segment were included in the final analyses, the steady state segment was extended on each end by accepting all transformed HRs equivalent to the mean + 2 SD. The non-transformed HR data corresponding to this extended steady state segment were averaged to determine the mean steady state HR, and the variance around the mean was calculated. All heartbeats in the transition period prior to the steady state segment were used to determine the rate of change for HR at the onset of breath-hold; the slope was determined by least squares regression analysis.

Pearson product moment correlation tests were used to assess the influence of age on resting HR, steady state HR during breath-hold, the variance in steady state HR during breath-hold, and the rate of change in HR during the transition from breathing to steady state bradycardia. Adults were excluded from the correlation analyses because their exact ages were unknown. The resting HR and steady state HR from all dolphins combined were compared by a *t*-test.

Average HR

The accuracy of determining HR from 10-s averages was assessed by comparing average HR recorded by the TDR to instantaneous HR from ECG recordings during voluntary breath-holds of similar duration performed by the same dolphins. HRs recorded for the entire breath-hold cycle were similar for each method ($t = 1.870$, $df = 4$, $P = 0.135$).

Bradycardia varies with dive duration (Ridgway et al. 1975), thus longer dives for each dolphin resulted in a more pronounced cardiac response. To ensure that the most pronounced cardiovascular response was analyzed and each dolphin contributed equally, the five longest dives performed by each dolphin were used for the analyses. The following were determined for each dive: maximum HR at the surface, mean steady state HR while diving (described above), minimum HR during submergence, and the percentage reduction in HR while diving, where percent change in HR is equivalent to:

$$[(\text{maximum surface HR} - \text{minimum diving HR}) / (\text{maximum surface HR})] \times 100 \quad (1)$$

Data for HR were grouped into five age classes, 1.5–2.5 years, 2.5–3.5 years, 3.5–4.5 years, 4.5–5.5 years, and adult. The two youngest age classes represent calves that are still developing oxygen stores (Noren et al. 2001, 2002). The two older immature age classes represent juveniles that have mature muscle and blood oxygen stores but have not yet attained adult body size. Maximum HR at the surface, mean steady state HR while diving, minimum HR during diving, and the percentage reduction in HR were compared across age classes using a one way ANOVA in combination with Tukey all pairwise comparisons.

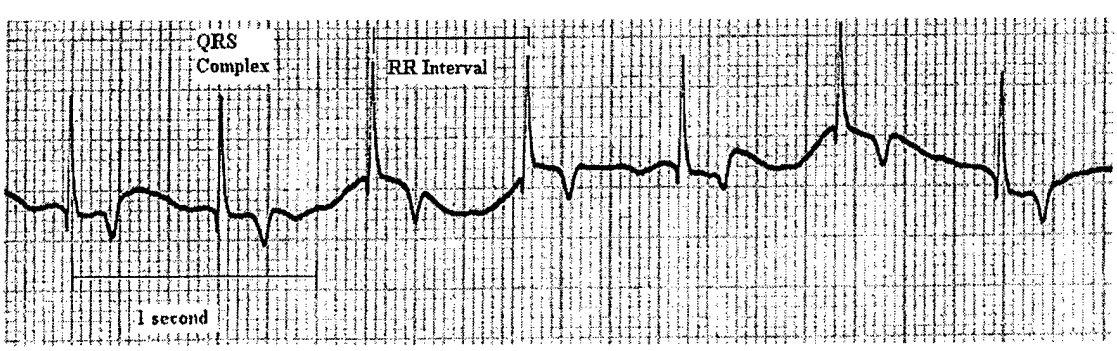

Fig. 1 Representative electrocardiogram trace recorded from a 1.7-year-old bottlenose dolphin calf during stationary respiration on the water surface. Time and a representative QRS complex and R-to-R interval, which were used to determine heart rate, are indicated

Developmental trends in cardiac control were also assessed for calves that were studied longitudinally over 2–3 consecutive years. Data obtained from individual calves were compared across years and differences in the level of bradycardia during diving throughout maturation were either determined by a *t*-test or one-way ANOVA in combination with Tukey all pairwise comparisons.

Dive performance

Similar to the HR analyses, differences in observed dive durations between age classes were quantified by a one way ANOVA in combination with a Tukey all pairwise comparison. Longitudinal analyses of dive capacity for individual calves were either determined by a *t*-test or a one-way ANOVA in combination with Tukey all pairwise comparisons.

To determine whether voluntary dives and their associated HRs were representative of maximal aerobic efforts, aerobic dive limits (ADLs) were determined for each dolphin in the study. ADLs were calculated by dividing total body oxygen stores by metabolic rate according to Kooyman (Kooyman 1989). Methods for calculating ADLs of immature and mature bottlenose dolphins are described in detail in Noren et al. (2002). Briefly, ADLs for all dolphins were calculated assuming a metabolic rate of two times basal metabolic rate (Kleiber 1975) as measured for adult bottlenose dolphins (Williams et al. 1993b). Values for the calculated aerobic dive limit (cADL) and the five longest dive durations for 1.7–5.4-year-old dolphins were plotted against age. Slopes for these relationships were determined by least squares regression analyses, and compared using one-way ANOVA.

Variables influencing HR

Because the older dolphins were larger and exhibited longer dive durations, it was necessary to differentiate between the effects of dive duration, body mass, and age on HR. Data from the longest dive performed by each dolphin were used in a forward stepwise regression to determine which variable (age, body mass, or dive duration) best predicts maximum HR at the surface, mean steady state HR during diving, minimum HR during diving, and percentage reduction in HR. Adults were excluded from these analyses, as their exact ages were unknown.

Results

Cardiac control during respiration and breath-hold

The mean resting HR during stationary respiration on the water surface was not associated with age ($n=11$, $r=-0.155$, $P=0.649$). Evidence of cardiac control in response to prolonged apnea was demonstrated by dolphins of all ages. HR declined significantly with the onset of breath-hold and the rate of change did not correlate with age for either voluntary breath-hold ($n=4$, $r=0.837$, $P=0.163$) or shallow diving ($n=14$, $r=-0.174$, $P=0.551$; Fig. 2). For all dolphins, mean resting HR was significantly greater than mean steady state HR during breath-hold ($t=5.561$, $df=15$, $P<0.001$). At the end of breath-hold, all dolphins demonstrated an anticipatory tachycardia as HR abruptly increased within a few seconds before breathing (Fig. 2).

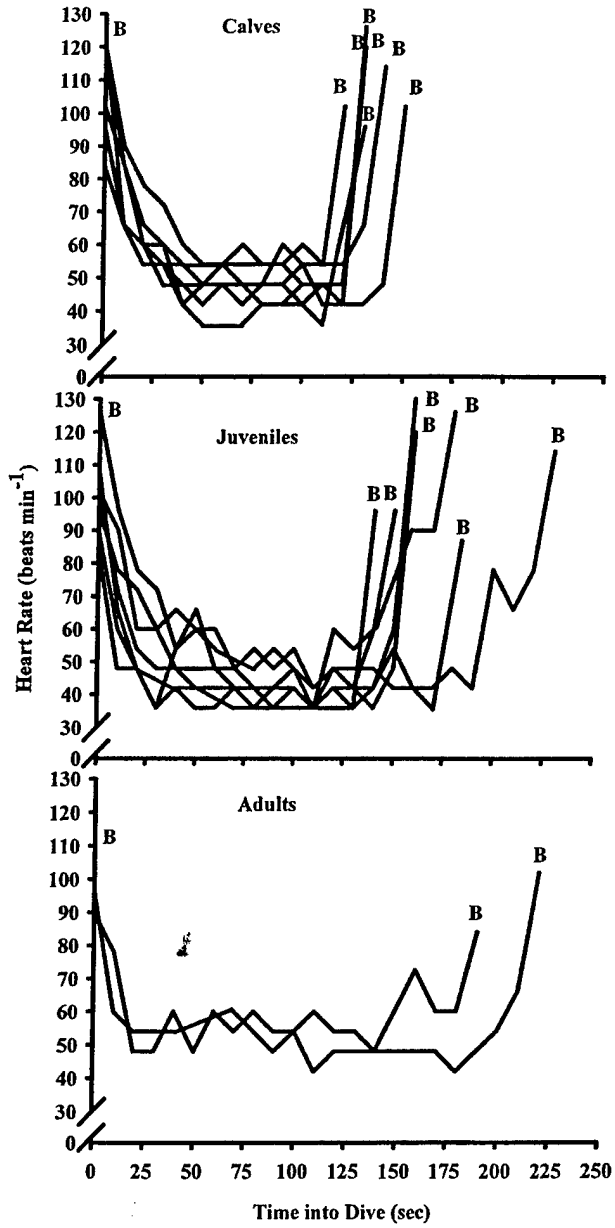

Fig. 2 Average heart rate (HR) throughout a shallow dive cycle for calves (1.5–3.5-year-olds), juveniles (3.5–5.5-year-olds), and adult bottlenose dolphins. HR was averaged over 10-s intervals using a time–depth recorder (TDR) microprocessor worn by the diving dolphins. The longest dive performed by each dolphin is shown. *B* indicates the point when the dolphins took a breath. All dolphins show a pattern of bradycardia during submergence and anticipatory tachycardia before surfacing

The effect of development on bradycardia

Mean steady state HR during voluntary breath-hold was not correlated with age ($n=4$, $r=-0.533$, $P=0.467$). The inability to detect a significant relationship between age and mean steady state HR during breath-hold may be a result of limited sample size; the 2-year-old calf (youngest animal in this portion of the study)

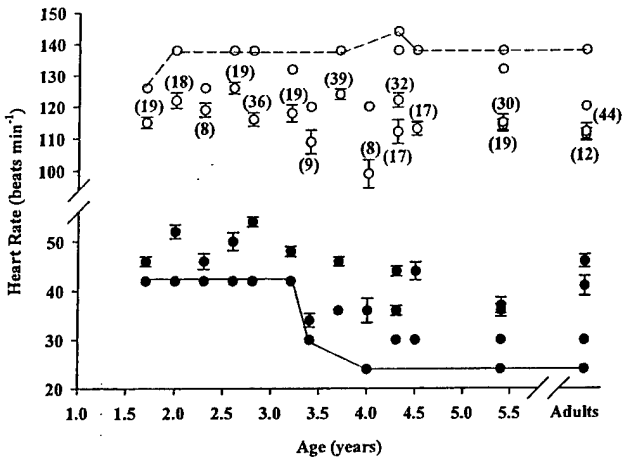

Fig. 3 Minimum and maximum HR recorded during shallow dive cycles > 1 min in relation to age for bottlenose dolphins. *Points with error bars* represent minimum HR during diving ± 1 SEM (*filled circles*) and maximum HR at the water surface ± 1 SEM (*unfilled circles*) for individual dolphins. *Filled circles connected by a solid line* represent the absolute minimum HR recorded while submerged. *Unfilled circles connected by a dashed line* represent the absolute maximum HR recorded at the surface. The *numbers in parentheses* are the number of dives

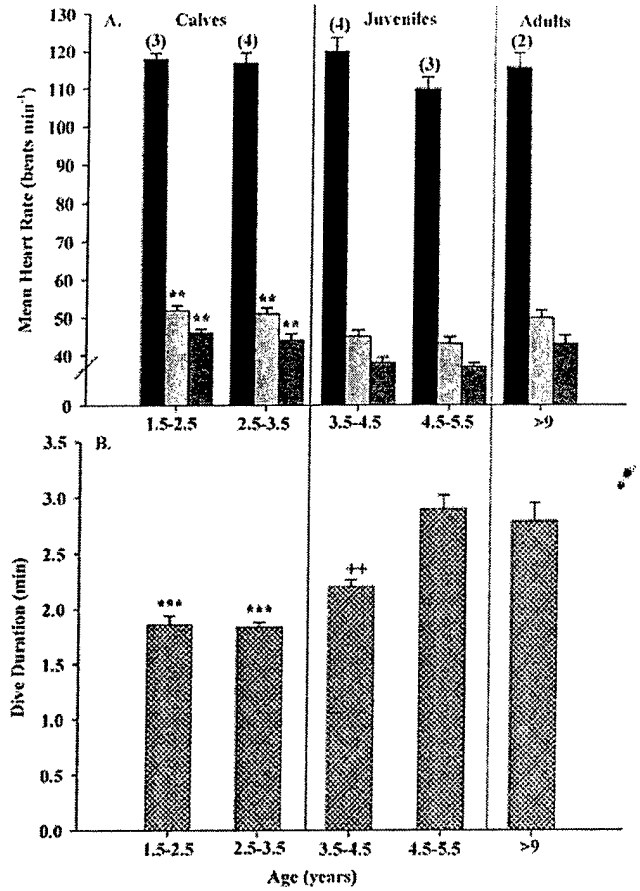

Fig. 4A–B HR (**A**) and dive duration (**B**) during shallow diving in relation to age class. *Bars with error lines* represent age class means + 1 SEM (includes data from the five longest dives performed by each dolphin). The number of animals in each age class is shown in *parenthesis*. **A** Maximum HR during surface breathing (*black bars*), mean steady state HR during diving (*light gray bars*), and minimum HR during diving (*dark gray bars*) are compared. Values for calves that are significantly greater then values for juveniles are denoted by *two asterisks*. Maximum HR at the surface was similar across age classes. See text for statistics. **B** *Cross-hatched bars* represent mean voluntary dive durations. Values for calves that are significantly lower than values for juveniles and adults are denoted by *three asterisks*. Values for the 3.5–4.5-year-old juvenile age class that are significantly lower than values for the 4.5–5.5-year-old juvenile and adult age classes are denoted by *two plus signs*. See text for statistics

demonstrated the highest mean steady state HR during apnea (66 ± 0.8 beats·min^{-1}) while the adult demonstrated the lowest (45 ± 1.3 beats·min^{-1}). The variance associated with the mean steady state HR during breath-hold (variance range: 8–20; SD range: 5–9) did not correlate with age ($r = 0.790$, $n = 4$, $P = 0.210$); the adult value for variance fell within the range demonstrated for immature dolphins. Thus, all dolphins showed similar abilities to maintain a stable HR during breath-hold.

Differences in minimum HR achieved during diving indicate that bradycardia is refined with maturation. The absolute minimum HR achieved during diving represents the most pronounced cardiovascular response; calves (< 3.4 years old) demonstrated HRs as low as 42 beats·min^{-1}, but older calves, juveniles, and adults could attain lower HRs (24–30 beats·min^{-1}; Fig. 3). In contrast to minimum HR, there was no discernable pattern associated with age for maximum HR recorded at the water surface prior to or after a dive (Fig. 3).

When grouped according to age class, mean steady state diving HR, minimum HR during submergence, and percent HR reduction while diving also indicate developmental trends for dolphins (Fig. 4a). Minimum and mean steady state HR during diving differed significantly among age classes (minimum HR: $F = 6.297$, $df = 4, 75$, $P < 0.001$; mean steady state HR: $F = 5.794$, $df = 4, 75$, $P < 0.001$). Tukey all pairwise comparisons demonstrated that juveniles (3.5–4.5-year-olds and 4.5–5.5-year-olds) maintain significantly lower minimum and mean steady state HR during diving compared to calves (1.5–2.5-year-olds and 2.5–3.5-year-olds; minimum HR: $q = 4.587, 5.721, 4.162, 5.382$; $P < 0.05$; mean steady state HR: $q = 3.997, 5.196, 4.090, 5.344$; $P < 0.05$). Values for minimum and mean steady state HR during diving were similar for juveniles and adults. Although values for minimum and mean steady HR during diving appeared lower in adults compared to calves, these differences were not significant. In contrast, maximum HR recorded during surfacing were similar across all age classes ($F = 1.507$, $df = 4, 75$; $P = 0.209$). A consequence of the enhanced ability to lower HR during submergence in older dolphins is a significantly greater percent reduction in HR during diving compared to younger dolphins ($F = 5.820$, $df = 4, 75$; $P < 0.001$). Tukey all pairwise comparisons demonstrated that juveniles maintained significantly greater reductions in HR (67–68%) during diving compared to calves (61–62%;

$q=5.321$, 4.831, 4.733, 4.225; $P<0.05$). The ability for HR reduction during diving in juveniles was similar to that observed in adults (66%). Although adults appeared to demonstrate a greater capacity for HR reduction during diving than calves, these differences were not significant.

Longitudinal measurements on individual dolphins further demonstrate enhanced cardiac control during diving with maturation (Fig. 5). The ability to reduce HR while diving improved with age for each of the three youngest calves in this portion of the study. As a result, the level of bradycardia during diving increased throughout maturation for these individuals (Calf 1: One way ANOVA $F=15.914$, $df=2, 12$; $P<0.001$, Tukey all pairwise $q=4.405$, 7.963; $P<0.05$; Calf 2: one way ANOVA $F=3.794$, $df=2, 12$; $P=0.053$, Tukey all pairwise comparison $q=3.061$, 3.617; $P<0.10$; Calf 3: One way ANOVA $F=4.406$, $df=2, 12$; $P=0.037$, Tukey all pairwise comparison $q=3.945$, $P<0.05$; Fig. 5). In contrast, the level of bradycardia during diving for the oldest calf, measured at 4.5 years and 5.4 years of age, did not change between years ($t=-2.150$, $df=8$, $P=0.064$). These results suggest that diving bradycardia is refined by approximately 3.5 years postpartum (Fig. 5).

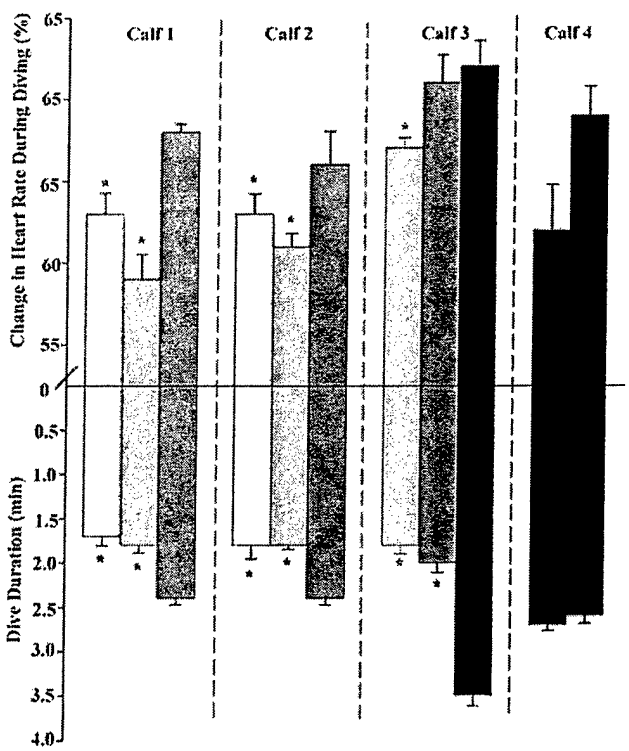

Fig. 5 The percentage reduction in HR during shallow diving and dive duration for four immature dolphins studied longitudinally over 2–3 consecutive years. Measurements for each calf are presented in longitudinal order. *Bars with error lines* represent the mean + 1 SEM for individuals and are colored according to age [1.5–2.5 years (*white*), 2.5–3.5 years (*light gray*), 3.5-4.5 years (*dark gray*), and 4.5–5.5 years (*black*)]. Intra-individual comparisons for Calf 1, 2, and 3 indicate differences between annual measurements and the *asterisk* denotes the measurements that were significantly different than the final (oldest) measurement. See text for statistics

The effect of development on dive duration

Dive duration was significantly longer for older bottlenose dolphins (Figs. 4b, 5, 6). Age class comparisons demonstrated these differences ($F=32.660$, $df=4, 75$; $P<0.001$; Fig. 4b), where calves had significantly shorter dive durations than 3.5–4.5-year-old juveniles ($q=4.108$, 4.713; $P<0.05$), 4.5–5.5-year-old-juveniles ($q=11.884$, 12.960; $P<0.05$) and adults ($q=9.541$, 10.282; $P<0.05$). Furthermore, 3.5–4.5-year-old juveniles had significantly shorter dive durations than the older juveniles ($q=8.596$, $P<0.05$) and adults ($q=6.433$, $P<0.05$).

A significant increase in dive duration with maturation was also evident for each of the three youngest calves studied longitudinally (Calf 1: one way ANOVA $F=19.476$, $df=2, 12$; $P<0.001$, Tukey all pairwise comparison $q=8.324$, 6.699; $P<0.05$; Calf 2: one way ANOVA $F=11.286$, $df=2, 12$; $P=0.002$, Tukey all pairwise comparison $q=6.134$, 5.442; $P<0.05$; Calf 3: one way ANOVA $F=70.275$, $df=2, 12$; $P<0.001$, Tukey all pairwise comparison $q=15.247$, 13.662; $P<0.05$; Fig. 5). As found for diving HR, the oldest calf showed no difference in dive duration at the age of 4.5 years and 5.4 years ($t=0.742$, $df=8$, $P=0.479$; Fig. 5).

Across all immature dolphins examined in this study, dive duration and cADL increased with age (Fig. 6). Although values for cADL are greater than the measured dive durations, the slopes of these relationships

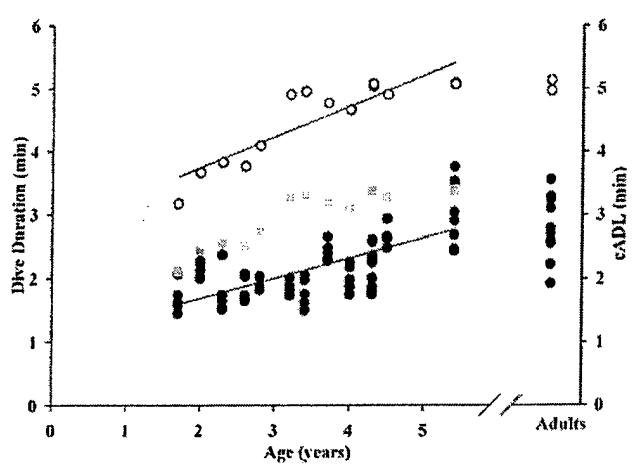

Fig. 6 Calculated aerobic dive limit and voluntary dive duration in relation to age. The calculated aerobic dive limit (*cADL; unfilled circles*) and the five longest dive durations (*filled circles*) for each dolphin are represented. *Solid lines* are the least squares linear regressions for the immature dolphins, where cADL = 0.5 age + 2.8 ($r^2=0.78$, $F=43.298$, $df=1, 12$; $P<0.001$) and dive duration = 0.3 age + 1.1 ($r^2=0.51$, $F=69.767$, $df=1, 68$; $P<0.001$). *Gray squares* represent cADLs that assume a metabolic rate of three times basal metabolic rate to account for additional metabolic costs for immature animals (Donohue et al. 2000)

were not significantly different ($F=3.645$, $df=1, 82$, $P=0.06$; Fig. 6); this suggests that the voluntary dives performed by the immature dolphins represented similar relative aerobic efforts.

Variables influencing HR

Although older dolphins had greater body mass and exhibited longer dive durations, results of the forward stepwise regression indicated that age, body mass, and dive duration were poor predictors of maximum HR at the surface. Age was the only variable that significantly predicted mean steady state HR during diving, minimum HR during diving, and the percentage reduction in HR during diving for 1.7–5.4-year-old dolphins according to:

$$\text{Mean steady state diving HR} = -3\ \text{age} + 56 \quad (2)$$

($r^2=0.33$, $F=5.810$, $df=1, 12$; $P=0.033$)

$$\text{Minimum HR during diving} = -4\ \text{age} + 54 \quad (3)$$

($r^2=0.53$, $F=13.46$, $df=1, 12$; $P=0.003$)

$$\text{HR reduction during diving} = 3\ \text{age} + 54 \quad (4)$$

($r^2=0.60$, $F=18.21$, $df=1, 12$, $P=0.001$), where HR is measured in beats per minute, HR reduction is as a percentage, and age is in years. These results indicate that the refinement of diving bradycardia is not influenced by changes in body mass or dive duration throughout maturation. Rather, the development of physiological processes as young dolphins age appears to be the major factor leading to an increased ability to reduce HR and achieve a more pronounced bradycardia response during diving.

Discussion

Maturation of HR in mammals: developing cardiac control

Across mammals, HR patterns of mature individuals demonstrate similar features. This includes sinus arrhythmia, the capability to rapidly transition between elevated and reduced HRs during the respiratory cycle, and the ability to maintain a stable HR once a steady state has been reached. Rather than an inherent feature, HR adjustment in response to respiratory events requires a refinement in cardiac control and improves with maturation in mammals. For example, puppies (Haddad et al. 1987) and southern elephant seal neonates (Falabella et al. 1999) show smaller differences in HR during their respiratory cycle compared to adults, and the change in HR associated with respiration occurs more gradually in the immature animals compared to the adults. Furthermore, the HRs of young northern (Castellini et al. 1994b) and southern (Falabella et al. 1999) elephant seal pups are more variable during sleep apnea than the HRs recorded during this period for older pups. After a period of postnatal development mature cardiac patterns appear, such that Northern elephant (Castellini et al. 1994a, 1994b) and harbor (*Phoca vitulina*; Lapierre et al. 2001; Greaves et al. 2001) seal pups demonstrate mature cardiac cycles associated with respiration before weaning.

Less detailed information concerning changes in cardiac control is available for young cetaceans due to the difficult logistics of attaining physiological data from this group. A mysticete calf (California gray whale, *Eschrichtius robustus*; Ponganis and Kooyman 1999) and a juvenile odontocete (harbor porpoise, *Phocoena phocoena*; Reed et al. 2000) demonstrated an ability to adjust HR during the respiratory cycle. Similarly, bottlenose dolphin calves as young as 1.7 years old demonstrate elements of cardiac control. Like mature bottlenose dolphins, calves lower HR in response to breath-hold and are capable of maintaining stable minimum HRs during breath-hold. Mean change in HR during the transition from breathing into breath-hold was 2.5 ± 0.9 beats $\text{min}^{-1} \cdot \text{s}^{-1}$, ($n=5$). For bottlenose dolphins, this development has occurred by the age of weaning (weaning occurs at approximately 1.5–1.7 years postpartum; Perrin and Reilly 1984). Thus, newly weaned bottlenose dolphin calves have the necessary cardiac control that would be required to elicit bradycardia while diving.

The effect of age on bradycardia: refining cardiac control

A similar pattern of accelerating and decelerating HR in response to breathing and breath-hold is a vital component of the dive response of marine mammals (Kooyman 1989), albeit in an exaggerated form. Presumably, the control mechanisms that govern cardiovascular responses to apnea on land may be used to modify cardiovascular responses during diving (Irving et al. 1935; Castellini et al. 1994a). Juvenile northern elephant seals show a similar cardiac response to both terrestrial and diving apneas, although the terrestrial response is less pronounced than the diving response (31% versus 64% reduction in HR; Andrews et al. 1997). By markedly reducing HR to a fraction of that exhibited when the animal is breathing, diving marine mammals are able to conserve limited on-board oxygen stores that support aerobic metabolism when submerged.

Studies of bradycardia during forced dives in young pinnipeds indicate that harbor (Harrison and Tomlinson 1960), fur (*Callorhinus ursinus*; Irving et al. 1963), and northern elephant (Hammond et al. 1969) seal pups are able to markedly lower HR in response to submergence. The level of bradycardia increases with age in harbor seals (Harrison and Tomlinson 1960) and fur seals (Irving et al. 1963). In contrast, freely diving juvenile elephant seals (Andrews et al. 1997), and forcibly

submerged neonatal (Hammond et al. 1969) and adult (Van Critters et al. 1965) elephant seals show similar levels of bradycardia.

As reported for harbor and fur seals, the present study demonstrates that bradycardia during diving changes with maturation in bottlenose dolphins. Absolute minimum HRs during shallow diving are lower in adults and juveniles than in calves (Fig. 3) with the result that mean steady state HR during diving is maintained at lower levels in older dolphins (Fig. 4a). Despite these absolute changes, differences between age classes for minimum and mean steady state HR during diving were only significant between calves and juveniles; calves were not significantly different from adults (Fig. 4a). One explanation for this discrepancy is that the full cardiac response in adults may not have been initiated because of their relatively short dive durations (Figs. 4b, 6). According to Williams et al. (1993a), adult bottlenose dolphins are capable of aerobically supported dive durations of 4.4 min. Without the "anticipation" of a long dive, which strongly influences the degree of bradycardia, the cardiac response can be highly variable (Kooyman 1989). Furthermore, Ridgway et al. (1975) demonstrated that the level of diving bradycardia varies with dive duration in adult bottlenose dolphins. If the adults in this study had prolonged dive duration, it is likely that the variability associated with the age class mean for mean steady state diving HR and minimum HR during diving would have been reduced and the actual values of these means may have been lowered. As a result, the ability to detect differences in diving HR between calves and adults would have been improved. Unlike the adult dolphins, the immature dolphins in this study were closer to their physiological dive limits during the diving trials (Fig. 6). Therefore, comparisons of diving HR between calves and juveniles were not encumbered by these factors. Regardless, the results of this study suggest that a mature bradycardia response during diving is established by approximately 3.5 years postpartum for bottlenose dolphins (Figs. 4a, 5).

Many factors undoubtedly influence the change in diving bradycardia that occurs during maturation. An evaluation of the relative effects of body mass, dive duration, and age demonstrates that throughout development, age is the primary predictor of minimum and mean steady state HR during diving for dolphins. This does not imply that this refinement in bradycardia is attributable simply to the lowering of HR with age as typically occurs in developing animals (Dittmer and Grebe 1959). For all dolphins in the present study, maximum HRs at the surface are identical while minimum HRs during diving decline with age (Figs. 3, 4a). These findings are similar to those reported in a preliminary study for diving harbor seal pups in which surface HRs did not change but HRs during submergence declined with age (Greaves et al. 2001). Therefore, the primary developmental change in cardiac function for a variety of marine mammals appears to occur on the physiological and/or psychogenic processes that control the ability to reduce HR while diving; see Kooyman (1989) for a review of these processes.

Physiological development: implications for diving capacity

The interrelationships between HR, metabolic rate, oxygen stores and diving duration (Kooyman 1989) suggest that an inability to reduce HR limits apnea duration during intermittent breathing and breath-hold diving. This has been demonstrated for several species of seals in which maturation of cardiac control coincides with increasingly prolonged apneas (Castellini et al. 1994b; Falabella et al. 1999; Lapierre et al. 2001; Greaves et al. 2001) and extended periods of submergence (Harrison and Tomlinson 1960; Irving et al. 1963). Yet, many of the postpartum changes in HR observed for marine mammals are not associated with a requirement to dive. Developmental changes in HR patterns are complete within 11 weeks of birth for southern elephant seals (Falabella et al. 1999) and 15 weeks for northern elephant seals (Castellini et al. 1994b), before the pups leave the beach. The refinement in cardiac control during diving for harbor seal pups occurs before weaning and is therefore, temporally separated from the requirement to dive during independent foraging (Greaves et al. 2001).

Unlike pinnipeds, dolphins are subject to the immediate demands of swimming and diving at birth and demonstrate a comparatively protracted developmental period. Although newly weaned dolphin calves as young as 1.7 years old have already developed several elements of cardiac control, the ability for bradycardia during diving does not approach mature levels until 3.5 years postpartum (Figs. 4a, 5). Similarly, the development of the oxygen stores in the skeletal muscles (Noren et al. 2001) and blood (Noren et al. 2002) of bottlenose dolphins are not fully developed until 3 years postpartum. These developmental factors in combination with increased body size act synergistically to enable dolphins to increase breath-hold capacity as they mature. As a result, the diving capability of immature dolphins remains limited until development is complete; voluntary dive durations do not reach adult values until 4.5 years postpartum (Figs. 4b, 5, 6). This may explain in part the long associations (3–6 years) observed between bottlenose dolphin mom-calf pairs in the wild (Scott et al. 1990).

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ORIGINAL PAPER

S. R. Noren · T. M. Williams · D. A. Pabst
W. A. McLellan · J. L. Dearolf

The development of diving in marine endotherms: preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence

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Abstract Myoglobin is an important oxygen store for supporting aerobic diving in endotherms, yet little is known about its role during postnatal development. Therefore, we compared the postnatal development of myoglobin in marine endotherms that develop at sea (cetaceans) to those that develop on land (penguins and pinnipeds). We measured myoglobin concentrations in the major locomotor muscles of mature and immature bottlenose dolphins (*Tursiops truncatus*) and king penguins (*Aptenodytes patagonicus*) and compared the data to previously reported values for northern elephant seals (*Mirounga angustirostris*). Neonatal dolphins, penguins, and seals lack the myoglobin concentrations required for prolonged dive durations, having 10%, 9%, and 31% of adult values, respectively. Myoglobin contents increased significantly during subsequent development. The increases in myoglobin content with age may correspond to increases in activity levels, thermal demands, and time spent in apnea during swimming and diving. Across these phylogenetically diverse taxa (cetaceans, penguins, and pinnipeds), the final stage of postnatal development of myoglobin occurs during the initiation of independent foraging, regardless of whether development takes place at sea or on land.

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S. R. Noren (✉) · T. M. Williams
Earth and Marine Science Building Room A316,
Department of Biology,
University of California at Santa Cruz,
Santa Cruz, CA 95064, USA
e-mail: snoren@biology.ucsc.edu
Fax: +1-831-4594882

D. A. Pabst · W. A. McLellan · J. L. Dearolf
Department of Biological Sciences and Center
for Marine Science,
University of North Carolina
at Wilmington,
Wilmington, NC 28403, USA

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Abbreviations *[Mb]* myoglobin concentration · *NST* nonshivering thermogenesis

Introduction

Marine mammals and birds routinely experience prolonged periods of apnea during diving. During these periods, aerobic metabolic processes are supported by the use of on-board oxygen stores. One important store is myoglobin, which supplies oxygen for the locomotor muscles that must provide propulsion during diving and operate in the absence of continuous oxygen delivery by the cardiovascular system. The larger the myoglobin oxygen store, the greater the aerobic dive duration (Kooyman 1989). Consequently, the skeletal muscles of marine mammals and diving birds maintain myoglobin contents that are approximately 10–30-times greater than their terrestrial counterparts (Scholander 1940; Castellini and Somero 1981). This adaptation appears to be especially important for cetaceans and penguins due to their comparatively higher reliance on muscle oxygen stores than pinnipeds, which tend to rely more on blood oxygen stores (Kooyman 1989).

Although it is well known that adult marine mammals and birds have comparatively high myoglobin contents, only a few studies have examined the development of this muscle characteristic in newborn and immature animals. Previous studies concerning changes in myoglobin content during development have primarily focused on pinnipeds (Thorson 1993; Kohin 1998; Burns et al. 2000) and seabirds (Weber et al. 1974; Haggblom et al. 1988; Ponganis et al. 1999). Both groups are born (pinnipeds) or hatched (seabirds) on land; during this time myoglobin content increases before their first trip to sea, primarily in the absence of diving and locomotor demands. In contrast cetaceans are born and develop at sea, and thus immediately encounter the demands of swimming

and diving. Consequently, we asked the question, does the development of muscle myoglobin content in cetaceans differ from that of other swimming and diving endotherms that undergo early development on land?

In this study we compare the postnatal development of the oxygen store in locomotor skeletal muscles of marine endotherms in three categories: marine-born marine mammals (bottlenose dolphin, *Tursiops truncatus*), terrestrial-born marine birds (king penguins, *Aptenodytes patagonicus*), and terrestrial-born marine mammals (northern elephant seals, *Mirounga angustirostris*). Four other cetacean species (Pacific white-sided dolphin, *Lagenorhynchus obliquidens*; common dolphin, *Delphinus capensis*; striped dolphin, *Stenella coeruleoalba*; gray whale, *Eschrichtius robustus*) were sampled as available to determine whether postpartum development of myoglobin content is similar across cetacean species. Comparison of postnatal myoglobin contents across these diverse taxa revealed that neonatal diving marine endotherms have low muscle myoglobin contents, regardless of whether postnatal development occurs at sea or on land. Furthermore, increases in physical activity, thermal demands, and time spent in apnea during swimming and diving are factors that appear to influence myoglobin development. Finally, postnatal myoglobin development appears to be completed after the initiation of independent foraging.

Materials and methods

Experimental design

The postnatal development of myoglobin content of the primary locomotor muscle was examined for three categories of diving endotherms. Postnatal development on land and at sea was compared. The bottlenose dolphin was the primary species used to represent the first category, marine-born marine mammals. This category was supplemented with four other cetacean species (Pacific white-sided dolphin, common dolphin, striped dolphin, and gray whale) to determine whether the developmental pattern for muscle myoglobin content was similar across cetacean species. The king penguin represented the second category, terrestrial-born marine birds. Lastly, the northern elephant seal represented the third category, terrestrial-born marine mammals. Myoglobin contents of the *m. longissimus dorsi* of northern elephant seals were obtained from previous reports (Thorson 1993; Kohin 1998).

Specimens

Cetaceans

The Atlantic bottlenose dolphins used in this study were collected by the Northeast and Southeast Regional Marine Mammal Stranding Networks. Animals were divided into three age classes depending on the presence of neonatal characteristics and/or their length according to the methods of Dearolf et al. 2000. Floppy dorsal fin and floppy tailflukes were used to classify specimens as neonates, as these characteristics are common to dolphin calves that are less than 2-weeks-old (McBride and Kritzler 1951; Tavolga and Essapian 1957; Crockcroft and Ross 1990). All neonates were less than 120 cm. Animals that lacked neonatal characteristics but were less than 200 cm were classified as juveniles. The body lengths of our "juvenile" specimens ranged from 138 cm to 191 cm, therefore our "juvenile" age class represents animals that are less than 1.5-years-old, according to the mean length-at-age of bottlenose dolphins (Read et al. 1993). Dolphins 200 cm or greater were classified separately as "adults". The body lengths of our "adult" specimens ranged from 204 cm to 260 cm. A 204-cm animal is 1.5–3.4-years-old, therefore our "adult" age class represents animals that are at least 1.5–3.4-years-old or older according to the mean length-at-age of bottlenose dolphins (Read et al. 1993). Three to five individuals were analyzed for each age class depending on the availability of specimens. Additional cetacean species (Pacific white-sided, common, and striped dolphins, and gray whale) were acquired opportunistically from Northeast and Southeast Regional Marine Mammal Stranding Networks, NMFS, Southwest Fisheries Science Center, Los Angeles Natural History Museum, and Long Marine Lab. These specimens were assigned to three age classes (neonate, juvenile, and adult) according to the presence of neonatal characteristics and by body length determined during necropsy (A. Pabst, J. Heyning, D. Casper, personal communication). Muscle samples were taken only from carcasses that were considered in fresh condition (Smithsonian Condition Code 2). Samples were collected from a primary locomotor muscle (m. longissimus dorsi) and stored following protocols outlined previously in Noren and Williams (2000).

Penguins

The king penguin chicks examined in this study were hatched from eggs collected in the Antarctic late in the breeding season. The chicks were reared in a simulated Antarctic environment at Sea World in San Diego, California where temperature, light, and diet were controlled. Chicks were weighed often to ensure that good body conditions were maintained. All chicks used for this study had died of natural causes. A total of 23 chicks were used, ranging in age from 0 days to 136 days. The pectoralis muscle, the major locomotor muscle of this species, was dissected within 1–2 h of death and stored frozen at −80 °C until myoglobin content analysis. Penguins were assigned to age groups that were associated with specific developmental periods. The 0- to 6-day-old group represents chicks immediately following the energy demanding activity of pipping. Two groups, 8- to 29-day-old penguins and 33- to 51-day-old penguins, represent the early and late incubation/ brooding stage (Moore et al. 1999). Two groups, 59–84-day-old penguins and 136-day-old penguins, represent the early and late crèche/fasting stage (Moore et al. 1999). Since the oldest specimen studied was only 136-days-old, we included the myoglobin content of the adult king penguin from Kooyman (1989) for the purposes of our analyses.

Analyses

Myoglobin content

Myoglobin content ([Mb]), reported in g Mb (100 g wet muscle)$^{-1}$, was determined using the procedure of Reynafarje (1963). Slightly thawed muscle samples (approximately 0.5 g) were minced in a low ionic strength buffer (40 mM phosphate, pH = 6.6), and sonicated (Sonifier Cell Disrupter Model W185D, Heat systems – Ultrasonics) for 2–3 min on ice. Buffer to tissue ratio was 19.25 ml buffer g^{-1} wet tissue. The samples were centrifuged at −4 °C and 28,000*g* for 50 min (Sorvall RC – 5B refrigerated superspeed centrifuge, DuPont Instruments). The clear supernatant was extracted and then bubbled at room temperature with pure CO for approximately 8 min. We added 0.02 g sodium dithionite to ensure a complete reduction. The absorbance of each sample was read at room temperature at 538 nm and 568 nm on a spectrophotometer (Shimadzu UV – visible spectrophotometer Bio spec – 1601). All samples were run in triplicate.

Validation for the assay

As controls for the assay, myoglobin contents were determined for the *m. longissimus dorsi* of a 1-week-old northern elephant seal pup and New Zealand white rabbit, and compared to previously pub-

lished values. The [Mb] of the seal pup, 2.4 ± 0.2 g (100 g wet muscle)$^{-1}$, and rabbit muscle, 0.08 ± 0.06 g (100 g wet muscle)$^{-1}$, in the present study were similar to values reported by Thorson (1993) and Castellini and Somero (1981) [2.9 and 0.04 g (100 g wet muscle)$^{-1}$, respectively].

Statistics

Statistical analyses were computed using Sigma Stat Software (Jandel Scientific 1995). Myoglobin contents for dolphin and penguin age classes are reported as means ± 1 SEM. A one-way analysis of variance with a Tukey all pairwise multiple comparison test was used to assess inter-age variability of muscle myoglobin content for the bottlenose dolphin, king penguin, and elephant seal. Inter-age variability of muscle myoglobin content for the common dolphin was determined by a *t*-test. Linear regressions were determined by least squares method; significance of the regressions was determined using *F*-tests. Ninety-five percent confidence intervals are shown for significant regressions. A Basic program outlined by Yeager and Ultsch (1989) was used to determine the statistical breakpoints in the data for length or age versus myoglobin content. Results were considered significant at $P \leq 0.05$.

Results

Development of skeletal muscle in cetaceans (marine-born marine mammals)

For the bottlenose dolphin, myoglobin content increased with age and the differences between all age classes (neonate, juvenile, and adult) were significant ($F = 28.45$, $P < 0.001$, $df = 11$, $n = 12$; Table 1). Furthermore, muscle myoglobin contents for bottlenose dolphins were described by two relationships depending on length, and hence age. Myoglobin increased linearly with total body length up to 191 cm. This was followed by a breakpoint between 191–204 cm, suggesting that adult myoglobin values are obtained within this range of body lengths for bottlenose dolphins. For the animals analyzed in this study, myoglobin content reached a plateau when body length was equal to or exceeded 204 cm (representing the adult age class). Mean myoglobin content at the plateau was 2.76 ± 0.15 g (100 g wet muscle)$^{-1}$ for the adult bottlenose dolphins (Fig. 1A).

The adult muscle of the common dolphin had significantly greater myoglobin contents than that in the neonate muscle ($t = 5.51$, $P = 0.012$, $df = 3$, $n = 4$; Table 1). Small sample sizes for the Pacific white-sided dolphin, striped dolphin and gray whale precluded statistical analyses. However, there was an overall trend showing an increase in myoglobin content with older age classes in all cetacean species examined (Table 1).

Development of skeletal muscle in penguins (terrestrial-born marine birds)

As found for the cetaceans, myoglobin contents for the skeletal muscles of king penguins differed significantly between age classes (Table 2; Fig. 2B, $F = 4.27$, $P = 0.019$, $df = 21$, $n = 24$). An all pairwise test showed the myoglobin content of adult muscle was significantly greater than muscle from all chick age classes ($P < 0.05$). The myoglobin content of the 136-day age class was significantly greater than all of the younger chick age classes (0–6, 8–29, 33–51, and 59–84-day age classes at $P < 0.05$). The 8–29-day age class had the lowest mean myoglobin content, 0.27 ± 0.04 g (100 g wet muscle)$^{-1}$. The relationship between age and muscle myoglobin content was described by two linear regressions with a breakpoint between 43–46 days. For penguin chicks ≤43-days-old, myoglobin content was negatively correlated with age. For older chicks, muscle myoglobin content increased with age (Fig. 1B). The highest myoglobin content for king penguins measured in this study was 1.06 g (100 g wet muscle)$^{-1}$ for the 136-day-old chick. This is considerably lower than the adult level of 4.3 g (100 g wet muscle)$^{-1}$ reported by Kooyman (1989).

Development of skeletal muscle in seals (terrestrial-born marine mammals)

For the purpose of comparison, previous reports of myoglobin content from the *m. longissimus dorsi* of different age classes of northern elephant seals [7, 30, 60,

Table 1 Body length and myoglobin content of cetaceans at different age classes (n = sample size; length and Mb reported as means ± 1SEM)

Cetacean species	Age class (n)	Length (cm)	% Adult length	[Mb] [g (100 g wet muscle^{-1})]	% Adult [Mb]	Reference
Bottlenose dolphin	Neonate (3)	110.5 ± 2.6	49%	0.27 ± 0.02	10%	Present study
(*Tursiops truncatus*)	Juvenile (4)	161 ± 11.1	72%	1.58 ± 0.34	57%	Present study
	Adult (5)	223.9 ± 9.6	100%	2.76 ± 0.15	100%	Present study
Pacific white-sided dolphin	Fetus (1)	70.4	34%	0.15	4%	Present study
(*Lagenorhynchus obliquidens*)	Juvenile (1)	185	90%	2.93	85%	Present study
	Adult (2)	205 ± 2.0	100%	3.45 ± 0.25	100%	Noren and Williams (2000)
Common dolphin	Neonate (2)	95.5 ± 5.3	45%	0.70 ± 0.44	20%	Present study
(*Delphinus capensis*)	Adult (3)	211.1 ± 7.7	100%	3.58 ± 0.32	100%	Noren and Williams (2000)
Striped dolphin	Juvenile (1)	153	66%	3.94	68%	Present study
(*Stenella coeruleoalba*)	Adult (1)	233	100%	5.78	100%	Noren and Williams (2000)
Gray whale	Neonate (1)	–	–	0.13	–	Present study
(*Eschrichtius robustus*)	Juvenile (1)	–	–	0.22	–	Castellini and Somero (1981)

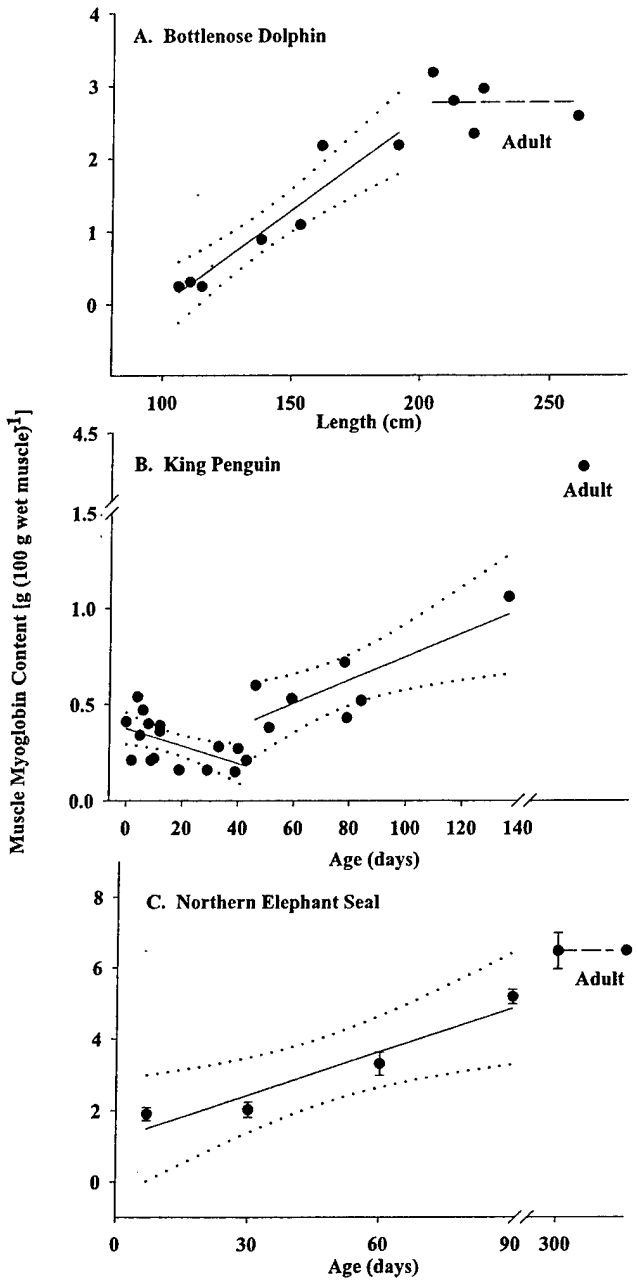

Fig. 1 Myoglobin content [g (100 g wet muscle)$^{-1}$] in relation to length (cm) as an index of age for bottlenose dolphins (**A**), and age (days) for king penguins (**B**) and northern elephant seals (**C**). *Solid lines* represent linear regressions determined by least squares method. *Dotted lines* represent the 95% confidence intervals. *Horizontal dashed lines* represent the average adult value for the muscle myoglobin content. **A** For dolphins, myoglobin content increased linearly with length up to 191 cm. This relationship is described by [Mb] = 0.03 length − 2.55 ($r^2 = 0.89$, $F = 39.42$, $P = 0.002$, $df = 6$, $n = 7$). **B** For penguins, myoglobin content was negatively correlated with age from 0 days to 43 days according to the relationship [Mb] = −0.005 age + 0.38 ($r^2 = 0.32$, $F = 6.48$, $P = 0.02$, $df = 15$, $n = 16$). For older chicks, muscle myoglobin content is positively correlated with age according to the relationship: [Mb] = 0.006 age + 0.14 ($r^2 = 0.65$, $F = 9.10$, $P = 0.03$, $df = 6$, $n = 7$). The adult value is from Kooyman (1989). **C** For seals, myoglobin content increased linearly with age for animals ≤90-days-old, as described by [Mb] = 0.04 age + 1.22 ($r^2 = 0.92$, $F = 23.16$, $P = 0.041$, $df = 3$, $n = 4$). Values for 0–300 -days-old seals are from Kohin (1998). The average adult value was calculated from sub-adult and adult categories from Thorson (1993)

and 90-day age classes from Kohin (1998) and 300-day, sub-adult and adult age classes from Thorson (1993)] were evaluated statistically. The combined data set for the seals demonstrated an increase in skeletal muscle myoglobin content with age. Myoglobin content differed significantly between age classes ($F = 33.48$, $P < 0.001$, $df = 33$, $n = 34$). An all pairwise test showed that the myoglobin contents for the 7-day and 30-day age classes were significantly less than those reported for the 60, 90, 300-day, sub-adult, and adult age classes ($P < 0.05$). The myoglobin content for the 60-day age class was significantly less than older age classes ($P < 0.05$). Like the bottlenose dolphin and king penguin, muscle myoglobin content showed a biphasic relationship with age for the northern elephant seal (Fig. 1C). Muscle myoglobin content for northern elephant seals increased in a linear manner with age up to 90-days-old. A breakpoint occurred between 90-days-old and 300-days-old, suggesting that adult myoglobin values are obtained within this range of ages for northern elephant seals. For the range of animals studied in Thorson (1993) and Kohin (1998), myoglobin reached a plateau for animals that were 300-days and older. Because there were no statistical differences in the myoglobin contents of the sub-adult and adult age classes from Thorson (1993), these age classes were combined to represent the overall adult age class. Mean myoglobin content for the combined 300-day and adult age class at the plateau was 6.48 g (100 g wet muscle)$^{-1}$.

Discussion

Previous studies examining the development of the oxygen stores and cardiorespiratory control for diving have focused on terrestrial-born, marine endotherms such as seabirds (Weber et al. 1974; Merino and Barbosa 1997; Ponganis et al. 1999) and pinnipeds (Thorson 1993; Castellini et al. 1994; Horning and Trillmich 1997a; Burns et al. 2000). These studies demonstrated the necessity of a postnatal development period to acquire the enhanced whole body oxygen stores and heart rate control of adults. These developmental changes were critical for increasing dive duration with age in both seabirds (Ponganis et al. 1999) and pinnipeds (Thorson 1993; Horning and Trillmich 1997b; McCafferty et al. 1998).

Unlike these other groups of divers, cetaceans encounter the demands of swimming and diving immediately after birth. The only two studies to examine postpartum development of diving characteristics in cetaceans suggest that the locomotor muscles of immature dolphins have low aerobic capacity (Dolar et al. 1998; Dearolf et al. 2000). The results of the present study provide further support for these findings. In view of the similarity in pattern for pinnipeds, penguins and cetaceans it appears that diving marine endotherms require a period of postnatal development before myoglobin contents reach adult levels, regardless of whether development takes place on land or at sea (Fig. 1A–C).

Table 2 Myoglobin content of seabirds at different age classes (n = sample size: Mb reported as means ± 1SEM for this study)

Seabird species	Age class (n)	[Mb] [g (100 g wet muscle^{-1})]	% Adult [Mb]	Reference
King penguin (*Aptenodytes patagonicus*)	0- to 6-day-old chick (5)	0.39 ± 0.13	9%	Present study
	136-day-old chick (1)	1.06	25%	Present study
	Adult	4.3	100%	Kooyman (1989)
Pigeon guillemot (*Cepphus columba*)	Chick	Not detectable	0%	Haggblom et al. (1988)
	Fledgling	0.52	24%	
	Adult	2.16	100%	
Emperor penguin (*Aptenodytes forsteri*)	Pre-molt Chicks	1.55	24%	Ponganis et al. (1999)
	Post-molt juveniles	2.0	31%	
	Adult	6.4	100%	
Adelie penguin (*Pygoscelis adeliae*)	Chick (one-third fledged)	0.10	3%	Weber et al. (1974)
	Young adult	1.16	40%	
	Adult	2.88	100%	
Gentoo penguin (*Pygoscelis papua*)	Young chick	0.05	1%	Weber et al. (1974)
	Adult	4.42	100%	

Factors influencing the maturation of muscle myoglobin content

Factors such as changes in physical activity, thermal demands, and exposure to hypoxia have been shown to increase myoglobin content in endotherm locomotor muscles. For example, treadmill-conditioned bar-headed geese (Saunders and Fedde 1991) and dive-conditioned tufted ducks (Stephenson et al. 1989) showed increases of 31% and 57% in myoglobin contents in the primary locomotor muscles from pre-conditioned levels, respectively. Morrison et al. (1966) demonstrated that myoglobin contents in red-backed voles in the winter show a 2.5-fold increase associated with increased metabolic output from the shivering muscles. Likewise, diving muskrats experienced an 18% increase in myoglobin content in the locomotor muscles during winter that was associated with an increased dependence on diving and the hypoxic conditions of winter lodges (MacArthur 1990). These findings indicate the malleable nature of myoglobin and these factors may explain the changes we observed in myoglobin content for the skeletal muscles of immature marine mammals and birds. Throughout their early lives, marine mammals and birds experience changes in physical activity, thermal demands, and time spent in apnea during swimming and diving that may influence the postnatal enhancement of myoglobin concentrations in the muscle.

From the moment of birth, cetaceans experience the demands of thermoregulation, swimming, and diving in the marine environment. Changes in swimming style and increased time spent in apnea during swimming and diving throughout postpartum development undoubtedly influence myoglobin development in dolphin calves. The swimming style of newborn dolphins is qualitatively different from that of older animals. The predominate position for neonate dolphins swimming with their mothers is the "echelon" position, flanking the mother near the dorsal fin region (Gubbins et al. 1999). In this swimming position, an infant dolphin has a decreased cost of transport because it is carried by the pressure wave created by its mother's larger body (Williams et al. 1992). This position enables the calf to maintain the group speed with a decreased tailbeat frequency (Norris and Prescott 1961). Calves 1 week of age spend 67% of their time swimming in "echelon" position when swimming in association with their mothers; by the time calves are 1 year of age this decreases to 23% (Gubbins et al. 1999). Dolphins also increase diving and breath-holding capacities with age. Wild dolphins begin foraging between the ages of 4 months and 11 months (Perrin and Reilly 1984), and detailed observations of a captive dolphin calf showed the most dramatic increase in breath-hold ability at 6 months (Peddemors 1990). Heightened demands on the skeletal muscle from increased independent swimming and increased time spent in apnea during swimming and diving could be associated with the development of higher muscle myoglobin content observed in the juvenile age class (Table 1, Fig. 2A).

Weaning, the attainment of fully independent foraging, occurs at 18–20 months (Perrin and Reilly 1984), corresponding to a body length of 170–180 cm in bottlenose dolphins (Barros and Odell 1990). Because this length is approximately 10 cm longer than the average length of our juvenile age class, it is likely that the animals in this age class were not weaned. According to their body length, our adult age class consists of dolphins that were most likely weaned. Muscle myoglobin contents for the juveniles were lower than those observed for adults (Table 1, Fig. 2A), suggesting that suckling juvenile dolphins require further muscle development before they attain the aerobic capacities of adults and can be successfully weaned (Fig. 2A). Previous studies have suggested that echolocation and other foraging-related behaviors are learned during the prolonged period of nursing in cetaceans (Leatherwood and Reeves 1983). The present study indicates that the pro-

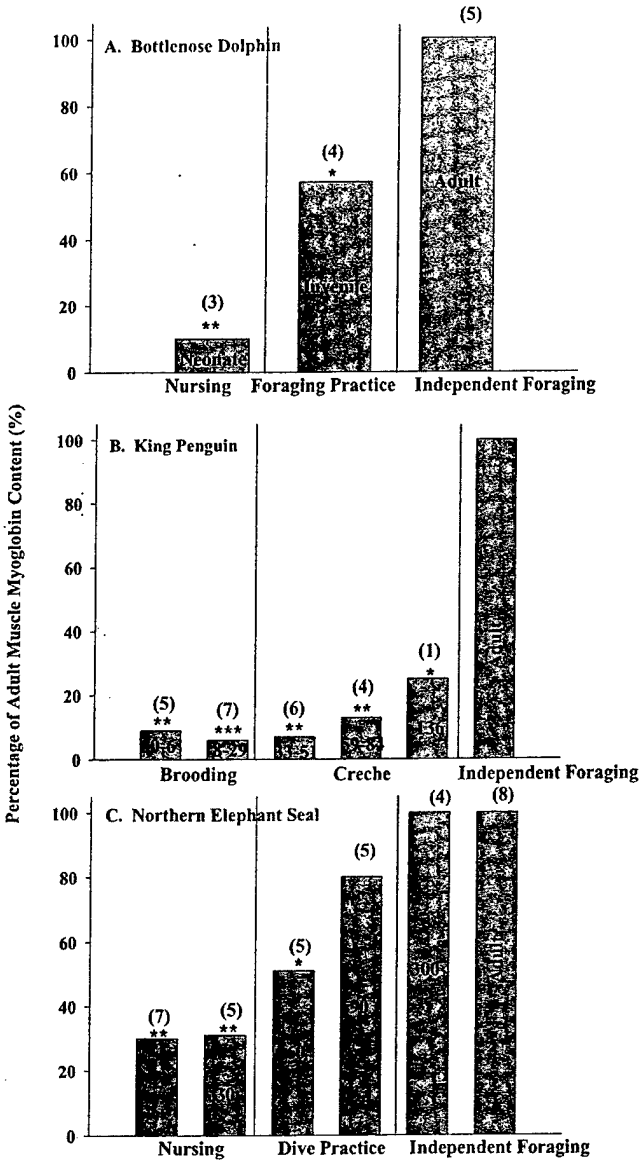

Fig. 2 Muscle myoglobin content as a percentage of adult values for bottlenose dolphins (**A**), king penguins (**B**), and northern elephant seals (**C**) at different activity states during development. *Solid vertical lines* represent transitions between stages. *Numbers in parentheses* indicate the sample size for each age class. *Heights of the bars* show the mean value for each age category. Age classifications used in this study are written in the bars. **A** Bottlenose dolphins. (**significantly less than juvenile and adult age classes, *significantly less than adult age class, $P < 0.05$). **B** King penguins. The adult value is from Kooyman (1989). (***significantly less than 59–84 day, 136 day, and adult age classes, **significantly less than 136 day and adult age classes, *significantly less than adult age class, $P < 0.05$). **C** Northern elephant seals. Pup age classes (7–300 days) from Kohin (1998). Adult value calculated from sub-adult and adult categories from Thorson (1993). (**significantly less than 60 day, 90 day, 300 day, and adult age classes, *significantly less than 90 day, 300 day, and adult age classes, $P < 0.05$)

longed nursing period may also allow time for important physiological changes to occur within the developing skeletal muscles that will enhance dive capacity and ensure successful foraging at weaning.

Despite hatching and developing on land, king penguins show a surprisingly similar pattern in myoglobin development to that of cetaceans. King penguin chicks do not go to sea until fledging at approximately 350 days after hatching (Adams and Klages 1987). As the penguin chick ages, there is an overall increase in muscle myoglobin content (Fig. 2B). Several factors may facilitate the increase in myoglobin content that occurs in chicks older than 43 days (Fig. 1B). First, chicks at this age join other chicks in a crèche for a 4-month overwintering fast. At this stage, the chicks are considerably more active (Moore et al. 1999). Consequently, conditioning associated with the increased activity could enhance myoglobin content. Second, the climate extreme of the overwintering fast may also enhance skeletal muscle myoglobin content. Skeletal muscle has been proposed as a possible site of nonshivering thermogenesis (NST) in king penguin chicks (Duchamp et al. 1989). Furthermore, cold-acclimated king penguin chicks have increased muscle oxidative capacity (Duchamp et al. 1991) which is likely accompanied by increases in myoglobin content. Finally, birds also increase the mass specific pectoral muscle mass during ontogeny to increase their capacity for NST (Aulie 1976; Marsh and Wickler 1982). There is an increase in mass-specific pectoral muscle mass with age in king penguins between 46 days and 136 days (oldest specimen examined; T.M. Williams unpublished data), suggesting that king penguin chicks do rely on muscles for thermoregulation.

Unfortunately, there were insufficient samples from king penguins to determine whether myoglobin development is complete before the first foraging trip. The oldest chick examined in this study was 136-days-old, while fledging requires 350 days (Adams and Klages 1987). The myoglobin content of the 136-day-old chick was only 25% of the value for adult king penguins [4.3 g (100 g wet muscle)$^{-1}$, Kooyman 1989]. We would expect further increases in myoglobin content in the 200 days before the first foraging trip, however, other penguin species show only 24–40% of adult values at the time of fledging (Table 2). It is possible that the first foraging trips by king penguins occur before myoglobin development is complete. Increased time spent in apnea during swimming and diving may then contribute to the completion of the development of the muscle oxygen store.

Like the penguins, elephant seals are born on land and experience a terrestrial, postnatal developmental period. During the relatively inactive period of nursing (0–30 days), myoglobin content remains low (Fig. 2C). Over the subsequent 2.5-month post-weaning fast, pups become more active on the beach and myoglobin content increases significantly from 30 days to 60 days of age (Kohin 1998). Further increases occur from 60 days to 90 days of age (Kohin 1998) as pups increase the proportion of time spent in water (Thorson 1993). Ninety-day-old pups have approximately 80% of adult myoglobin content prior to departing on their first foraging trip, while 300-day-old northern elephant seals return from their first trip to sea with 100% of the adult

value (Thorson 1993; Kohin 1998). This suggests that ocean experience and the associated increased time spent in apnea during swimming and diving catalyzes the final stage in muscle oxygen store development.

In addition to increased activity levels and the demands of diving as plausible factors that may increase myoglobin concentration in northern elephant seals, thermoregulatory factors, as we suggested for king penguins, may also play a role. Because increased myoglobin content enhances overall aerobic capacity, it is important for NST and shivering thermogenesis. In harp seals, nonshivering thermogenic capacity reaches a maximum at the time of transition to aquatic life approximately 30 days after birth (Blix and Steen 1979). For northern elephant seal pups, NST or shivering thermogenesis may be particularly beneficial for the pup at the end of the post-weaning fast as the pup enters the highly conductive marine environment with its depleted blubber layer.

Duration of muscle development

Although these three taxa show similar patterns in terms of increasing myoglobin content with age, the time required to attain adult levels varies. For example, bottlenose dolphin calves and king penguin chicks begin with similar proportions of the adult myoglobin content, at 10% and 9%, respectively. However, the time it takes for complete maturation of the muscle oxygen store varies between groups. Myoglobin content of a 90-day-old northern elephant seal is 80% of the adult myoglobin content. In comparison, a 136-day-old king penguin has only 25% of the adult myoglobin content. Although king penguin chicks were not studied to the point of fledging, based on conclusions from other penguins (Table 1), we can hypothesize that a 350-day-old newly fledged king penguin may still not have adult myoglobin contents. Meanwhile, it takes at least 1.5 years for bottlenose dolphins to reach adult myoglobin contents in the primary locomotor muscle. Interestingly, when both juvenile seals and dolphins begin to practice hunting, they show similar proportions of their adult values (64% and 57%, respectively), marking the final stage of myoglobin enhancement (Fig. 2). From these data, it appears that the duration of myoglobin development is dependent on the initiation of independent foraging by the young. Northern elephant seals, which start independent foraging at 3 months of age, show the shortest period of muscle myoglobin development, obtaining adult values sometime between 3-months-old and 10-months-old. In comparison, bottlenose dolphins, which start independent foraging at 18–20 months, experience the longest period of myoglobin development, obtaining adult values sometime between 18-months-old and 41-months-old.

To summarize, although the demands of locomotion, diving, and thermoregulation differ throughout maturation, cetaceans, penguins, and pinnipeds show similar patterns in myoglobin development from birth or hatching to adulthood. The possible effects of physical conditioning, thermal demands, and the increased time spent in apnea during swimming and diving on the postnatal development of muscle myoglobin content are apparent for all three taxa. The time it takes for complete maturation of the muscle oxygen store varies between groups depending on when the animal begins independent foraging. The final stage of postnatal development of myoglobin occurs during the initiation of independent foraging whether the animal is born at sea or born/hatched on land.

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Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling?

A. M. Springer[a,b], J. A. Estes[c], G. B. van Vliet[d], T. M. Williams[e], D. F. Doak[e], E. M. Danner[e], K. A. Forney[f], and B. Pfister[g]

[a]Institute of Marine Science, University of Alaska, Fairbanks, AK 99775; [c]United States Geological Survey, Center for Ocean Health, Santa Cruz, CA 95060; [d]P.O. Box 210442, Auke Bay, AK 99821; [e]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064; [f]National Marine Fisheries Service, Santa Cruz, CA 95060; and [g]National Marine Fisheries Service, Seattle, WA 98115

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Populations of seals, sea lions, and sea otters have sequentially collapsed over large areas of the northern North Pacific Ocean and southern Bering Sea during the last several decades. A bottom-up nutritional limitation mechanism induced by physical oceanographic change or competition with fisheries was long thought to be largely responsible for these declines. The current weight of evidence is more consistent with top-down forcing. Increased predation by killer whales probably drove the sea otter collapse and may have been responsible for the earlier pinniped declines as well. We propose that decimation of the great whales by post-World War II industrial whaling caused the great whales' foremost natural predators, killer whales, to begin feeding more intensively on the smaller marine mammals, thus "fishing-down" this element of the marine food web. The timing of these events, information on the abundance, diet, and foraging behavior of both predators and prey, and feasibility analyses based on demographic and energetic modeling are all consistent with this hypothesis.

The abrupt decline of the western stock of Steller sea lions (*Eumetopias jubatus*)[h] across most of the northern North Pacific Ocean and southern Bering Sea is one of the world's most well known yet poorly understood marine conservation problems. For years, scientists attributed this decline to nutritional limitation, the presumed consequence of a climate regime shift and/or competition with regional fisheries (1). Although fisheries and regime shifts undoubtedly influenced both the fishes and their associated food webs (2–5), several recent reviews of the available information on sea lions and their environment, including an assessment by the National Research Council, cast doubt on the nutritional limitation hypothesis (6, 7), notwithstanding evidence from field and laboratory studies that diet quality is a factor in sea lion energetics (8). The doubt stems from three main findings. First, most measures of behavior, physiology, and morphology from surviving adult sea lions and pups in the western Gulf of Alaska and Aleutian Islands are inconsistent with nutritional limitation. These animals have better body condition, reduced foraging effort, and reduced field metabolic rates relative to similar measures from the increasing sea lion population in southeast Alaska (7). Second, sea lion prey is abundant in most areas of the decline (9). Known changes in prey availability and other features of the oceanic ecosystem are particularly incongruous with the most precipitous phase of the decline, which occurred during the mid- to late 1980s, and can be accounted for only by greatly increased adult mortality (6). Third, populations of piscivorous sea birds, many of which feed on earlier life stages of the same fish species consumed by sea lions, have remained stable or increased in the same area and over the same period that the sea lions have declined (10). Top-down forcing now appears to have been an important contributor to declines of Steller sea lions and other marine mammal populations in the region (6). Likely top-down forcing factors include purposeful shooting, incidental mortality in fishing gear, and predation. We will suggest that increased predation was paramount among these factors, and that altered food web dynamics brought about by human overharvesting initiated the change.

A Megafaunal Collapse

Steller sea lions are only one of several marine mammal species in the far North Pacific region whose numbers have crashed in recent decades. Northern fur seal (*Callorhinus ursinus*), harbor seal (*Phoca vitulina*), and sea otter (*Enhydra lutris*) populations have also fallen precipitously. Causes of the pinniped declines are poorly known, except that incidental mortality from commercial fishing activities and intentional harvesting in the 1960s and early 1970s appear to explain substantial portions of the initial declines. The failure of these factors to explain the continued rapid collapses, the failure of the nutritional limitation hypothesis to explain the decline of the western stock of Steller sea lions, the recent demonstration that harbor seals thrive on prey with a wide range of nutritional quality (11), and the discovery that killer whales (*Orcinus orca*) were likely responsible for the sea otter decline (12), led us to suspect that the pinniped declines also were caused by increased killer whale predation.[i]

If this explanation is indeed true, why did the collapse occur? We propose that decimation of the great whales during the modern era of industrial whaling ultimately caused the declines by forcing the great whales' foremost natural predators, killer whales, to turn elsewhere for food.

Killer Whales Prey on Great Whales

Our hypothesis rests on the supposition that the great whales were an important prey resource for killer whales before industrial whaling severely reduced their numbers. Although there is debate over the nature and importance of killer whale predation on great whales (13, 14), this supposition is supported by several lines of evidence. Killer whales are known to attack and consume all species of great whales (15, 16). Such attacks have been observed regularly in modern times, despite the reduced abundance of most great whale stocks. Early whalers apparently recognized the importance of killer whale–great whale interactions: historical accounts from that era referred to these animals as "whale killers," a term that later was transposed to killer whales (17). Scars and rake marks from the teeth of killer whales on living great whales support the idea that killer whale attacks are fairly common (18), although the rate of scarring appears to

[b]To whom correspondence should be addressed. E-mail: ams@ims.uaf.edu.

[h]Steller sea lions range across the North Pacific Ocean from California to Japan. The western stock of this species, which ranges westward from Cape Suckling (longitude 144° W), was listed as Endangered under the U.S. Endangered Species Act in 1997.

[i]The absence of beach-stranded carcasses is one of the most intriguing and perplexing features of these declines. Sea otter mortality from nutritional limitation, disease, and pollution typically results in large numbers of stranded carcasses. Pinnipeds often sink when killed at sea, although many such individuals float to the surface and wash ashore later. Malnourished or diseased pinnipeds commonly haul out to die. The near absence of stranded carcasses and a lack of reports of distressed animals on beaches or of emaciated animals taken by subsistence hunters thus are most consistent with losses to predators.

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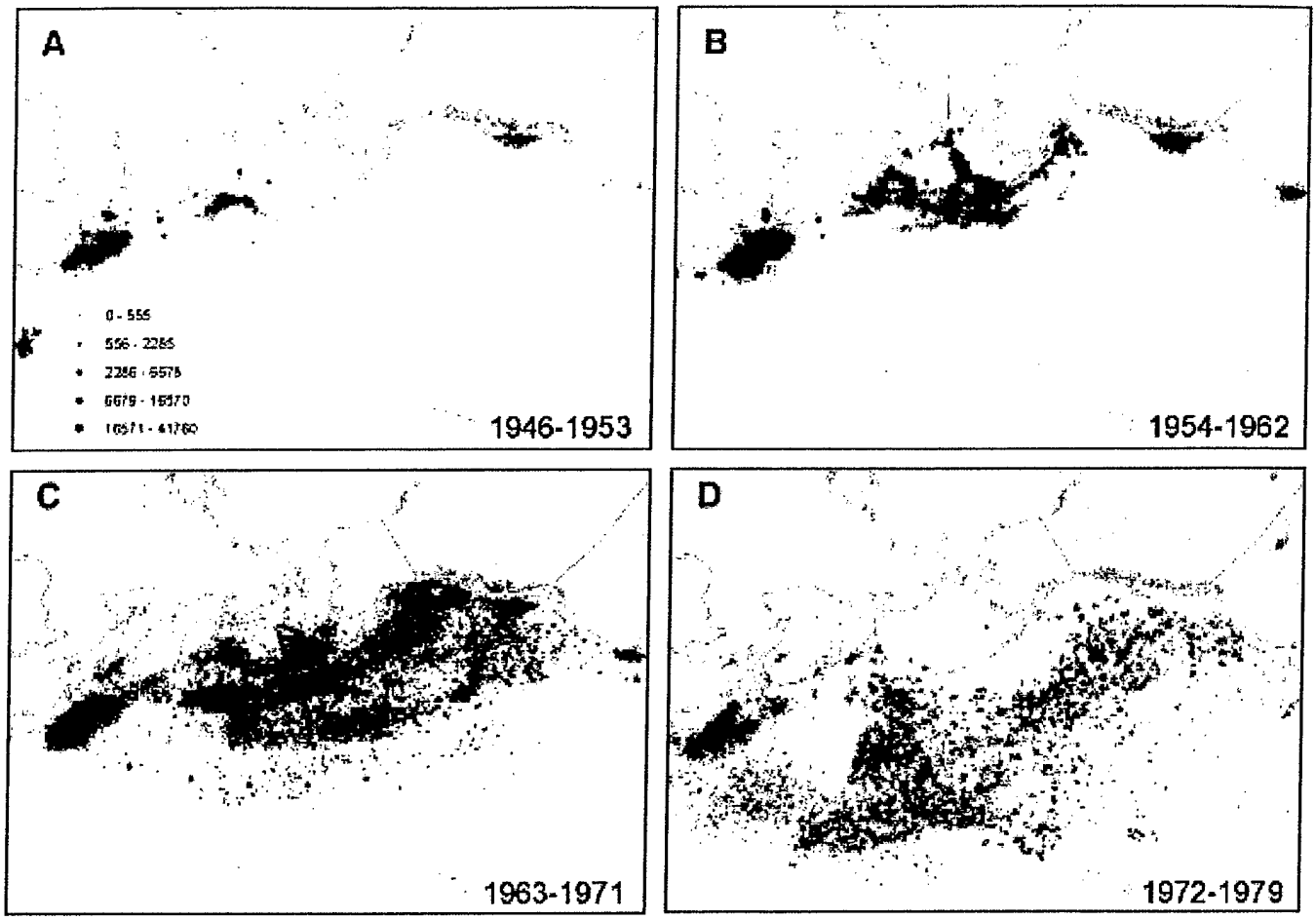

Fig. 1. Geography of reported whale harvests (all species) in the North Pacific Ocean and Bering Sea from 1946 through 1976. Data (latitude/longitude and number of individuals) are from International Whaling Commission records and are binned by sequential 7- to 8-year intervals to show temporal trends.

vary by region and species. Measured scarring on 20–40% of the individuals in some large whale species is not unusual; the highest known scarring rate is >60% reported for sperm whales in the southern ocean (19).

Several features of great whale life history and behavior may also function to reduce the likelihood of killer whale predation. For instance, sperm whales, long thought to be immune to killer whales, are now known to be preyed on by them and to assume stereotypical formations to ward off the attacks (20, 21). Many large whale species migrate from high-latitude feeding grounds to low-latitude calving grounds. Because of their very large size, this behavior does not confer a thermal benefit or energy saving, even to calves (13). The lack of thermal benefit raises the question of why large whales undertake such long migrations to nutritionally impoverished tropical oceans. Corkeron and Connor (13) contend this behavior may substantially reduce losses from killer whale predation by placing the most vulnerable newborns in environments where killer whales are comparatively rare. Likewise, the northward migration of bowhead whales (*Balaena mysticetus*) from wintering and feeding areas in the extremely productive northwestern Bering Sea to summering areas in the comparatively impoverished Beaufort Sea may reduce their exposure to killer whale predation (22). It has been further suggested that the failure of bowheads in the eastern Canadian Arctic to recover from commercial whaling is due in part to predation by killer whales (23, 24).

Industrial Whaling in the North Pacific Ocean

Modern industrial whaling in the North Pacific Ocean began in the late 1940s as Japan and the Soviet Union turned a maritime technology that developed during World War II toward postwar economic growth. Several species, including North Pacific right whales (*Eubalena japonica*), bowhead whales, humpback whales (*Megaptera novaeangliae*), blue whales (*Balaenoptera musculus*), and gray whales (*Eschrichtius robustus*), were depleted some 50–100 years earlier (25–27), but the more abundant fin whales (*Balaenoptera physalus*), sei whales (*Balaenoptera borealis*), and sperm whales (*Physeter macrocephalus*) were not exploited in large numbers until after the war. Our analysis of the depletions is based on International Whaling Commission records, which include geographical coordinates and species of all legally killed whales reported by whaling nations. These "official" records minimize the true magnitude of the catch in the North Pacific because of underreporting by the Russian fleet, by as much as 60% in the case of sperm whales taken between 1949 and 1971 (28), and because some unknown proportion of all kills were animals that were struck and lost. Nonetheless, the data provide a reasonable indication of the timing and spatial pattern of the whale declines.

Early postwar whale landings were mostly from the far western North Pacific Ocean (Fig. 1*A*), presumably because at the time, Japan was the region's only significant whaling nation, and great whales were still abundant throughout the North Pacific; thus, the Japanese whalers did not have to venture far from their home ports. Other nations, mainly the Soviet Union, subsequently entered the whale fishery. As stocks close to the home ports were progressively reduced, the fishery spread eastward and intensified (Fig. 1 *B* and *C*). By the early 1970s, the whaling industry had

abandoned this region because of severely depleted stocks and catch restrictions imposed by the International Whaling Commission and moved south into the central North Pacific (Fig. 1*D*) to exploit smaller Bryde's whales (*Balaenoptera brydei*) and female sperm whales.

The vast majority of whales were removed from rich summer feeding grounds in a small portion of the northern North Pacific Ocean and Bering Sea. In waters within 370 km (200 nautical miles) of the Aleutian Islands and north coastal Gulf of Alaska alone, a minimum of 62,858 whales and an estimated 1.8 million tonnes of whale biomass were taken between 1949 and 1969. As a measure of the magnitude of change in whale abundance in this region over this time, only 156 whales were harvested there after 1969. Altogether, at least a half million great whales were removed from the North Pacific Ocean and southern Bering Sea during this period. By the mid-1970s, all great whale stocks in the North Pacific Ocean were severely diminished. Although some species have exhibited remarkable recoveries (e.g., gray whale and humpback whale), the combined current biomass (1990s and early 2000s) is estimated to be only ≈14% of preexploitation levels (B.P., unpublished data).

The extreme, rapid, concentrated reduction of whale biomass from the northern North Pacific Ocean must have profoundly influenced the workings of the ecosystem by altering population level interaction strengths of two general kinds: those extending downward in the food web from the great whales to their prey and those extending upward in the food web from the great whales to their predators. Our focus is on the potential consequences of altered interaction strengths between the great whales and their predators.

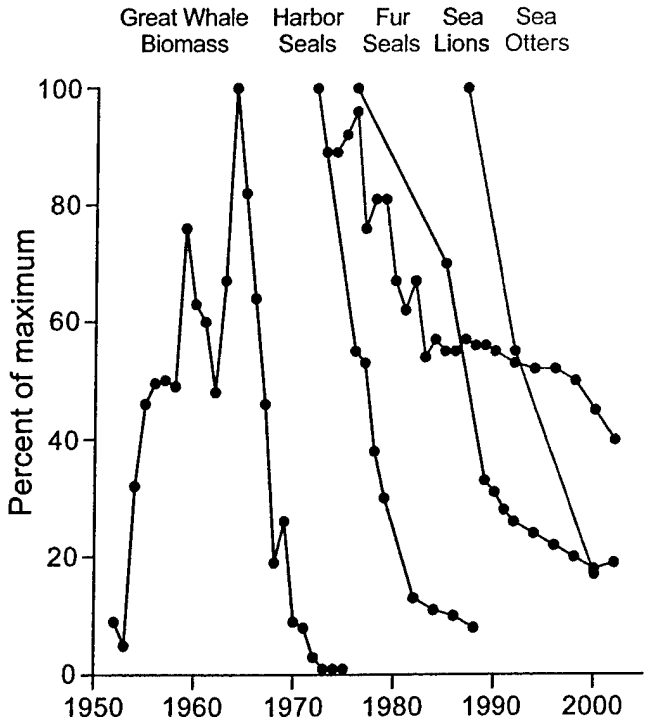

Fig. 2. The sequential collapse of marine mammals in the North Pacific Ocean and southern Bering Sea, all shown as proportions of annual maxima. Great whales: International Whaling Commission reported landings (in biomass) within 370 km of the Aleutian archipelago and coast of the western Gulf of Alaska. Harbor seals: counts and modeled estimate (1972) of Tugidak Island (36). Fur seals: average pup production on St. Paul and St. George islands, Pribilof Islands (from ref. 37 and A. E. York, personal communication). Steller sea lions: estimated abundance of the Alaska western stock (from ref. 38). Sea otters: counts of Aleutian Islands (from ref. 39). For fur seals and harbor seals, 100% represents population sizes at the time effects of excessive harvesting ended and "unexplained" declines began.

Response of Killer Whales to Whaling

Before commercial whaling, the great whales likely provided an important food resource for killer whales in the North Pacific Ocean, just as gray whales do today along their eastern Pacific migratory route (29–31). Killer whales are organized around cultural matrilines with foraging preferences that define distinct ecotypes (32). Three killer whale ecotypes are recognized in the eastern North Pacific Ocean: transients, which feed largely on other marine mammals; residents, which feed largely on fish; and offshores, whose diet is less known (33, 34). Shifts in diet within specific ecotypes are known or suspected. For example, in the Southern Ocean, one particular ecotype (or species) feeds mostly on large cetaceans at high latitude during the austral summer and pinnipeds, fish, and squid at lower latitude during the austral winter (35). Because mammal-eating killer whales in the North Pacific feed on a wide variety of marine mammals, and because killer whales alter their diets in response to changing prey availability, the decline of great whales could have led to increased consumption of other marine mammal species by at least some of the whale-eating killer whales.

The sequential declines of pinnipeds and sea otters after human depletion of the great whales (Fig. 2) are consistent with this expectation. Pinniped populations in the Aleutian Islands, Bering Sea, and Gulf of Alaska began to fall during the 1960s and 1970s, shortly after the whale fishery collapsed and after the cessation of human harvest, but in advance of the late 1970s regime shift.[j] Harbor seals declined first (36),[k] followed by fur seals and then sea lions. Killer whales may have preferred harbor seals and fur seals to sea lions for nutritional or behavioral reasons, such as the higher energy density of harbor seals and the ease of capturing and handling both species because of their smaller size and less aggressive nature.

We surmise that as the last of the pinnipeds became comparatively rare, some of the killer whales that preyed on them further expanded their diet to include the even smaller and calorically least profitable sea otters. Sea otter populations in the Aleutian Islands began to collapse in ≈1990, after the pinniped declines, and by the late 1990s their numbers had decreased by an order of magnitude in many areas, converging on a common low density throughout the archipelago (39) and causing sea urchins to overgraze the kelp forest ecosystem (12).[l] Our subsequent analyses of the likely reason for these changes are limited to the Aleutian archipelago, because this is where our

[j]Initial declines of fur seals on the Pribilof Islands (in the Bering Sea) and harbor seals on Tugidak Island (in the Kodiak archipelago, depicted in Fig. 2) prior to the 1970s were caused in substantial part by excessive human killing, of fur seals during an experimental harvest in 1956–1968 and of harbor seals by a commercial harvest in 1964–1972. After cessation of these harvests, numbers of both species continued to decline because of elevated mortality of juveniles and adults. It is particularly noteworthy that these "unexplained" declines began well in advance of the climate regime shift of 1977, which has been blamed for altering many facets of marine ecosystems of the North Pacific (3–5).

[k]Although these data are from a single location, Tugidak Island, they are representative of the timing and magnitude of harbor seal declines that occurred elsewhere. For instance, the harbor seal population at Otter Island (in the Pribilof Islands), which numbered ≈1,200 when first counted in 1974, declined 40% from 1974 to 1978 and an additional 70% from 1978 to 1995 (L. Jemison, personal communication). Similar harbor seal declines, although not quantified, have occurred throughout the Aleutian archipelago (J.A.E., unpublished observations).

[l]A corollary is that the increase in abundance of killer whales in the late 1980s on the continental shelf of the eastern Bering Sea, in the region of the Pribilof Islands and in Bristol Bay (40, 41), also resulted from the collapse of pinnipeds in the Aleutian Islands. The increase of killer whales on the shelf was accompanied by the resumption of the overall decline of fur seals at the Pribilofs after a brief interval of stability at St. Paul Island (Fig. 2) and by numerous observations of attacks on a variety of marine mammal species in Bristol Bay.

field studies were done, and it is the region from which we have the best information on key players.

Killer Whale Abundance

Killer whales were long thought to be too rare to account for the pinniped declines,[m] but current information indicates this is not the case. By using standard line transect techniques (42), killer whale density in waters up to 370 km south of the eastern and central Aleutian archipelago was conservatively estimated at 3.6 individuals per 1,000 km^2, based on 2,897 km of shipboard search effort during a 1994 survey (K.A.F., unpublished data). [This estimate is comparable to densities of 2.5 per 1,000 km^2 for the southeast Bering Sea (43) and 2.3–7.6 per 1,000 km^2 for Antarctic waters (44).] If the density were similar in the western Aleutian Islands, the estimate of 3.6 individuals per 1,000 km^2 would translate into an abundance of 3,888 killer whales (95% confidence interval, 1,707–8,857) in waters within 370 km (1,080,000 km^2) of the entire archipelago. This estimate presumably includes killer whales of all three ecotypes.

Demographic Influences of Killer Whale Predation

Although changes in fish stocks due to fishing or climate regime shifts may have contributed to the losses (45), as did directed killing by people (6), both the sea otter and sea lion declines could be accounted for by remarkably small changes in killer whale foraging behavior. We computed these changes by combining estimates of the abundance and nutritional requirements of killer whales, the nutritional value of sea lions and sea otters, and the number of additional deaths required to explain the observed sea lion and sea otter declines in the Aleutian archipelago. We were unable to conduct similar analyses for harbor seals, because the predecline population size there is unknown.

Population matrix models were used to estimate the number of additional deaths required to drive the sea otter and sea lion declines. These models were parameterized by using published life table data for Steller sea lions (46), age-specific fertility and mortality rates for sea otters (12), and predecline abundance estimates for both species (39, 46). We then fit the added mortality required to generate the observed speed and magnitude of population declines for each species. For sea otters, we assumed age independence and a constant number of animals lost per year (12). The resulting loss estimate was 9,982 deaths per year from 1991 through 1997. For Steller sea lions, we used maximum likelihood methods (47) to fit the demographic model with an added time-varying logit function for predation risk. The age-specific probability of elevated mortality is unknown for Steller sea lions, and thus a series of models was fitted, ranging from age constancy to 5-fold higher predation risk for pups and younger animals. These models predict from as many as 15,006 additional animals lost to predation in the Aleutian Islands in 1979 to as few as 170 in 2000.

Caloric values for sea otters were determined by bomb calorimetry of homogenized whole carcasses and measurements of adult body mass (12). Resulting estimates range from 41,630 to 61,540 kcal per individual. Caloric values for Steller sea lions, determined similarly for skeletal muscle and blubber, ranged from 1.5 to 6.7 $kcal \cdot g^{-1}$ wet weight. These latter data were combined with published estimates of body mass and composition for pups, adult females, and adult males to provide estimates of caloric value for individual sea lions (T.M.W., unpublished data).

[m]Dahlheim, M. E. (1994) *Abundance and Distribution of Killer Whales in Alaska* (Unpublished Report, National Oceanic and Atmospheric Agency, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle).

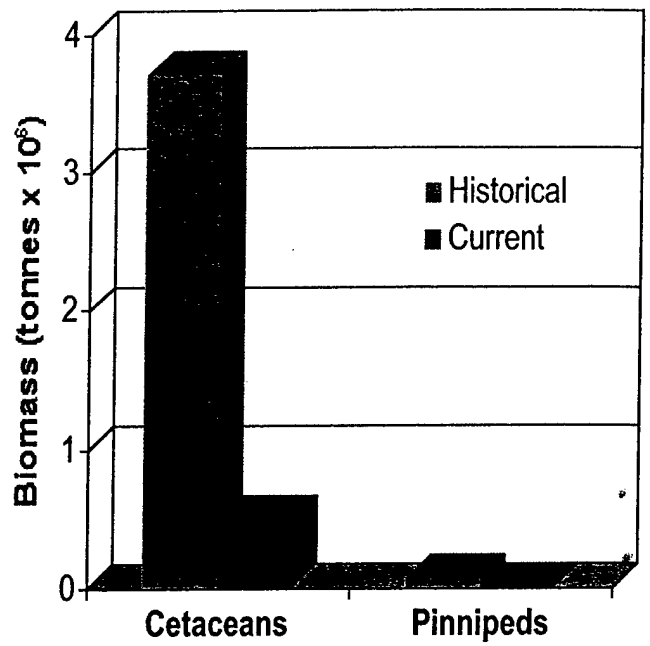

Fig. 3. Biomass estimates for great whales and pinnipeds before and after recent declines in the Aleutian Islands and Bering Sea region. These estimates were derived from current and historical estimates of abundance and per capita biomass, in some cases adjusted for estimates of sex and size composition (from B.P., unpublished work). Historic and current abundance estimates are species-specific. "Historical" is defined as the period before large-scale commercial exploitation, ranging from the mid-1800s to the mid-1900s. "Current" is defined as the most recent available estimate of abundance, reflecting population levels during the mid-1990s to early 2000s.

The nutritional requirements of killer whales were estimated from field metabolic rates and assimilation efficiency. Field metabolic rate estimates ranged from 163,738 to 243,501 $kcal \cdot day^{-1}$, depending on sex and age [Barrett-Lennard *et al.* (48) estimated similar metabolic rates for free-ranging killer whales]. Assimilation efficiency was taken as 82% (49).

These data can be translated into potential killer whale dietary change in various ways. If we assume the change was spread evenly across all of the region's 3,888 killer whales, then a dietary shift of <1% in total caloric intake (0.99% for sea lions; 0.17% for sea otters) is sufficient to drive the respective population declines. In view of the killer whale's complex social structure and associated dietary variation, a larger dietary change by some smaller number of individuals is more likely. If we assume that ≈7% of the killer whale population are transient mammal eaters (P. Wade, personal communication), the resulting 272 killer whales is >10-fold larger than the minimum number needed to drive the Steller sea lion decline and >45-fold larger than the minimum number needed to drive the sea otter decline if they derived 100% of their total caloric intake from either species. These various estimates show that our conclusions are robust to anything but massive errors in the input parameters, something we believe is unlikely.

The inability of sea otters and pinnipeds to sustain increased mortality from redirected killer whale predation ultimately derives from their much smaller aggregate biomass compared with that of the great whales (Fig. 3). When all of these marine mammals were maximally abundant, the estimated biomass of great whales was ≈60-fold larger than the combined total for pinnipeds and sea otters. These gross inequalities suggest that the great whales were capable of sustaining vastly more killer

whales than were the pinnipeds and sea otters, despite the fact that in some cases only portions, e.g., tongues, of great whales are consumed. From these estimates and analyses, it is easy to see how industrial whaling could have caused killer whales to "fish down" (50) other components of the marine mammal food web.

Discussion

Our proposed explanation for the collapse of sea otters and pinnipeds in the northern North Pacific Ocean and southern Bering Sea, although speculative, is based on a logical interpretation of known patterns and feasibility analyses of the hypothesized causal process. Although killer whales likely drove the sea otter declines and are known to prey on harbor seals, northern fur seals, and sea lions, there is presently no direct evidence that killer whale predation drove the pinniped declines. In contrast with the sea otters, detailed field studies of killer whales and pinnipeds are lacking from the most critical time periods. Studies of the modern-day predator–prey system in the western Gulf of Alaska and Aleutian Islands are unlikely to resolve this matter, because pinnipeds and sea otters are now relatively rare and their populations comparatively stable, and numbers of mammal-eating killer whales in the region also may be much reduced. Thus, few losses from predation would be expected, and the demographic significance of those that might be seen would be difficult to interpret. However, it is worth mentioning that recent localized declines of harbor seals (www.sfgate.com/cgi-bin/article.cgi?file=/news/archive/2003/02/24/state1900EST7458.DTL) and Steller sea lions[n] elsewhere have been attributed to killer whale predation. A further complication is that some recovering whale populations, particularly gray, humpback, and bowhead whales, are increasingly providing alternate prey resources for killer whales in this region.

The most promising source of information on the cause of the pinniped declines is the retrospective analysis of materials from individual pinnipeds or killer whales that were alive during various stages of the megafaunal collapse. Recently published nitrogen isotope analyses of pinniped bones obtained during this period provide no indication of dietary change (51), a finding that appears to be inconsistent with nutritional limitation. Isotopic studies of killer whale bones and teeth could provide a more definitive test of our hypothesis by establishing whether these large predators altered their diets after the great whale reductions. It is worth noting that if the North Pacific killer whale population has remained numerically stable with a stationary age distribution over this period, ≈28–39% of the individuals alive in 1965 during the final binge of commercial whaling would still be alive in 2002. For the longer-lived females alone, 39–57% survival from 1965 is expected.[o]

There is growing evidence that large animals play important roles in ecosystem dynamics (53–57). Furthermore, retrospective analyses of numerous coastal marine systems demonstrate or suggest a pervasive influence from the historical removal of these large animals (58). Many ecosystems function in vastly different ways today than they did when large animals were common, and there is no reason to believe the open sea is an exception. If our hypothesis is correct, either wholly or in significant part, commercial whaling in the North Pacific Ocean set off one of the longest and most complex ecological chain reactions ever described, beginning in the open ocean >50 years ago and leading to altered interactions between sea urchins and kelp on shallow coastal reefs.

Whaling was a global endeavor (59), and thus ecosystem-level effects of commercial whaling undoubtedly occurred elsewhere in the world oceans. The depletion of baleen whales in the Southern Ocean is thought by some to have substantially altered krill abundance and therefore the dynamics of interactions between krill and krill consumers (60, 61). Moreover, the Southern Ocean is a region where the great whales were exploited in even larger numbers than they were in the North Pacific, pinnipeds and killer whales were abundant, and various southern elephant seal (*Mirounga leonina*) populations have declined (62–64). Barrat and Mougin (62) hypothesized that these declines were caused by whaling and increased killer whale predation, an identical explanation to the one we are proposing for the North Pacific. It is surprising to us that these proposals for community-level influences of whales and whaling have had so little effect on subsequent research. Both are supported by logic and a variety of indirect evidence, and neither has been reasonably discounted, so far as we know.

Although substantial uncertainty remains concerning the degree to which whales and whaling influenced the structure and dynamics of ocean ecosystems in top-down ways, these influences must have been sizeable. A greater appreciation of this fact is needed to properly understand the function of the oceans, now and in the past.

[n]Maldini, D., Maniscalco, J. & Burdin, A. (2002) *Fourth International Orca Symposium and Workshop* (Centre National de la Recherche Scientifique, Villiers en Bois, France), pp. 92–94 (www.cebc.cnrs.fr/Fr_collo/ORCA.pdf).

[o]Survival estimates were calculated from two-sex matrix models by using demographic rates from ref. 52.

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Intermittent Swimming by Mammals: A Strategy for Increasing Energetic Efficiency During Diving[1]

TERRIE M. WILLIAMS[2]

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

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[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 diving). 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.*, 1993*a*) 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

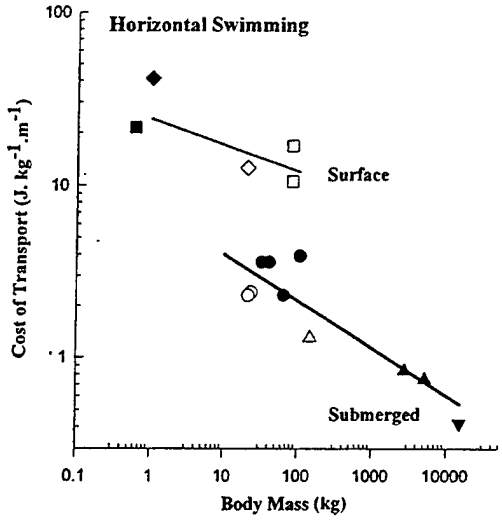

FIG. 1. Total cost of transport (COT) in relation to body mass for surface and submerged swimming mammals moving in a horizontal path. Solid lines represent the least squares regressions through the data points and are presented in the text. Data points represent individual studies and species: surface 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.*, 1993*a*), 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

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

where COT is in $J \cdot kg^{-1} \cdot m^{-1}$ 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

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

where COT is in $J \cdot kg^{-1} \cdot m^{-1}$ 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 twofold (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

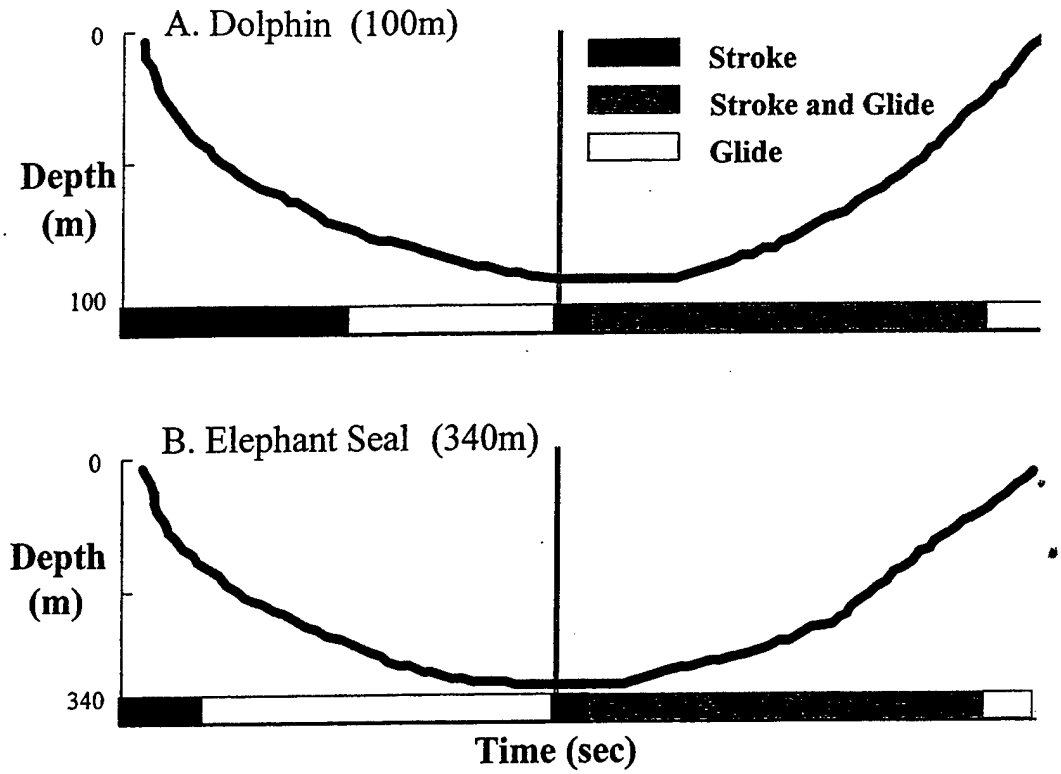

FIG. 2. Representative dive profiles and locomotor modes for an adult bottlenose dolphin performing a 100 m dive (A) and a juvenile northern elephant seal during a 340 m dive. Dark curves denote the change in depth with time during the dive. Horizontal boxes along each dive indicate the preferred locomotor 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 $m \cdot sec^{-1}$. 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 remaining 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 $mlO_2 \cdot kg^{-1}$) 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.*, 1993*b*, 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 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.

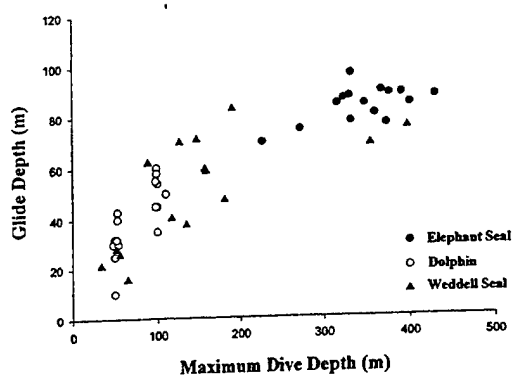

FIG. 3. Depth at the start of the gliding during descent in relation to maximum depth of the dive. Each point represents a single dive for northern elephant seals (closed circle), bottlenose dolphins (open circle) and Weddell seals (closed triangle).

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.

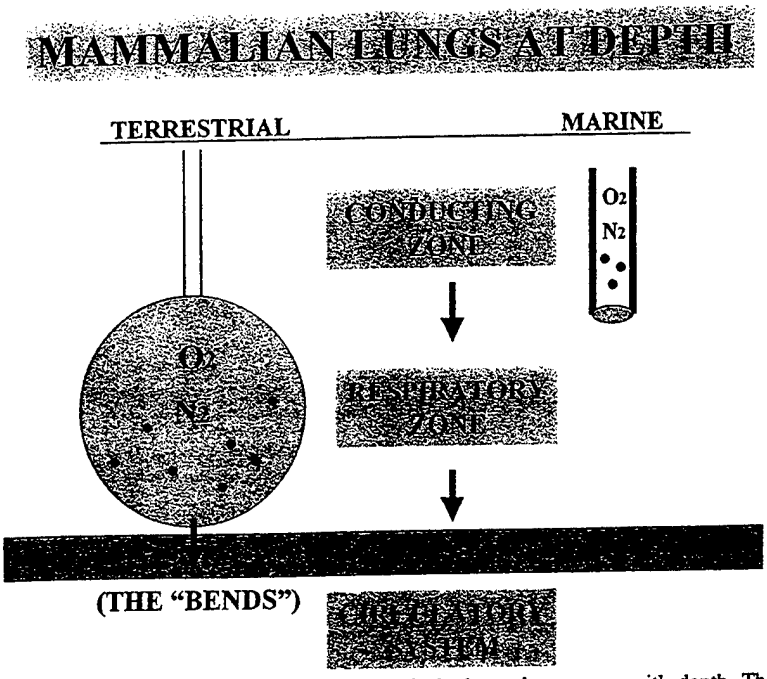

FIG. 4. Changes in the mammalian lung with increases in hydrostatic pressure with depth. The alveoli (gray circle) of terrestrial mammals trap air due to the collapse of connecting airways. Trapped gases remain in the alveolar respiratory zone and may be absorbed into the circulatory system resulting 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 airways (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 Sinnett, 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 interrelationship 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).

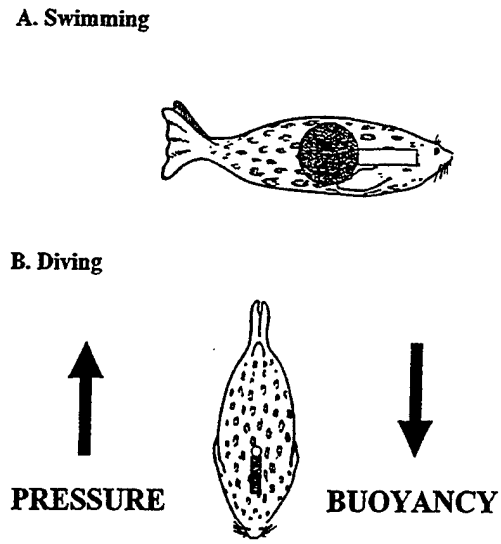

FIG. 5. Relative differences in lung volume of a Weddell seal during horizontal swimming near the water surface (A) and vertical diving (B). Increases in hydrostatic pressure during descent result in compression and a decrease in volume of the lungs. Buoyancy decreases concomitantly. Circle = respiratory 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).

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 $O_2 \cdot kg^{-1}$)					
	Descent		Ascent			
	Stroke Period	Glide Period	Stroke Period	Glide Period	Total Cost	% Total O_2 Store
Dolphin						
Intermittent Locomotion	8.9	5.1	19.4	0.4	33.8	102%
Continuous Locomotion	17.2	—	20.6	—	37.8	114
Phocid Seal						
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 example the rate of oxygen consumption for har- bor seals is 4.6 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$ during res and 12.9 $mlO_2 \cdot kg^{-1} \cdot min^{-1}$ during swimmin at approximately 2.0 $m.sec^{-1}$ (Davis *et al.* 1985). Rates of oxygen consumption deter mined for bottlenose dolphins are 4.($mlO_2 \cdot kg^{-1} \cdot min^{-1}$ during rest and 8.: $mlO_2 \cdot kg^{-1} \cdot min^{-1}$ during swimming at 2. $m \cdot sec^{-1}$ (Williams *et al.*, 1992). Assumin that oxygen consumption during passiv gliding approximates resting levels, then theoretical dive to 200 m by an adult harbc seal will require 43 $mlO_2 \cdot kg^{-1}$ if the anima continuously strokes during descent and as cent. A dive incorporating prolonged per ods of gliding as in Figure 2 will need onl 29.5 $mlO_2 \cdot kg^{-1}$. For dolphins, a strokin dive to 200 m in depth will use 37. $mlO_2 \cdot kg^{-1}$ compared to 33.8 $mlO_2 \cdot kg^{-1}$ fc a gliding dive of similar depth.

The benefit of these energetic savings b comes apparent when the size of the oxyge reserve available during submergence considered. The total oxygen store for a adult, 145 kg bottlenose dolphin is 33 $mlO_2 \cdot kg^{-1}$ (Williams *et al.*, 1993*b*), ar 65.0 $mlO_2 \cdot kg^{-1}$ for a 24 kg harbor se (Kooyman, 1989). In terms of the total o ygen reserve available, the gliding seal pe forming a 200 m dive realizes a 23% sa ings and the dolphin a 12% savings. Ir tially, these savings may appear trivi However, a 12% savings in the oxyg store for the diving dolphin translates ir an additional 1.0 min of gliding or 0.5 m of swimming at 2.0 $m \cdot sec^{-1}$ assuming t metabolic rates described above. For t phocid seal, a 23% saving in the oxyg store represents 3.0 additional minutes gliding or 1.1 min of swimming at : $m \cdot sec^{-1}$.

Many additional factors not accoun for in these simple calculations will also fect the actual cost of diving in mar mammals. Metabolic depression duri submergence, dive depth, gliding durati angles of descent and ascent, velocity, use of stroke and glide locomotion, and interactive effects of drag and buoyant fc es during a dive will influence total er getic requirements. For example, metab depression during diving (Hochach 1992) would have an additional conserv

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.

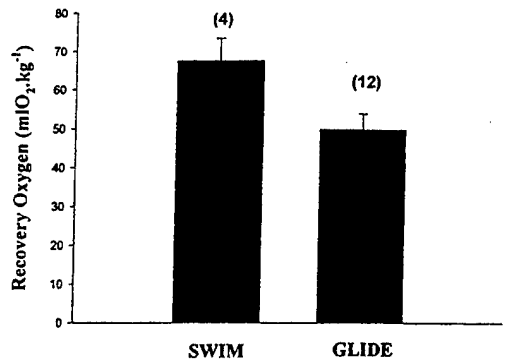

FIG. 6. Post-dive oxygen consumption of Weddell seals travelling 1,750–1,850 m beneath the Antarctic sea ice. Dives incorporating prolonged glide sequences (Glide) are compared to dives completed by continuous or stroke and glide swimming (Swim). Height of the bars and vertical lines denote mean values + 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.

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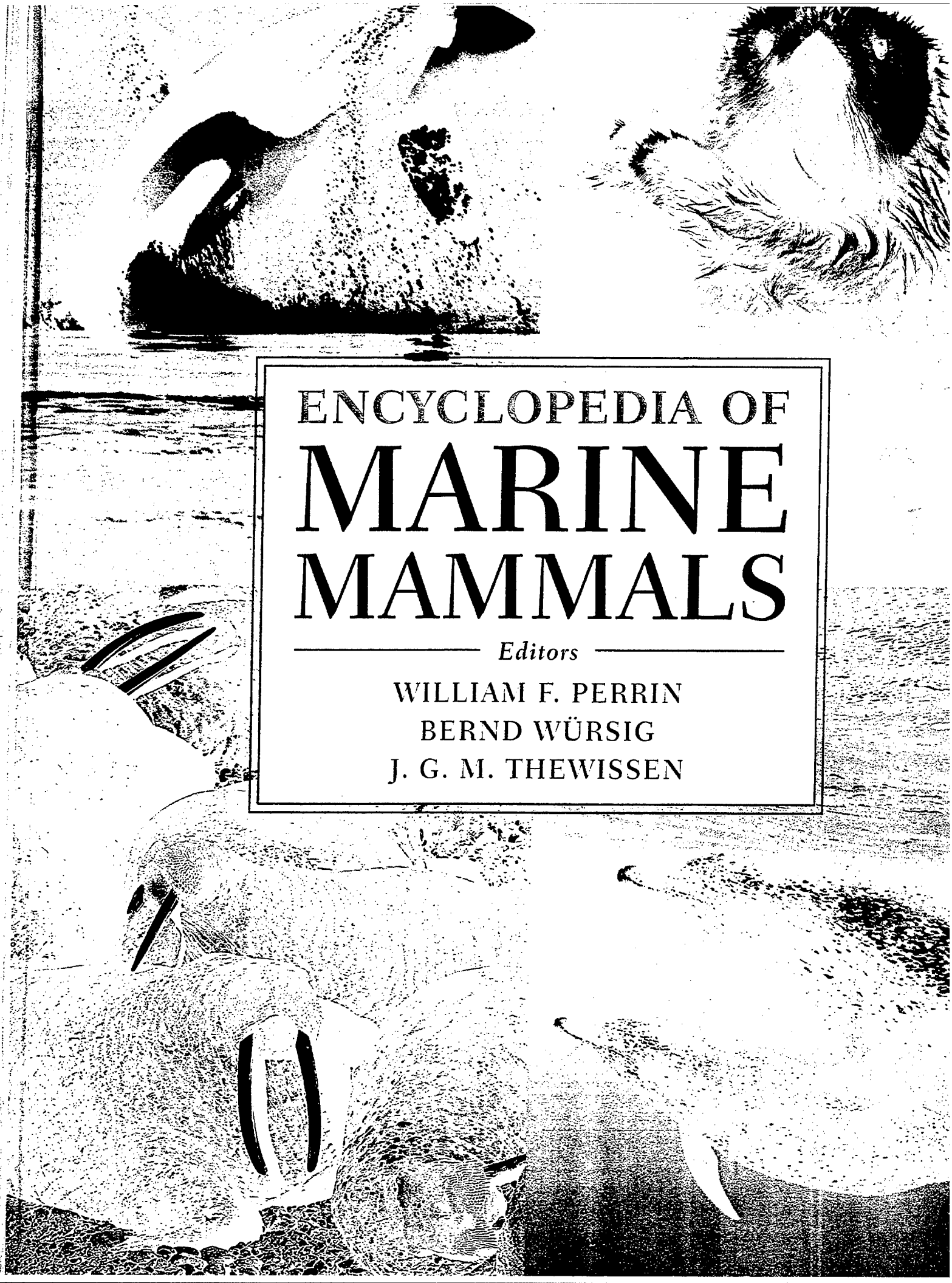

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Swimming

TERRIE M. WILLIAMS
University of California, Santa Cruz

The primary mode of locomotion for marine mammals, with the possible exception of polar bears (*Ursus maritimus*), is swimming. For dolphins, porpoises, and whales it is the only form of locomotion. The duration of swimming among these mammals may be as short as several seconds when moving between prey patches or as long as several months during seasonal migrations across entire ocean basins. Although swimming by marine mammals often appears effortless, it is in reality a delicate balance between precise body streamlining, exceptional thrust production by specialized propulsive surfaces, and locomotor efficiency (Fig. 1).

I. Hydrodynamics and Body Streamlining

One of the most characteristic features of marine mammals is a streamlined body shape. This is not surprising when one considers the forces that the animal has to overcome in order to move through water. When a swimmer moves through water a force, termed drag, acts backward on it resisting its forward motion. The equation describing total body drag is given by

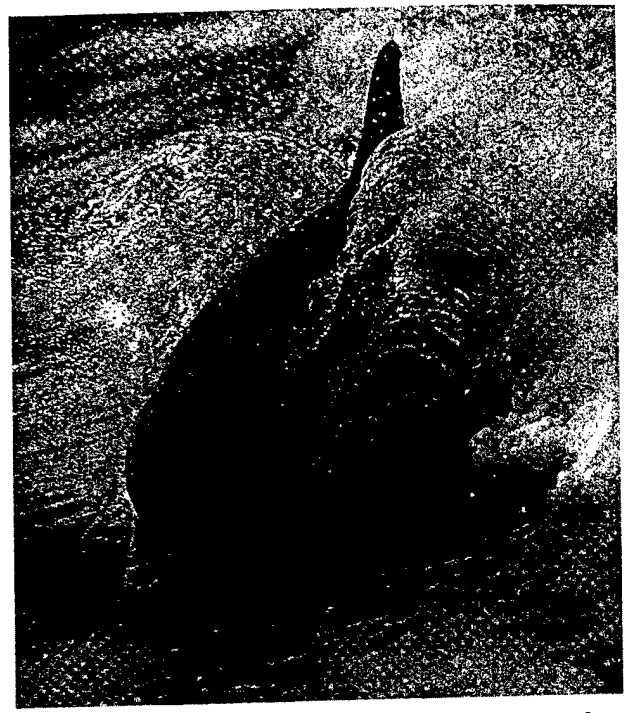

Figure 1 *A bottlenose dolphin swimming at high speed on the water surface. The generation of waves by the dolphin's movements leads to increases in body drag and elevated energetic costs during surface swimming.*

$$\text{drag} = 1/2pV^2ACd, \quad (1)$$

where p is the density of the fluid, V is the velocity of the fluid relative to the body, A is a characteristic area of the body, and Cd is the drag coefficient (a factor that takes into account the shape of the swimmer). Four primary types of drag contribute to total body drag: (1) skin friction drag, which is a tangential force resulting from shear stresses in the water sliding by the body; (2) pressure drag, which is a perpendicular force on the body associated with the pressure of the surrounding fluid; (3) wave drag, which occurs when a swimmer moves on or near the water surface; and (4) induced drag, which is associated with water deflection off of hydrofoil surfaces such as fins, flukes, or flippers. Of these, pressure drag is the component most influenced by body streamlining in marine mammals. The more streamlined a body, the lower the pressure drag and consequently the lower the total body drag of the swimmer.

Mammals whose lifestyles or foraging habits involve prolonged periods of swimming have streamlined body shapes. In contrast to the lanky appearance and appendages of terrestrial mammals, marine mammals tend to have a reduced appendicular skeleton and characteristic teardrop body profile. External features that may disrupt water flow across the body are also reduced or absent in many species of marine mammal. These

features include the pinnae (external ears), limbs, and long fur. In highly specialized swimmers such as dolphins the skin contains microscopic ridges that help to direct the flow of water in a controlled manner down the body. All of these adaptations prevent the onset of turbulence in the water surrounding the swimmer, thereby reducing total body drag.

Hydrodynamic theory describes the streamlined body shape as one in which a rounded leading edge slowly tapers to the tail, and total length is three to seven times maximum body diameter. The ratio of these morphological measurements, termed the fineness ratio, can be written

$$\text{fineness ratio} = \frac{\text{maximum body length}}{\text{maximum body diameter}}. \qquad (2)$$

The optimum fineness ratio that results in minimum drag with maximum accommodation for volume is 4.5. Calculations of the fineness ratio for a wide variety of marine mammals show that many species have body shapes that conform to the ideal hydrodynamic range (Fig. 2). A review by Fish (1993) showed that many cetaceans, pinnipeds, and sirenians have body shapes with fineness ratios that range from 3.0 to 8.0. The species examined included seals, sea lions, and odontocete whales, which are considered by many to typify a streamlined body profile. However, even the mysticete whales with enlarged heads and jaws specialized for filter feeding maintain a streamlined body profile (Fig. 2).

Despite nearly ideal body streamlining, all marine mammals must contend with drag forces when moving through the water. These forces can be a considerable challenge for the swimmer and will influence how quickly the animal will be able to move. It is apparent from Eq. (1) that the velocity of the swimmer will have a large impact on total body drag. As the swimmer moves faster, body drag increases exponentially. An example of the relationship between total body drag and velocity is presented in Fig. 3 for the sea otter (*Enhydra lutris*). Whether the sea otter swims on the water surface or submerged, body drag increases with velocity. However, body position clearly affects the level of total body drag encountered by the sea otter. At all comparable swimming speeds, body drag is higher for the otter moving on the water surface than when it is swimming submerged.

The same results have been found for other swimmers, including humans and harbor seals (*Phoca vitulina*). In general, body drag for a swimmer moving on or near the water surface is four to five times higher than the level of drag encountered by the submerged swimmer moving at the same speed. Much of this increase in drag at the water surface is due to energy wasted in the formation waves. This can be avoided if the swimmer is able to submerge to a depth equivalent to three body diameters. For a seal or small whale with a maximum body diameter of 1 m, this would mean changing swimming position to at least 3 m in depth to avoid wave drag and the consequent

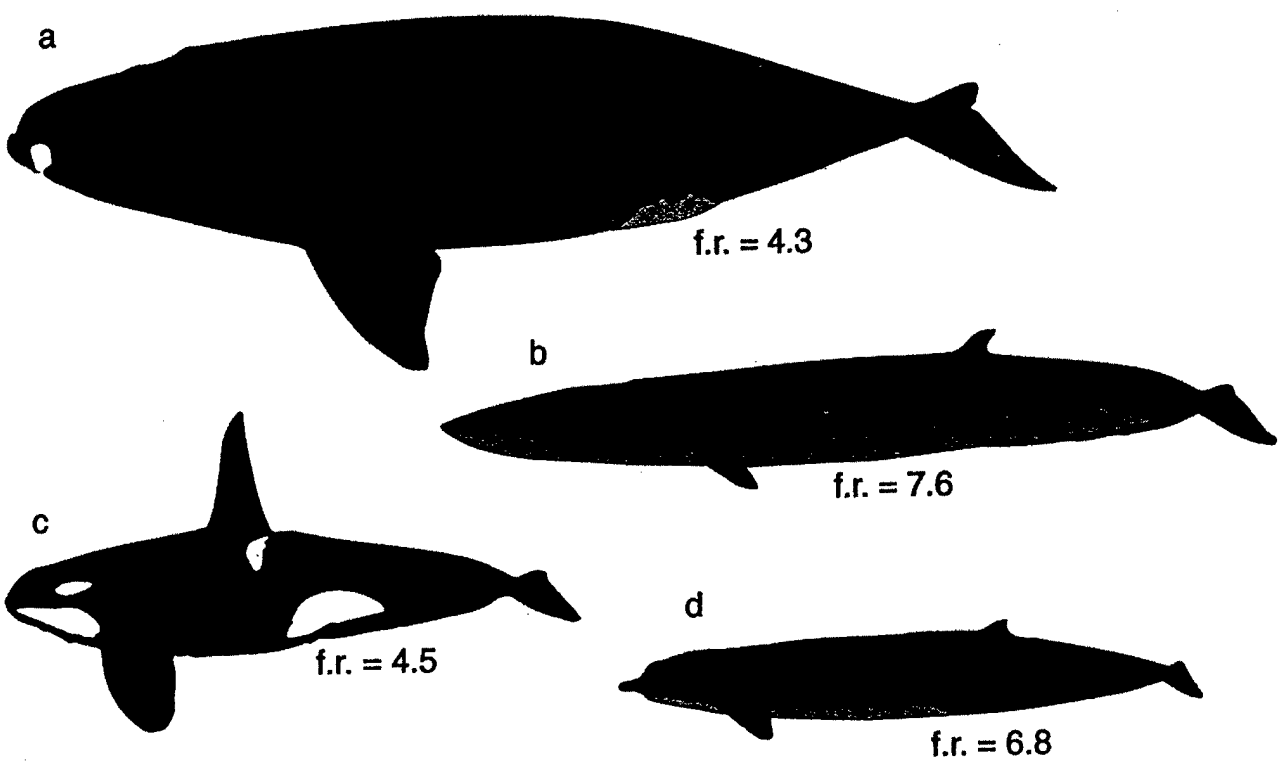

Figure 2 *Body shapes and fineness ratios for cetaceans. Shapes can range from the robust bowhead whale (a) to the long thin tapered body of the rorqual whales (b) and beaked whales (d). The killer whale (c) has the optimum shape in terms of fineness ratio and streamlining. From Berta and Sumich (1999), "Marine Mammals: Evolutionary Biology," Academic Press.*

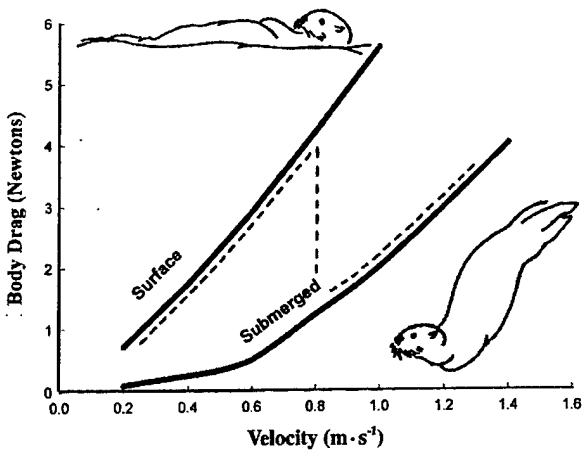

Figure 3 *Comparison of body drag for surface and submerged sea otters in relation to swimming speed. Note that at all comparable speeds, body drag of the sea otter on the water surface is higher than when the otter is submerged. The dashed line denotes the preferred swimming speeds of surface and submerged sea otters.*

elevation in total body drag. This is one of the reasons that swimming is comparatively difficult for humans—all of our performances take place on the water surface where wave drag, and hence total body drag, is the highest.

The ability to swim submerged for prolonged periods is one of the most important adaptations for increasing swimming efficiency and performance in marine mammals. The sea otter provides an excellent example of the advantage provided by this adaptation. Sea otters restrict prolonged periods of surface swimming to speeds less than 0.8 m · sec^{-1} and to a maximum body drag of 4.2 N (Fig. 3). For high-speed swimming, sea otters change to a submerged mode of locomotion. In doing so, drag is reduced by 3.5 times and the sea otter is able to reach speeds of 1.4 m · sec^{-1} before body drag once again exceeds 4.0 N. Thus, behavioral changes by the sea otter take into account the differences in drag associated with body position in the water and allow the animal to extend its range of swimming speeds. Several other behavioral strategies, such as porpoising and wave riding, are also used by marine mammals to avoid elevated body drag while swimming and are discussed in Section IV.

II. Kinematics

A hallmark of marine mammal swimming is the use of lift-based propulsion that allows thrust to be generated through the entire stroke cycle. This capability is found in highly adapted marine species such as pinnipeds and cetaceans. It contributes to an increase in locomotor efficiency in marine mammals, especially when compared to the inefficient drag-based swimming styles of humans and terrestrial mammals (Fig. 4).

Marine mammals use a wide variety of swimming styles to move through the water (Table I). The most terrestrial species of this group, the POLAR BEAR and sea OTTER, swim by alternate strokes of the forelimbs or hindlimbs, respectively. Polar bears use a dog style of forelimb paddling with the hindlimbs dragged passively behind or used as an aid to steering. Sea otters are unique among marine mammals in their ability to lie on their backs during surface swimming. Propulsion is provided by either simultaneous or alternate strokes of the hindlimbs. When on the surface, sea otters can also swim ventral surface (belly) down using the hind paws for propulsion. The front paws are held against the submerged chest and do not play a role in propulsion during this mode of swimming. Stroke frequency

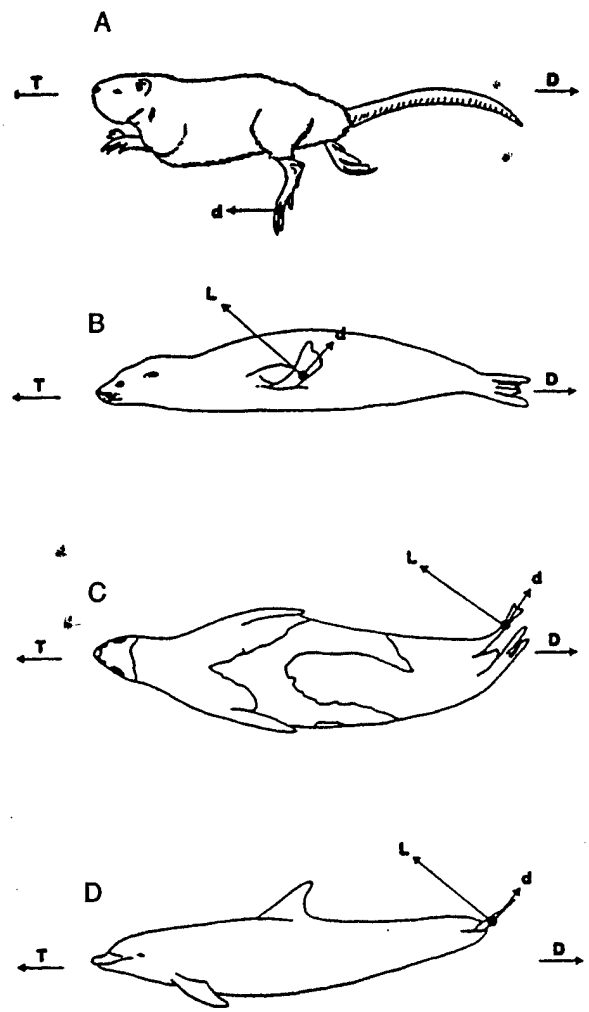

Figure 4 *Swimming modes for semiaquatic and marine mammals. The muskrat (A) is a semiaquatic mammal that uses drag-based propulsion by paddling its hind feet. Otariids (B), phocid seals (C), and cetaceans (D) use life-based propulsion that may involve fore flippers (sea lion), lateral body undulation (seal), or dorsoventral undulation (dolphin). Major forces on the animals and propulsive surfaces are shown. T denotes thrust, and D shows the direction of body drag on the animals. L and d illustrate lift and drag forces on the appendages, respectively. From Fish (1993).*

TABLE I
A Comparison of Swimming Characteristics for Four Major Classes of Marine Mammals

	Sea otter	*Otariid*	*Phocid*	*Small cetacean*
Routine speed (m/sec)	<0.8 (surface) <1.4 (submerged)	2.0–3.0	1.2–2.0, sprints to 4.0	2.0–4.0, sprints to 10.0
Hydrodynamics	Surface/submerged	Submerged	Submerged	Submerged
Kinematics				
Mode	Paddle, row (surface) Undulate (submerged)	Pectoral	Lateral Carangiform	Dorsoventral Thunniform
Energetics[a]				
COT measured	12.0 (surface)			
COT predicted	6.0 (submerged)	2.3–4.0	2.3–4.0	2.1–2.9

[a]The energetic cost of transport (COT) was measured for animals swimming in a flume or swimming freely in open water. The ratio of these values and the predicted values for fish of similar body mass are presented.

has been measured for swimming sea otters and ranges from approximately 30 to 80 strokes per minute while swimming on the water surface.

Polar bears and sea otters are the only marine mammals that rely primarily on drag-based modes of swimming. These modes of swimming have two distinct phases during the stroke cycle: a power phase when thrust is produced and a recovery phase when the foot is repositioned for the next stroke. During the power phase the foot is moved backward relative to the body. Drag created by this motion is subsequently translated into thrust and the animal moves forward through the water. The enlarged hind flippers of sea otters and fore paws of polar bears enable the animals to increase propulsive efficiency by moving a large mass of water during this power phase. The recovery phase of the stroke is only used to bring the limb back to its starting position and occurs without the generation of thrust. Because thrust is produced only during part of the stroke cycle, drag-based modes of swimming are comparatively inefficient.

When sea otters want to move quickly through the water they switch to an undulatory mode of swimming involving dorsoventral body flexion and simultaneous movements of paired hind flippers. The tail and hind flippers are held straight back and trail the undulatory movements of the trunk. The stroke frequency of sea otters remains relatively constant at 55 strokes per minute during submerged undulatory swimming, which suggests that underwater speed is elevated by increasing stroke amplitude.

As observed for submerged swimming sea otters, dolphins and whales use undulatory modes of propulsion. The primary propulsive movements of all cetaceans occur in the vertical plane with the posterior third of the body undulating in a dorsoventral direction. Termed thunniform swimming or carangiform swimming with a semilunate tail, this mode of locomotion is characterized by an undulatory wave that travels with increasing amplitude down the body, caudal peduncle, and finally the flukes (Fig. 5). "Semilunate" refers to the crescent shape of the flukes. This mode of propulsion is shared by other fast-swimming vertebrates, including tuna, hence the name "thunniform." Undulatory propulsion in cetaceans is considered highly efficient and can generate high levels of thrust on both the upstroke and the downstroke. There is no recovery phase and propulsion can be produced throughout the stroke cycle. Stroke frequency using this mode of swimming varies with the speed and size of the cetacean. The range of stroke frequencies for bottlenose dolphins swimming in a pool is 60–180 strokes $\cdot$ min^{-1}. Stroke frequency decreases with increasing body size among the cetaceans. Thus, we find that the largest species of swimming mammal, the 100-ton blue whale (*Balaenoptera musculus*), uses stroke frequencies that are only one-tenth of the range observed for bottlenose dolphins (*Tursiops* spp.). Recent measurements of the stroke frequency of blue whales ascending during a dive were 6–10 strokes $\cdot$ min^{-1}.

Swimming by pinnipeds differs markedly among EARED SEALS (otariids) and true seals (the phocids). Otariids use pectoral appendages to generate propulsive forces during swimming, with the hind flippers trailing passively or occasionally used for steering. In this way, sea lions and fur seals resemble penguins and sea turtles during swimming. Detailed kinematic analyses have been conducted for California sea lions (*Zalophus californianus*) swimming in a flume. These studies revealed three distinct phases to the stroke: (1) the power phase, (2) a paddle phase, and (3) a recovery phase. The majority of thrust is produced during the paddle phase when the fore flippers are moved quickly and forcibly from the water flow to the sides of the animal's body. Stroke frequency for these sea lions increased with swimming speed and ranged from 15 to 50 strokes $\cdot$ min^{-1} as the animals increased speed from 0.5 to 3.0 m $\cdot$ sec^{-1}. In addition to stroke frequency, sea lions increase the amplitude of the fore flipper stroke during high-speed swimming.

When viewed in cross section, the fore flipper of the sea lion resembles a hydrofoil. This specialized shape allows the flipper to produce thrust during the power and recovery phases of the stroke cycle. As found for cetaceans, the specialized flip-

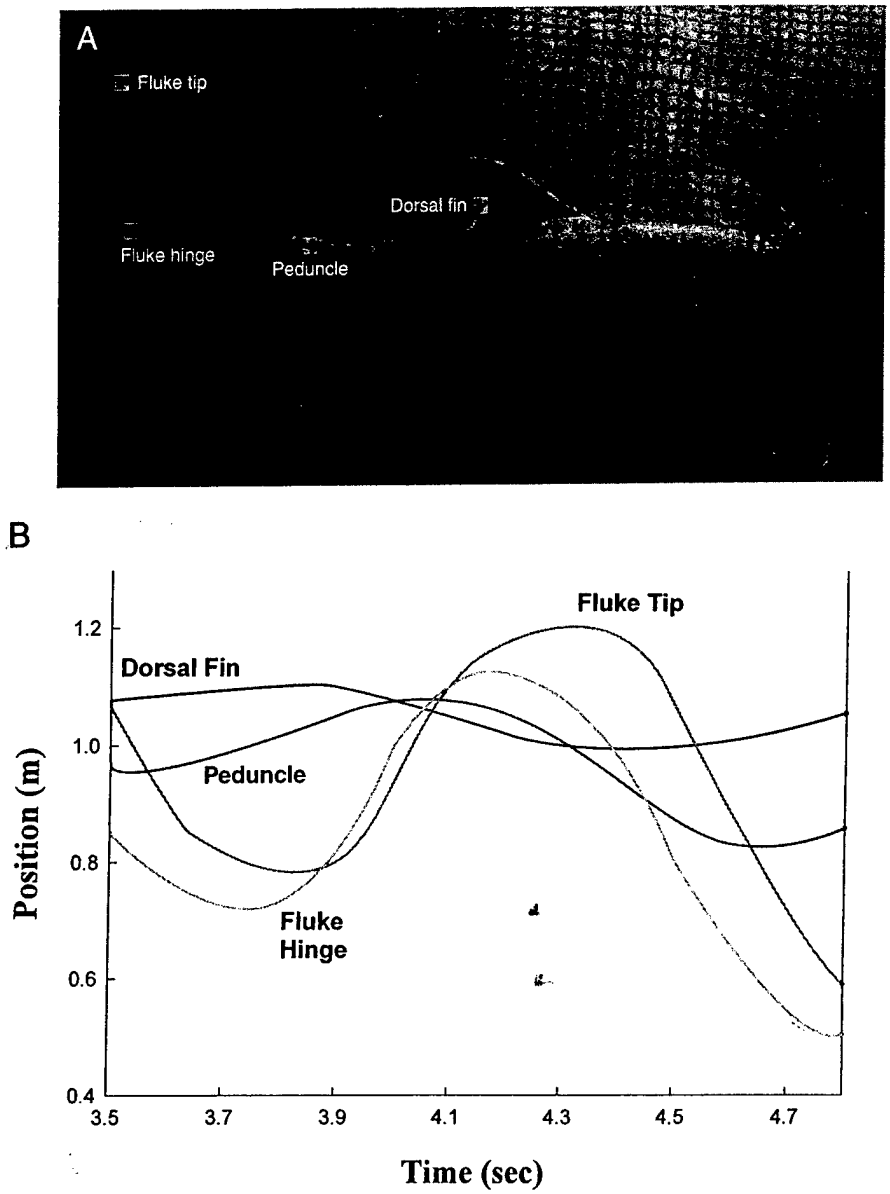

Figure 5 *Video image (A) and range of movement (B) of four anatomical sites during a single stroke for a swimming bottlenose dolphin. Squares correspond to the lines illustrating the movements for each site. Note the traveling wave as it passes from the dorsal fin to the peduncle, fluke hinge, and finally the fluke tip. From Skrovan* et al. *(1999).*

per movements of otariids result in thrust production throughout the stroke cycle and contribute to overall locomotor efficiency. Several other advantages are provided by fore flipper propulsion. These include stability at slow speeds and maneuverability at high speeds. Consequently, otariids are champion underwater acrobats and are capable of rapid changes in direction and acceleration.

Phocid seals and WALRUSES (*Odobenus rosmarus*) differ from otariids in terms of swimming style and rely on alternate sweeps of the hind flippers for propulsion. In addition to the flippers, the posterior half of the body flexes during each stroke with the result that body flexion provides nearly 90% of the change in amplitude during the stroke cycle. In phocid seals, both hind flippers are swept in the same direction as the posterior portion of the body during each half of the stroke cycle. The leading flipper remains closed and the trailing flipper maximally expands during the sweep to one side. Once the flippers have moved to the maximum lateral position, the flippers switch their open and closed positions in preparation for the reverse lateral sweep. By reversing the role of each flipper during lateral

sweeps, one flipper is able to provide thrust while the other flipper recovers. The result, once again, is the ability to produce propulsive thrust during the entire stroke cycle. Stroke frequency in phocids increases linearly with swimming speed. For harbor seals trained to swim at 1.0 to 1.4 m · sec^{-1} in a water flume, stroke frequency ranged from 60 to 78 strokes · min^{-1}.

III. Energetics

The energetic cost of swimming has been measured for numerous species of semiaquatic and marine mammals using a wide variety of techniques. Smaller swimmers, such as sea otters, seals, and sea lions, have been studied while they swam against a current in water flumes. Similar to placing a human on a treadmill, flume studies have enabled scientists to measure how much energy a swimmer expends while moving at different speeds. Often oxygen consumption is measured during these tests by using a face mask or metabolic hood connected to an oxygen gas analyzer. By training animals to breathe into a metabolic hood, expired respiratory gases can be collected and analyzed for oxygen content. For larger, more powerful swimmers, such as dolphins and whales, most flumes are not adequate in terms of size or challenging water speeds. Instead, investigators have relied on a variety of novel techniques for determining the energetic cost of swimming in cetaceans. Techniques have included using trained dolphins that match their swimming speed to that of a moving boat in open water or having whales swim to metabolic stations where expired gases can be collected for analysis.

To compare swimmers of different size, it is useful to convert the metabolic measurements into a cost of transport. Defined as the amount of fuel it takes to transport one unit of body weight over a unit distance, the cost of transport is analogous to the fuel rating of an automobile. In this case, the cost of transport indicates the "gas per mile" used by the swimmer rather than the "miles per gas" achieved by automobiles. The total cost of transport is calculated from the following equation:

$$\text{total cost of transport} = \frac{\text{oxygen consumption}}{\text{swimming speed}}, \qquad (3)$$

where oxygen consumption is in $mlO_2 \cdot kg^{-1} \cdot sec^{-1}$ and speed is in m · sec^{-1}, which results in a cost of transport in $mlO_2 \cdot kg^{-1} \cdot m^{-1}$. These values are usually converted to an energetic term and are expressed as Joules expended per kg of body weight per meter traveled ($J \cdot kg^{-1} \cdot m^{-1}$). The conversion calculation assumes a caloric equivalent of 4.8 kcal per liter of oxygen consumed and a conversion factor of 4.187×10^3 J/kcal.

Comparisons of the cost of transport for a wide variety of mammalian swimmers indicate that swimming is energetically expensive for mammals in comparison to fish. The total cost of transport for swimming mammals can also be divided into two distinct groups: semiaquatic mammals and marine mammals (Fig. 6). Swimming costs for semiaquatic mammals, such as minks, muskrats, and humans, are two to five times higher than observed for marine mammals. These high energetic swimming costs are attributed to a wide variety of factors, including elevated body drag associated with a surface swimming position (Fig. 3) and low propulsive efficiency associated with drag-based propulsion.

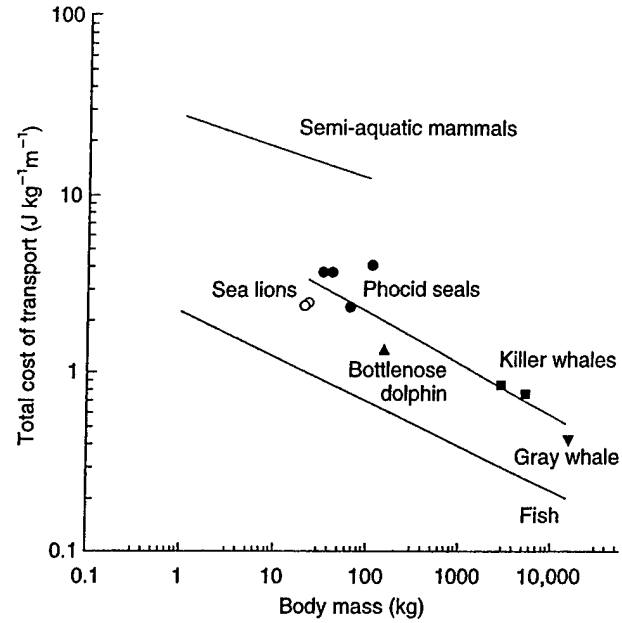

Figure 6 *Total energetic cost of transport in relation to body mass for different classes of swimmers. Marine mammals include gray seals and harbor seals, California sea lions, bottlenose dolphins, killer whales, and a gray whale. The least-squares regression through the data points for marine mammals is presented in the text. This regression is compared to the regressions for swimming semiaquatic mammals (upper solid line) and the predicted regression for salmonid fish (lower solid line). From Williams (1999).*

Mammals specialized for swimming demonstrate comparatively lower energetic costs. The total cost of transport in relation to body mass for swimming marine mammals ranging in size from a 21-kg California sea lion to a 15,000-kg gray whale (*Eschrichtius robustus*) is described by

$$\text{total cost of transport} = 7.79\ \text{mass}^{-0.29}, \qquad (4)$$

where the cost of transport is in $J \cdot kg^{-1} \cdot m^{-1}$ and body mass is in kilograms. Interestingly, the style of swimming used by marine mammals did not affect the cost of transport relationship. Species and swimming styles represented in this equation include sea lions using pectoral fins for propulsion, phocid seals using lateral undulation of paired hind flippers, and odontocete and mysticete whales using dorsoventral undulation of flukes.

As illustrated in Fig. 6, the energetic cost of swimming for marine mammals is greater than predicted for salmonid fish of similar body size. Despite specialization of the body and propulsive surfaces for aquatic locomotion, the cost of transport for swimming by seals and sea lions is 2.3 to 4.0 times higher than predicted for swimming fish. Values for cetaceans are somewhat lower and range from 2.1 to 2.9 times values predicted for fish. Differences in the total cost of transport between marine mammals and fish are due in part to the amount of energy expended for maintenance functions, particularly thermoregula-

tion and the support of a high core body temperature. As endotherms, mammals expend more energy to support the production of endogenous heat than ectothermic fish. In addition, many marine mammals show exceptionally high metabolic rates while resting in water in comparison to terrestrial mammals resting in air. A consequence of these high maintenance costs is an overall increase in the total energy expended during swimming, especially when compared to fish.

IV. Swimming Speeds and Behavior

Although body size varies considerably among marine mammals from the 20-kg sea otter to the 122,000-kg blue whale, routine swimming is limited to a surprisingly narrow range of speeds. Many species of marine mammal routinely swim between approximately 1.0 and 3.6 m · sec^{-1} regardless of body size (Fig. 7). Within this range, pinnipeds generally select slower routine traveling speeds than cetaceans, and mysticete whales swim slower than odontocetes. For example, average swimming speeds for a wide variety of otariids and phocids range from 1.3 to 2.0 m · sec^{-1}. The massive mysticete whales are only slightly faster; routine speeds for this group of marine mammals range from 2.1 to 2.6 m · sec^{-1}. Although they are not the largest marine mammals, odontocetes tend to move the fastest during routine travel. The slowest of the odontocetes represented in Fig. 7 was the beluga whale (*Delphinapterus leucas*) with a routine speed of 1.8 m · sec^{-1}. In comparison, the killer whale (*Orcinus orca*) demonstrates the fastest routine speed of the marine mammals measured to date and averages 3.6 m · sec^{-1} during casual swimming. These speeds are even more remarkable when compared to the efforts of humans. The routine speed of humans during freestyle swimming is approximately 1.0 m · sec^{-1}, about the same speed as a sea otter swimming underwater.

As would be expected, the sprinting speeds of marine mammals are considerably faster than routine speeds and show much variation among the species measured. Most of the information regarding sprint swimming performance in marine mammals is for cetaceans. However, the speed of adult Weddell seals (*Leptonychotes weddellii*) chasing fish beneath the Antarctic sea ice has been measured and was found to exceed 4.0 m · sec^{-1} during the hunt. Among cetaceans, sprint speeds are even higher. The range of sprinting speeds measured for mysticete whales is 4.1 to 13.3 m · sec^{-1} (Fig. 7); sprint swimming by odontocetes is within the upper end of this range and averages 6.1 to 12.5 m · sec^{-1}. Killer whales remain the fastest of the odontocetes measured and can sprint at 12.5 m · sec^{-1}. This is nearly six times faster than the maximum performance of human swimmers in Olympic sprint competition.

Because marine mammals must surface periodically to breathe, they are subject to high levels of drag associated with the effects of wave formation and splashing, especially during high-speed swimming. To help minimize body drag and energetic costs during these surface intervals, marine mammals have developed a number of unique behavioral strategies to accommodate

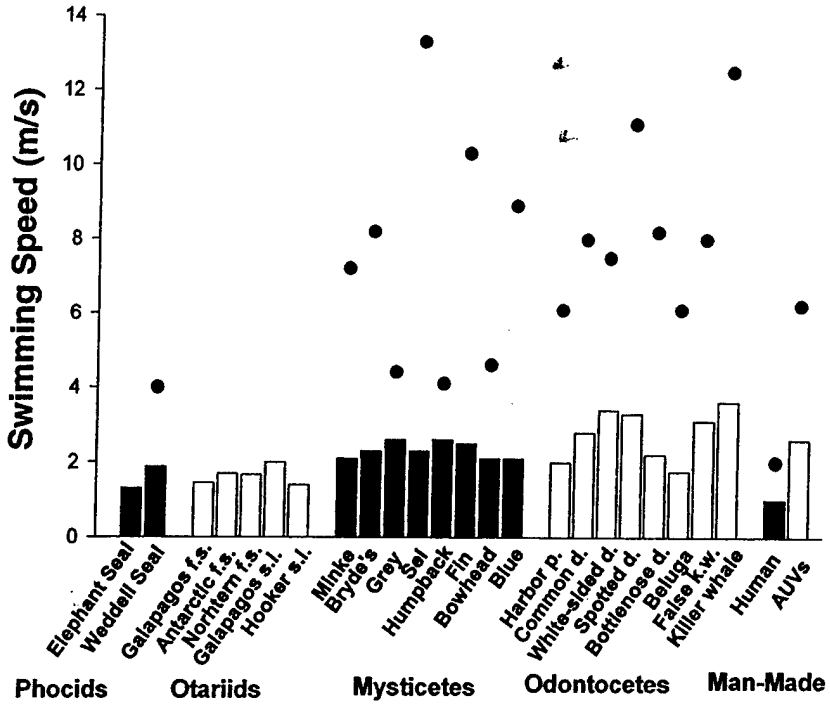

Figure 7 *Swimming speeds for marine mammals. Routine speeds of phocid seals, otariids, mysticetes, odontocetes, humans, and autonomous underwater vehicles (AUVs) are shown. Filled circles above the bars denote the sprinting speeds recorded for each species. Note the similar range of routine speeds for these marine mammals regardless of body size.*

breathing while swimming fast. Porpoising is one such highly visible behavioral strategy used by small cetaceans and some pinnipeds moving at high speed near the water surface. Rather than stroke continuously, the animals leap into the air and simply avoid the elevated wave drag that occurs when swimming near the water surface to breathe. Theoretically, this behavior results in an energetic savings to the animal, although the cost of surface swimming versus leaping has yet to be measured.

Wave riding is another strategy that enables the swimmer to avoid the work of continuous stroking while moving near the water surface. In a study involving bottlenose dolphins trained to swim freely or wave ride next to a moving boat, investigators found that heart rate, respiration rate, and energetic cost were reduced for animals riding the bow wave of the boat. This behavior enabled the dolphins to nearly double their forward traveling speed with only a 13% increase in energetic cost. Consequently, it is not surprising that marine mammals routinely ride waves generated by the wind, surf, the wake of boats, and even large whales. What appears to be an amusing activity also provides an energetic benefit to the swimmer.

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 (*Mirounga* spp.) 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 allow the animals to remaining submerged except for brief surface intervals to breathe.

V. The Special Case of Swimming at Depth

Most of our information about swimming in marine mammals is from animals moving near the water surface. However, the majority of swimming by these animals occurs at depth in conjunction with diving. When descending or ascending during a dive, marine mammals must contend with buoyant forces and hydrostatic pressure, as well as body drag. As discussed earlier, drag forces resist both forward progression and limb movements of the swimmer. In contrast, 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 pressure results from the weight of the water column above the marine mammal.

The magnitude of buoyant forces and hydrostatic pressure on the swimming marine mammal will depend on where in the water column activity takes place. Hydrostatic pressure increases progressively by 1 ATM for every 10.1 m an animal descends in the water column. This will have a profound effect on compressible spaces or tissues, and hence buoyancy of the animal, especially for marine mammals that may descend and ascend hundreds of meters during the course of a dive. In addition, seasonal changes in blubber content, pregnancy, and lactation will have an effect on the overall buoyancy of the marine mammal.

A consequence of the interrelationships among depth, buoyancy, hydrostatic pressure, and body drag is that the physical forces influencing the animal swimming horizontally near the water surface are very different from those encountered by the diving animal moving vertically through the water column. Detailed studies on diving common bottlenose dolphins and elephant seals have shown that the animals are positively buoyant near the water surface and that buoyancy decreases as the animal descends during the dive. For example, the buoyancy of a bottlenose dolphin changes from positive (24 N) when near the water surface to negative (−26 N) once the animal exceeds 70 m in depth.

These changes in buoyancy are associated with changes in lung compression due to the increase in hydrostatic pressure as marine mammals descend on a dive. Thus, as dolphins, whales, and seals dive, hydrostatic pressure increases and the lungs progressively collapse with the result that overall buoyancy is changed. These marked changes in physical forces with depth affect both locomotor behavior and energetics of the marine mammal as it descends and ascends during a dive (Fig. 8).

Until recently, it was not possible to observe the swimming modes of marine mammals during deep dives. With the development of miniaturized video cameras and instrumentation worn by free-ranging marine mammals, new information about swimming at depth has been obtained (Fig. 9). Videos have revealed that bottlenose dolphins, elephant seals, Weddell seals, and blue whales switch between different modes of swimming during the dive, much like terrestrial mammals switch between gaits. Dive descents usually began with a period of continuous stroking. Once the marine mammals reach 70–80 m in depth they change to a passive glide for the remainder of the descent. For deep divers such as phocid seals, these gliding periods can be quite long. For example, prolonged gliding periods exceed 6 min for Northern elephant seals (*M. angustirostris*) traveling to nearly 400 m and Weddell seals descending to 540 m beneath the Antarctic sea ice. Nearly 80% of the descent of diving seals may be spent gliding passively rather than swimming actively on dives exceeding 200 m in depth.

The ascent portion of a dive requires more effort by marine mammals when compared to the descent. The beginning of the ascent represents the period of greatest swimming effort for mammalian divers. During this period, many species of pinniped and cetacean use sequential, large amplitude strokes to begin moving upward. As the ascent continues, the physical forces impacting the diver are once again altered as they move through the water column. Hydrostatic pressure decreases on ascent. Consequently, the lungs are able to reinflate and the buoyancy of the marine mammal increases. Swimming behavior reflects these changes with the result that the continuous stroking phase is followed by a stroke and glide mode of swimming, and finally a brief glide to the water surface.

By altering the mode of swimming to account for changes in the physical forces that occur during a dive, marine mammals are able to conserve limited oxygen reserves during submergence. One study investigating the metabolic rates of Weddell seals diving from an ice hole found that the incorporation of prolonged glides enabled seals to reduce the energetic cost of individual dives by 9–60%. Such an energetic savings could make the difference between completing the dive aerobically or anaerobically and can increase the time available for hunting or avoiding predators.

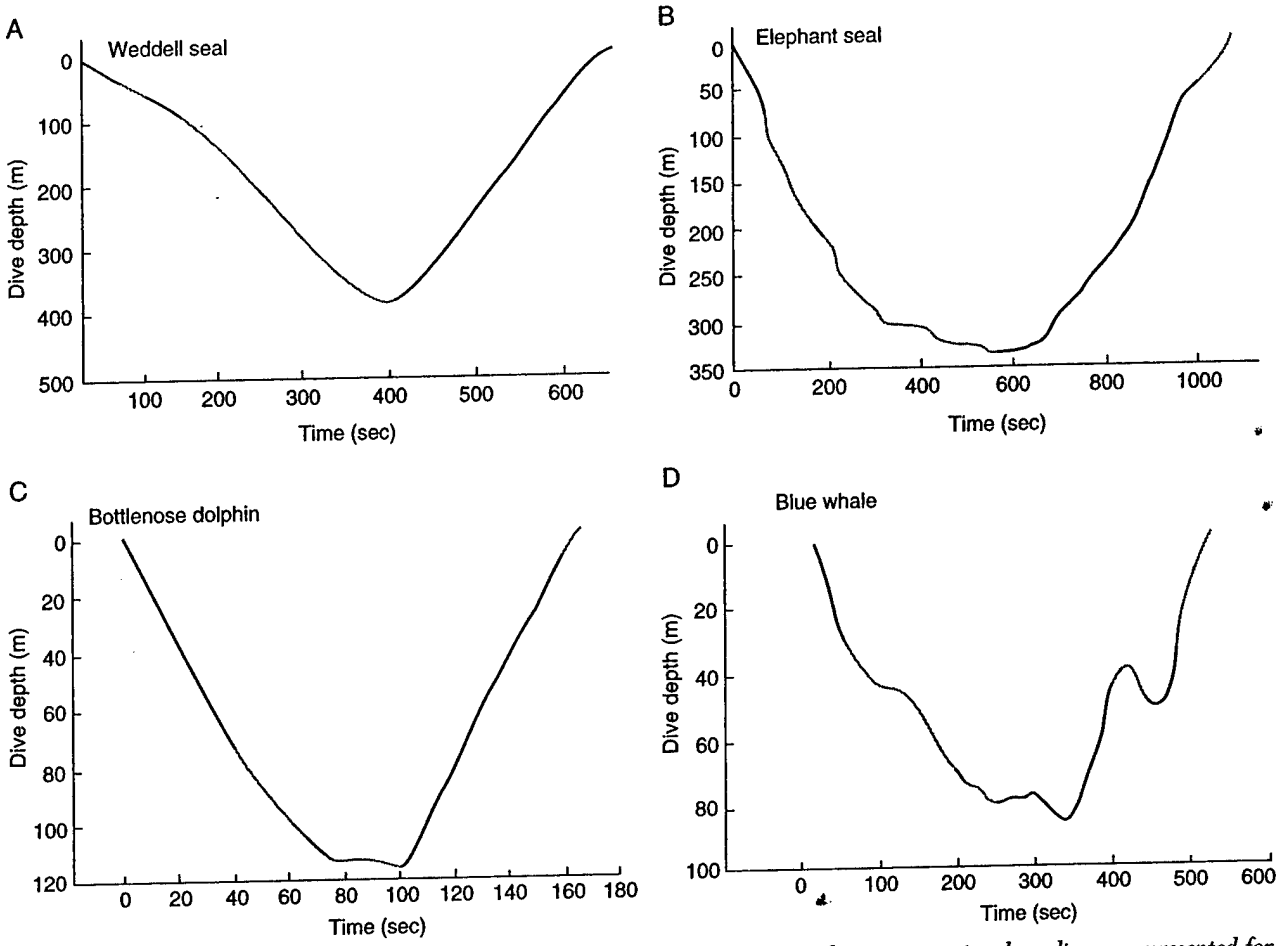

Figure 8 *Swimming and gliding activity of four species of diving marine mammal. Representative deep dives are presented for the Weddell seal (A), elephant seal (B), bottlenose dolphin (C), and blue whale (D). Each curve shows dive depth in relation to time elapsed during the dive. The shade of the line corresponds to stroking (black) and gliding (gray) periods. For each species the descent was characterized by prolonged periods of gliding. From Williams* et al. *(2000).*

Figure 9 *A bottlenose dolphin carries a video camera to record its swimming movements during deep dives. Courtesy of Kevin McDonnell.*

In summary, these studies demonstrate that swimming can be energetically expensive for mammals. Marine adapted species, including sea otters, pinnipeds, and cetaceans, have undergone marked morphological, physiological, and behavioral changes to increase their swimming efficiency. An especially important adaptation that distinguishes marine mammals from semiaquatic mammals is the ability to remains submerged for prolonged periods when swimming. However, prolonged submergence also requires specialized physiological responses associated with oxygen loading and utilization. A major benefit of these adaptations is a capacity for aquatic performance by marine mammals that far exceeds those of semiaquatic mammals and the best Olympic efforts of humans.

See Also the Following Articles

Breathing ■ Diving Physiology ■ Energetics ■ Locomotion, Terrestrial ■ Musculature ■ Pelvic Anatomy ■ Speed ■ Streamlining

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Systematics, Overview

ANNALISA BERTA
San Diego State University, California

Systematics is the study of biological diversity that has as its primary goal the reconstruction of phylogeny, the evolutionary or genealogical history of a particular group of organisms (e.g., species). Because of its emphasis on phylogeny, this discipline is often referred to as phylogenetic systematics or cladistics. Other related goals of systematics include determination of the times at which species originated and became extinct and the origin and rate of change in their characteristics. An important component of systematics is taxonomy, the identification, description, nomenclature, and classification of organisms. Systematics provides a framework for interpreting patterns and processes in evolution using explicit, testable hypotheses.

The rapid pace of research on marine mammals has resulted in renewed interest in their systematics. Phylogenetic systematic methodology as introduced here has gained near universal acceptance. [For a general introduction to the topic readers are referred to texts by Eldredge and Cracraft (1980), Wiley (1980), and Wiley *et al.* (1991).] In addition to their use in elucidating evolutionary relationships, phylogenies are now recognized as powerful tools for unveiling evolutionary patterns of marine mammal diversity in ecological and behavioral settings.

I. Basic Tenets of Phylogenetic Systematics

The recognition of patterns of relationship among SPECIES is founded on the concept of evolution. Patterns of relationship among species are based on changes in the characters of an organism. Characters are diverse, heritable attributes of organisms that include DNA base pairs, anatomical and physiological features, and behavioral traits. Two or more forms of a given character are termed *character states*. For example, among pinnipeds, the character contact between maxillary and frontal bones consists of three character states: (1) V shaped (in bears, extinct desmatophocids, *Enaliarctos,* and phocids), (2) W shaped (in otariids), and (3) transverse (walruses) as described by Berta and Sumich (1999). In the establishment of relationships among groups of organisms, phylogenetic systematics emphasizes evolutionary novelties (derived characters) in contrast to ancestral similarities (primitive characters).

The evolutionary history of a group of organisms can be inferred by sequentially linking species together based on their common possession of derived characters, also known as *synapomorphies.* If derived characters are unique to a particular taxon rather than showing relationships among taxa they are termed *autapomorphies.* An example of an autapomorphy is the transverse contact between maxillary and frontal bones seen only in walruses among pinnipedimorphs (living pinnipeds and their fossil relatives). Derived characters are considered to be *homologous,* a similarity that results from common ancestry. For example, the flipper of a seal and that of a walrus are homologous because their common ancestor had flippers. In contrast to homology, a similarity not due to homology is *homoplasy.* For example, the flipper of a pinniped and that of a whale are homoplasious as flippers because their common ancestor lacked flippers. Homoplasy may arise in one of two ways: convergence (parallelism) or reversal. *Convergence* is the independent evolution of a similar feature in two or more lineages. Thus seal flippers and whale flippers evolved independently as swimming appendages; their similarity is homoplasious by convergent evolution. *Reversal* is the loss of a derived feature coupled with the reestablishment of an ancestral feature. For example, in phocine seals (bearded seal *Erignathus barbatus*, hooded seal *Cystophora cristata*, and the Phocini) the development of strong claws, lengthening of the third digit of the foot, and deemphasis of the first digit of the hand are character reversals because none of them characterize phocids ancestrally but are present in terrestrial arctoid CARNIVORES, common ancestors of PINNIPEDS (Berta and Sumich, 1999).

Relationships among organismal groups are commonly represented in the form of a *cladogram,* a branching diagram that conceptually represents the best estimate of phylogeny (Fig. 1). Derived characters are used to link *monophyletic* groups, groups of taxa that consist of a common ancestor plus all descendants of that ancestor (referred to as a *clade*). For example, a hypothesis of relationships among pinnipedimorphs (inclusive group that includes all pinnipeds and their close fossil relatives) based on morphologic characters proposes that phocid seals (Phocidae) and an extinct lineage (Desmatophocidae) are more closely related to each other than either is to walruses (Odobenidae). Fur seals and sea lions (Otariidae) are positioned as the next closest relative to this clade (walruses + desmatophocids + phocids) with the fossil taxon *Enaliarctos* recognized as the most *basal* lineage (Berta and Sumich, 1999; Fig. 1). According to this hypothesis, relationships among pinnipedimorphs are depicted as sets of nested hierarchies. In this case, four monophyletic groups can be recognized. The most exclusive monophyletic group is that formed by phocid seals and desmatophocids, as this clade shares derived synapomorphies not also exhibited by walruses, otariids, or *Enaliarctos.* At

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Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration

S.R. Noren [a,b,*], T.M. Williams [a,b]

[a] *Department of Biology, Earth and Marine Sciences Building, University of California, Santa Cruz, CA 95064, USA*

[b] *Institute for Marine Sciences, Earth and Marine Sciences Building, University of California, Santa Cruz, CA 95064, USA*

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Abstract

Cetaceans exhibit an exceptionally wide range of body mass that influence both the capacities for oxygen storage and utilization; the balance of these factors is important for defining dive limits. Furthermore, myoglobin content is a key oxygen store in the muscle as it is many times higher in marine mammals than terrestrial mammals. Yet little consideration has been given to the effects of myoglobin content or body mass on cetacean dive capacity. To determine the importance of myoglobin content and body mass on cetacean diving performance, we measured myoglobin content of the *longissimus dorsi* for ten odontocete (toothed whales) and one mysticete (baleen whales) species ranging in body mass from 70 to 80 000 kg. The results showed that myoglobin content in cetaceans ranged from 1.81 to 5.78 g (100 g wet muscle)$^{-1}$. Myoglobin content and body mass were both positively and significantly correlated to maximum dive duration in odontocetes; this differed from the relationship for mysticetes. Overall, the combined effects of body mass and myoglobin content accounts for 50% of the variation in cetacean diving performance. While independent analysis of the odontocetes showed that body mass and myoglobin content accounts for 83% of the variation in odontocete dive capacity. © 2000 Elsevier Science Inc. All rights reserved.

Keywords: Cetaceans; Myoglobin; Body size; Diving capacity; Odontocetes; Mysticetes

1. Introduction

Cetaceans exhibit a 2200-fold increase in body mass from the smallest species, the 55 kg vaquita (*Phocoena sinus*; Evans, 1987), to the largest species, the 122 000 kg blue whale (*Balaenoptera musculus*; Laurie, 1933). Such a wide range of body masses results in an exceptionally large range of metabolic rates and capacities for oxygen storage in comparison to other marine mammal groups. Although both factors will impact diving capability (Kooyman et al., 1981), there is little information concerning the advantages or disadvantages associated with extreme body size and the capacity to adapt the mammalian body for prolonged periods of submergence. One important adaptation for diving exhibited by a wide range of diving mammals is the storage of oxygen in the skeletal muscles (Castellini and Somero, 1981). Myoglobin acts as the primary oxygen carrier in the skeletal muscles of these mammals. When perfusion to a muscle region is decreased, oxygen depletion of that area is retarded by the release of myoglobin-bound oxygen into the tissue (Salathe and Chen, 1993). Elevated myoglobin content in the skeletal muscle enables aerobic

* Corresponding author. Tel.: +1-831-4594133; fax: +1-831-4594882.

E-mail address: snoren@biology.ucsc.edu (S.R. Noren)

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metabolism to be maintained during apnea and appears to be an important adaptation for diving in birds and mammals. Consequently, myoglobin concentration is 10–30 times greater in the locomotor muscles of aquatic birds and mammals than in the muscles of their aerial or terrestrial counterparts (Kooyman, 1989).

For the species studied to date, cetaceans demonstrate a higher reliance on muscle oxygen stores than other marine mammal groups including pinnipeds. For example, ≈ 33, 38, and 51% of the total body oxygen store is found in the skeletal muscle of beluga whales (Shaffer et al., 1997), bottlenose dolphins (Williams et al., 1993) and narwhals (Williams unpublished observation), respectively. In comparison, otariids and phocids sequester a higher proportion of the total oxygen store in the blood; less than 33% of the oxygen reserve of pinnipeds is found in the skeletal muscle (Kooyman, 1989). A non-diving mammal, the human, stores only 15% of its oxygen reserve in the skeletal muscle.

In contrast to numerous investigations on pinniped muscles (Scholander, 1940; Lenfant et al., 1970; George et al., 1971; Castellini and Somero, 1981; Lydersen et al., 1992; Ponganis et al., 1993; Thorson 1993), comparatively few studies have examined the skeletal muscles of cetaceans or the adaptations of their muscles for diving. One previous study suggested that cetaceans with higher muscle myoglobin contents show longer dive durations (Snyder, 1983). A complicating factor, however, is the effect of body mass on dive performance in this diverse marine mammal group. In view of this, we examined the myoglobin content of the primary locomotor muscles of 11 species of cetaceans, ranging in size from the 70 kg common dolphin to the 80 000 kg bowhead whale. These data were then correlated with reported values for maximum dive duration for each species. We found that both muscle myoglobin content and body mass explained nearly 50% of the variation in dive performance across cetacean species. Differences in foraging behavior between the two cetacean suborders, odontocetes (toothed whales) and mysticetes (baleen whales), suggest that foraging behaviors may further influence these relationships.

Table 1
Myoglobin contents for the *longissimus dorsi* of the cetacean species examined in this study[a]

Cetacean species	*n*	[Mb] (g [100 g wet muscle]$^{-1}$)
Odontocetes		
Common dolphin (*Delphinus capensis*)	3	3.58 ± 0.32
Common dolphin (*Delphinus delphis*)	7	3.55 ± 0.27
Harbor porpoise (*Phocoena phocoena*)	2	4.03 ± 0.32
Striped dolphin (*Stenella coeruleoabla*)	1	5.78
Northern right whale dolphin (*Lissodelphis borealis*)	1	1.81
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	2	3.45 ± 0.25
Bottlenose dolphin (*Tursiops truncatus*)	6	2.66 ± 0.16
Pygmy sperm whale (*Kogia breviceps*)	1	4.33
Beluga whale (*Delphinapterus leucas*)	5	3.44 ± 0.39
Cuvier's beaked whale (*Ziphius cavirostris*)	2	4.32 ± 0.15
Mysticetes		
Bowhead whale (*Balaena mysticetus*)	5	3.54 ± 0.33

[a] All values are for site 1 illustrated in Fig. 1. *n*, represents the number of specimens for each species. Values are given as the mean ± 1 S.E.M.

2. Materials and methods

2.1. Animals

Muscle samples were obtained from ten odontocete species and one mysticete (Table 1). The cetaceans examined in this study were acquired from strandings, incidental fishery catches, or subsistence hunts. Muscle samples were taken only from mature animals that were considered in excellent condition based on their external appearance (i.e. no bloating or large external cuts). Depending on the availability of specimens, one to seven individuals of each species were analyzed.

2.2. Muscle sample collection

For the bowhead and beluga whales, muscle samples were collected on site soon after death. For all other species, whole carcasses were frozen at 0°C shortly after death and muscle samples were taken within 6 months postmortem. All muscle samples were stored at −80°C until analysis. Muscle samples were taken from the midbelly of the *longissimus dorsi* (Fig. 1). The *longissimus dorsi* is the primary locomotor muscle of

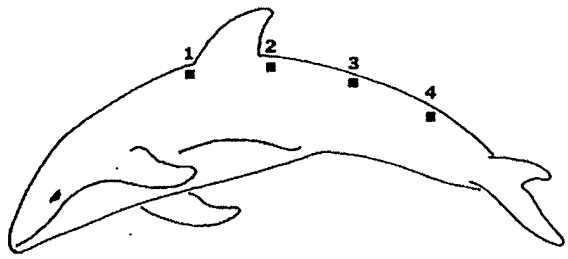

Fig. 1. Sample sites for skeletal muscle in cetaceans. Numbered black squares indicate the four areas along the *longissimus dorsi* where the muscle samples were taken. All muscles were sampled from the midbelly region at each site. Samples (≈ 6 g) were obtained from site 1 for all of the specimens in this study.

cetaceans and is one of two muscles that power the dolphin upstroke (Pabst, 1993). Recent research suggests that there is a gradient in myoglobin content between the midbelly and the peripheral regions of the *longissimus dorsi* of cetaceans (Harrison and Davis, 1998). The midbelly appears to contain the highest concentration of myoglobin. In addition, a small gradient in myoglobin content is found along the length of the muscle, with the area below the dorsal fin showing the highest content (Harrison and Davis, 1998). Sample site 1 in the present study (Fig. 1) was chosen to reflect the highest myoglobin content for the *longissimus dorsi* of each species. When available, samples were also taken from three other sites along the muscle (sites 2, 3, and 4; Fig. 1) for comparative purposes.

2.3. Myoglobin content

Myoglobin content ([Mb]), measured in g Mb (100 g wet muscle)$^{-1}$ was determined using the procedure of Reynafarje (1963). Slightly thawed muscle samples (≈ 0.5 grams) were minced in a low ionic strength buffer (40 mM phosphate, pH = 6.6), and sonicated (Sonifier Cell Disrupter Model W185D, Heat systems-Ultrasonics, Inc.) for 2–3 min on ice. The buffer to tissue ratio was 19.25 ml buffer per g wet tissue. The samples were centrifuged at −4°C and 28 000 g for 50 min (Sorvall RC-5B refrigerated superspeed centrifuge, DuPont Instruments). The clear supernatant was drawn, and bubbled at room temperature with pure CO for approximately 8 min. We added 0.02 g of sodium dithionite to ensure a complete reduction. The absorbance of each sample was read at room temperature at 538 and 568 nm on a spectrophotometer (Shimadzu UV-visible spectrophotometer Bio spec-1601). All samples were run in triplicate.

2.4. Standards for the assays

Myoglobin contents were determined for the main locomotory skeletal muscles of a New Zealand white rabbit and a 7 day old Northern elephant seal pup, and compared to previously published values. The [Mb] of the seal pup in the present study, 2.4 ± 0.2 g (100 g wet muscle)$^{-1}$, was similar to a previously published value for a 1–14 day old northern elephant seal pup (Thorson, 1993). The [Mb] for rabbit muscle, 0.08 ± 0.06 g (100 g wet muscle)$^{-1}$, was similar to previous reports for a New Zealand white rabbit (Castellini and Somero, 1981).

2.5. Dive duration

Maximum dive times for each species were obtained from previous studies that used time-depth recorders (TDRs) or trained animals. Timed observations of dive durations for wild, uninstrumented animals were included only if no other data source was available. *Kogia breviceps* was not used in the diving analyses because the only dive data available for this species was acquired from a rehabilitated animal that had been housed in a shallow pool for several months before release (Höhn et al., 1995). We used maximum dive durations rather than average dive times in these analyses for several reasons. First, few diving records for cetaceans report average dive durations; of the 15 species used in our analyses, only six have average dive times reported in the literature. Second, average values are a poor indicator of an animal's diving capabilities. This is illustrated by comparing average and maximum dive durations of the six cetacean species for which both values are available. Average dive duration is 1.1 min for the harbor porpoise (Westgate et al., 1995), 0.4 min for the Pacific white-sided dolphin (Black, 1994), 0.4 min for the bottlenose dolphin (Mate et al., 1995), 12.9 min for the beluga whale (Martin et al., 1993), 38 min for the sperm whale (Watkins et al., 1993), and 6.3 min for the bowhead whale (Wursig et al., 1984). These values represent less than 20% of the maximal dive durations reported for these species. The

beluga and sperm whales are exceptions; their average dive durations are 70 and 52% of their maximum dive durations, respectively. Similar to studies examining aerobic function in terrestrial mammals (Weibel et al., 1987), we have chosen to use extreme performance in this study to understand the physiological capacities of diving in cetaceans.

2.6. Statistics

Variability between the myoglobin contents of skeletal muscle sites, and between species was determined by Kruskal–Wallis one way analysis of variance on ranks. In addition, Dunn's method for all pairwise comparison procedures was used for interspecies comparisons. Species specific muscle myoglobin contents determined in the present study were combined with previously published values for other cetacean species for further analyses. The inclusion of previously reported values ensured that the myoglobin-dive duration relationships determined in this study were inclusive of as many cetacean species possible. The same species were subsequently used in body mass-dive duration relationships. Least squares methods were used for the linear regressions of myoglobin content versus maximum dive duration, and for body mass in relation to maximum dive duration. The regressions for body mass were plotted on logarithmic scales due to the large range in body mass (70–80 000 kg). The reported linear equation for this plot was log transformed. Significance of the regressions was determined using an F-test. A Pearson correlation test was used to determine the correlation between body mass and muscle myoglobin. The simultaneous effects of body mass and muscle myoglobin content on maximum dive performance were assessed using a forward stepwise regression. Results were considered significant when $P \leq 0.05$. All statistical tests were calculated using standard software programs (Sigma Stat, Jandel Scientific, 1995).

3. Results

3.1. Myoglobin content

Myoglobin contents for each of the four sampling sites and the average value for the four sites were not significantly different in 10 specimens of *Lagenorhynchus obliquidens*, *Delphinus delphis* and *Delphinus capensis* ($H = 1.11$, df $= 4$, $P = 0.89$). Therefore, values for site 1 (Fig. 1) are used as a representative of the entire muscle; these are reported as mean values ± 1 S.E.M.

Myoglobin contents for the *longissimus dorsi* of cetaceans measured in this study are presented in Table 1. There was a 3-fold increase in myoglobin content from the lowest value in the Northern right whale dolphin, 1.81 g (100 g wet muscle)$^{-1}$, to the highest value in the striped dolphin, 5.78g (100 g wet muscle)$^{-1}$. The one mysticete examined in this study, the bowhead whale, had a myoglobin content of 3.54 g (100 g wet muscle)$^{-1}$; that was within the mid-range of values for the odontocetes. The interspecific differences in myoglobin contents were significant ($H = 18.37$, df $= 10$, $P = 0.049$, $n = 11$) although an all pairwise test was unable to identify the particular species that were different.

For review, previously published myoglobin contents for the skeletal muscles of cetaceans are presented in Table 2. The combined myoglobin data for all cetacean species, including previously reported values and data from the present study, show that the range of myoglobin values for the mysticetes (0.91–3.54 g [100 g wet muscle^{-1}]) are at the lower range of myoglobin values for the odontocetes (1.81 to 7.87 g [100 g wet muscle^{-1}]) (Tables 1 and 2).

3.2. Myoglobin content and body mass relationships with dive capacity

The results of the literature search for the accumulation of the body mass and dive capacity data for the cetacean species used in the analyses for this study are presented in Table 3.

Myoglobin content of the skeletal muscle correlated poorly with maximum dive duration for all cetaceans ($r^2 = 0.28$, $F = 5.03$, $P = 0.04$, $n = 15$). When the two cetacean suborders were analyzed independently, we found that the correlation increases for odontocetes while the relationship for mysticetes was not significant (Fig. 2). For odontocetes, maximum dive duration increased with myoglobin content according to the relationship:

$$\text{Odontocete maximum dive duration} = 8.31\ \text{Mb} - 13.10\ (r^2 = 0.36,\ F = 5.69,\ P = 0.04,\ n = 12)$$

Table 2
Previously reported myoglobin contents for cetacean skeletal muscle

Cetacean species	[Mb] (g [100 g wet muscle]$^{-1}$)	References
Odontocetes		
Indus river dolphin (*Platanista indi*)	2.6	(Blessing, 1972)
Spotted dolphin (*Stenella attenuata*)	2.54	(Castellini and Somero, 1981)
Spinner dolphin (*Stenella longirostris*)	5.5	(Dolar et al., 1999)
Fraser's dolphin (*Lagenodelphis hosei*)	7.1	(Dolar et al., 1999)
Humpback dolphin (*Sousa chinensis*)	2.5	(Harrison and Davis, 1998)
Narwhal (*Monodon monoceros*)	7.87	(Williams unpubl. observ.)
False killer whale (*Pseudorca crassidens*)	6.3	(Harrison and Davis, 1998)
Northern bottlenose whale (*Hyperoodon ampullatus*)	6.34	(Scholander, 1940)
Sperm whale (*Physeter macrocephalus*)	5.03	Avg. of Scholander (1940) and Tawara (1950)
Mysticetes		
Sei whale (*Balaenoptera borealis*)	0.91	(Tawara, 1950)
Fin whale (*Balaenoptera physalus*)	2.42	Avg. of Scholander (1940) and Hochachka and Foreman (1993)

Table 3
Body mass and maximum dive durations for cetaceans[a]

Cetacean species	Mass[d] (kg)	Max. dive (min)	Method[b]	References[c]
Odontocetes				
Common dolphin (*Delphinus capensis*)	70[e]	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Common dolphin (*Delphinus delphis*)	70[e]	5	TDR	(Heyning and Perrin, 1994; Evans, 1971)
Harbor porpoise (*Phocoena phocoena*)	70[h]	5.35	TDR	(Westgate et al., 1995)
Spotted dolphin (*Stenella attenuata*)	75[e]	4.7	TDR	(Perrin et al., 1987; Scott et al., 1993)
Northern right whale dolphin (*Lissodelphis borealis*)	115[e]	6.25	O	(Jefferson et al., 1993; Leatherwood and Walker, 1979)
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	120	6.2	E	(Whole body specimen mass from present study; Black, 1994)
Bottlenose dolphin (*Tursiops truncatus*)	200[e]	8	E	(Evans, 1987; Ridgway and Harrison, 1986)
Pygmy sperm whale (*Kogia breviceps*)	363[e]	12	TDR	(Evans, 1987; Hohn et al., 1995)
Beluga whale (*Delphinapterus leucas*)	1400[f]	18.3	TDR	(Bryden, 1972; Martin et al., 1993)
Narwhal (*Monodon monoceros*)	1500[h]	25	TDR	(Heide-Jφrgensen and Dietz, 1995)
Cuvier's beaked whale (*Ziphius cavirostris*)	2953[f]	30	O	(Bryden, 1972; Houston, 1991)
Northern bottlenose whale (*Hyperoodon ampullatus*)	6700[e]	60	O	(Evans, 1987; Reeves et al., 1993)
Sperm whale (*Physeter macrocephalus*)	36,700[g]	73	TDR	(Omura, 1950; Watkins et al., 1993)
Mysticetes				
Sei whale (*Balaenoptera borealis*)	23,000[g]	20	O	(Lockyer and Waters, 1986 Martin, 1990)
Fin whale (*Balaenoptera physalus*)	33,000[g]	14	TDR	(Lockyer and Waters, 1986; Watkins et al., 1981)
Bowhead whale (*Balaena mysticetus*)	80,000[e]	31	TDR	(Evans, 1987; Wursig et al., 1984)

[a] Species: listed are limited to those with known myoglobin contents and dive behaviors.
[b] Dive data acquired by: TDR, time depth recorder; E, experimental dive; or O, observation.
[c] References: body mass reference first, followed by dive duration reference.
[d] Mass given, unless otherwise noted in table, is represented as.
[e] Average mass for the species.
[f] Calculated mass from body length-mass equations.
[g] Mass corrected by 6% for loss associated with piecemeal weighing.
[h] Estimated mass of animal from which dive data was acquired.

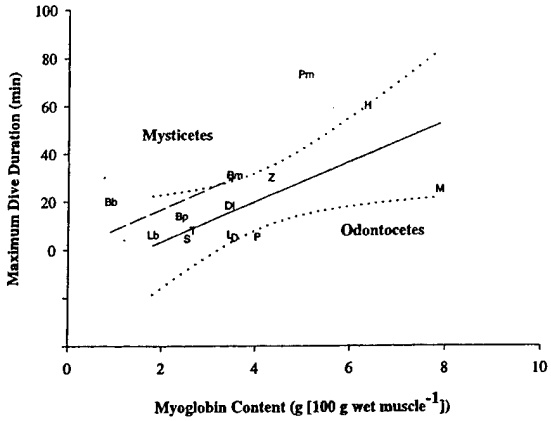

Fig. 2. Maximum dive duration in relation to skeletal muscle myoglobin content for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 1, Table 2, and Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).

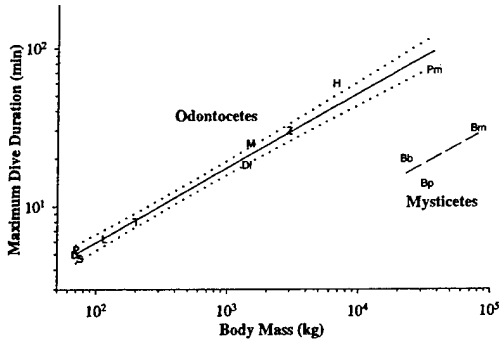

Fig. 3. Maximum dive duration in relation to body mass for odontocetes (solid line) and mysticetes (dashed line). Relationships are least squares linear regressions as described in the text. Dotted lines are the 95% confidence intervals around the regression for odontocetes. Genus initials denote data points; species initial is included if the genus initial is redundant. See Table 3 for references. (Odontocetes: S, *Stenella attenuata*; D, *Delphinus delphis* and *Delphinus capensis*; P, *Phocoena phocoena*; L, *Lagenorhynchus obliquidens* and *Lissodelphis borealis*; T, *Tursiops truncatus*; Dl, *Delphinapterus leucas*; M, *Monodon monoceros*; Z, *Ziphius cavirostris*; H, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*; Mysticetes: Bb, *Balaenoptera borealis*; Bp, *Balaenoptera physalus*; Bm, *Balaena mysticetus*).

where duration is in min and muscle myoglobin is in g Mb (100 g wet muscle)$^{-1}$. For mysticetes, the relationship between myoglobin content and maximum dive duration was not significant ($r^2 = 0.33$, $F = 0.48$, $P = 0.61$, $n = 3$).

Similar results were found for the body mass and dive capacity analyses. A significant correlation was found between maximum dive duration and body mass for all cetaceans in this study ($r^2 = 0.72$, $F = 33.49$, $P < 0.001$, $n = 15$). Again the relationships differed between the two cetacean suborders. Odontocetes exhibit a significant correlation between maximum dive duration and body mass (Fig. 3) according to the relationship:

$$\text{Odontocete max. dive duration} = 0.68\ (\text{body mass})^{0.47}$$

$$(r^2 = 0.98,\ F = 463.92,\ P < 0.001,\ n = 12)$$

where duration is in min and body mass is in kg. The same relationship was not significant for mysticetes ($r^2 = 0.54$, $F = 1.15$, $P = 0.48$, $n = 3$) (Fig. 3).

Pearson correlation tests showed that cetacean muscle myoglobin content and body mass, and odontocete muscle myoglobin content and body mass are not correlated ($r = -0.08$, $P = 0.77$, $n = 15$ and $r = 0.49$, $P = 0.16$, $n = 10$, respectively). Because these two variables are independent, we ran forward stepwise regression analyses to determine the combined influence of these two characteristics (muscle myoglobin content and body mass) on maximum dive duration. For all cetaceans combined, muscle myoglobin and body mass together explained 50% of the variation in maximum dive duration across species (myoglobin $r^2 = 0.28$, $P = 0.017$; body mass delta $r^2 = 0.22$, $P = 0.042$). For odontocete species only, body mass and muscle myoglobin together explained 83% of the variation in maximum dive duration across odontocete species (body mass $r^2 = 0.69$, $P < 0.001$; myoglobin delta $r^2 = 0.14$, $P = 0.023$). A similar test for the mysticete species was not possible due to the small sample size available for analyses.

4. Discussion

Limits to aerobic diving are determined by the size of the oxygen store as well as the rate in which this store is utilized. Because skeletal mus-

cles provide the power for swimming, an important factor in determining maximum dive duration of marine mammals is size of the on-board oxygen stores to support metabolic processes at the level of the working skeletal muscle (Hochachka, 1986). Previous studies have demonstrated that aerobic metabolic processes within the muscle may be maintained during prolonged periods of submergence by utilization of oxygen stored in myoglobin (Kooyman, 1989). From the present study it appears that the combined effect

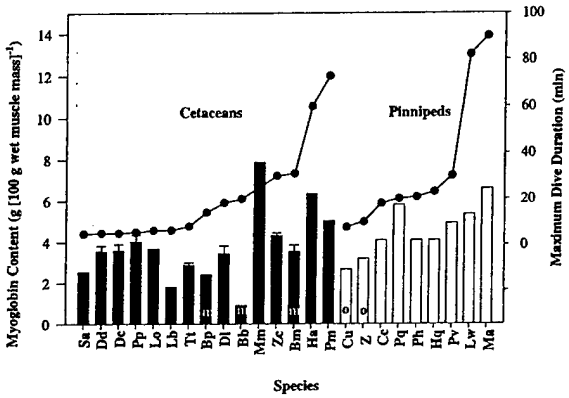

Fig. 4. Muscle myoglobin content (bars) and maximum dive duration (-●-) for cetaceans (black bars) and pinnipeds (white bars). Individual species are presented in order of increasing dive duration. 'm' denotes mysticetes and 'o' denotes otariids. Initials denote genus and species. Note that our calculations show that in pinnipeds, myoglobin concentration correlates with maximum dive duration according to the relationship, dive duration = 18.7 [Mb] − 51.4 ($r^2 = 0.58$, $F = 9.82$, $P = 0.017$, $n = 9$). The relationship between maximum dive duration and myoglobin content is more variable in cetaceans as described in the text. See Table 1, Table 2, and Table 3 for cetacean references. (Sa, *Stenella attenuata*; Dd, *Delphinus delphis*; Dc, *Delphinus capensis*; Pp, *Phocoena phocoena*; Lo, *Lagenorhynchus obliquidens*; Lb, *Lissodelphis borealis*: Tt, *Tursiops truncatus*; Bp, *Balaenoptera physalus*; Dl, *Delphinapterus leucas*; Bb, *Balaenoptera borealis*; Mm, *Monodon monoceros*; Zc, *Ziphius cavirostris*; Bm, *Balaena mysticetus*; Ha, *Hyperoodon ampullatus*; Pm, *Physeter macrocephalus*). Pinniped references Otariids: Cu, *Callorhinus ursinus*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Gentry et al., 1986); Z, *Zalophus californianus*: [Mb] (Castellini and Somero, 1981), Dive (Feldkamp et al., 1989). Phocids: Cc, *Cystophora cristata*: [Mb] and Dive (Scholander, 1940); Pg, *Phoca groenlandica*: [Mb] and Dive (George et al., 1971); Ph, *Phoca hispida*: [Mb] (Lydersen et al., 1992), Dive (Parsons, 1977); Hg, *Halichoerus grypus*: [Mb] (Scholander, 1940), Dive (Lavigne and Kovacs, 1988); Pv, *Phoca vitulina*: [Mb] (Lenfant et al., 1970; Castellini and Somero, 1981), Dive (Kooyman et al., 1972); Lw, *Leptonychotes weddelli*: [Mb] (Ponganis et al., 1993), Dive (Castellini et al., 1993); Ma, *Mirounga angustirostris*: [Mb] (Thorson, 1993), Dive (Le Boeuf et al., 1993).

of muscle myoglobin content as well as body mass dictates the limits to diving performance in cetaceans. As discussed below, feeding behaviors unique to odontocetes and to mysticetes may have refined these relationships over evolutionary time.

By itself, myoglobin content of the skeletal muscle is a poor predictor of maximum dive duration when cetaceans are considered as a single group (Fig. 4). However, when the two cetacean suborders are analyzed independently, we find a close correlation between myoglobin content and maximum dive duration, particularly for the odontocetes (Fig. 2). Thus, the four odontocete species exhibiting the longest maximum dive durations (25–73 min) have high myoglobin contents ranging from 4.32 to 7.87 g (100 g wet muscle)$^{-1}$. In comparison, short duration divers among the odontocetes with maximum dive durations of 5 to 18.3 min maintain comparatively lower myoglobin contents (1.81 to 4.03 g [100 g wet muscle]$^{-1}$). These results suggest that high myoglobin content within the skeletal muscles serves as an important adaptation for prolonging dive duration in odontocetes. Indeed, some of the longest dives for cetaceans occur among the odontocetes, including the narwhal, Cuvier's beaked whale, Northern bottlenose whale, and sperm whale (Table 3).

In contrast to the results for odontocetes, the relationship between myoglobin content and maximum dive duration for mysticetes was not significantly correlated (Fig. 2). This may be due in part to the low sample size available for analysis for the mysticetes (Tables 1 and 2). These results differ from Snyder (1983) who suggested that large cetaceans have elevated myoglobin contents that correspond to increased dive duration. The results also differ from the pattern reported for pinnipeds, a mammalian group that demonstrates a distinct positive correlation between myoglobin content and maximum dive time (Fig. 4). Furthermore, pinnipeds may be subdivided into two groups, shorter diving otariids that maintain low myoglobin contents and longer diving phocids with higher myoglobin contents. The current study did not find a similar distinction between the two groups of cetaceans, the mysticetes and odontocetes (Fig. 4).

The wide range of body masses among cetacean species has a demonstrable effect on the range of maximum dive durations reported for these mammals (Table 3). Although body mass was posi-

tively correlated with maximum dive duration for cetaceans, the effect of body mass differs between the two cetacean suborders. A strong correlation between body mass and maximum dive duration was found for odontocetes; the same relationship was not significant for mysticetes (Fig. 3). Again, this may have been related to the small sample size of mysticetes examined. To maintain equivalent sample sizes for the myoglobin-dive duration and body mass-dive duration analyses, we limited our analyses to those species in which myoglobin content was measured or known. Although it was difficult to draw conclusions in the present study, previous investigations have reported a positive correlation between body mass and dive duration for mysticetes (Schreer and Kovacs, 1997).

For Weddell seals (Kooyman et al., 1983), other pinnipeds (Costa, 1991), and the pekin duck (Hudson and Jones, 1986) large body size provides an advantage for diving in terms of the absolute size of oxygen stores and relative decrease in mass specific metabolic rate. Similarly, both muscle myoglobin content and body mass influence dive capacity in cetaceans. These two characteristics explain nearly 50% of the variation in dive performance across a wide range of cetacean species including odontocetes and mysticetes. When odontocetes are considered separately, muscle myoglobin content and body mass accounts for 83% of the variation in dive performance.

Increased body size preadapts large cetaceans for prolonged dive durations due to two factors; (1) an increase in the absolute muscle mass and consequently an increase in absolute muscle oxygen stores; and (2) a decrease in mass specific metabolic rate. Metabolic rate only increases by a mass exponent 0.75 for resting mammals (assuming cetaceans follow the same allometric trend presented for other animals by Kleiber 1975) and by 0.71 for swimming transport costs in marine mammals (Williams, 1999). The lower mass specific energetic demands of large cetaceans in comparison to smaller cetaceans slow the relative depletion of oxygen during breath-hold. Thus, the larger cetacean is able to prolong its dive time beyond that of smaller cetaceans despite similar mass specific muscle oxygen stores. A comparison of the 80 000 kg bowhead whale and the 70 kg common dolphin demonstrates these relationships. These species represent two size extremes among cetaceans that have similar myoglobin contents in the locomotor muscles (Table 1). Based on the Kleiber (1975) regression, the mass specific metabolic rate of the common dolphin is 10 times greater than that of the bowhead whale. The theoretical consequence is a lower oxygen utilization rate for the larger cetacean, and sparing of limited oxygen stores in the skeletal muscle. With similar myoglobin contents per gram of muscle, the difference in oxygen utilization rate permits longer dive durations in the larger cetacean. TDR records support this, and we find a 6-fold greater maximum dive duration for the bowhead whale in comparison to the common dolphin (Table 3). Admittedly, further research is required to provide empirical evidence regarding the scaling of oxygen demand in this taxonomic group. However, these simple calculations demonstrate the importance of body size on metabolic rate and its potential effect on diving performance.

Despite the small sample sizes for mysticetes in this study, it appears that the relationships between myoglobin content and maximum dive duration (Fig. 2) and body mass and maximum dive duration (Fig. 3) are different for the two cetacean sub groups. One possible explanation for this is differences in preferred feeding behaviors and consequently different selective pressures for prolonged diving in odontocetes and mysticetes. The largest species in this study, the bowhead whale, dives between 0.1–31 min with an average dive duration of 12.08 ± 9.15 min (Wursig et al., 1984). These whales are described as skimmer feeders and forage primarily at the water surface, exhibiting a stereotypic basic pattern of short dive durations (Wursig et al., 1984; Dorsey et al., 1989). Other mysticete species show similar surface foraging behaviors. For example, in the Gulf of California and coastal California the majority of dives by fin whales rarely exceed 12 min and 200 m in depth (Croll personal communication). This depth represents only 12 times the animals' body length and suggests that large mysticetes may rarely approach their physiological limits for diving. In view of this, many species of mysticetes may be under little selective pressure for developing physiological adaptations, such as high myoglobin contents, that prolong dive duration. Conversely, the sperm whale, the largest odontocete, forages at depths of up to 2250 m (Ridgway and Harrison, 1986) for durations of 73 min (Watkins et al., 1993). When feeding behavior is

taken into account, it is not surprising that large odontocetes show exceptionally high myoglobin contents in the skeletal muscles while large mysticetes do not (Figs. 2 and 4, Tables 1 and 2).

In summary, the results of the present study demonstrate how myoglobin concentration in the skeletal muscles and body mass mutually influence dive duration in cetaceans. These two characteristics combined account for nearly 50% of the variation in dive capacity across cetacean species that vary in body mass from 70 to 80 000 kg. As found for other marine mammals, enhanced oxygen storage capacity due to high myoglobin concentrations is an important adaptation for diving in cetaceans. Balancing this store and oxygen utilization rate will dictate the duration of aerobically supported dives for these animals (Kooyman, 1989). Due to the wide range of body masses among cetaceans, differences in oxygen utilization rate as modulated by mass specific metabolic rate, is an especially important factor in defining aerobic dive capacity. Differences observed between the two cetacean suborders suggest that odontocetes and mysticetes have been under different selective pressures for developing physiological adaptations for prolonged dive duration. Among cetaceans, mysticetes show average myoglobin contents and rely on the relatively low oxygen consumption rates associated with large body size to support relatively short dives. The trend for smaller odontocetes is elevated muscle myoglobin contents prolonging dive durations. Large odontocete species, such as the bottlenose whale and sperm whale, combine both large body mass and high myoglobin contents in the skeletal muscles. As a result, these cetaceans are capable of prolonged dives at remarkable depths making them the champion divers among cetaceans.

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The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke

Terrie M. Williams[1,*], Lee A. Fuiman[2], Markus Horning[3] and Randall W. Davis[3]

[1]*Department of Ecology and Evolutionary Biology, Center for Ocean Health, Long Marine Laboratory, 100 Shaffer Road, University of California at Santa Cruz, Santa Cruz, CA 95060, USA,* [2]*University of Texas at Austin, Department of Marine Science, Marine Science Institute, 750 Channel View Drive, Port Aransas, Texas 78373, USA* and [3]*Department of Marine Biology, Texas A&M University at Galveston, 5007 Avenue U, Galveston, TX 77553 USA*

*Author for correspondence (e-mail: williams@biology.ucsc.edu)

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Summary

Foraging by mammals is a complex suite of behaviors that can entail high energetic costs associated with supporting basal metabolism, locomotion and the digestion of prey. To determine the contribution of these various costs in a free-ranging marine mammal, we measured the post-dive oxygen consumption of adult Weddell seals (*N*=9) performing foraging and non-foraging dives from an isolated ice hole in McMurdo Sound, Antarctica. Dives were classified according to behavior as monitored by an attached video-data logging system (recording activity, time, depth, velocity and stroking). We found that recovery oxygen consumption showed a biphasic relationship with dive duration that corresponded to the onset of plasma lactate accumulation at approximately 23 min. Locomotor costs for diving Weddell seals increased linearly with the number of strokes taken according to the relationship: locomotor cost = –3.78+0.04 × stroke number (r^2=0.74, *N*=90 dives), where locomotor cost is in ml O_2 kg^{-1}. Foraging dives in which seals ingested *Pleuragramma antarcticum* resulted in a 44.7% increase in recovery oxygen consumption compared to non-foraging dives, which we attributed to the digestion and warming of prey. The results show that the energy expended in digestion for a free-ranging marine mammal are additive to locomotor and basal costs. By accounting for each of these costs and monitoring stroking mechanics, it is possible to estimate the aerobic cost of diving in free-ranging seals where cryptic behavior and remote locations prevent direct energetic measurements.

Key words: Weddell seal, *Leptonychotes weddellii*, dive, oxygen consumption, locomotor cost, plasma lactate, stroke frequency, foraging energetics.

Introduction

Foraging by large predators comprises complex, potentially energetically demanding behaviors, depending on the type of prey involved (Stephens and Krebs, 1986). Activities such as locating, pursuing and capturing prey, as well as processing and assimilating food, as occurs in active hunting mammalian predators, can each represent a significant energetic cost to the animal. For example, the maximum aerobic energy used during locomotion can reach 10–30 times resting levels in a wide variety of terrestrial mammals (Taylor et al., 1980, 1987) and 4–11 times resting levels in marine mammals (Elsner, 1986; Williams et al., 1993). Digesting and absorbing prey can also be expensive, with both the quality and the quantity of the food affecting energetic costs. For both terrestrial (Kleiber, 1975) and marine (Costa and Williams, 1999) carnivores, metabolic rate may increase 30–67% over resting levels following the ingestion of prey. Termed the heat increment of feeding (HIF), this metabolic effect may last for hours. For example, in one marine carnivore, the sea otter *Enhydra lutris*, metabolic rate remained elevated for 4–5 h, peaking at 54% above resting levels following a high protein meal, and provided a thermoregulatory benefit for the animal (Costa and Kooyman, 1984).

Energy intake from prey ingestion must exceed these costs if a predator is to achieve a net positive energy balance. This in turn will dictate the efficiency of the predator, and ultimately its survival (Stephens and Krebs, 1986).

For aquatic birds and mammals, the problem of balancing foraging costs and benefits is complicated by the limited availability of oxygen when diving. Dunstone and O'Connor (1979a,b) investigated the trade-offs associated with underwater predation by air-breathing carnivores, using the American mink (*Mustela vison* Schreber) hunting fish as a model system. These investigators demonstrated an interaction between foraging economics, as predicted by optimality models (Charnov, 1976), and the preferred hunting strategies of the mink, as constrained by oxygen reserves. In this

relatively simple situation, foraging economics explained 51% of the variance in hunting patterns of the mink while oxygen constraints accounted for another 23%.

Kramer (1988) expanded on these studies by predicting optimum foraging patterns of diving birds and mammals based on the physiological and morphological characteristics that dictate oxygen gain during surface intervals. Theoretically, increased distance to feeding sites resulted in longer dive durations and surface times for breathing. Many species of marine mammal fit this pattern (Costa and Gales, 2003), although hunting behavior, type of prey taken and type of dive (e.g. exploratory *versus* hunting) can modify the response.

For actively foraging marine mammals, each energetic demand may simultaneously draw on limited oxygen stores. As a result, the combined energetic costs of locomotion and digestion while submerged can overwhelm the metabolic capacity of some marine mammals, forcing a selection between physiological activities when diving. Indirect evidence is provided from studies on northern elephant seals, which show a temporal separation between the cost of diving and of prey assimilation during submergence (Crocker et al., 1997). Following possible prey ingestion, elephant seals suspend swimming activity, which theoretically allocates a greater proportion of the oxygen reserve to metabolic processes necessary for warming the food, digestion and assimilation. In this way sequential diving may continue and the seal remains within its aerobic diving limits as it forages and processes prey. Similarly, the exceptionally high costs (as estimated from post-dive surface intervals) associated with lunge feeding by blue whales and fin whales confines submergence by these huge marine mammals to comparatively short bouts (Acevedo-Gutierrez et al., 2002).

Except for indirect evidence (Ponganis et al., 1993; Crocker et al., 1997; Acevedo-Gutierrez et al., 2002) and theoretical models (Williams et al., 1996), little is known regarding the energetic cost of foraging dives in marine mammals. This is due in part to the difficulty of simultaneously measuring metabolic rate and foraging behavior in free-ranging diving mammals. To address this problem, we measured the energetic cost of foraging and non-foraging dives in Weddell seals by using open flow respirometry and an isolated ice hole technique coupled with an animal-borne video-data logging system. Energetic costs associated with locomotion and prey warming and assimilation were measured, and the contribution of these costs to the total energetic demands of foraging determined. Using these results, we developed an energetics model to predict the cost of a dive by Weddell seals, based on stroking costs and the post-absorptive or post-prandial state of the animal.

Materials and methods

Experimental design

This study was conducted in McMurdo Sound, Antarctica (77.86°S, 166.22°E) in November and December of 1997, 1998 and 1999. An isolated ice hole paradigm (Kooyman et al., 1973; Castellini et al., 1992) was used in which Weddell seals dived from a man-made hole that had been drilled through the ice. The hole was located where the surrounding sea ice was free of other holes or cracks within a 3–4 km radius, thus ensuring that the animals would return to the isolated hole to breathe. No other restrictions were placed on the seals' behavior and the animals were able to dive freely to the ocean bottom at approximately 585 m in depth. Each seal was instrumented and released into the isolated hole, which was periodically covered with a metabolic dome for collection of expired gases between dives. The dome was removed at 6 h intervals for retrieval of videotapes and data from instrumented seals as they rested on the water surface. Seals routinely dived and rested in the hole for 3–5 days. Afterwards a secondary hole was opened in the ice and used by the seals to haul out.

A climate-controlled research hut was placed over the isolated hole and served as the laboratory for the experiments. Location of the hut and ice hole was approximately 10 km west of Cape Armitage, Ross Island, adjacent to the McMurdo ice shelf.

Animals

Nine adult Weddell seals *Leptonychotes weddellii* Lesson (1 female, 8 males; body mass=387.4±6.6 kg, mean ± S.E.M.) were used in these studies. The seals were captured with a purse-string net on the sea ice near Ross Island and transported approximately 15 km to the isolated ice hole (1.3 m diameter hole in a 2.5 m long × 1.5 m wide shelf) that had been cut into the sea ice. After a 24–48 h holding period the animals were instrumented with a video-data recording system, an indwelling intravertebral extradural vein catheter and swimming stroke monitor, as described in Davis et al. (1999). Following the experiments, the instruments and catheter were removed and the seals returned to their point of capture.

Aerobic and anaerobic costs of diving

Aerobic costs of diving were determined from the rate of oxygen consumption, as measured by open flow respirometry (Williams et al., 2001) following the protocols of Castellini et al. (1992). Breathing by the seals before and after dives was restricted to a Lexan™ dome (2.4 m long × 1.1 m wide × 0.4 m high) mounted at the water level over the isolated ice hole. Air was drawn through the chamber using a vacuum pump (Sears 2.0 hp Wet/Dry Vac; Chicago, IL, USA) at 510–550 l min^{-1}. Flow rates were monitored continuously with a dry gas flow meter (American Meter Co. Inc., DTM-325, San Leandro, CA, USA). At these flow rates the fractional concentration of oxygen in the dome remained above 0.2000 except for the initial seconds following a dive. Samples of air from the exhaust port of the dome were dried (Drierite; Hammond Drierite Co., Xenia, OH, USA) and scrubbed of carbon dioxide (Sodasorb; Chemetron, St Louis, MO, USA) before entering an oxygen analyzer (Sable Systems International, Inc., Henderson, NV, USA; and AEI Technologies S3-A, Pittsburgh, PA, USA). The percentage of oxygen in the expired air was monitored continuously and recorded once per second

on a personal computer using Sable Systems software. Rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77. This respiratory quotient was later confirmed in independent tests using simultaneous $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ measurements for a subset of the seals. All values were corrected to STPD.

The entire system was calibrated daily with dry ambient air (20.94% O_2) and every 3–4 days with dry span gases (16.0% O_2) and N_2 gas according to Fedak et al. (1981). The flow of calibration gases into the dome was controlled and monitored by an electronic flow meter (Model #FMA-772V; Omega, Manchester, UK) that was accurate to within 1% of total flow. Calibration of the flow meter was checked before and after the study with nitrogen gas and a rotameter (Cole-Palmer Instruments, Chicago, IL, USA). The theoretical fraction of O_2 leaving the dome was calculated according to Davis et al. (1985) and compared to measured values from the oxygen analyzer.

Oxygen consumption during the dive was calculated from the difference between total recovery oxygen consumption and resting rates in water following the procedures of Hurley and Costa (2001) and Scholander (1940). Prior to the diving experiments, baseline post-absorptive oxygen consumption rates were determined for each Weddell seal resting in the ice hole (Williams et al., 2001). These were later validated with rates determined during prolonged (>20 min) rest periods between dives by foraging and non-foraging seals. Following a dive, oxygen consumption was monitored continuously, and diving metabolism calculated from the recovery oxygen consumed in excess of resting rates for either post-absorptive or post-prandial seals as determined from feeding behavior logged by the animal-borne video-data recorder (see below). Only post-dive recovery periods in which the seals rested quietly and remained on the surface long enough for oxygen consumption to return to within 2% of baseline levels were used in this analysis. In this way, the potential effects of sequential dives on oxygen consumption were avoided.

To assess the contribution of anaerobic metabolism during diving, plasma lactate concentration was measured in post-dive blood samples drawn from an indwelling catheter placed in the extradural vein of the seals. Because the metabolic dome prevented access to the catheter, blood samples were collected in a separate series of dives covering the range of dive durations observed for the respirometry tests. Samples (5–10 ml) were drawn within 1.5–5.0 min of resurfacing from a dive to correspond with peak recovery lactate levels (Qvist et al., 1986). Serial blood samples for seven dives confirmed that peak changes in pH and [lactate] occurred during this period of recovery. Chilled blood samples were immediately centrifuged (approximately 1000 *g* for 10 min) and the plasma stored in cryovials at –30°C until analysis. Total plasma [lactate] was determined using a portable lactate analyzer (YSI 1500 Sport Lactate Analyzer, Yellow Springs, OH, USA) calibrated daily with zero and lactate standard solutions.

Foraging behavior

The underwater foraging behavior of the seals was recorded continuously using a video-data logging system carried by the free-ranging animals. Details of the instrumentation and attachment procedures have been described previously by Davis et al. (1999) and Fuiman et al. (2002). Briefly, seals were sedated with an intramuscular injection of ketamine hydrochloride (2 mg kg^{-1}; Fort Dodge Laboratories, Fort Dodge, IA, USA) and diazepam (0.1 mg kg^{-1}; Steris Corporation, Phoenix, AZ, USA) and weighed. A low light-sensitive camera with an array of near-infrared LEDs was mounted on a small piece of neoprene rubber glued to the fur on the head of the seal, providing a view of the animal's eyes and muzzle, and of the water for approximately 70 cm in front of the nose. Illumination from the LEDs was invisible to the seals and their prey. The camera was attached by a cable to a torpedo-shaped, reinforced housing (35 cm long × 13 cm diameter) that contained an 8 mm videotape recorder and microprocessor (Pisces Designs, San Diego, CA, USA). The video housing rested in a molded, non-compressible foam cradle that was attached to a neoprene rubber pad on the dorsal midline of the seal below the shoulders. The video images were synchronized with measurements of depth from a pressure transducer, swimming speed from a flow meter, compass bearing (Davis et al., 1999) and swimming stroke activity (described below).

The instrument pack and housing were neutrally buoyant in water. The frontal area of the instruments represented less than 5.5% of the frontal area of the seal, and was within the suggested limits and shapes for instrumented free-ranging swimming animals (Wilson et al., 1986; Culik et al., 1994). To assess the potential effects of the instruments on swimming effort, we compared metabolic rates of seals with (N=82 dives) and without (N=63 dives) the video system and camera. Dive durations ranged from 1.4 to 44.0 min and there was no significant difference in recovery oxygen consumption (Mann–Whitney nonparametric test at P=0.917) for the two groups (Fig. 1).

Each 8 mm videotape was duplicated in VHS format immediately after recovery. Videotapes were screened for encounters with prey, almost entirely fishes. The species of fish were identified by size, shape and pigmentation according to Fuiman et al. (2002).

Stroke mechanics and locomotor costs

The mode of swimming (burst-and-coast, continuous stroking, gliding), relative stroke amplitude and stroke frequency were determined for the seals from a single axis accelerometer (±2 g; 6 cm long × 3 cm wide × 2.0 cm high; Ultramarine Instruments, Galveston, TX, USA) mounted on a neoprene pad at the base of the tail of the seals. Lateral sweeps of the posterior half of the body and the hind flippers, characteristic of phocid swimming (Fish et al., 1988), were monitored by the accelerometer. Output from the accelerometer was recorded at 16 Hz with a microprocessor and synchronized with dive depth, time and video images.

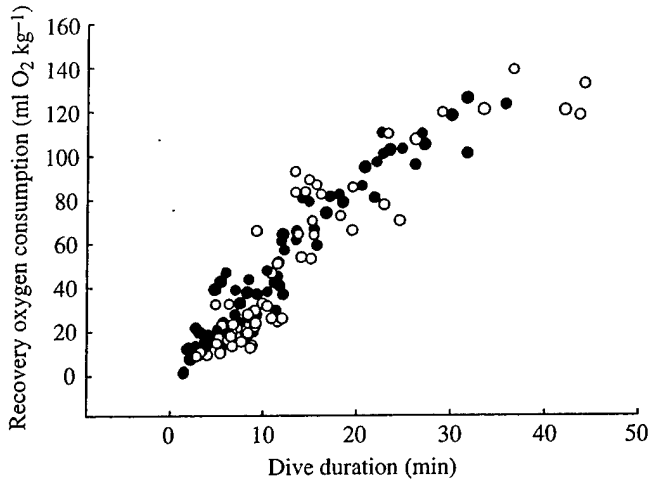

Fig. 1. Post-dive oxygen consumption in relation to dive duration for Weddell seals diving with (closed circles) and without (open circles) the video-data logging system. Each point represents an individual dive. No statistical difference was found in oxygen consumption between the groups (see text), although uninstrumented seals tended to perform the longest dives.

Accuracy of the accelerometer in detecting stroke movements was tested by comparing the output of the microprocessor to video sequences obtained on dives in which the camera was directed backwards on the seal. In this way, the correspondence between peak flipper excursions and peak output from accelerometer microprocessor was confirmed.

To determine the amount of oxygen expended for locomotion, we examined the relationship between total oxygen consumed during the post-dive recovery period and the number of strokes performed during a dive. Prolonged (>12 s) periods of gliding characteristic of the descent (Williams et al., 2000) were accounted for by assuming that metabolism remained at resting levels when the seal was not actively stroking. Therefore, locomotor costs during a dive were determined from the difference between total recovery oxygen and maintenance costs according to the equation:

$$\text{Locomotor cost} = V_{O_2\text{rec}} - (\text{BMR}t)\,, \qquad (1)$$

where locomotor cost and $V_{O_2\text{rec}}$ (recovery oxygen consumption) are in ml O_2 kg^{-1}, BMR is the basal metabolic rate in ml O_2 kg^{-1} min^{-1} (according to Kleiber, 1975) and t is dive duration in min. Previous experiments on quiescent, submerged pinnipeds have demonstrated that maintenance costs approach Kleiber's BMR predictions (Hurley and Costa, 2001). Therefore, we assumed that the predicted BMR was a reasonable approximation of the maintenance costs for the diving seals in the present study. To avoid complications associated with anaerobiosis and feeding, only aerobic, post-absorptive dives were used for calculations of locomotor costs.

Statistics

Linear regressions for the relationships between recovery oxygen consumption and dive duration, and plasma lactate concentration and dive duration, were determined by least-squares methods using statistical software (Jandel Scientific Software 1995). Dives were classified as aerobic or anaerobic depending on increases in post-dive plasma lactate concentration above resting levels. To assess the effect of the heat increment of feeding on metabolic rate, we calculated the residuals for total recovery oxygen consumption of post-prandial and post-absorptive seals. Dives were classified as feeding dives if the seals ingested a fish or performed a dive within 5 h of ingesting a large meal (i.e. >5 *Pleuragramma antarcticum*). The latter was used to account for the prolonged metabolic effect associated with heating and assimilating a protein meal, characteristic of marine mammals (Costa and Kooyman, 1984). The recovery oxygen consumption residuals of these dives were then compared to similar residuals for seals performing non-foraging dives (SYSTAT 1998; SPSS, Inc.).

The effects of the instrumentation on diving performance were determined by comparing metabolic rates of seals with and without instrumentation. Because the test for normality failed, a Mann–Whitney nonparametric test was used (Zar, 1974). All mean values are ± 1 S.E.M. unless otherwise noted.

Results

Aerobic and anaerobic cost of diving

The effect of dive duration on aerobic and anaerobic responses by adult Weddell seals is shown in Fig. 2. As reported previously for diving Weddell seals (Kooyman et al., 1980), plasma lactate concentration remained at resting levels (mean=2.10±0.35 mmol l^{-1}, N=38 dives) until the dive duration exceeded 23 min (Fig. 2A). Longer dives resulted in a linear increase in peak post-dive plasma [lactate] that was described by the equation:

$$\text{Plasma [lactate]} = 3.09 + 0.37t\,, \qquad (2)$$

(r^2=0.47, N=15 dives, P<0.005), where plasma [lactate] is in mmol l^{-1}.

Total oxygen consumption during the post-dive recovery period also showed a biphasic relationship with dive duration (Fig. 2B). Using the breakpoint in plasma lactate concentration at 23 min to define aerobic and anaerobic dives, we found that recovery oxygen consumption of aerobic dives increased linearly as described by the equation:

$$V_{O_2\text{rec}} = -8.20 + 4.74t\,, \qquad (3)$$

(r^2=0.85, N=137 dives, P<0.001). Dives longer than 23 min resulted in a second linear relationship in which recovery oxygen consumption increased with dive duration according to the equation:

$$V_{O_2\text{rec}} = 74.27 + 1.10t\,, \qquad (4)$$

(r^2=0.29, N=37 dives, P<0.001).

As reported by Castellini et al. (1992) and Ponganis et al. (1993), the rate of oxygen consumption ($\dot{V}_{O_2}$) measured after

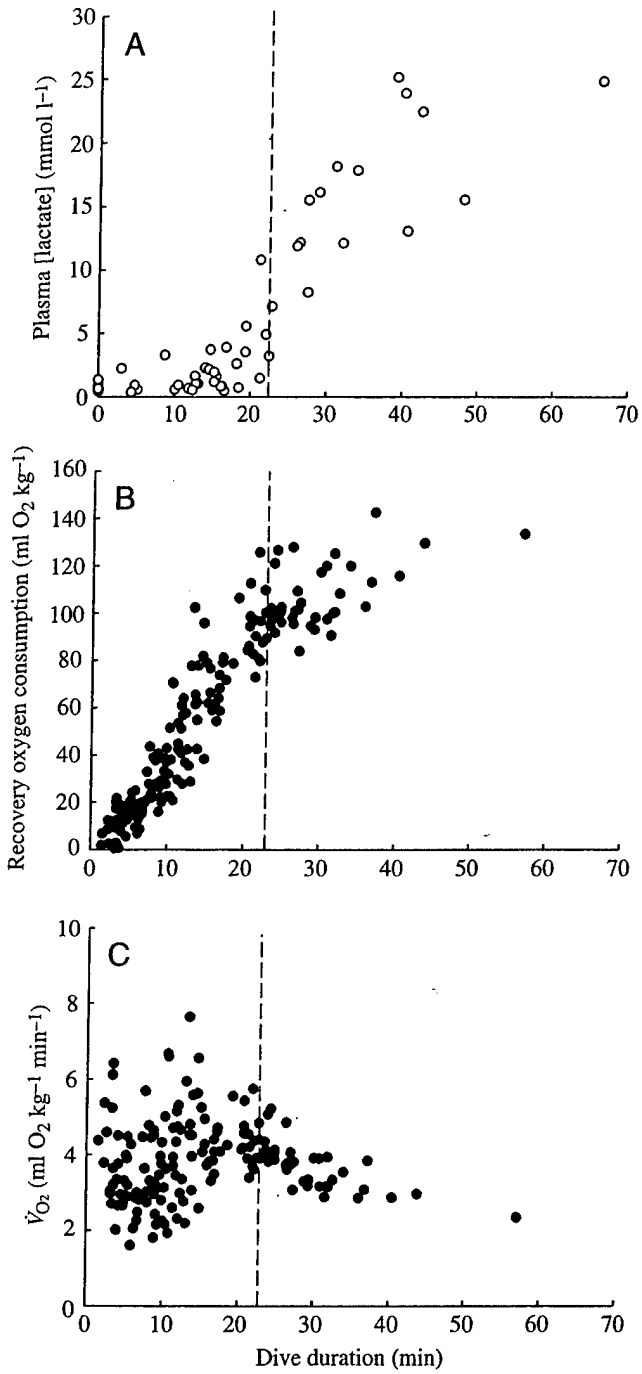

Fig. 2. Changes in plasma lactate concentration (A), recovery oxygen consumed (B) and post-dive oxygen consumption rate (C) in relation to dive duration for nine adult Weddell seals. Measurements were taken during the recovery period immediately following each dive. Points represent individual dives for an animal. The dashed vertical line denotes the change from aerobic to anaerobic dives, as indicated by the increase in plasma [lactate] above resting levels. Equations for statistical relationships are provided in the text.

diving was highly variable for dives of shorter duration than the aerobic dive limit (Fig. 2C). For dives shorter than 23 min, $\dot{V}_{O_2}$ ranged from 1.61 to 7.64 ml O$_2$ kg^{-1} min^{-1} and showed no

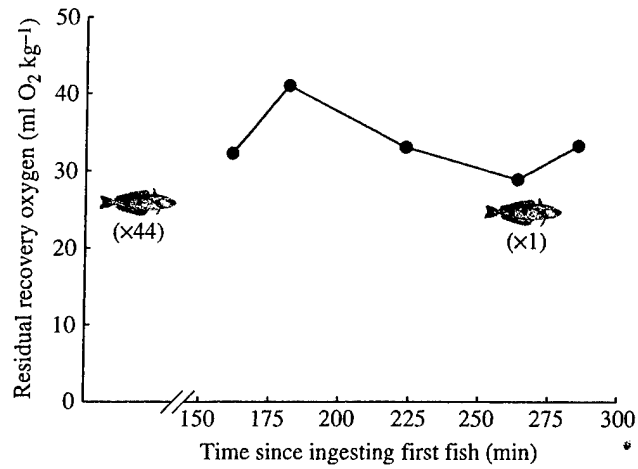

Fig. 3. Residuals for recovery oxygen consumption of a foraging Weddell seal. Data are presented in relation to time following first fish ingestion in a feeding bout. The final five dives of a sequence consisting of 11 foraging dives are shown. Each point represents the residual for the recovery period following a dive. Fish indicate times when we observed the seal eating *Pleuragramma antarcticum*. 44 fish were ingested at the beginning of this bout, with one additional fish caught on the tenth dive of the sequence. Residuals were determined by comparing the observed post-dive recovery oxygen consumption to predicted values based on Fig. 2B and Equation 3.

pattern with dive duration. The mean of this range, 3.84±0.39 ml O$_2$ kg^{-1} min^{-1} (N=5 seals), was similar to the average metabolic rate measured for animals resting on the water surface. This value is 23.2% lower than reported by Castellini et al. (1992) for short dives by Weddell seals, which may be attributed to differences in the classification of short dives (<23 min in the present study, compared with <14 min in Castellini et al., 1992). For longer dives, $\dot{V}_{O_2}$ decreased with dive duration according to the relationship:

$$\dot{V}_{O_2} = 5.63 - 0.07t\,, \qquad (5)$$

(r^2=0.50, N=37 dives, P<0.001).

Feeding costs

Antarctic silverfish *Pleuragramma antarcticum* Boulenger were the common prey item of foraging Weddell seals in this study (Fuiman et al., 2002), and ingestion was associated with a higher recovery oxygen consumption than post-absorptive dives of similar duration (Figs 3, 4). The elevation in metabolism lasted for several hours after a foraging dive, suggesting a thermogenic effect associated with the heating and assimilation of the fish. An example of the response is illustrated in Fig. 3 for a Weddell seal performing repetitive dives into an aggregation of silverfish. During a feeding bout of 11 sequential dives the seal ingested 44 fish in the first four dives as well as an additional fish during the tenth dive of this sequence. Residuals for the recovery oxygen consumption showed that metabolic rate remained elevated an average of 33.73±1.98 ml O$_2$ kg^{-1} for over 5 h, although fish were not necessarily caught on every dive.

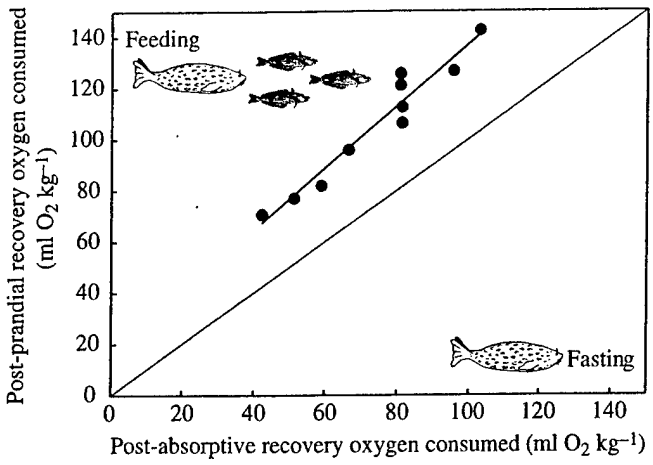

Fig. 4. Recovery oxygen consumption of feeding (post-prandial) and fasting (post-absorptive) dives in free-ranging Weddell seals. Each point represents a feeding dive paired with a fasting dive of equal distance traveled (within 6.8±1.7%) and duration (within 8.3±1.7%) for two male seals of identical body mass (398 kg). The diagonal line through the origin represents the line of equality for the cost of feeding and fasting dives. The short line denotes the least-squares linear regression through the data points, as described in the text.

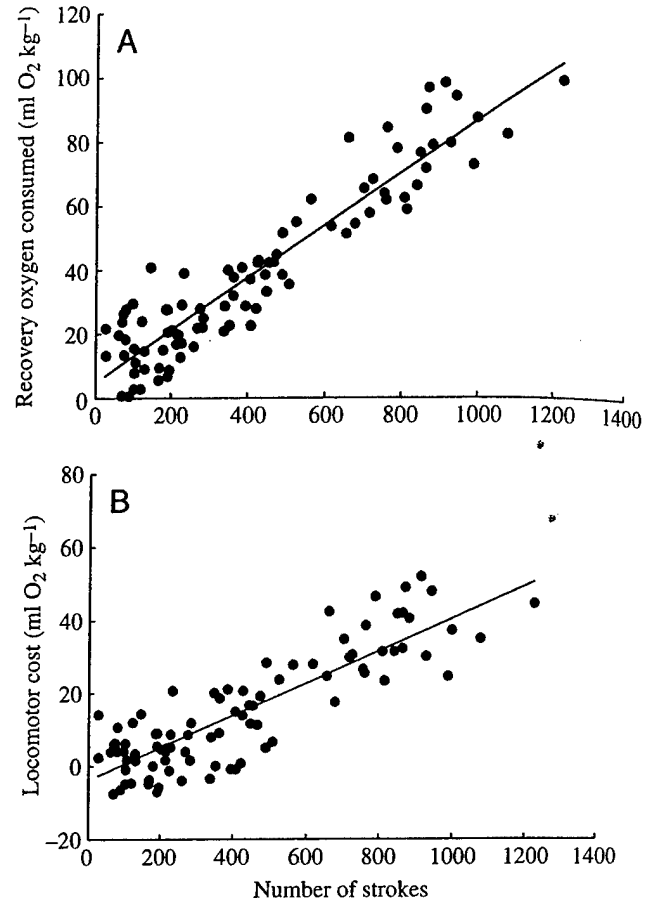

Fig. 5. Recovery oxygen consumed (A) and locomotor costs (B) of diving Weddell seals in relation to the total number of strokes taken during a dive. Measurements were taken during the post-dive recovery period. Points represent individual dives. Solid lines are the least squares linear regressions through the data points as described in the text. Note that only aerobic dives, as determined from Fig. 2 were used in these analyses.

When comparing the post-dive recovery oxygen consumed for post-absorptive and post-prandial seals, we found that dives associated with feeding were consistently more costly than non-feeding dives of similar duration and distance (Fig. 4). In this subset of dives, the total distance traveled ranged from 1178 m to 5012 m, while duration of the dives ranged from 10.6 min to 37.1 min. Together these resulted in a range of energetic costs for feeding and non-feeding dives as described by the equation:

$$\text{Post-prandial } V_{O_2\text{rec}} = 16.19 + 1.21 \times \text{post-absorptive } V_{O_2\text{rec}}\,, \quad (6)$$

(r^2=0.94, N=10, P< 0.001).

All paired dives fell above the line of equality with an average post-dive oxygen consumption that was 44.7±3.6% (N=10 paired dives) higher for feeding dives than non-feeding dives. A similar elevation in metabolic rate following the ingestion of prey was observed for one seal at rest. $\dot{V}_{O_2}$ for the quiescent, post-absorptive seal determined prior to diving was 4.42 ml O_2 kg^{-1} min^{-1}. During an extended recovery period following a foraging dive, the same animal showed a resting $\dot{V}_{O_2}$ of 6.78 ml O_2 kg^{-1} min^{-1}, representing a 53% increase in metabolic rate attributed to the assimilation of prey.

Locomotor and stroking costs

Total recovery oxygen consumed during the post-dive period of aerobic dives increased linearly with the number of strokes executed (Fig. 5A) according to the equation:

$$V_{O_2\text{rec}} = 4.74 + 0.08S_n\,, \quad (7)$$

(r^2=0.87, N=90 dives, P<0.001), where S_n is stroke number.

As might be expected, there was a linear increase in locomotor costs as the number of strokes increased (Fig. 5B). The relationship for aerobic dives was described by:

$$\text{Locomotor cost} = -3.78 + 0.04S_n\,, \quad (8)$$

(r^2=0.74, N=90 dives, P<0.001). Based on the slope of this relationship, the net cost per stroke for an adult Weddell seal is 0.044 ml O_2 kg^{-1} (mean=0.036±0.007 ml O_2 kg^{-1} stroke^{-1}, N=90 dives).

Discussion

The foraging energy budget

For Weddell seals the energy expended for foraging includes significant costs associated with swimming as well as with the warming, digestion and assimilation of ingested prey. A generalized model describing the energetic demands of a free-ranging animal in a thermally neutral environment states that total energetic cost=basal metabolic cost + locomotor cost + feeding cost (Costa and Williams, 1999). In this model,

thermoregulatory costs are considered minor relative to the remaining costs or are offset by either skeletal muscle activity or the heat produced by the assimilation of prey. For the following analysis, we will assume that thermoregulatory costs of the diving Weddell seal are likewise included in the remaining energetic costs.

There has been considerable discussion concerning the basal metabolic rate (BMR) of marine mammals, but with little resolution (Lavigne et al., 1986; Andrews, 2002). Current evidence suggests that the BMR of many pinnipeds and cetaceans ranges from 1.4 to 2.1 times that predicted for domestic animals (Kleiber, 1975) and approximates that of other carnivorous mammals (McNab, 2000) when marine mammals are resting on the water surface (Williams et al., 2001). We found similar results for resting Weddell seals. The BMR of Weddell seals was 4.07±0.21 ml O_2 kg^{-1} min^{-1} in air and 3.58±0.24 ml O_2 kg^{-1} min^{-1} in water. The latter value was within 14% of that reported by Castellini et al. (1992) for Weddell seals resting in an isolated ice hole, and 1.6× the Kleiber (1975) prediction. BMR decreased by approximately 10% if the seals went into prolonged apneas during the rest period. In view of this, it is likely that the metabolic rate of inactive seals is lower when submerged for prolonged periods than when resting and breathing apneustically on the water surface. Evidence for this is provided by sleeping and diving Weddell seals (present study; Castellini et al., 1992) and California sea lions trained to station underwater (Hurley and Costa, 2001). For both species, post-submergence metabolism indicates a flexible resting metabolic rate depending on the duration of breath-hold. In Weddell seals, prolonged breath-holding while sleeping on the water surface or during long (>14 min) dives resulted in the lowest metabolic rates (Castellini et al., 1992). The metabolic rate of sea lions resting on the water surface was 2–3 times predicted values (Kleiber, 1975); this decreased to predicted levels when the animals remained submerged for 7 min (Hurley and Costa, 2001).

We found a similar result for Weddell seals when extrapolating the relationship between recovery oxygen consumption and stroke count (Fig. 5A) to zero strokes performed (i.e. submerged resting). The calculated submerged metabolic rate of Weddell seals was 2.47 ml O_2 kg^{-1} min^{-1}, and was within 10% of the Kleiber (1975) prediction. Therefore, we used this value to represent the minimum basal metabolic costs of the diving Weddell seal in our energetic analyses, recognizing that this minimum value may vary slightly for short duration dives (Fig. 2C).

Of the two remaining costs, the energy expended for locomotion can be considerably higher than both resting and assimilation costs. Overall, locomotor activity resulted in a 1.3- to 3.5-fold increase in metabolism over resting rates, depending on the duration of the dive (Fig. 6). Because oxygen consumption increased linearly with the number of strokes taken during a dive (Fig. 5), the resulting net cost per stroke remained constant at 0.044 ml O_2 kg^{-1} $stroke^{-1}$. Consequently, each swimming stroke performed by the seal had a predictable effect on the oxygen reserves of the animal, more so than the

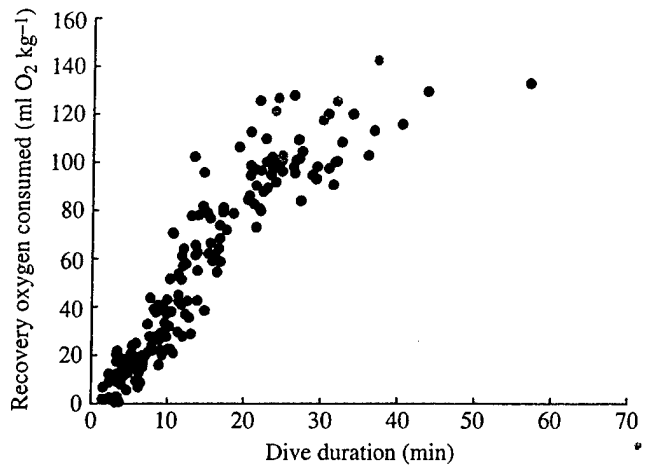

Fig. 6. The effects of behavior on recovery oxygen consumption in diving Weddell seals. Each point represents an individual dive for an animal as shown in Fig. 2B, now color coded for feeding behavior as determined from video sequences, and aerobic limits determined from blood [lactate] values. Aerobic and anaerobic dives for non-foraging seals are shown in black and dark blue circles, respectively. Post-dive oxygen consumption increased in foraging seals, and is indicated by red (aerobic dives) and light blue (anaerobic dives) circles.

duration of the dive because gliding can represent a large fraction of the total dive duration (Williams et al., 2000; Davis et al., 2001).

Similar analyses have been conducted for running animals, in which the cost of terrestrial locomotion has been attributed to cost of each step (Alexander and Ker, 1990; Kram and Taylor, 1990). However, the cost per stroke of diving Weddell seals was considerably less than reported for stride costs of running mammals. Using the same methods as Taylor et al. (1982), the total cost per stroke for Weddell seals was calculated by dividing the recovery oxygen consumption (ml O_2 kg^{-1}) by the number of strokes taken during the preceding dive, using a conversion factor of 20.1 J/ml O_2. Note that this value differs from the net cost per stroke presented above, and does not account for the oxygen consumed during gliding periods. The resulting value, 2.39 J kg^{-1} $stroke^{-1}$ for swimming Weddell seals, compares with 5.0 J kg^{-1} $stride^{-1}$ for running mammals (Taylor et al., 1982). For runners ranging in body mass over four orders of magnitude the metabolic energy consumed at equivalent speeds remained nearly constant. Likewise, total stroke costs varied little for five species of phocid seal (Fig. 7). The total cost per stroke ranged from 1.44 J kg^{-1} $stroke^{-1}$ for a 97 kg harp seal to 2.87 J kg^{-1} $stroke^{-1}$ for a 33 kg harbor seal.

The difference between step and stroke costs among mammals may be explained in part by the different physical forces that must be overcome during running and swimming (Dejours, 1987). Among runners, smaller plantar areas reduce the cost of overcoming gravitational and frictional forces during locomotion. Conversely, propulsive surfaces are often enlarged in aquatic mammals that must overcome

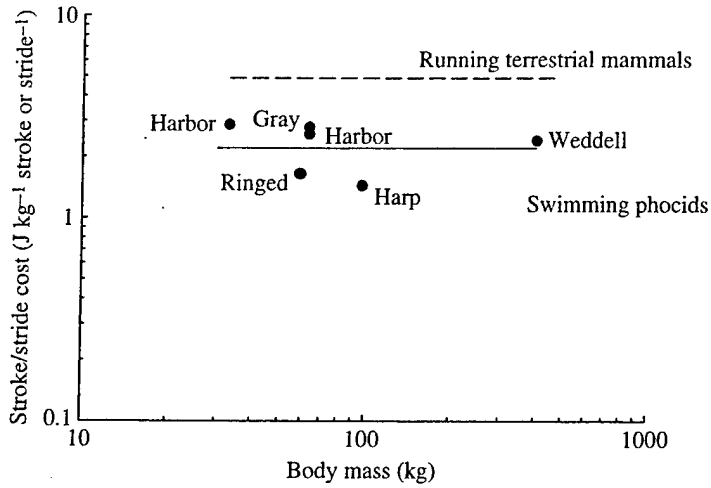

Fig. 7. Total cost of a stroke or stride in relation to body mass f swimming phocid seals and running mammals. Each poi represents the mean stroke costs calculated from the oxyg consumption and stroke frequency of harbor (Davis et al., 198 and gray, ringed and harp (Innes, 1984; Fish et al., 1988) sea swimming in a flume. Weddell seal data are from the prese study. The solid line is the mean total cost per stroke for fi species of swimming phocid seal. The dashed line is the me cost per stride for running terrestrial mammals from Taylor et a (1982).

hydrodynamic drag (Fish, 1993). The distance traveled per step (Kram and Taylor, 1990) or stroke (T. M. Williams, unpublished data) will also affect the energetic cost of running and swimming, respectively. In the present study, it was not possible to differentiate between large and small amplitude strokes, and a closer examination of the data from tail-mounted accelerometers may allow investigators to classify unique stroke types (e.g. accelerative, maintenance, braking, steering), each with a different energetic cost. Such analyses of these individual stroke types may allow us to further refine the locomotor costs associated with propulsive movements by large and small phocid seals.

The final component of the generalized energetic model is the energy required for prey warming, digestion and assimilation (Fig. 6). For the Weddell seals in this study, feeding resulted in a 44.7% increase in metabolic rate over a wide range of dive durations and distances traveled (Fig. 4). The pattern was similar to that described by Ponganis et al. (1993) for a juvenile Weddell seal presumed to be foraging on *Pleuragramma antarcticum*. It is unlikely that these increases were due to added locomotion associated with capturing fish as both resting and diving metabolic rates increased following feeding. Interestingly, the metabolic effect was apparent for dives in which fish were ingested as well as dives taking place as long as 5 h after fish ingestion (Fig. 3). This suggests that the digestion, assimilation and warming of prey elevate metabolism in foraging seals. Wilson and Culik (1991) have shown a similar response in another diving endotherm, the Adelie penguin. For these birds cold ingesta resulted in a marked energetic effect independent of the heat increment of feeding.

The high energetic demands associated with foraging suggest a selective advantage for aquatic mammals demonstrating high locomotor and assimilation efficiencies. By reducing the energy expended for travel and for processing prey, limited oxygen reserves could be extended and the duration of underwater hunting prolonged. Relatively little is known about reducing assimilation costs *per se*, although the timing and type of prey ingested has been shown to have an effect on total energetic cost in marine mammals (Costa and Kooyman, 1984; Bowen et al., 2002), and may be regulate (Crocker at al., 1997). In comparison, several strategie enable swimmers to increase locomotor efficienc Intermittent forms of swimming in particular have bee shown to reduce the cost of forward movement in a wid variety of aquatic animals. Burst-and-coast swimming b fishes (Weihs, 1974; Fish et al., 1991), and porpoising (Au an Weihs, 1980), wave-riding (Williams et al., 1992) an prolonged gliding (Costa and Gales, 2000; Williams et al 2000; Davis et al., 2001) by marine mammals lead to reduce locomotor costs. Gliding is an exaggerated from of intermitten propulsion that has recently been observed for many divin animals including Weddell seals, blue whales and elephan seals (Williams et al., 2000; Davis et al., 2001), bottlenos dolphins (Skrovan et al., 1999), right whales (Nowacek et al. 2001), Adelie penguins (Sato et al., 2002) and other divin birds (Lovvorn and Jones, 1991; Lovvorn et al., 1999). Th change from constant to interrupted propulsion acts to reduc the total number of strokes required to complete a dive, an thus enables the animal to conserve limited oxygen store during submergence (Williams, 2001).

Budgeting the number of strokes serves as such an energ conserving strategy for diving Weddell seals due to th relationship between recovery oxygen consumption and stroke count (Fig. 5). Maximum aerobic efficiency is achieved b traveling the greatest distance on the fewest number of strokes a task that may be accomplished by taking advantage o buoyancy changes with depth and using intermitten propulsion (Williams et al., 2000; Sato et al., 2003). This relationship also provides a useful tool for assessing the energetics of diving for free-ranging seals. If, as in running animals (Alexander and Ker, 1990), activity is priced by each locomotor movement, then the cost of diving may be predicted from the sum of individual stroking costs.

Predicting foraging costs for a free-ranging marine predator

The underwater location and cryptic feeding behavior of marine mammals makes the determination of foraging energetics particularly challenging for this group. Over the past 30 years, a variety of approaches have been used to study the energetics of these animals at sea. These can be generally categorized as indirect measurements and time budget analyses in which field observations of behaviors are matched with metabolic rates determined in captivity (Butler and Jones, 1997; Costa, 2002). The former includes the dilution of

isotopically labeled water and the use of physiological variables as surrogates for metabolism. For example, breathing rates (Sumich, 1983; Kreite, 1995), heart rate (Williams et al., 1992; Boyd et al., 1995; Butler and Jones, 1997), and swimming speed (Kshatriya and Blake, 1988; Hind and Gurney, 1997) have been used to estimate the energetics of free-ranging marine mammals. However, several factors such as the effect of diving bradycardia on heart rate and the effect of prolonged gliding sequences on swimming speed can obscure the actual activity level of the animal, thereby rendering the use of these indirect measures inaccurate for some diving birds and mammals or for some types of dives.

Alternatively, the relationship between energetic cost and stroke count allows the energetic demands of a dive to be predicted from propulsive movements. For Weddell seals that are not foraging, or at least have not fed within 3 h of a dive the aerobic cost of a dive is described by the equation:

$$\text{Non-feed}V_{O_2\text{rec}} = \text{BMR}t + \text{locomotor cost} = (9.98M_b^{-0.25})t + 0.04S_{tot}, \quad (9)$$

where $V_{O_2\text{rec}}$ is in ml O_2 kg^{-1}, M_b is body mass in kg, t is dive duration in min and S_{tot} is the total number of strokes taken. The BMR of mammals from Kleiber (1975) is 2.5 ml O_2 kg^{-1} min^{-1} for the seals in the present study. If the foraging behavior of the seal is monitored or if the animal has been known to feed, then the resulting aerobic cost will be approximately 44.7% higher (Figs 3, 6) than predicted by this equation. The cost of a foraging dive may be calculated by combining Equation 9 with the equation describing the effect of feeding (Equation 6):

$$\text{Feed}V_{O_2\text{rec}} = 16.19 + (12.08M_b^{-0.25})t + 0.05S_{tot}. \quad (10)$$

Because meal size, prey composition, and the time of feeding may affect the results (Costa and Williams, 1999), this is considered a preliminary estimate of the actual costs within 3 h of fish ingestion. Furthermore, seals exceeding aerobic diving limits will incur anaerobic costs in addition to the aerobic costs presented here.

This method enables energetic costs to be assessed for free-ranging animals in which direct energetic measurements are impossible and avoids the potential problems associated with using heart rate or swimming speed as predictors for metabolism (see McPhee et al., 2003). In addition, the relative cost of discrete behaviors (i.e. locating, chasing or traveling to prey) or segments of a dive (i.e. ascent, bottom or descent periods) can be estimated by counting the number of strokes performed during these periods.

In summary, the cost of foraging by Weddell seals entails many energetic components associated with locomotion and the ingestion of prey. The relative proportion of energy allocated to each of these components by a Weddell seal changes with the distance traveled on a foraging dive. For example, locomotor costs will increase proportionately on longer distance dives as the total number of strokes increases. Many questions remain regarding the effects of meal size and prey type on feeding costs, as well as variation in basal metabolism during prolonged submergence. However, by accounting for each of these costs and monitoring stroking mechanics, dive duration and feeding behavior, it is possible to estimate the aerobic demands of diving in free-ranging seals where the cryptic behavior and remote location prevent direct energetic measurements.

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A killer appetite: metabolic consequences of carnivory in marine mammals☆

Terrie M. Williams[a,*], J. Haun[b], R.W. Davis[c], L.A. Fuiman[d], S. Kohin[e]

[a]*Department of Biology, EMS-A316, University of California, Santa Cruz, CA 95064, USA*
[b]*SPAWAR Systems Center, D35, 53560 Hull Street, San Diego, CA 92152-6506, USA*
[c]*Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77553, USA*
[d]*Department of Marine Science, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX 78373, USA*
[e]*Department of Physiology, University of California, San Diego, CA 92093, USA*

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Abstract

Among terrestrial mammals, the morphology of the gastrointestinal tract reflects the metabolic demands of the animal and individual requirements for processing, distributing, and absorbing nutrients. To determine if gastrointestinal tract morphology is similarly correlated with metabolic requirements in marine mammals, we examined the relationship between basal metabolic rate (BMR) and small intestinal length in pinnipeds and cetaceans. Oxygen consumption was measured for resting bottlenose dolphins and Weddell seals, and the results combined with data for four additional species of carnivorous marine mammal. Data for small intestinal length were obtained from previously published reports. Similar analyses were conducted for five species of carnivorous terrestrial mammal, for which BMR and intestinal length were known. The results indicate that the BMRs of Weddell seals and dolphins resting on the water surface are 1.6 and 2.3 times the predicted levels for similarly sized domestic terrestrial mammals, respectively. Small intestinal lengths for carnivorous marine mammals depend on body size and are comparatively longer than those of terrestrial carnivores. The relationship between basal metabolic rate (kcal day^{-1}) and small intestinal length (m) for both marine and terrestrial carnivores was, BMR = 142.5 intestinal length$^{1.20}$ ($r^2 = 0.83$). We suggest that elevated metabolic rates among marine mammal carnivores are associated with comparatively large alimentary tracts that are presumably required for supporting the energetic demands of an aquatic lifestyle and for feeding on vertebrate and invertebrate prey. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Basal metabolic rate; Carnivore; Dolphin; Marine mammal; Small intestine; Weddell seal; Herbivore

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*Corresponding author. Tel.: +1-831-459-5123; fax: +1-831-459-4882.
E-mail address: williams@biology.ucsc.edu (T.M. Williams).

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1. Introduction

Diving marine mammals spend considerable time and energy in locating, pursuing, capturing and processing prey. For these activities to be energetically profitable, two physiological requirements must be met. First, more energy must be acquired from the intake of prey than is spent in obtaining and processing them. Second, marine mammals that forage while submerged must be capable of hunting under a constraint of limited oxygen availability (Dunstone and O'Connor, 1979).

Based on these requirements, there is considerable selective pressure for energetic efficiency during underwater hunting by marine mammals. In conventional foraging models, energetic profitability of specific prey and the efficiency of the predator are often expressed in terms of cost/benefit ratios calculated from the ratio of energy gained to energy expended during foraging (Stephens and Krebs, 1986). The duration of hunting by marine mammal predators is also defined by energy expenditure, as oxygen reserves in the blood, muscles and lungs are consumed during a dive (Kooyman, 1989).

Despite the importance of energy expenditure in evaluating foraging costs and overall energetic efficiency of a predator, there is much confusion regarding the metabolic rates of marine mammals. Even the relatively simple measure of basal metabolic rate (BMR) has not been clearly defined for this group. Currently, a question remains regarding whether or not the basal metabolic rates of marine mammals are higher (Irving, 1973; Liao, 1990), lower, or identical (Lavigne et al., 1986; Innes and Lavigne, 1991) to predictions for terrestrial mammals of comparable size. The confusion is due, in part, to a poor understanding of the underlying factors that set metabolic rates in marine mammals, and the impact of diving responses on these factors.

Recent studies on a variety of small vertebrates, including rodents (Konarzewski and Diamond, 1995; Koteja, 1996), birds (Piersma et al., 1996; Burness et al., 1998) and lizards (Garland, 1984), indicate that the organs associated with the processing and distribution of nutrients are coupled to the metabolic rate of the animal. Among a wide variety of terrestrial animals, metabolic rates are influenced by the quality of the diet, as well as digestive tract design and function. Sustained metabolic rates and metabolic ceilings, which ultimately set the limits for foraging behavior, reproductive output and geographic distribution, are linked to the digestive tract's ability to process food (Peterson et al., 1990). As a consequence, the size of the organs comprising the gastrointestinal tract often reflects the immediate metabolic demands of the animal. For example, cold exposure (Koteja, 1996), food habits (McNab, 1986), foraging methods (Jackson, 1992) and ecological conditions (Piersma et al., 1996) that lead to variability in basal metabolic rate have been associated with alterations in the size of the alimentary tract.

To provide a better understanding of the metabolic demands of marine mammals and the organs that must support these demands, we examined the relationship between BMR and gastrointestinal length in cetaceans and pinnipeds. Metabolic measurements were conducted on two species: an odontocete, the bottlenose dolphin (*Tursiops truncatus*) and a phocid, the Weddell seal (*Leptonychotes weddelli*). These data were combined with basal metabolic rates reported for other carnivorous marine mammals measured under comparable conditions. The relationship between gastrointestinal tract morphology and metabolic demand was determined using data for six species of marine mammal, in which both BMR and small intestinal length were measured or known. Similar analyses were conducted for five species of carnivorous terrestrial mammal. The results of this study indicate that the BMR of marine mammals resting on the water surface is higher than predicted for terrestrial mammals. This elevated metabolism is associated with a comparatively large alimentary tract that is presumably required for supporting an aquatic lifestyle and for feeding on vertebrate and invertebrate prey.

2. Materials and methods

2.1. Animals

Three mature, male bottlenose dolphins (mean body mass = 148.6 kg) were used in the metabolic studies. The animals were maintained in floating net pens at the US Navy Marine Mammal Program (SPAWAR, San Diego, CA), and had been at the facility for over 2 years before the mea-

surements were conducted. All animals were fed daily on a diet of mackerel, herring, and smelt supplemented with vitamins. Water temperature in the pens reflected seasonal ambient conditions in the ocean. Average water temperature in the pens during the experimental period was 15.4°C. T_{air} was 15.5°C. The dolphins were trained for 2–3 weeks prior to experimentation to rest quietly in a water-filled metabolic box

Seven mature, male Weddell seals (mean body mass = 388.5 kg) were captured on the sea ice near McMurdo Station, Antarctica. The animals were transported approximately 7 miles from the point of capture to an isolated ice hole (2.4-m-long × 1.1-m-wide shelf with a 1.0-m-diameter hole) that had been cut into the sea ice. All seals were held for 24–48 h and fitted with dive recorders and video instrumentation packs (Davis et al., 1999) before release into the isolated hole. A video recording system and camera mounted on the animals continuously monitored hunting behavior to ensure that the animals were post-absorptive prior to the metabolic measurements. Water temperature in the ice hole was −1.4 to −0.8°C during the experimental period. T_{air} was 1.7–3.6°C.

2.2. Basal metabolic rate

2.2.1. Dolphins

Metabolic measurements were carried out during March–April. Each animal was fasted overnight and placed in an insulated metabolic box the following morning. Water temperature in the box was controlled by a saltwater heat exchanger and ranged from 3.7 to 28.9°C. Only one water temperature was tested on each experimental day. Depending on the animal and the experimental water temperature, metabolic measurements were carried out continuously over 2–3 h. Experiments were conducted on sedentary animals and were terminated if the animal became active. Core body temperature was determined continuously during the experiments with a digital thermometer and flexible rectal probe (Physitemp Inc, Clifton, NJ).

2.2.2. Weddell seals

All metabolic measurements were carried out during the Antarctic austral summer (October–December) and followed the protocols of Castellini et al. (1992). Instrumented seals were released into the ice hole and were free to dive and rest. Resting metabolic measurements were made on sedentary animals as they floated on the water surface. Only resting periods lasting at least 2 h were used in the analyses. Respiratory rate and apneic periods were recorded visually and acoustically on videotape.

2.2.3. Oxygen consumption

Oxygen consumption was determined using open-flow respirometry systems. Breathing by the animals was restricted to a Plexiglas dome (1.1 m long × 0.8 m wide × 0.8 m high for dolphins; 2.4 m long × 1.1 m wide × 0. 4 m high for seals) mounted at the water level of the metabolic box or ice hole. Air was drawn through the chamber with a vacuum pump (Sears 2.0 Hp Wet/Dry Vac). Flow rate was monitored with a calibrated, dry gas-flow meter (American Meter Co Inc, DTM-325, San Leandro, CA) and was maintained at 45–65 l min^{-1} for the dolphins and 510–550 l min^{-1} for the seals. At these flow rates, the fractional concentration of oxygen in the domes remained above 0.2000. Samples of air from the exhaust port of the domes were dried (Drierite) and scrubbed of CO_2 (Sodasorb) before entering the oxygen analyzer (AEI Technologies S3-A, Pittsburgh, PA). The percentage of oxygen in the exhaust air was monitored continuously during the experiments, and recorded with a personal computer using Sable Systems software (Salt Lake City, UT). The output from the oxygen analyzer was monitored every second and averaged for each minute. These values were converted to oxygen consumption ($\dot{V}_{O_2}$) using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77. The lowest value for oxygen consumption averaged over 10–30 min during each 2–3-h experimental session was used in the analyses of basal metabolic rate. All values were corrected to STPD.

The entire system was calibrated daily (dolphins) or immediately before and after measurements (seals) with dry ambient air (20.94% O_2) and 100% nitrogen gas according to Fedak et al. (1981). The theoretical fraction of O_2 leaving the dome was calculated (Davis et al., 1985) and compared to the measured values from the oxygen analyzer. The flow of calibration gases into the dome was controlled and monitored by an electronic flowmeter (Omega, Model #FMA-772V) that was accurate to within 1%. Calibra-

tions of the flow meter were conducted with nitrogen gas and a rotameter (Cole-Palmer Instruments) before and after the studies.

2.3. Length of the small intestine

The length of the small intestine for a wide variety of terrestrial and marine mammals was compiled from published literature. Because diet influences gastrointestinal morphology, including intestinal length in mammals (Stevens and Hume, 1995), the published data used in the present study were limited to carnivorous species, except for comparisons with herbivores. Care was also taken to limit the data to adult, non-pregnant, non-lactating animals. Values for post-prandial animals were excluded whenever the presence of food in the intestinal tract was indicated.

2.4. Statistics

The lower critical temperature for the dolphins was determined from the intersection of multiple regressions using Yeager and Ultsch (1989). Because warm water tests were terminated if core temperature of the dolphins fluctuated $> 0.1°C$, it was not possible to conduct a similar analysis for the upper critical temperature. Instead, upper critical temperature for the dolphins was based on fluctuations in core body temperature and *t*-tests conducted for metabolic rates determined at 16, 23 and 29°C.

Differences in the means for the metabolic rates of resting and intermittently breathing seals were determined from *t*-tests using statistical software (Jandel Scientific Software, 1995). Allometric regressions for basal metabolic rate in relation to body mass, and relationships for basal metabolic rate vs. intestinal length, and intestinal length ratio vs. body length, were determined using least squares methods (Jandel Scientific Software, 1995). Data are reported as means ± S.E.M., unless otherwise indicated.

3. Results

3.1. Basal metabolic rate

The metabolic rate of dolphins resting on the water surface was dependent on water temperature (Fig. 1). Metabolic rates recorded in this

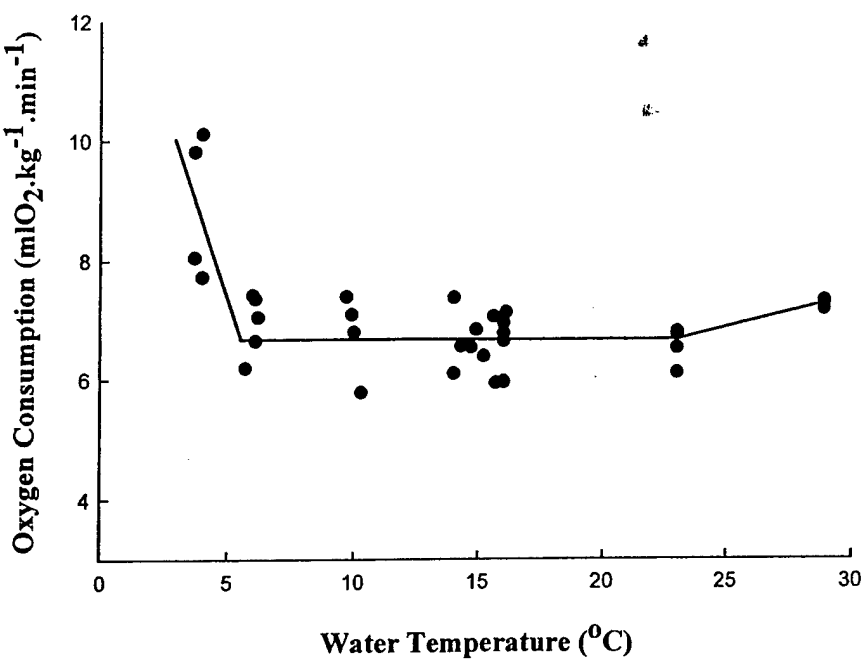

Fig. 1. Resting metabolic rate of three adult, post-absorptive bottlenose dolphins in relation to water temperature. Acclimatization temperature for the dolphins was $T_{water} = 15.4°C$. Each point represents a single metabolic measurement for an individual dolphin. The horizontal line represents the average metabolic rate within the thermal neutral zone (defined in text).

experiment ranged from 5.78 to 10.12 ml O_2 kg^{-1} min^{-1}, with higher metabolic rates occurring at both the high and low water-temperature extremes. The mean minimum metabolic rate for the three dolphins resting on the water surface was 6.53 ± 0.16 ml O_2 kg^{-1} min^{-1} ($n = 9$) at $T_{water} = 15.4$°C (acclimatization temperature), and was within 8% of that reported by Ridgway and Patton (1971) for a 128-kg dolphin at $T_{water} = 17$°C. Metabolic rate of the dolphins remained at this level until T_{water} was lower than 5.9 or higher than 23.0°C. These water temperatures were considered the lower and upper critical temperatures, respectively, for bottlenose dolphins acclimatized to 15.4°C, as defined by a significant increase in metabolic rate at 3.9 ($n = 4$, $P = 0.029$) and 29.0°C ($n = 4$, $P = 0.004$).

Weddell seals rested on the water surface for periods of up to 6 h. Respiratory cycles alternated between eupnea during quiescent, alert periods and intermittent breathing patterns during sleep. The metabolic rate of alert Weddell seals resting at $T_{water} = -1.4$ to -0.8°C was 3.58 ± 0.24 ml O_2 kg^{-1} min^{-1} (Fig. 2). This decreased to 3.20 ± 0.06 ml O_2 kg^{-1} min^{-1} when the seal was sleeping and breathing intermittently. However, the difference in metabolic rates between the two conditions was not statistically significant ($n = 7$ seals, $t = 1.892$, $P = 0.09$). These results are within 14% of metabolic rates previously reported for resting and sleeping Weddell seals by Castellini et al. (1992), measured under identical conditions.

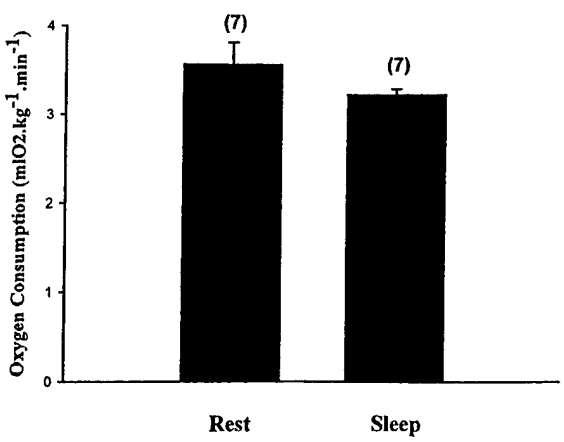

Fig. 2. Metabolic rate of seven adult, post-absorptive Weddell seals resting or sleeping on the water surface. Resting values are for alert, inactive animals breathing continuously. These data are compared to values for the same seals breathing intermittently during sleep. Height of the columns and lines represent means + S.E.M. Numbers in parentheses indicate the number of seals.

3.2. Length of the small intestine

Intestinal length for marine carnivores correlated with body size and ranged from 11.4 m in the smallest species, the sea otter (*Enhydra lutris*; Kenyon, 1969), to 100 m in the largest species, the fin whale (*Balaenoptera physalus*; Stevens and Hume, 1995). Values for similarly sized otariids and phocids ranged from 14.5 to 38.0 m in adult animals (Burns, 1981a,b; King, 1983; Stevens and Hume, 1995; Martensson et al., 1998). Owing to their comparatively large body size, small intestinal length was greater for mysticete whales (range 61.2–100.0 m) than for odontocetes (range 30.0–66.0 m) (Stevens and Hume, 1995). The ratio of small intestinal length to total body length correlated negatively with body length in marine mammals (Fig. 3a), and was described by the regression

$$\text{Intestinal length / body length ratio} = 17.6\,\text{body length}^{-0.41} \quad (n = 25 \text{ species}, r^2 = 0.49)$$

where body length is in m. In comparison, small intestinal length increased with body length in these marine mammals (Fig. 3b) and was described by:

$$\text{Intestinal length} = 16.7\,\text{body length}^{0.60} \quad (n = 25 \text{ species}, r^2 = 0.77)$$

where lengths are in m.

Comparable measurements for carnivorous terrestrial mammals ranging in mass from 1.0 to 190.0 kg showed relatively smaller intestinal lengths than for marine species (Fig. 3a,b). Like marine mammals, the length of the small intestines depended on body size, and ranged from 1.2 m for the domestic cat (*Felis catus*; Stevens and Hume, 1995) to 8.7 m for a male African lion (*Panthera leo*; Davis, 1962). The ratio of intestinal length to body length was 2.4–4.9 and did not change with body length for the range of terrestrial species examined in this study (Davis, 1962; Stevens and Hume, 1995).

4. Discussion

4.1. Interrelationships between resting metabolic rate and the alimentary tract of carnivorous marine mammals

In a review of studies reporting basal metabolic rates for marine mammals, Lavigne et al. (1986) recognized that, in many cases, the defined conditions for assessing basal metabolism had not been met. These conditions specify mature, post-absorptive animals resting in a thermally neutral environment. Consequently, the authors suggested that the elevated BMRs reported for many

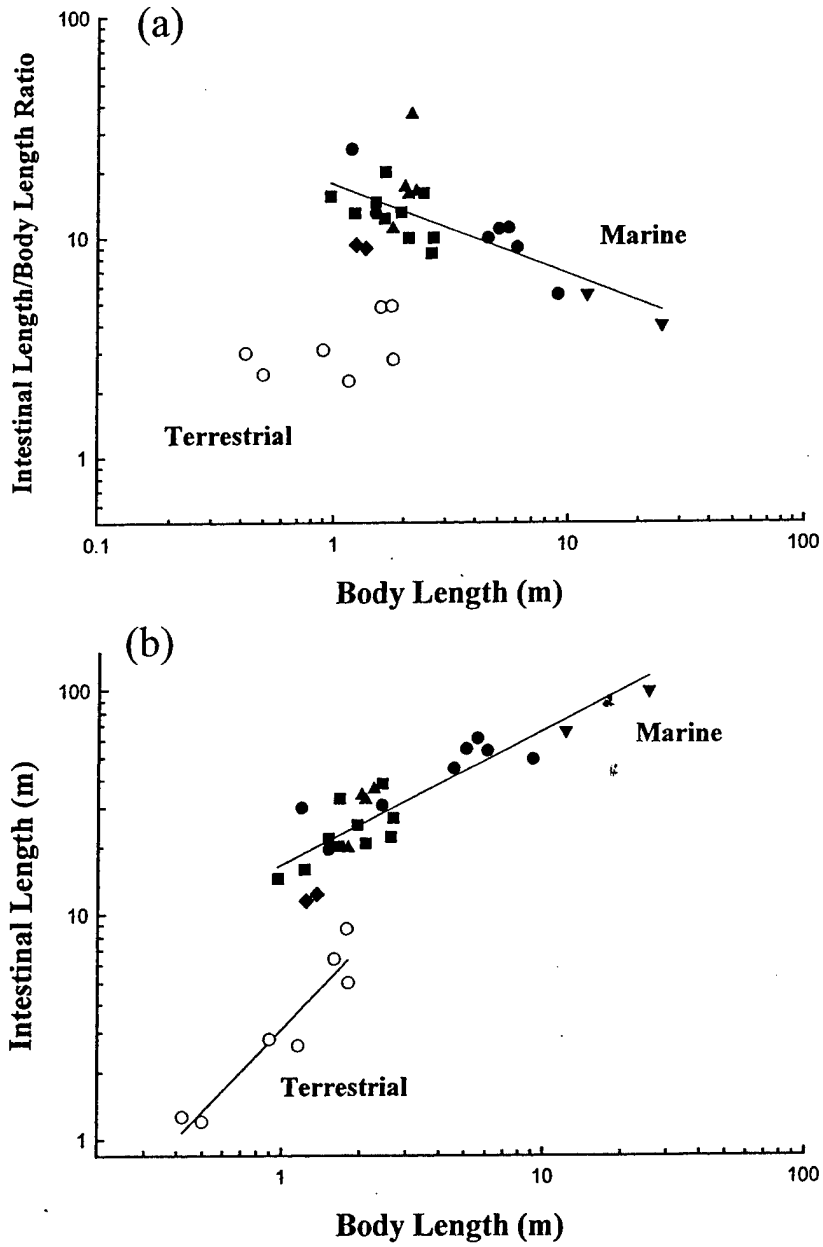

Fig. 3. The ratio of small intestinal length to total body length (a) and intestinal length (b) in relation to body length for carnivorous mammals. Data for marine mammals are denoted by the closed symbols and include sea otters (diamonds), odontocetes (circles), phocid seals (squares), otariids (triangles), and mysticete whales (down-pointed triangles). Terrestrial carnivores are shown by the open circles and include mink, human, cat, dog, leopard, and African lions. The solid lines denote the least squares regressions through the data points and are presented in the text for marine mammals. The regression for terrestrial mammals in (b) is intestinal length = 3.1 body length$^{1.22}$ ($n = 6$ species, $r^2 = 0.90$).

marine mammals were an artifact due to inappropriate comparisons with terrestrial mammals. Results from the present study, in which these conditions were met (assuming acclimatization temperature and minimum oxygen consumption occur within the thermal neutral zone; Bartholomew, 1977), indicate that other factors may also be involved.

In general, we find that the metabolic rates of marine mammals resting on the water surface are higher than those of terrestrial mammals resting in air (Fig. 4). Basal metabolic rates of the bottlenose dolphins and Weddell seals measured here were 2.3- and 1.6-fold the predicted levels for domestic terrestrial mammals (Kleiber, 1975), respectively. When measured under similar conditions, the metabolic rates of other species of resting marine mammal follow a similar pattern. Killer whales trained to breathe into a respiratory balloon (Kriete, 1995) showed metabolic rates that were 1.6-fold those predicted by Kleiber for a 3750-kg adult male, and 1.4-fold those predicted for a 2692-kg adult female. A 73-kg adult female California sea lion resting in a water-filled metabolic chamber had a minimum resting metabolic rate that was 2.1-fold that predicted (Liao, 1990). Sea otters, with an admittedly elevated mustelid metabolism (Iverson, 1972), show resting rates that are 2.8-fold the predictions when resting quietly on the water surface in a metabolic hood at $T_{water} = 20.0°C$ (Williams, 1989).

A better predictor of the basal metabolic rates for these species of marine mammal can be found in the scaling equation for vertebrate-eaters presented in McNab (1988) (Fig. 4). This agreement may not be surprising, since the species represented in this equation include marine, terrestrial and semi-aquatic mammals. When only terrestrial carnivorous mammals are considered, the differences in BMR between marine and terrestrial groups remain, despite similar food habits. For example, the BMR of a 73-kg California sea lion (Liao, 1990) is 2.3-fold that of a 59-kg cougar (Corts, 1984); a 20-kg sea otter (Williams, 1989) maintains a BMR that is 3.5-fold that of a 14.1-kg dog (Kleiber, 1975). In general, the BMRs reported for many carnivorous terrestrial mammals, including cats, dogs, arctic foxes, red foxes and cougars (reviewed by McNab, 1988), are within 4–23% of the predictions of Kleiber (1975). In

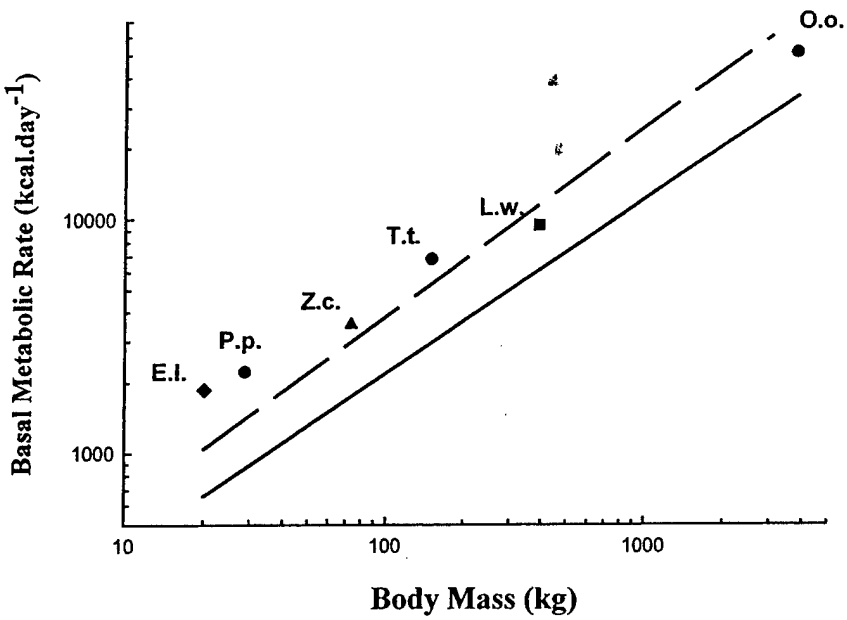

Fig. 4. Basal metabolic rate for marine mammals resting on the water surface in relation to body mass. Each point represents the mean values for sea otters (E.l. diamond; Williams, 1989), harbor porpoise (P.p. circle; Kanwisher and Sundnes, 1965), California sea lions (Z.c. triangle; Liao, 1990), bottlenose dolphins (T.t. circle; present study), Weddell seals (L.w. square, present study), and killer whales (O.o. circle; Kriete, 1995). The solid line is the predicted regression for basal metabolic rate in domestic terrestrial mammals according to Kleiber (1975). The dashed line is the regression for vertebrate eaters, which includes marine, semi-aquatic and terrestrial mammals from McNab (1988).

comparison, the BMR of carnivorous marine mammals ranges from 1.4- to 2.8-fold that predicted.

One confounding factor for marine mammals is the physiological adjustment that occurs with the dive response. In a study using adult California sea lions trained to submerge in a pool, Hurley (1996) found a graded resting metabolic response that correlated with the duration of submergence. Metabolic rates measured on the water surface were 2–3-fold those predicted for domestic terrestrial mammals by Kleiber (1975). These rates were reduced and approached the predicted levels when the measurement period included prolonged submergence. Undoubtedly, the variation in measured BMR for these sea lions can be attributed in part to changes in metabolic demands of specific tissues during submergence. This may also explain the variability in basal metabolic rate reported for marine mammals in comparison to terrestrial mammals.

Several studies have provided explanations to account for the comparatively high metabolic rates of resting marine mammals, regardless of their surface or submerged position (reviewed in Lavigne et al., 1986). These include elevated food consumption of captive subjects, cold acclimatization leading to high thermoregulatory energetic costs, body composition, and high protein diets. Certainly, the high thermal conductivity of water in comparison to air at the same temperature can result in elevated levels of heat loss and increased metabolic demands for mammals resting in water (Dejours, 1987). In addition, the maintenance of metabolically active tissues will influence overall metabolic rate, which in turn could limit dive duration in marine mammals (Ridgway, 1985).

An especially relevant factor in setting the metabolic rate of an animal is the capacity of the body to deliver nutrients to active tissues (Armstrong, 1983). Consequently, the high energetic requirements of marine mammals may place a correspondingly high demand on the gastrointestinal tract. Previous studies examining diverse vertebrate species with different food habits have demonstrated that the metabolic demands faced by an animal have an important bearing on the design and function of the gastrointestinal tract (Stevens and Hume, 1995). Both inter- (Daan et al., 1990) and intraspecific (Konarzewski and Diamond, 1995) variation in basal metabolic rate among terrestrial mammals may be explained by variation in the mass of metabolically active organs that support the processing and delivery of nutrients. Thus, the small intestines, as well as the heart, kidney, and liver, comprise a small proportion (< 17%) of the total body mass of mice, but account for nearly 50% of the variation in BMR in this species (Konarzewski and Diamond 1995).

The proposed demand on the gastrointestinal tract of marine mammals is reflected in the length of the small intestines for otariids, phocids, odontocetes, mysticetes and a mustelid, the sea otter (Fig. 3a,b). Many investigators have noted the exceptional length of the small intestines of marine mammals. It remains one of the most striking features of the gastrointestinal tract of both pinnipeds (Eastman and Coalson, 1974; King, 1983) and cetaceans (Slijper, 1976; Stevens and Hume, 1995). Although the length of the small intestine in many terrestrial carnivores approaches six-fold total body length, it ranges from seven- to 40-fold body length in otariids and phocids (King 1983). Among odontocetes and mysticetes, this length ratio ranges from four- to 23-fold body length, depending on the species (Stevens and Hume, 1995).

Currently, the reason for the exceptional length of the small intestines in marine mammals is not known. Thermoregulatory factors, parasitic infestation necessitating a larger gut, and increased time for enzymatic or microbial breakdown and absorption of ingested whole prey have been suggested (Eastman and Coalson, 1974; King, 1983). The linked ancestral history of cetaceans and herbivorous mammals may also explain similarities in alimentary tract length for both of these groups (Stevens and Hume, 1995), but does not apply to other marine mammal lineages. The current study indicates that metabolic demands associated with an aquatic lifestyle and with carnivory may be key factors. The length of the small intestines is a major distinguishing feature between marine and terrestrial carnivores, and is correlated with metabolic rate. A single regression describes the relationship between basal metabolic rate and total length of the small intestine for both mammalian groups (Fig. 5):

$$\text{Basal metabolic rate} = 142.5 \text{ intestinal length}^{1.20}$$

$$(n = 11 \text{ species}, r^2 = 0.83)$$

where metabolic rate is in kcal day^{-1} and intestinal length is in m. This relationship differs from that of mammalian herbivores, which shows correspondingly lower basal metabolic rates and shorter intestinal lengths (Fig. 5). Based on these differences, there appears to be a cost with carnivory that is associated with an increase in length of the small intestines. For both carnivorous and herbivorous groups, marine-living species represent the upper extremes of these relationships. Thus, an aquatic lifestyle appears to add a second influencing factor on the relationship between basal metabolic rate and intestinal length.

By maintaining a large alimentary tract, marine mammals obtain both the advantages inherent with being able to meet elevated metabolic demands and the disadvantages associated with supporting a metabolically active tissue. A large digestive tract provides an advantage for marine predators that feed on prey that is only intermittently available or patchily distributed in the environment (Gaskin, 1978). In this way, large quantities of prey can be consumed, processed and absorbed when it is suddenly available (Slijper, 1976). The processing of prey items that are high in fat content or possess chitinous exoskeletons will also be facilitated (Stevens and Hume, 1995). By enhancing assimilation efficiency, comparatively high metabolic rates can be supported, with the concomitant advantages of higher rates of sustained activity, independence from environmental temperature fluctuations, faster growth, and higher reproductive output (Konarzewski and Diamond, 1995).

Despite these advantages, there is a metabolic trade-off associated with maintaining a large digestive tract. Because the gastrointestinal tract is a metabolically intense organ in vertebrates, both in terms of protein synthesis and energy utilization, it is expensive to maintain (Stevens and Hume, 1995). Comparative tissue respiration rates and organ masses indicate a disproportionate metabolic demand by the alimentary tract, which ranks fourth in whole-organ oxygen consumption out of 14 organs examined in the rat (Schmidt-Nielsen, 1984).

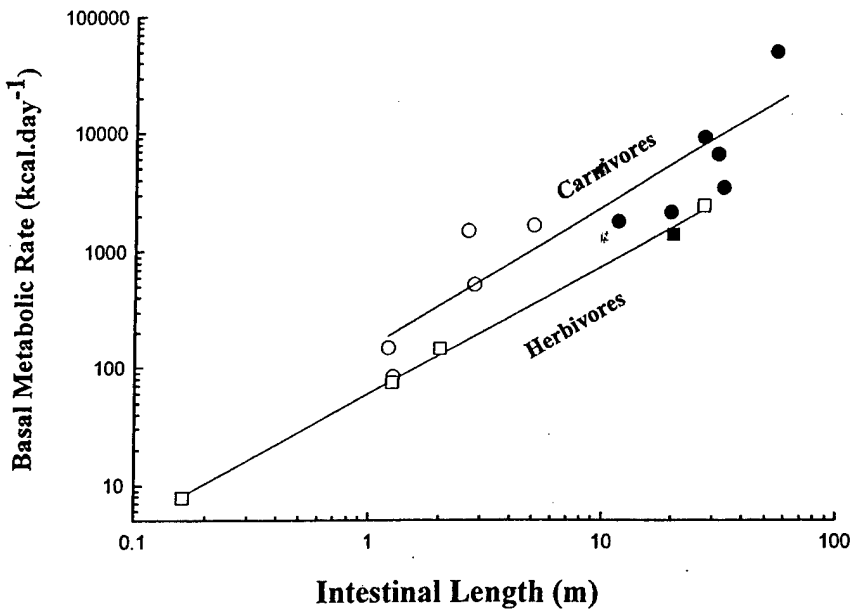

Fig. 5. Basal metabolic rate of carnivorous marine (closed circles) and terrestrial (open circles) mammals in relation to intestinal length. Each point represents the mean value for each species. The solid line for carnivores is the least squares linear regression through the data, as described in the text. Basal metabolic rates for marine mammals are from Fig. 4; intestinal lengths are from Fig. 3. Terrestrial mammal basal rates are from Brody (1945); human), Kleiber (1975); dog, cat), McNab (1986); mink), and Corts (1984, cougar); intestinal lengths are from Fig. 3. Values for representative marine (closed square) and terrestrial (open square) herbivorous mammals are provided for comparison, and include vole, woodchuck, rabbit, sheep and manatee (metabolic rates reviewed in McNab, 1988; intestinal lengths for terrestrial herbivores are from Stevens and Hume, 1995; intestinal length for the manatee is from Reynolds and Rommel, 1996). The least squares regression (solid line) for herbivores is BMR = 61.6 intestinal length$^{1.10}$ ($n = 5$ species, $r^2 = 0.99$).

Interestingly, selective redistribution of blood away from the alimentary tract during diving could reduce these costs in marine mammals, and may explain part of the variability in resting metabolic rates of surface and submerged California sea lions reported by Hurley (1996). Previous studies have demonstrated that the function of splanchnic organs varies with dive duration (Davis et al., 1983), and that blood flow is markedly reduced to the intestines during forced dives in Weddell seals (Zapol et al., 1979). In a study of seven species of polar phocid seals, Martensson et al. (1998) reported no correlation between intestinal length relative to body length and diving capacity. This would be expected if the metabolic demands of maintaining the gastrointestinal tract were reduced during submergence. Crocker et al. (1997) have suggested a trade-off between the metabolic demands of processing food and locomotion in northern elephant seals. Rather than try to simultaneously meet the energetic demands of both, elephant seals may reduce locomotor costs by drifting when increased energy is needed for processing ingested prey. Clearly, further studies examining the function of these tissues will be needed to assess differences in metabolic costs for maintaining gastrointestinal activity for marine and terrestrial predators.

In summary, the present study demonstrates that the metabolic rates of many species of carnivorous marine mammal are elevated when compared to levels for carnivorous terrestrial mammals. These elevated metabolic rates are associated with comparatively large alimentary tracts in marine mammals that are likely required for supporting the energetic demands of an aquatic lifestyle and for feeding on vertebrate and invertebrate prey. Although a large alimentary tract affords several adaptive advantages for marine mammals, it is energetically expensive to maintain. It is possible that physiological changes associated with the dive response may aid in defraying these costs during submergence, and this warrants further investigation of gastrointestinal function in marine predators.

Acknowledgements

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