Biomechanics and Energetics in Aquatic and Semiaquatic Mammals: Platypus to Whale*

Frank E. Fish[†]

Department of Biology, West Chester University, West Chester, Pennsylvania 19383

ABSTRACT

A variety of mammalian lineages have secondarily invaded the water. To locomote and thermoregulate in the aqueous medium, mammals developed a range of morphological, physiological, and behavioral adaptations. A distinct difference in the suite of adaptations, which affects energetics, is apparent between semiaquatic and fully aquatic mammals. Semiaquatic mammals swim by paddling, which is inefficient compared to the use of oscillating hydrofoils of aquatic mammals. Semiaquatic mammals swim at the water surface and experience a greater resistive force augmented by wave drag than submerged aquatic mammals. A dense, nonwettable fur insulates semiaquatic mammals, whereas aquatic mammals use a layer of blubber. The fur, while providing insulation and positive buoyancy, incurs a high energy demand for maintenance and limits diving depth. Blubber contours the body to reduce drag, is an energy reserve, and suffers no loss in buoyancy with depth. Despite the high energetic costs of a semiaquatic existence, these animals represent modern analogs of evolutionary intermediates between ancestral terrestrial mammals and their fully aquatic descendants. It is these intermediate animals that indicate which potential selection factors and mechanical constraints may have directed the evolution of more derived aquatic forms.

Introduction

It has been asked by the opponents of such views as I hold,

how, for instance, a land carnivorous animal could have been converted into one with aquatic habits; for how could the animal in its transitional state have subsisted? It would be easy to show that within the same group carnivorous animals exist having every intermediate grade between truly aquatic and strictly terrestrial habits; and as each exists by a struggle for life, it is clear that each is well adapted in its habits *to* its place in nature. (Darwin 1859)

Darwin considered two of the more vexing questions in evolution: how did aquatic mammals arise, and how did the mammals existing in the transitional state survive? From observations of mink (*Mustela vison*) and black bear (*Ursus americanus*), Darwin concluded that with acceptable energy supplies (i.e., food) these animals could exist in the intermediate state and, by natural selection, lead to more specialized aquatic forms. Recently, these questions are being answered by examination of energy budgets through the fields of ecological physiology and functional morphology (e.g., Fish et al. 1997; Hind and Gurney 1997; Pfeiffer and Culik 1998; Williams 1999). Both fields seek to identify adaptations for enhancing survival in particular environments.

With approximately 70% of the planet's surface covered by water, it is not surprising that a wide variety of mammalian lineages have secondarily invaded the aquatic environment. However, moving into the viscous medium of water, where Archimedes' principle dominates, from the less viscous, gravity-dominated terrestrial environment has presented biomechanical and energetic hurdles to these mammals (Fish 1992, 1996; Williams 1999).

Those animals in the most energetically precarious position are semiaquatic mammals. Semiaquatic mammals occupy the intermediate position between terrestrial and aquatic animals (Fish and Baudinette 1999), in which they are not specialized for either environment. Their energetic performance in each environment is limited by an anatomy and physiology that are compromises to the disparate forces experienced on land and in water. Despite the increased aquatic habits, propulsive appendages of semiaquatic mammals were modified only slightly from the weight-bearing, inverted pendular struts necessary for terrestrial locomotion (Alexander 1991; Fish 1993*b*, 1996; Thewissen and Fish 1997).

Whereas swimming by semiaquatic mammals is associated with inefficiencies and high energetic costs (Fish 1992; Williams 1999), the converse is considered true for aquatic mammals. Aquatic mammals are far removed from their terrestrial an-

cestors and as such are specialized to live and forage primarily in water. In this regard, evolution of the propulsive appendages has shaped these structures into high-efficiency hydrofoils that effect locomotion by transferring momentum to fluid surroundings. This change in limb structure, although negatively impacting an aquatic mammal's performance on land, enhanced performance in the water.

Despite these apparent differences, all lineages of aquatic mammals had terrestrial ancestors and thus underwent a semiaquatic phase (Barnes et al. 1985; Gingerich et al. 1994; Thewissen et al. 1994; Zimmer 1998). The evolution of increased aquatic habits in many mammals necessitated the evolution of adaptations that allowed aquatic mammals to optimize energy use by reduction of resistive forces, improvement in propulsive force production and efficiency, thermoregulation, and control of buoyancy (Fish 1996; Williams 1999). Because modern semiaquatic mammals are the best representations of the transitional aquatic forms (Fish 1996; Thewissen and Fish 1997), direct comparison of energetics can point to the potential selective factors and mechanical constraints that directed the evolution of more derived aquatic forms.

Diversity of Semiaquatic and Aquatic Mammals

What defines a transitional or intermediate form? This is no trivial question but an important concern in evolutionary biology (Thewissen and Fish 1997; Shipman 1998; Zimmer 1998). With regard to this discussion, what is a semiaquatic mammal? Bats can swim (Craft et al. 1958), and certain species prey on fish (Altenbach 1989; Fish et al. 1991); however, we would be hard pressed to define any member of the Chiroptera as semiaquatic. How can one recognize a truly semiaquatic species versus a terrestrial mammal that occasionally crosses bodies of water or simply falls in? With the exception of apes and giraffe, terrestrial mammals are regarded to swim instinctively (Howell 1930; Dagg and Windsor 1972; Hickman 1984).

For this discussion, modifications of morphology and locomotor modes associated with aquatic specialization will be used to separate aquatic and semiaquatic mammals. It should be noted that these modifications show a gradation associated with the terrestrial-aquatic continuum. Direct comparison of semiaquatic and aquatic mammals shows a number of factors that can influence energetic performance (Table 1).

Aquatic mammals primarily inhabit the marine environment, although the river dolphins (e.g., *Inia, Platanista*), Baikal seal *(Phoca sibirica)*, and manatee (*Trichechus*) are notable exceptions. Freshwater habitats generally are used by semiaquatic mammals. River otters *(Lutra canadenesis)* will forage in coastal marine habitats (Stenson et al. 1984), but the species is largely distributed along the rivers and lakes throughout North America. The less specialized morphology and use of freshwater habitats limit semiaquatic species to swim at the water surface and make shallow dives. Animals swimming at the surface encounter increased resistance through wave drag (Lang and Daybell 1963; Hoerner 1965; Hertel 1966; Fish 1982a; Williams 1983a, 1989). In the ocean, aquatic mammals like the sperm whale *(Physeter macrocephalus)* can dive to depths as great as 2,250 m and remain submerged for 138 min (Rice 1989). When fully submerged, drag is primarily generated from frictional forces between the body and the water (Webb 1975).

With the exception of *Hippopotamus*, semiaquatic mammals are small in size, $<10^2$ kg. The restriction in body size could be in part because of the phylogeny. Semiaquatic mammals occur in groups of small body size, although the semiaquatic representatives are generally larger than closely related terrestrial forms (Wolff and Guthrie 1985). Limits on body size are necessary because of the restricted size of many freshwater habitats. Alternatively, the marine habitat is immense enough to accommodate the largest mammal that has ever lived. While the blue whale (*Balaenoptera musculus:* >30 m long, 10^5 kg) represents the maximum size, the sea otter, *Enhydra lutris,* represents the minimum for marine mammals at 16 **kg.** Large body size is associated with mechanisms that enhance swimming performance, such as streamlined body shapes that minimize drag and propulsors that maximize thrust (Webb and De Buffrenil 1990).

Semiaquatic mammals show little streamlining, and the propulsive appendages, although larger than in their terrestrial counterparts, are relatively smaller than fully aquatic mammals (Howell 1930; Mordvinov 1976; Williams 1989; Fish 1993b; Thewissen and Fish 1997). These appendages act like paddles

Table 1: Differences between semiaquatic and aquatic mammals

Factor	Semiaquatic	Aquatic
Aquatic environment	Freshwater	Marine
Swimming position	Surface	Submerged
Maximum diving depth	Shallow	Deep (2–2,250 m)
Propulsive force	Drag	Lift
Propulsive appendages	Paddle	Hydrofoil (winglike)
Predominate resistive force	Wave drag	Frictional drag
Insulation	Fur	Blubber
Size	.01–4,500 kg	16–64,348 kg

and produce thrust using a hydrodynamically generated resistive force (Fish 1984, 1996). Highly derived aquatic mammals employ a winglike hydrofoil that is oscillated to produce thrust (Lighthill 1969; Fish et al. 1988).

The final major difference between semiaquatic and aquatic mammals that could influence their energetic performance is the type of insulation. As with their terrestrial relatives, semiaquatic mammals insulate their bodies with fur, although this fur has a higher hair density (Kenyon 1969; Sokolov 1982; Fish and Baudinette 1999). So long as the fur is of a nonwettable type (hydrophobic), it can be an effective thermal barrier in both air and water (Johansen 1962; Irving 1973). For small semiaquatic mammals, fur can provide sufficient insulation without restricting terrestrial movement because of its light weight. Blubber is used by aquatic mammals. In terms of both volume and mass, blubber is a poorer insulator than fur (Parry 1949; Hart and Fisher 1964; Irving 1973). However, a large blubber layer provides sufficient insulation, can be used as a high-energy reserve during periods of fasting, and aids in sculpting of the body for streamlining.

Physical and Mechanical Environment

Propulsion in an aquatic medium is the result of the transfer of momentum from the animal to the environment, whereas the momentum transferred from the water to the animal is responsible for resistive forces (Webb 1988). The primary resistive hydrodynamic force for steady swimming by mammals is drag. The components of drag vary in accordance with (1) flow conditions around the animal, (2) proximity to the water surface (air-water interface), and (3) the relative predominance of inertial, viscous, and gravitational forces. Flow conditions and predominant forces are determined by the size and speed of the animal in conjunction with density, ρ, and viscosity, μ. The total drag, D, for a body can be determined according to the equation:

$$D = 0.5 \times \rho \times S \times U^2 \times C_D, \qquad (1)$$

where S is the wetted surface area of the body, U is velocity, and C_D is the dimensionless drag coefficient (Webb 1975; Vogel 1994). C_D represents a way of comparing streamlining in various animals. Towing and gliding experiments showed that aquatic mammals (otariid seals, phocid seals, cetaceans) had values of C_D of 0.003–0.018, which were at least 28% lower than C_D for the semiaquatic beaver (*Castor canadensis;* Fish 1992). The sea otter, however, has a C_D of 0.006 (Williams 1989). Higher values of C_D for aquatic mammals were obtained from calculations using hydromechanical models for actively swimming animals (Webb 1975; Chopra and Kambe 1977; Fish et al. 1988; Fish 1993c, 199827). These higher values for actively swimming animals are expected because the movements of the body and

propulsors modify the water flow adjacent to the body and increase the drag (Lighthill 1971).

When animals are swimming submerged, frictional and pressure components of drag dominate (Webb 1975; Fish 1993b). Frictional drag originates from fluid viscosity, which produces shear stresses in the boundary layer (a layer of water extending out from the body to the point at which it is moving at 99% of free-stream speed; Prandtl and Tietjens 1934). The magnitude of frictional drag will depend on S and flow conditions (laminar, turbulent, or transitional) within the boundary layer (Webb 1975). For large aquatic mammals operating at high swimming speed, transition from laminar to turbulent flow conditions can occur (Gray 1936; Williams and Kooyman 1985; Fish and Hui 1991). A boundary layer with turbulent flow produces the highest frictional drag (Webb 1975).

Pressure drag arises from pressure differences in the flow outside of the boundary layer because of distortion of the flow around the body. Deflection of this outer flow due to body shape produces pressure gradients from varying flow velocities. The pressure differential from leading to trailing edges of the body is the source of the drag (Webb 1975; Vogel 1994). Streamlining minimizes drag by reducing the magnitude of the pressure gradient over the body. Increased pressure drag can occur due to interaction of the boundary layer and adverse pressure gradients resulting in separation of the boundary layer from the body. Interaction of the boundary layer and the outer flow produces a net pressure force that acts in opposition to forward motion as kinetic energy is lost in the wake. Drag is minimized when separation is avoided.

Mammals swimming at or near the water surface also experience frictional and pressure components of drag. Particularly for semiaquatic mammals, proximity to the surface incurs additional resistance from gravitational forces in production of surface waves. Kinetic energy from the animal motion is lost as it is changed into potential energy in the formation of waves (Denny 1993; Vogel 1994). This wave drag can reach a maximum of five times frictional drag (Hertel 1966). Maximum wave drag occurs when the body is just submerged at a relative depth of 0.5 of maximum body diameter (Hoerner 1965; Hertel 1966; Marchaj 1991; Vogel 1994). When towed at the surface, the drag on harbor seals (*Phoca vitulina*) was measured at 2.5 times the submerged value at the identical velocity (Williams and Kooyman 1985). Similarly, drag on mink carcasses at the water surface was seven to 10 times greater than the calculated drag when submerged (Williams 1983a). Wave drag is negated with increasing or decreasing submergence depths; that is, it becomes unimportant at depths greater than two to three times body diameter or when the animal becomes airborne (Lang and Daybell 1963; Hertel 1966).

As opposed to submerged swimming with an exponential rise in drag with increasing velocity, the relationship between drag and velocity for surface swimming is more complex. While moving at the water surface, the body of an animal will act
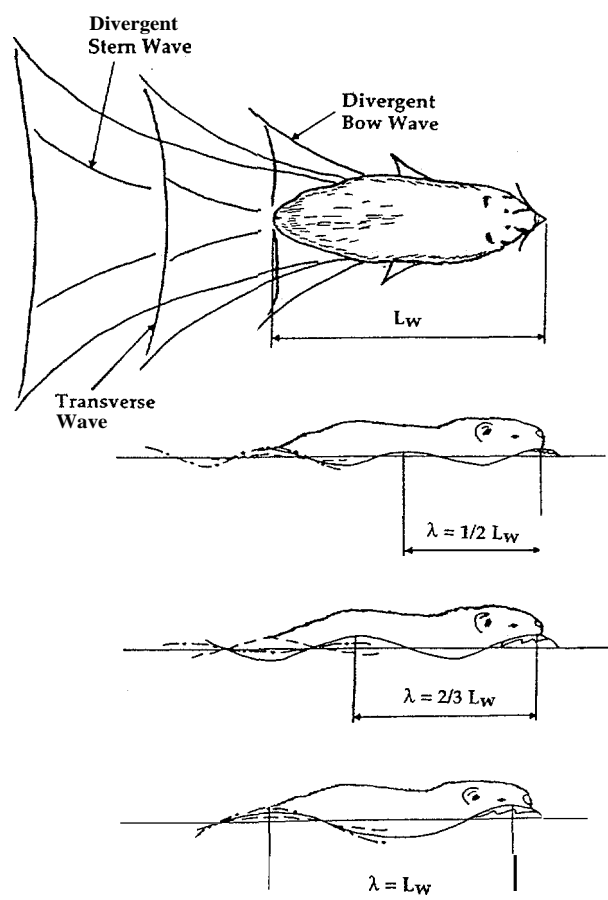
Figure 1. Wave pattern for surface-swimming semiaquatic mammal. Upper figure shows dorsal view of wave pattern with diverging and transverse wave systems generated at the bow and stern of the animal. Lower figures show lateral views of the transverse wave systems with increasing velocity. As speed increases, wavelength of the bow wave (A) increases as a fraction of the waterline length (L_w). At hull speed ($A = L_w$), the bow wave equals the L_w of the body, and the animal is effectively trapped in a wave trough, limiting higher surface-swimming speeds. The lines in the wake represent the bow wave *(solid lines)*, stern wave *(dashed lines)*, and resultant wave from the interference of the bow and stern wave *(dashed-dotted lines)*. Modified from Marchaj **(1964).**

like a displacement hull of a ship, producing two distinct systems of waves (Fig. 1): bow-wave system and stern-wave system (Taylor 1933). These systems are composed of diverging and transverse waves that each contributes half of the wave drag (Hoerner 1965).

The diverging waves from bow and stern cannot interfere with one another; however, the transverse bow waves can be superimposed on the transverse stern waves because wavelength is variable with respect to speed (Marchaj 1964; Hoerner 1965). With increasing speed, the wavelength of the bow-wave system increases and interferes with the waves generated at the stern

(Taylor 1933; Marchaj 1964). Depending on the phase relationship, the bow and stern waves can produce a positive or negative interference. Thus, the drag on a body can be exaggerated when wave crests are synchronized and can be reduced when a wave crest and trough destructively interfere. As a result, for a body moving at the surface, the drag as a function of velocity shows "humps" and "hollows" (Taylor 1933; Lang and Daybell 1963; Hoerner 1965).

Speed at the water surface is constrained by the formation of surface waves (Prange and Schmidt-Nielsen 1970; Fish 1982a; Williams 1989; Aigeldinger and Fish 1995). When the wavelength of the bow wave is equal to waterline length of the body, this effectively traps the animal in the trough of the bow wave, ultimately limiting further increases in speed (Denny 1993; Vogel 1994). To move faster, an animal would have to swim over or through the bow wave, both of which are energetically very costly. This effective speed limit for a conventional displacement hull, such as a ship or muskrat, is called the hull speed (Prange and Schmidt-Nielsen 1970). Surface-swimming animals rarely exceed hull speed (Fish 1982a; Williams 1989; Fish and Baudinette 1999) and are capable of greater speeds by submerged swimming (Williams 1989; Fish et al. 1997), porpoising (Au and Weihs 1980), and hydroplaning (Aigeldinger and Fish 1995).

Propulsive Forces **and Swimming Modes**

Thrust is the reaction force to drag for an animal swimming at a constant velocity. Thrust is generated by actively transferring momentum from the moving parts of the body (i.e., propulsors) to the water. The rate of momentum exchange between the propulsor and the water determines the amount of thrust generated (Daniel et al. 1992). The propulsors most efficiently maximize thrust by accelerating a large mass of fluid but at a low velocity (Alexander 1983). Propulsors, therefore, are large in span and area (Blake 1981; Webb 1988; Fish 1993b). Hence, an increased volume of water is accelerated during the excursion of the propulsor.

The propulsors of swimming mammals can be classified as drag-based oscillatory, lift-based oscillatory, and undulatory (Webb and Blake 1985). Oscillatory propulsion uses motions of the paired appendages (i.e., feet) or a highly modified lunate tail (i.e., flukes), whereas undulatory propulsion uses movements of the body and tail.

Drag-based oscillation occurs in semiaquatic mammals using movements of the appendages with power and recovery phases (Howell 1930; Tarasoff et al. 1972; Williams 1983a; Fish 1984, 1996). In the power stroke, thrust is generated as the foot is swept posteriorly, producing a large pressure drag oriented in the direction of motion of the body. Drag is maximized by an increase in surface area from elongation of the digits, fringe hairs on the digits, and interdigital webbing (Howell 1930; Tarasoff 1972; Mordvinov 1976; Fish 1993b; Thewissen and Fish
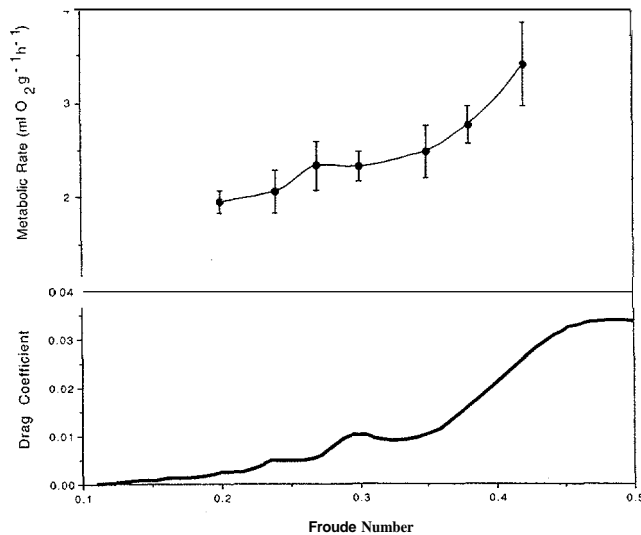
Figure 2. Comparison of trends of mean metabolic rate ($\pm$ SD) of surface-swimming *Hydromys* (*above*; Fish and Baudinette 1999) with wave drag for a model ship hull (*below*, redrawn from Hoerner 1965) with respect to Froude number (ratio of inertial to gravitational forces); Froude number $= U/(gL_w)^{1/2}$, where U is the velocity, L_w is the waterline length along the longitudinal axis of the body, and g is the gravitational acceleration, 9.8 m/s^2. The pattern of humps and hollows is dependent on Froude number. Humps occur at critical Froude number values of 0.20, 0.28, and 0.45, with hollows between these values (Taylor 1933; Hoerner 1965). Froude number of 0.45 corresponds to the hull speed.

1997). Drag generated in the recovery phase has an orientation opposite to the direction of body motion and adds to the resistance on the body. This increased drag on the foot is reduced by decreasing the area by adduction of the digits and decreasing the forward velocity of the foot (Fish 1984).

Propulsion by drag-based oscillation is produced by the motion of various combinations of the paired appendages (quadrupedal, pectoral, pelvic) either alternately or simultaneously and oriented in either the parasagittal or horizontal planes (Howell 1930; Fish 1993*b*, 1996). Movement of the appendages in the parasagittal plane is referred to as "paddling," whereas movements in the horizontal plane are "rowing."

The most highly derived aquatic mammals (i.e., Cetacea, Pinnipedia, Sirenia) swim with flippers or flukes by lift-based oscillation (Lighthill 1969; Fish 1993*b*). These propulsors produce thrust by acting as a hydrofoil (Lighthill 1969; Webb 1975, 1988; Feldkamp 1987*a*, 1987*b*; Fish 1998*a*). The oscillating hydrofoil is canted at an angle to the flow (i.e., angle of attack). A lift is produced so that its vector is inclined in the forward direction and can be resolved into thrust (Daniel et al. 1992; Vogel 1994).

To maximize lift, the propulsor is maintained at an angle of attack (<30°) throughout the stroke cycle (Fish et al. 1988; Fish

1993*c*). Angle of attack is controlled by a jointed system at the narrow base of the propulsor (Webb 1975, 1988; Fish et al. 1988). Thrust from lift is also maximized by providing the propulsor with a high aspect ratio (span^2/area) shape (Webb 1975). High aspect ratio reduces energy losses by decreasing the magnitude of the drag due to lift (Bushnell and Moore 1991). Aspect ratio for cetacean flukes is 3.2–5.4 (Fish 1998*b*), phocid hind flippers is 3.4–4.0 (Fish et al. 1988), and otariid fore flippers is 7.5–8.5 (Feldkamp 1987*b*).

For undulatory swimming, the body and tail are bent into a wave that travels backward at a velocity faster than the animal is moving forward (Webb 1988). As each section of the body accelerates laterally, it faces caudally at an angle to the mean motion of the body. Fluid adjacent to the accelerated section produces a reaction force with a component in the direction of thrust (Lighthill 1971; Webb 1988; Daniel et al. 1992).

Although most fish use undulation, the number of mammals swimming by undulatory propulsion is limited. The giant otter shrew, *Potamogale velox*, has a deep, laterally compressed tail that may be used for undulatory propulsion. The muskrat, *Ondatra zibethicus*, undulates its laterally compressed tail when paddling at the surface, but the tail accounts for only 1.4% of the entire thrust production (Fish 1982*b*, 1984). The river otter, *Lutra canadensis*, dorso ventrally undulates the body and tail in conjunction with simultaneous paddling efforts of the hind feet (Tarasoff et al. 1972; Fish 1994). Thrust produced by undulation in *Lutra* may be low compared to the paddling stroke because the tail tapers to a narrow tip. The tail tip has the largest amplitude and potentially would affect the greatest volume of water, but the tapered tip reduces momentum exchange. The beaver and the giant otter, *Pteronura brasiliensis*, have broad tails that when undulated could produce large amounts of thrust (Rue 1964; Fish 1994); whereas the sea otter, *Enhydra lutris*, with a short tail, uses undulation with the broad hind feet (Kenyon 1969; Tarasoff et al. 1972; Williams 1989).

The propulsive efficiency (thrust power/total mechanical power output) of the three swimming modes varies in accordance with the degree of aquatic specialization (Weihs and Webb 1983; Fish 1993*b*, 1996). Drag-based oscillation has the lowest propulsive efficiency (<0.33; Fish 1984, 1992). This low efficiency occurs because thrust is generated through only half of the stroke cycle (Fish 1984). Energy is lost to increased resistive drag as the foot is repositioned during the recovery phase. In addition, approximately 40%–50% of the total energy expended through the stroke is lost in acceleration of the mass of the limb and the water entrained to the foot (Fish 1993*b*). Propulsive efficiency for the drag-based oscillation is higher at low speeds, whereas the other propulsive modes have maximum efficiency at high speeds (Webb 1984; Vogel 1994).

Fish, which swim solely by undulation, exhibit a mechanical efficiency of 0.5–0.8 (Webb 1978; Vogel 1994). For mammals such as *Lutra*, the propulsive efficiency of its undulatory swimming may be less than that calculated for fish. A lower efficiency

Table 2: Cost of transport (CT) and swimming speed (U) of semiaquatic and aquatic mammals

Species	Mass (kg)	CT (J/Nm)	× Fish CT (m/s)[a]	U	Mode[b]	Depth	Reference
Semiaquatic:							
Ornithorhynchus anatinus	1.24	.506	2.4	1.0	R	Submerged	Fish et al. 1997
Castor canadensis	18.6	.360	3.4	.9	P	Submerged	Allers and Culik 1997
Hydromys chrysogaster	.73	2.631	11.1	.57	P	Surface	Fish and Baudinette 1999
Ondatra zibethicus	.65	2.179	8.9	.75	P	Surface	Fish 1982*a*
Mustela vison	.97	4.39	19.9	.75	P	Surface	Williams 1983*a*
Amblonyx cinerea	3.1	1.47	8.9	1.0	U	Submerged	Borgwardt and Culik 1999
Lutra lutra	6.2	.95	6.8	1.3	U	Submerged	Pfeiffer and Culik 1998
Enhydra lutris	19.85	.748	7.2	.8	U	Submerged	Williams 1989
E. lutris	19.85	1.281	12.3	.8	P	Surface	Williams 1989
Homo sapiens (front crawl)	69.3	1.15	15.1	.8	P	Surface	Holmér 1974
H. sapiens (breast stroke)	76.3	1.25	16.8	.6	P	Surface	Holmér 1974
H. sapiens (butterfly)	81.3	1.76	24.1	1.17	P	Surface	Holmér 1974
H. sapiens (front crawl)	70.0	1.71	22.6	1.68	P	Surface	DiPrampero 1986
Aquatic:							
Zalophus californianus	21	.235	2.3	2.0	FO	Submerged	Williams et al. 1991
Z. californianus	36.4	.385	4.3	2.0	FO	Submerged	Kruse 1975
Z. californianus	30.3	.390	4.2	1.8	FO	Submerged	Kruse 1975
Z. californianus	22.7	.245	2.4	1.8	FO	Submerged	Feldkamp 1987*b*
Z. californianus	19	.410	3.9	2.6	FO	Submerged	Feldkamp 1987*b*
Z. californianus	62	.310	4.0	1.4	FO	Submerged	Costello and Whittow 1975
Phoca groenlandica	105	.2	2.9	1.0	HO	Submerged	Britsland and Ronald 1975
P. groenlandica	105	.15	2.2	1.1	HO	Submerged	Innes 1984
P. groenlandica	105	.134	2.0	1.1	HO	Submerged	Innes 1984
P. groenlandica	62	.157	2.0	1.1	HO	Submerged	Innes 1984
P. groenlandica	66	.281	3.7	1.1	HO	Submerged	Innes 1984
Phoca hispida	59	.149	1.9	1.1	HO	Submerged	Innes 1984
P. hispida	47	.191	2.3	1.1	HO	Submerged	Innes 1984
Phoca vitulina	42.5	.203	2.4	1.0	HO	Submerged	Craig and Påsche 1980
P. vitulina	33	.367	4.0	1.4	HO	Submerged	Davis et al. 1985
P. vitulina	63	.235	3.0	1.4	HO	Submerged	Davis et al. 1985
P. vitulina	32	.367	4.0	2.2	HO	Submerged	Williams et al. 1991
Halichoerus grypus	85	.166	2.3	1.1	HO	Submerged	Innes 1984
H. grypus	70	.226	3.0	1.1	HO	Submerged	Innes 1984
H. grypus	104	.398	5.8	1.3	HO	Submerged	Fedak 1986
H. grypus	270	.23	4.3	1.3	HO	Submerged	Thompson et al. 1993
H. grypus	85	.312	4.3	1.3	HO	Submerged	Thompson et al. 1993
Tursiops truncatus	145	.132	2.1	2.1	CO	Submerged	Williams et al. 1993
Phocoena phocoena	41.5	.205	2.4	2.0	CO	Submerged	Worthy et al. 1987
Orcinus orca	5,153	.077	3.0	3.1	CO	Submerged	Kriete 1995
O. orca	2,738	.085	2.8	3.1	CO	Submerged	Kriete 1995
Eschrichtius robustus	15,000	.043	2.2	2.1	CO	Submerged	Sumich 1983
Balaenoptera acutorostrata	4,000	.026	.9	3.25	CO	Submerged	Blix and Folkow 1995

[a] Multiples of CT for salmonoid fish based on data from Brett (1964).

[b] CO = caudal oscillation. FO = fore-flipper oscillation. HO = hind-flipper oscillation. P = paddling, R = rowing, U = undulation.

would be due to the tapering structure of the tail in conjunction with the simultaneous use of paddling by the hind feet.

High-speed swimming for aquatic mammals is accomplished with lift-based thrust production (Fish et al. 1988; Fish 1992, 1996). Lift-based oscillation is associated with the radiation into pelagic habitats where steady swimming is required (Webb and de Buffrenil 1990). Because of the high lift-to-drag ratio of the propulsors and nearly continuous production of thrust, this mode is characterized by high propulsive efficiencies. By using the unsteady lifting-wing theory (Chopra and Kambe 1977), I found the propulsive efficiencies for four species of cetaceans were 0.75–0.9 (Fish 1993c, 1998b). Maximum efficiencies were achieved within the range of normal cruising speeds (0.8–1.5 body lengths/s). For pinnipeds, oscillation of the fore flippers by *Zalophus* and hind flippers by *Phoca* provide maximum efficiencies of 0.8 and 0.88, respectively (Feldkamp 1987b; Fish et al. 1988).

The magnitude of the propulsive efficiency is dependent on the design of the propulsor with the aspect ratio being the most important morphological parameter (Bose and Lien 1989; Liu and Bose 1993; Fish 1998a, 1998b). High aspect ratio reduces drag while maximizing thrust. The fin whale (*Balaenoptera physalus*), with a 6.1-aspect ratio flukes, has a higher maximum propulsive efficiency than the beluga whale (*Delphinapterus leucas*) and white-sided dolphin (*Lagenorhynchus acutus*), with aspect ratios of 3.3 and 2.7, respectively (Liu and Bose 1993).

Energetics

The energy to produce the thrust and overcome the resistance of the aquatic medium is supplied by the metabolism. The metabolic response minus the fraction of the metabolism for physiological maintenance and inefficiencies of the muscles and transmission of force is a reflection of the mechanical forces encountered during swimming. The metabolism of swimming mammals has been measured through oxygen consumption, respiratory frequency, and heart rate (Fish 1982b; Sumich 1983; Williams 1983a; T. M. Williams et al. 1992; Kriete 1995). Each method uses a variety of assumptions, although the former is the most straightforward. In addition, metabolic studies have used animals swimming in open water (Sumich 1983; T. M. Williams et al. 1992), circular pools (Kruse 1975; Markussen et al. 1992), and flumes (Fish 1982a; Williams 1983a, 1989; Davis et al. 1985; Feldkamp 1987b; Allers and Culik 1997; Fish et al. 1997; Pfeiffer and Culik 1998; Fish and Baudinette 1999).

As physical work load due to hydrodynamic resistance increases directly with swimming velocity, the metabolic work performed by a swimming animal should increase similarly with speed. The drag increases with the velocity (eq. [1]), and the power output increases with U^3 (power = force × velocity). The metabolic rate, representing the power input, should increase curvilinearly with increasing velocity according to the power function (i.e., $y = ax^b$) with an exponent $b > 1$ (Videler

1993). Studies of submerged, swimming mammals showed this trend for metabolism (Holmér 1972; Kruse 1975; Davis et al. 1985; Feldkamp 1987b; Williams et al. 1991; Kriete 1995; Hind and Gurney 1997; Pfeiffer and Culik 1998; Borgwardt and Culik 1999).

For semiaquatic mammals swimming at the surface, the dominant component of drag (wave drag) does not increase as a simple power function relationship with velocity as discussed above. The relationship between wave drag and velocity is described with a polynomial function (Hoerner 1965). For surface swimming by the Australian water rat, *Hydromys chrysogaster*, the increase in metabolic rate with velocity was reminiscent of the complex pattern of the humps and hollows for drag on bodies at the surface rather than the simple power function of submerged bodies (Fig. 2; Fish and Baudinette 1999). Thus, animals could reduce the energy cost of surface swimming by choosing velocity in which destructive interference between bow and stern waves would occur.

To standardize the metabolic response for comparison of the large ranges of body sizes and swimming speeds displayed by mammals, aerobic efficiency and cost of transport (CT) are used. Each represents an efficiency by which the metabolic power input is converted to thrust production (Tucker 1970, 1975; Schmidt-Nielsen 1972; Williams 1987; Fish 1992). Both aerobic efficiency and CT assume that the metabolic rate is aerobic with little or no contribution for anaerobic mechanisms.

Aerobic efficiency is calculated as the ratio of the aerobically supplied power input to the thrust power output (=drag power output). The power output is determined from hydrodynamic models based on swimming kinematics (Fish 1984) or from drag determinations based on towing and gliding animals (Williams 1983a, 1989; Feldkamp 1987b). This latter technique can produce an overestimate of efficiency because the drag will be larger for actively swimming animals compared to rigid bodies (Lighthill 1971).

In general, aquatic mammals have lower aerobic efficiencies than semiaquatic mammals (Fish 1992, 1996). Aerobic efficiencies for *Enhydra*, *Mustela*, and *Ondatra* were 0.021, 0.014, and 0.045, respectively (Williams 1983a, 1989; Fish 1984). Aquatic mammals, such as *Zalophus* and *Phoca*, have efficiencies of 0.15–0.30 at high and routine swimming speeds (Williams and Kooyman 1985; Feldkamp 1987b; Williams et al. 1991). These higher values reflect the greater efficiency of the lift-based propulsion versus drag-based propulsion (Fish 1996).

Analysis of aerobic efficiency has been limited because energetic studies of locomotion rarely examined both metabolic power input and mechanical power output. Examination of the CT represents an approach whereby locomotor energetics can be compared without consideration of power output (Videler 1993). CT is defined as the metabolic energy required to transport a unit mass a unit distance and is calculated by dividing the mass-specific metabolic rate by the swimming velocity (Fish
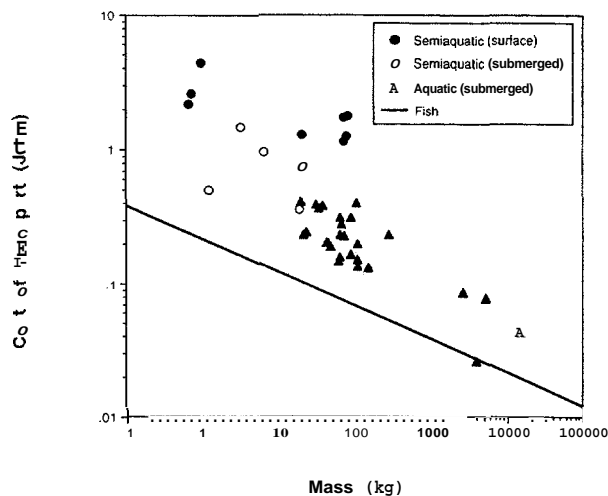
Figure 3. Minimum cost of transport (CT$_{min}$) as a function of body mass for semiaquatic mammals swimming submerged and at the surface and aquatic mammals swimming submerged. Solid line represents the extrapolated line for CT$_{min}$ of fish according to the equation CT $= 2.15M^{-0.25}/9.8$ (Williams 1999). See Table 2 for data.

1992). CT is inversely proportional to the efficiency (Tucker 1970). CT is calculated as

$$CT = MR(M \times g \times U)^{-1}, \qquad (2)$$

where MR is the metabolic rate J/s, M is body mass in kg, g is the gravitational acceleration of 9.8 m/s^2, and U is velocity in m/s (Videler and Nolet 1990). The units of CT are J/Nm, which makes CT dimensionless. For swimming, CT typically displays a U-shaped curve where it reaches a minimum value within the midrange of velocities (Williams 1987).

The minimum CT (CT$_{min}$) is the most efficient and is considered to occur at the velocity in which the animal can cover the largest distance for the smallest energy cost. Examination of CT$_{min}$ between semiaquatic and aquatic mammals provides a "fair comparison" for interpretation of differences in locomotor energetics (Videler 1993). Furthermore, comparisons of CT$_{min}$ values are made with salmonid fish of equivalent size (Williams 1999), based on data from Brett (1964). Fish have the lowest CT$_{min}$ for any vertebrate (Tucker 1970, 1975; Schmidt-Nielsen 1972; Videler 1993). The data for CT$_{min}$ of semiaquatic and aquatic mammals is displayed in Table 2. Although not considered a semiaquatic mammal, humans *(Homo sapiens)* are listed in Table 2. In most cases, CT$_{min}$ was determined from animals over a range of velocities. However, some measurements were taken at a single speed chosen by the animal and assumed to represent the velocity at which CT$_{min}$ occurred. The decrease in CT$_{min}$ with increasing body mass is believed to be primarily the result of higher optimum swimming speeds of large animals (Videler and Nolet 1990).

When CT$_{min}$ is examined, a distinct separation is apparent between surface-swimming semiaquatic mammals and semiaquatic and aquatic mammals swimming submerged (Fig. 3). Semiaquatic mammals paddling on the surface have high CT$_{min}$ of nine to 24 times the value predicted for fish due to the inefficiency of their propulsive system and drag penalty from wave formation (Fish 1982a, 1992, 1996; Williams 1983a, 1993b, 1989, 1999; Baudinette and Gill 1985; Videler and Nolet 1990). The mink has the highest CT$_{min}$ for any mammalian swimmer. Mink use a quadrupedal paddling mode that is considered primitive and inefficient due to active use of a greater muscle mass compared to hind-limb bipedal paddling (Williams 1983a; Fish 1992, 1993b, 1996). Submerged swimmers have CT$_{min}$ values 0.94 to nine times the predicted value for fish. Aquatic and semiaquatic mammals are able to reduce the high energy cost of wave drag by swimming submerged (Williams 1989; Fish 1996). Sea otters swimming submerged have an oxygen consumption 41% lower than when surface swimming (Williams 1989). The locomotor strategy of submerged swimming can result in increased efficiency by reduction of drag. Aquatic mammals are adapted for using this strategy by swimming for prolonged periods below the surface. To prevent increased energy cost when coming to the surface to breathe, these animals limit such times and quickly ventilate the lungs before submerging. Free-ranging dolphins ventilate in 0.38 s (Hui 1989). A variation on this strategy is to prolong ventilation time while reducing drag by porpoising (**Au** and Weihs 1980; Hui 1987, 1989; Williams 1987; Fish and Hui 1991).

Specialized lift-based swimming modes that use oscillation
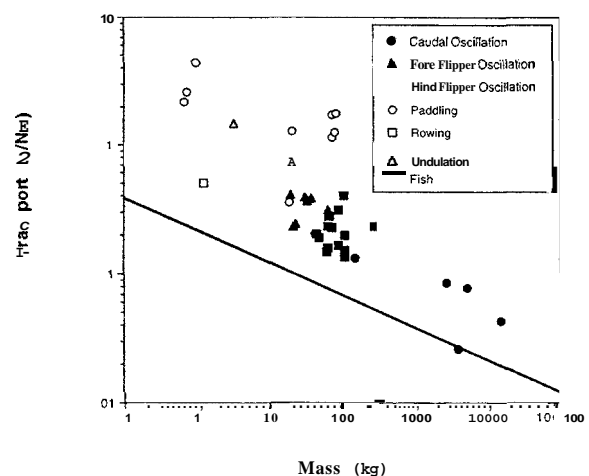

Figure 4. Minimum cost of transport (CT$_{min}$) as a function of body mass for different swimming modes used by mammals. Generally, paddling is the most inefficient means of swimming, whereas oscillation of a hydrofoil is the most efficient with the lowest CT$_{min}$. Solid line represents the extrapolated line for CT$_{min}$ of fish according to the equation CT $= 2.15M^{-0.25}/9.8$ (Williams 1999). See Table 2 for data.
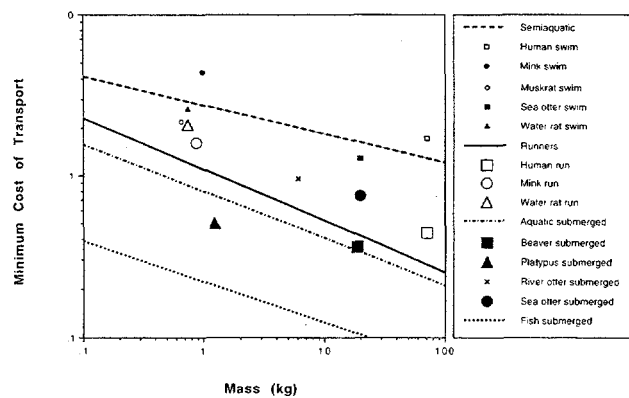
Figure 5. Minimum cost of transport (CT_{min}) versus body mass. Symbols represent CT_{min} values for paddling semiaquatic and terrestrial mammals when surface swimming, CT_{min} values for running by semiaquatic and terrestrial mammals, and CT_{min} values for submerged swimming by semiaquatic mammals. Data from Fish (1982a), Williams (1983a, 1993b, 1989), DiPrampero (1986), Allers and Culik (1997), Fish et al. (1997), Pfeiffer and Culik (1998), and Fish and Baudinette (1999). Lines represent the extrapolated CT_{min} for semiaquatic paddlers ($CT = 26.81M^{-0.18}/9.8$), runners ($CT = 10.7M^{-0.32}/9.8$), marine mammals swimming submerged ($CT = 7.79M^{-0.29}/9.8$), and submerged swimming fish ($CT = 2.15M^{-0.25}/9.8$; Williams 1999).

of flippers or flukes have low CT_{min} for aquatic mammals, whereas paddling has the highest CT_{min} and undulation is intermediate (Fig. 4). It is surprising, therefore, that the beaver and the platypus *(Ornithorhynchus anatinus)*, which swim by paddling and rowing, respectively, should have low values of CT_{min}. CT_{min} for the beaver and the platypus are, respectively, **3.4** and 2.4 times greater than fish CT_{min}, which are within the range for highly derived aquatic mammals.

Low CT_{min} for beaver and platypus may be a function of their swimming modes. The beaver swims underwater with simultaneous strokes of the hind feet in conjunction with undulations of the broad tail (Rue 1964; Allers and Culik 1997). The combination of propulsors could permit enhanced thrust production and propulsive efficiency. For the platypus, the rowing represents a drag-based mode with its associated inefficiencies (Fish 1992, 1996; Fish et al. 1997). However, the kinematics of the rowing mode are different from paddling (Fish 1984) and show similarities with more derived lift-based pectoral oscillation (Feldkamp 1987a). I argued that the platypus represents a possible modern analog to an intermediate swimming mode between drag-based and lift-based pectoral oscillation (Fish 1996).

Lowered CT_{min} for the platypus may be due to a depressed metabolism (Fish et al. 1997). The platypus maintains a resting metabolic rate in water 37%−54% lower than eutherian mammals (Grant and Dawson 1978). Submerged swimming by platypus and other mammals also produces pronounced bradycardia with an associated hypometabolism (Castellini 1988;

Williams et al. 1991; Butler and Jones 1997). Reduced maintenance costs during submerged swimming would decrease total swimming costs.

Williams (1999) has asserted that the maintenance costs of semiaquatic and aquatic mammals is higher than for their terrestrial counterparts. Examination of the resting and active metabolic rates of semiaquatic and aquatic mammals showed that, when maintenance costs were omitted, giving a net CT, aquatic mammals have similar locomotor costs with fish. Because fish and aquatic mammals use the same high-efficiency swimming modes, the implication is that mammals have a large component of their total locomotor budget devoted to maintenance of endothermy. The maintenance costs of dolphins, pinnipeds, and sea otters is 22%−77% of the total CT (Williams 1999). In addition, the similarity of locomotor cost of aquatic mammals with fish, which have the lowest CT among vertebrates, indicates that these mammalian specialists have reached an optimum in terms of energetic performance (Williams 1999). Recently, Alexander (1999) validated Williams (1999) conclusions by analyzing the mechanical power for swimming. As the mechanical power of moving through water at a velocity U **is** proportional to U^3, the metabolic rate is $R + kU^3$, where R is the resting rate and k is a constant. The cost of locomotion is $(R + kU^3)/U$, and the cost is minimal at $U = (R/2k)^{0.33}$. A high R would give a high U, with an associated increased locomotor cost (Alexander 1999).

CT for aquatic mammals is similar to the CT for running by terrestrial mammals (Williams 1999). However, CTs for these locomotor specialists are lower than for semiaquatic mammals (Fig. 5) as a consequence of the compromise between move-
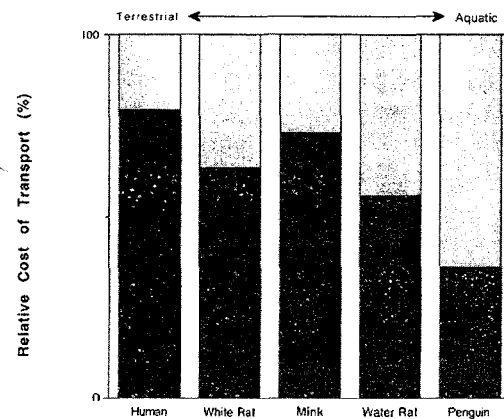

Figure 6. Relative cost of transport (CT) for running and swimming of terrestrial (human, mink, rat; Taylor et al. 1970; Holmér and Åstrand 1972; Williams 1983a, 1983b; DiPrampero 1986; Benthem et al. 1994), semiaquatic (water rat; Fish and Baudinette 1999), and aquatic animals (penguin; Pinshow et al. 1977; Baudinette and Gill 1985). With increasing aquatic adaptation, there is a reversal in the magnitude of CT between swimming and running.
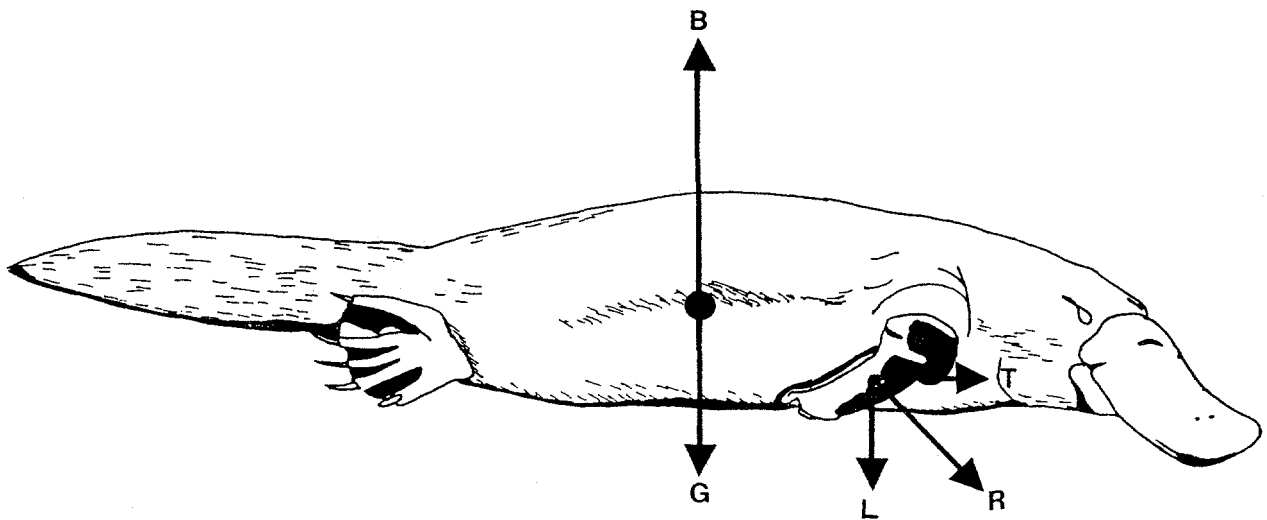
Figure 7. Submerged swimming by a rowing platypus indicating components of the hydrodynamic force *(R)* generated by posterior sweep of forefoot. Anteriorly directed component supplies the thrust *(T)*, whereas the dorsally oriented negative lift *(L)* counters the positive buoyancy *(B)*, which is opposed to the force of gravity (G).

ment on land and in water (Fish 1982*a*, 1992, 1996; Williams 1983*a*, 1989, 1999; Fish and Baudinette 1999). Williams (1999) considered that passage through this semiaquatic state by the ancestors of aquatic mammals represented an "energetic hurdle." To vault this hurdle, semiaquatic mammals would have to gain a selective advantage. Indeed, movement into water would lower predation pressures, open up unexploited food resources, and limit competition. Compared to the bulk of mammalian species, semiaquatic mammals comprise only a small percentage. On the entire continent of Australia, the platypus and the Australian water rat are the only semiaquatic mammals. As the only aquatic predators (Troughton 1941; Grant 1989), this monotreme and rodent exploited an energetically rich niche left vacant by the endemic marsupials.

Whereas both aquatic and terrestrial mammals are considered to have maximized energetic efficiency during locomotion (Williams 1999), the influence of conflicting forces incurs energetic trade-offs on mammals that operate in both terrestrial and aquatic regimes. The expected consequence of these trade-offs for semiaquatic mammals would be variable energetic effectiveness associated with the degree of adaptation to either environment (Fish and Baudinette 1999). I advised that studies on the locomotor energetics of semiaquatic animals should involve direct comparison of terrestrial and aquatic performance (Fish 1992). Unfortunately, there is a paucity of direct comparisons of locomotor energetics between running and swimming for semiaquatic species. Only studies on the Australian water rat (Fish and Baudinette 1999) and mink (Williams 1983*a*, 1983*b*) were performed in such a manner. The only other mammals for which comparative data for running

and swimming are available are humans (Holmér and Åstrand 1972; DiPrampero 1986) and white rats *(Rattus norvegicus;* Taylor et al. 1970; Benthem et al. 1994).

Comparison of relative CT (percentage of combined CT for running and swimming) from the terrestrial mammals to aquatic mammals indicates that the difference in CT between swimming and running is low for the semiaquatic water rat (Fig. 6; Fish and Baudinette 1999). Terrestrial animals have high CT values for swimming relative to their CT for running. Humans, white rats, and mink have swimming CT approximately 1.8 to four times greater than running CT (Taylor et al. 1970; Williams 1983*a*, 1983*b*; DiPrampero 1986; Benthem et al. 1994). The aquatic penguin can move on land with a bipedal waddling gait that is 1.8 times the energy cost of swimming (Pinshow et al. 1977; Baudinette and Gill 1985; Fish and Baudinette 1999). The sea lion, *Zalophus,* has a metabolic cost for swimming that is less than for comparatively sized mammalian runners at the same speeds (Feldkamp 1987*b*). The reversal of CT from running to swimming for more aquatic animals coincides with a suite of adaptations that enhance aquatic locomotion. However, the intermediate position of semiaquatic mammals results in greater locomotor costs due to their inability to specialize in either environment.

Buoyancy, Blubber, and Bubbles

The evolution from a terrestrial lifestyle to a fully aquatic existence in mammals required the development of buoyancy control mechanisms for stabilization in water (Stein 1989; Fish and Stein 1991; Fish 1993*a*). Buoyancy control has major im-

PELVIC
OSCILLATION

CAUDAL
OSCILLATION

PECTORAL
OSCILLATION

LATERAL
UNDULATION

DORSOVENTRAL
UNDULATION

ALTERNATE
PELVIC
ROWING

SIMULTANEOUS
PELVIC
PADDLING

PECTORAL
ROWING

ALTERNATE
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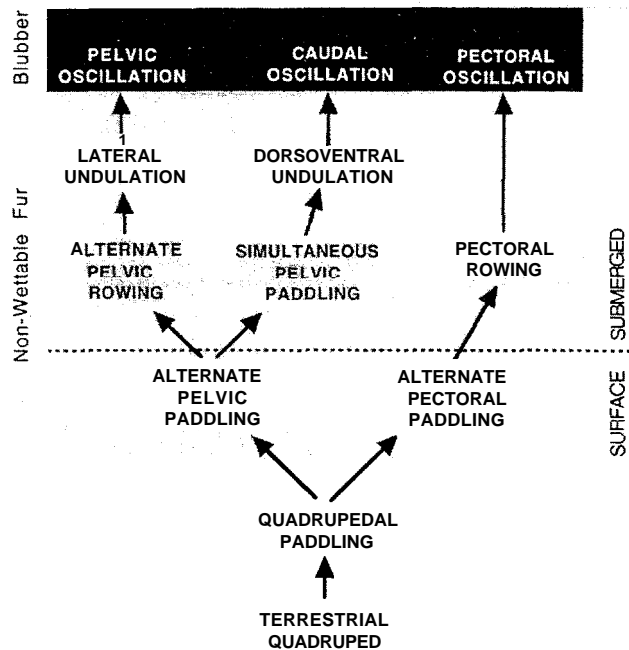PADDLING

QUADRUPEDAL
PADDLING

TERRESTRIAL
QUADRUPED

Figure 8. Model for sequence of swimming mode transitions. Surface-swimming mammals use alternate paddling modes and possess non-wettable fur *(gray),* which provides positive buoyancy. With a shift to submerged swimming, semiaquatic mammals adopted swimming modes that increased performance and countered the buoyancy of the fur. Increased time in the water coincided with the evolution of highly efficient lift-based swimming modes using oscillating hydrofoils and replacement of fur with blubber *(black)* as a means of thermal protection and control of buoyancy with deeper diving.

plications on locomotor energetics with respect to the ability to float at the water surface and dive and surface easily (Johansen 1962). Such activities are associated with foraging and escaping predation. For semiaquatic and aquatic mammals, a distinct division exists in use of fur and blubber for buoyancy control. This division is associated also with the insulatory capacity of fur and blubber in the different environments in which they operate.

Although diving periodically when foraging, semiaquatic mammals operate primarily at the water surface. Possession of large, low-density, air-filled spaces provides positive buoyancy and decreases the effort needed to float. Sea otters maintain buoyancy in part with lungs that are two times larger than that of other similarly sized mammals (Kooyman 1973; Tarasoff and Kooyman 1973). The nonwettable fur of the sea otter is extremely dense (1,008–1,573 hairs/mm²) entrapping a large volume of air for buoyancy (Kenyon 1969; Tarasoff 1974; T. D. Williams et al. 1992). The density of hairs in the pelage of semiaquatic mammals is high in comparison with terrestrial and aquatic mammals (Tarasoff 1974; Sokolov 1982; Fish and Baudinette 1999). The volume of air entrapped in the fur of

muskrats represents 21.5% of the animal's total volume and lowers its specific weight to 0.79 (Johansen 1962).

Although the positive buoyancy afforded by fur will reduce energy costs at the surface, buoyancy is a major determinant of locomotor costs when diving (Loworn et al. 1991). Buoyancy has a higher cost associated with it compared to drag (Loworn and Jones 1991). To submerge, a positively buoyant animal can expend at least 95% of its total mechanical energy to work against the buoyant force (Stephenson et al. 1989). The buoyancy of a diving sea otter can be 20 times greater than the drag on the body (Loworn and Jones 1991). Semiaquatic mammals use hydrodynamically generated forces to overcome buoyancy (Alexander 1990; Taylor 1994). Muskrats and platypuses adopt rowing as the submerged propulsive mode (Mizelle 1935; Howell 1937; Fish et al. 1997) and can generate a downward force to oppose positive buoyancy (Fig. 7).

As depth increases, the air in the lungs and fur will compress reducing buoyancy. When the buoyant force matches the weight of water displaced by the body, neutral buoyancy is achieved and the animal does not sink or rise to the surface. At this depth, the hydrodynamic cost of overcoming buoyancy is zero. Below a depth where neutral buoyancy is achieved, a diving animal will have to work harder to ascend or keep from sinking. This may limit the operating depth for semiaquatic mammals. The deepest semiaquatic diver is the sea otter, which was reported to descend to a maximum depth of 97 m, although most foraging dives are no deeper than 55 m (Kenyon 1969, 1981).

The overall cost to use fur in water is high. Although fur has exceptional insulative properties in air, which is beneficial to the terrestrial component of a semiaquatic existence, insulation by fur is reduced in water (Scholander et al. 1950; Johansen 1962; Frisch et al. 1974; Morrison et al. 1974; Doncaster et al. 1990). Insulatory reduction is attributed to water infiltration and reduction of the thermal gradient due to compression of the fur by the surrounding water. Compression of air in fur with increasing depth also limits its effectiveness as a thermal barrier. Maintenance of the air layer requires a large fraction of the daily energy budget devoted to grooming (Kenyon 1969; Williams 1989).

Blubber offers a structure for aquatic mammals that, compared to fur, requires lower maintenance costs, is not prone to fouling, is an effective thermal barrier in water, can be used as an energy reserve, facilitates streamlining, has springlike properties to reduce locomotor effort, and acts to provide buoyancy (Parry 1949; Scholander et al. 1950; Lang 1966; Kooyman 1973; Brodie 1975; Fish 1993b; Loughlin 1994; Pabst 1996).

Buoyancy from blubber is not depth sensitive. The lipid composition of blubber makes it essentially incompressible relative to air but not as buoyant (Loworn and Jones 1991). Without large lungs (Kooyman 1973; Tarasoff and Kooyman 1973), aquatic mammals offset the high density of the body tissues (i.e., bone, muscle) with a thick layer of blubber. Approximately

20%–30% of the total mass of marine mammals is blubber, providing higher buoyancy than terrestrial mammals (Kooyman 1973). Exhalation before diving by marine mammals has been considered a mechanism to prevent decompression sickness; however, this behavior may effectively reduce buoyancy to decrease the energy cost of swimming during the initial descent (Kooyman 1973). When diving deeply (>20 m), buoyancy is primarily a function of the blubber and hydrodynamic mechanisms because of lung collapse (Ridgway et al. 1969; Ridgway and Howard 1979).

Buoyancy in aquatic mammals plays a significant role in the energetics of diving. By allowing the body to be neutrally or slightly negatively buoyant, an animal foraging on the bottom can conserve its oxygen reserves and increase its dive time. Increased bottom time allows for maximizing energy intake (Kramer 1988; Thompson et al. 1993). During deep dives, marine mammals can reduce energy costs of transiting to the bottom by using intermittent swimming behaviors (Williams et al. 1996). Diving dolphins use gliding to reduce locomotor energy costs when they are negatively buoyant during descent and positively buoyant during ascent (Skrovan et al. 1999).

Summary

The evolution of increased aquatic habits lead through a number of transitional stages and parallel pathways with regard to swimming performance and buoyancy control (Fig. 8; Fish 1996). To accommodate their amphibious habits, semiaquatic mammals retained use of their limbs for terrestrial locomotion with only a slight modification for swimming. This limited semiaquatic mammals to swimming using drag-based paddling modes. These modes, although inefficient, are effective at the water surface. With increasing adaptation for movement in water, the energetic cost of locomotion on land became more expensive than movement in water. The need for a lightweight insulation that functioned in both air and water and increased buoyancy resulted in the development of nonwettable fur. As semiaquatic mammals became more adept at foraging beneath the water surface, new propulsive modes were used to increase performance (i.e., reduce energy cost, increase speed) while working against the positive buoyancy of the fur. The high energy costs associated with greater maintenance costs, swimming at the water surface, work against positive buoyancy when diving, and inefficient swimming modes represented an "energetic hurdle" to the evolution of full aquatic mammals (Williams 1999). The shift to high-efficiency, lift-based propulsive modes and use of blubber coincided with greater time in the water and increased foraging depth by aquatic mammals.

Acknowledgments

Literature Cited

Aigeldinger T.L. and F.E. Fish. 1995. Hydroplaning by ducklings: overcoming limitations to swimming at the water surface. J Exp Biol 198:1567–1574.

Alexander R.M. 1983. Animal Mechanics. Blackwell Scientific, Oxford.

———. 1990. Size, speed and buoyancy adaptations in aquatic animals. Am Zool 30:189–196.

———. 1991. Energy-saving mechanisms in walking and running. J Exp Biol 160:55–69.

———. 1999. One price to run, swim or fly? Nature 397: 651–653.

Allers D. and B.M. Culik. 1997. Energy requirements of beavers (Castor canadensis) swimming underwater. Physiol Zool 70: 456–463.

Altenbach J.S. 1989. Prey capture by the fishing bats Noctilio leporinus and Myotis vivesi. J Mammal 70:421–424.

Au D. and D. Weihs. 1980. At high speeds dolphins save energy by leaping. Nature 284:548–550.

Barnes L.G., D.P. Domning, and C.E. Ray. 1985. Status of studies on fossil marine mammals. Mar Mamm Sci 1:15–53.

Baudinette R.V. and P. Gill. 1985. The energetics of flying and paddling in water: locomotion in penguins and ducks. J Comp Physiol 155B:373–380.

Benthem L., J.W. Bolhuis, J. van der Leest, A.B. Steffens, J.P. Zock, and W.G. Zijlstra. 1994. Methods for measurement of energy expenditure and substrate concentrations in swimming rats. Physiol Behav 56:151–159.

Blake R.W. 1981. Influence of pectoral fin shape on thrust and drag in labriform locomotion. J Zool (Lond) 194:53–66.

Blix A.S. and L.P. Folkow. 1995. Daily energy expenditure in free living minke whales. Acta Physiol Scand 153:61–66.

Borgwardt N. and B.M. Culik. 1999. Asian small-clawed otters: resting and swimming metabolic rates. J Comp Physiol 169B: 100–106.

Bose N. and J. Lien. 1989. Propulsion of a fin whale (Balaenoptera physalus): why the fin whale is a fast swimmer. Proc R Soc Lond B Biol Sci 237:175–200.

Brett J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Board Can 21:1183–1226.

Brodie P.F. 1975. Cetacean energetics, an overview of intraspecific size variation. Ecology 56:152–161.

Bushnell D.M. and K.J. Moore. 1991. Drag reduction in nature. Annu Rev Fluid Mech 23:65–79.

Butler P.J. and D.R. Jones. 1997. Physiology of diving of birds and mammals. Physiol Rev 77:837–899.

Castellini M.A. 1988. Visualizing metabolic transitions in

aquatic mammals: does apnea plus swimming equal "diving"? Can J Zool 66:40–44.

Chopra M.G. and T. Kambe. 1977. Hydrodynamics of lunate-tail swimming propulsion. 2. J Fluid Mech 79:49–69.

Costello R.R. and G.C. Whittow. 1975. Oxygen cost of swimming in a trained California sea lion. Comp Biochem Physiol 50:645–647.

Craft T.J., M.I. Edmunson, and R. Agee. 1958. A comparative study of the mechanics of flying and swimming in some common brown bats. Ohio J Sci 58:245–249.

Craig A.B., Jr. and A. Påsche. 1980. Respiratory physiology of freely diving harbor seals (Phocu vitulina). Physiol Zool 53: 419–432.

Dagg A.I. and D.E. Windsor. 1972. Swimming in northern terrestrial mammals. Can J Zool 50:117–130.

Daniel T.L., C. Jordon, and D. Grunbaum. 1992. Hydromechanics of swimming. Pp. 17-49 in R.M. Alexander, ed. Advances in Comparative and Environmental Physiology. Vol. 2. Springer, Berlin.

Darwin C. 1859. On the Origin of Species by Means of Natural Selection. John Murray, London.

Davis R.W., T.M. Williams, and G.L. Kooyman. 1985. Swimming metabolism of yearling and adult harbor seals Phoca vitulina. Physiol Zool 58:590–596.

Denny M.W. 1993. Air and Water. Princeton University Press, Princeton, N.J.

DiPrampero P.E. 1986. The energy cost of human locomotion on land and in water. Int J Sports Med 7:55–72.

Doncaster C.P., E. Dumonteil, H. Barre, and P. Jouventin. 1990. Temperature regulation of young coypus (Myocastor coypus) in air and water. Am J Physiol 259:R1220–R1227.

Fedak M.A. 1986. Diving and exercise in seals: a benthic perspective. Pp. 11–32 in A. Brubakk, J.W. Kanwisher, and G. Sundnes, eds. Diving in Animals and Man. Kongsvold Symposium. Royal Norwegian Society of Sciences and Letters, Trondheim.

Feldkamp S.D. 1987a. Foreflipper propulsion in the California sea lion, Zalophus californianus. J Zool (Lond) 212:43–57.

———. 1987b. Swimming in the California sea lion: morphometrics, drag and energetics. J Exp Biol 131:117–135.

Fish F.E. 1982a. Aerobic energetics of surface swimming in the muskrat Ondatra zibethicus. Physiol Zool 55:180–189.

———. 1982b. Function of the compressed tail of surface swimming muskrats (Ondatra zibethicus). J Mammal 63: 591–597.

———. 1984. Mechanics, power output and efficiency of the swimming muskrat (Ondatra zibethicus). J Exp Biol 110: 183–201.

———. 1992. Aquatic locomotion. Pp. 34–63 in T.E. Tomasi and T.H. Horton, eds. Mammalian Energetics: Interdisciplinary Views of Metabolism and Reproduction. Cornell University Press, Ithaca, N.Y.

———. 1993a. Comparison of swimming kinematics between terrestrial and semiaquatic opossums. J Mammal 74:275–284.

———. 1993b. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. Aust J Zool 42:79–101.

———. 1993c. Power output and propulsive efficiency of swimming bottlenose dolphins (Tursiops truncatus). J Exp Biol 185:179–193.

———. 1994. Association of propulsive swimming mode with behavior in river otters (Lutra canadensis). J Mammal 75: 989–997.

———. 1996. Transitions from drag-based to lift-based propulsion in mammalian swimming. Am Zool 36:628–641.

———. 1998a. Biomechanical perspectives on the origin of cetacean flukes. Pp. 303–324 in J.G.M. Thewissen, ed. The Emergence of Whales. Plenum, New York.

———. 1998b. Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological correlates with swimming performance. J Exp Biol 201:2867–2877.

Fish F.E. and R.V. Baudinette. 1999. Energetics of locomotion by the Australian water rat (Hydromys chrysogaster): comparison of swimming and running in a semiaquatic mammal. J Exp Biol 202:353–363.

Fish F.E., R.V. Baudinette, P. Frappell, and M. Sarre. 1997. Energetics of swimming by the platypus (Ornithorhynckus anatinus): metabolic effort associated with rowing. J Exp Biol 200:2647–2652.

Fish F.E., B.R. Blood, and B.D. Clark. 1991. Hydrodynamics of the feet of fish-catching bats: influence of the water surface on drag and morphological design. J Exp Zool 258:164–173.

Fish F.E. and C.A. Hui. 1991. Dolphin swimming: a review. Mammal Rev 21:181–195.

Fish F.E., S. Innes, and K. Ronald. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. J Exp Biol 137:157–173.

Fish F.E. and B.R. Stein. 1991. Functional correlates of differences in bone density among terrestrial and aquatic genera in the family Mustelidae (Mammalia). Zoomorphology 110: 339–345.

Frisch J., N.A. Britsland, and J. Krog. 1974. Insulation of furs in water. Comp Biochem Physiol 47A:403–410.

Gingerich P.D., S.M. Raza, M. Arif, M. Anwar, and X. Zhou. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. Science 368:844–847.

Grant T.R. 1989. The Platypus. New South Wales University Press, Kensington.

Grant T.R. and T.J. Dawson. 1978. Temperature regulation in the platypus, Ornithorhynchus anatinus: production and loss of metabolic heat in air and water. Physiol Zool 51:315–332.

Gray J. 1936. Studies in animal locomotion. VI. The propulsive powers of the dolphin. J Exp Biol 13:192–199.

Hart J.S. and H.D. Fisher. 1964. The question of adaptations

to polar environments in marine mammals. Fed Proc 23: 1207–1214.

Hertel H. 1966. Structure, Form, Movement. Reinhold, New York.

Hickman G.C. 1984. Swimming ability of talpid moles, with particular reference to the semi-aquatic *Condylura cristata*. Mammalia 48:505–513.

Hind A.T. and W.S.C. Gurney. 1997. The metabolic cost of swimming in marine homeotherms. J Exp Biol 200:531–542.

Hoerner S.F. 1965. Fluid-Dynamic Drag. S.F. Hoerner, Brick Town, N.J.

Holmér I. 1972. Oxygen uptake during swimming in man. J Appl Physiol 33:502–509.

———. 1974. Energy cost of arm stroke, leg kick, and the whole stroke in competitive swimming styles. Eur J Appl Physiol 33:105–118.

Holmér I. and P.-O. Åstrand. 1972. Swimming training and maximal oxygen uptake. J Appl Physiol 33:510–513.

Howell A.B. 1930. Aquatic Mammals. Charles C. Thomas, Springfield, Ill.

———. 1937. The swimming mechanism of the platypus. J Mammal 18:217–222.

Hui C.A. 1987. The porpoising of penguins: an energy-conserving behavior for respiratory ventilation. Can J Zool 65: 209–211.

———. 1989. Surfacing behavior and ventilation in free-ranging dolphins. J Mammal 70:833–835.

Innes H.S. 1984. Swimming energetics, metabolic rates and hind limb muscle anatomy of some phocid seals. PhD diss. University of Guelph, Ontario.

Irving L. 1973. Aquatic mammals. Pp. 47–96 in G.C. Whittow, ed. Comparative Physiology of Thermoregulation. Vol. 3. Academic Press, New York.

Johansen K. 1962. Buoyancy and insulation in the muskrat. J Mammal 43:64–68.

Kenyon K.W. 1969. The sea otter in the eastern Pacific Ocean. N Am Fauna 68:1–352.

———. 1981. Sea otter *Enhydra lutris* (Linnaeus, 1758). Pp. 209–223 in S.H. Ridgway and R.J. Harrison, eds. Handbook of Marine Mammals. Vol. 1. Academic Press, London.

Kooyman G.L. 1973. Respiratory adaptations in marine mammals. Am Zool 13:457–468.

Kramer D.L. 1988. The behavioral ecology of air breathing by aquatic animals. Can J Zool 66:89–94.

Kriete B. 1995. Bioenergetics in the killer whale, *Orcinus orca*. PhD diss. University of British Columbia, Vancouver.

Kruse D.H. 1975, Swimming metabolism of California sea lions, *Zalophus californianus*. MS thesis. San Diego State University.

Lang T.G. 1966. Hydrodynamic analysis of dolphin fin profiles. Nature 209:1110–1111.

Lang T.G. and D.A. Daybell. 1963. Porpoise performance tests in a seawater tank. Naval Ordnance Test Station Tech. Publ. 3063. Naval Ordnance Test Station, China Lake, Calif. NAVWEPS Rep. 8060.

Lighthill J. 1969. Hydrodynamics of aquatic animal propulsion: a survey. Annu Rev Fluid Mech 1:413–446.

———. 1971. Large-amplitude elongated-body theory of fish locomotion. Proc R Soc Lond B Biol Sci 179:125–138.

Liu P. and N. Bose. 1993. Propulsive performance of three naturally occurring oscillating propeller planforms. Ocean Eng 20:57–75.

Loughlin T.R. 1994. Marine Mammals and the Exxon Valdez. Academic Press, San Diego, Calif.

Loworn J.R. and D.R. Jones. 1991. Effect of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks. Can J Zool 69:2879–2887.

Loworn J.R., D.R. Jones, and R.W. Blake. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. J Exp Biol 159: 89–108.

Marchaj C.A. 1964. Sailing Theory and Practice. Dodd, Mead, New York.

———. 1991. Aero-Hydrodynamics of Sailing. International Marine, Camden, Maine.

Markussen N.H., M. Ryg, and N.A. Britsland. 1992. Metabolic rate and body composition of harbour seals, *Phoca vitulina*, during starvation and refeeding. Can J Zool 70:220–224.

Mizelle J.D. 1935. Swimming of the muskrat. J Mammal 16: 22–25.

Mordvinov Y.E. 1976. Locomotion in water and the indices of effectiveness of propelling systems for some aquatic mammals. Zool Zh 55:1375–1382.

Morrison P., M. Rosenmann, and J.A. Estes. 1974. Metabolism and thermoregulation in the sea otter. Physiol Zool 47: 218–229.

Britsland N.A. and K. Ronald. 1975. Energetics of the free diving harp seal (*Pagophilus groenlandicus*). Rapp P-V Reun Comm Int Explor Sci Mer Mediterr 169:451–454.

Pabst D.A. 1996. Springs in swimming animals. Am Zool 36: 723–735.

Parry D.A. 1949. The structure of whale blubber, and a discussion of its thermal properties. Q J Microsc Sci 90:13–25.

Pfeiffer P. and B.M. Culik. 1998. Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.). J Comp Physiol 168B:143–148

Pinshow B., M.A. Fedak, and K. Schmidt-Nielsen. 1977. Terrestrial locomotion in penguins: it costs more to waddle. Science 195:592–594.

Prandtl L. and O.G. Tietjens. 1934. Applied Hydro- and Aeromechanics. Dover, New York.

Prange H. and K. Schmidt-Nielsen. 1970. The metabolic cost of swimming in ducks. J Exp Biol 53:763–777.

Rice D.W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. Pp. 177–233 in S.H. Ridgway, and R. Harrison, eds.

Handbook of Marine Mammals. Vol. 4. River Dolphins and the Larger Toothed Whales. Academic Press, London.

Ridgway S.H. and R. Howard. 1979. Dolphin lung collapse and intramuscular circulation during free diving: evidence from nitrogen washout. Science 206:1182–1183.

Ridgway S.H., B.L. Scronce, and J. Kanwisher. 1969. Respiration and deep diving in the bottlenose porpoise. Science 166: 1651–1654.

Rue L.L., III. 1964. The World of the Beaver. Lippincott, Philadelphia.

Schmidt-Nielsen K. 1972. Locomotion: energy cost of swimming, flying, and running. Science 177:222–228.

Scholander P.F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. Biol Bull 99:225–236.

Shipman P. 1998. Taking Wing: *Archaeopteryx* and the Evolution of Bird Flight. Simon & Schuster, New York.

Skrovan R.C., T.M. Williams, P.S. Berry, P.W. Moore, and R. Davis. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. J Exp Biol 202:2749–2761.

Sokolov V.E. 1982. Mammal Skin. University of California Press, Berkeley.

Stein B.R. 1989. Bone density and adaptation in semiaquatic mammals. J Mammal 70:467–476.

Stenson G.B., G.A. Badgero, and H.D. Fisher. 1984. Food habits of the river otter *Lutra canadensis* in the marine environment of British Columbia. Can J Zool 62:88–91.

Stephenson R., J.R. Loworn, M.R.A. Heieis, D.R. Jones, and R.W. Blake. 1989. A hydromechanical estimate of the power requirements of diving and surface swimming in lesser scaup (*Aythya affinis*). J Exp Biol 147:507–519.

Sumich J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. Can J Zool 61:647–652.

Tarasoff F.J. 1972. Comparative aspects of the hind limbs of the river otter, sea otter and seals. Pp. 333–359 in R.J. Harrison, ed. Functional Anatomy of Marine Mammals. Vol. 1. Academic Press, London.

———. 1974. Anatomical adaptations in the river otter, sea otter and harp seal with reference to thermal regulation. Pp. 111–141 in R.J. Harrison, ed. Functional Anatomy of Marine Mammals. Vol. 2. Academic Press, London.

Tarasoff F.J., A. Bisaillon, J. Pierard, and A.P. Whitt. 1972. Locomotory patterns and external morphology of the river otter, sea otter, and harp seal (Mammalia). Can J Zool 50: 915–929.

Tarasoff F.J. and G.L. Kooyman. 1973. Observations on the anatomy of the respiratory system of the river otter, sea otter, and harp seal. I. The topography, weight, and measurements of the lungs. Can J Zool 51:163–170.

Taylor C.R., K. Schmidt-Nielsen, and J.L. Raab. 1970. Scaling of energetic cost of running to body size in mammals. Am J Physiol 219:1104–1107.

Taylor D.W. 1933. The Speed and Power of Ships. Ransdell, Washington, D.C.

Taylor M.A. 1994. Stone, bone or blubber? buoyancy control strategies in aquatic tetrapods. Pp. 151–161 in L. Maddock, Q. Bone, and J.M.V. Rayner, eds. Mechanics and Physiology of Animal Swimming. Cambridge University Press, Cambridge.

Thewissen J.G.M. and F.E. Fish. 1997. Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence. Paleobiology 23:482–490.

Thewissen J.G.M., S.T. Hussain, and M. Arif. 1994. Fossil evidence for the origin of aquatic locomotion in Archaeocete whales. Science 263:210–212.

Thompson D., A.R. Hiby, and M.A. Fedak. 1993. How fast should I swim? behavioural implications of diving physiology. Symp Zool Soc Lond 66:349–368.

Troughton E. 1941. Australian water-rats: their origin and habits. Aust Mus Mag 7:377–381.

Tucker V.A. 1970. Energetic cost of locomotion in animals. Comp Biochem Physiol 34:841–846.

———. 1975. The energetic cost of moving about. Am Sci 63: 413–419.

Videler J.J. 1993. Fish Swimming. Chapman & Hall, London.

Videler J.J. and B.A. Nolet. 1990. Cost of swimming measured at optimum speed: scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. Comp Biochem Physiol 97A:91–99.

Vogel S. 1994. Life in Moving Fluids. Princeton University Press, Princeton, N.J.

Webb P.W. 1975. Hydrodynamics and energetics of fish propulsion. Bull Fish Res Board Can 190:1–158.

———. 1978. Hydrodynamics: non-scombroid fish. Pp. 189–237 in W.S. Hoar and D.J. Randall, eds. Fish Physiology, Locomotion. Vol. 7. Academic Press, New York.

———. 1984. Body form, locomotion and foraging in aquatic vertebrates. Am Zool 24:107–120.

———. 1988. Simple physical principles and vertebrate aquatic locomotion. Am Zool 28:709–725.

Webb P.W. and R.W. Blake. 1985. Swimming. Pp. 110–128 in M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds. Functional Vertebrate Morphology. Harvard University Press, Cambridge, Mass.

Webb P.W. and V. De Buffrenil. 1990. Locomotion in the biology of large aquatic vertebrates. Trans Am Fish Soc 119: 629–641.

Weihs D. and P.W. Webb. 1983. Optimization of locomotion. Pp. 339–371 in P.W. Webb and D. Weihs, eds. Fish Biomechanics. Praeger, New York.

Williams T.D., D.D. Allen, J.M. Groff, and R.L. Glass. 1992. An analysis of California sea otter (*Enhydra lutris*) pelage and integument. Mar Mamm Sci 8:1–18.

Williams T.M. 1983*a*. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. J Exp Biol 103:155–168.

———. 1983*b*. Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body of running energetics and gait patterns. J Exp Biol 105:283–295.

———. 1987. Approaches for the study of exercise physiology and hydrodynamics in marine mammals. Pp. 127–145 in A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. Approaches to Marine Mammal Energetics. Special Publication no. 1. Society for Marine Mammology, Lawrence, Kans.

———. 1989. Swimming by sea otters: adaptations for low energetic cost locomotion. J Comp Physiol 164A:815–824.

———. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Philos Trans R Soc Lond B Biol Sci 353:1–9.

Williams T.M., W.A. Friedl, M.L. Fong, R.M. Yamada, P. Sedivy, and J.E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355: 821–823.

Williams T.M. and G.L. Kooyman. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. Physiol Zool 58:576–589.

Williams T.M., G.L. Kooyman, and D.A. Croll. 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. J Comp Physiol 160B:637–644.

Williams T.M., S.F. Shippee, and M.J. Rothe. 1996. Strategies for reducing foraging costs in dolphins. Pp. 4–9 in S.P.R. Greenstreet and M.L. Tasker, eds. Aquatic Predators and Their Prey. Fishing News, Oxford.

Wolff J.O. and R.D. Guthrie. 1985. Why are aquatic small mammals so large? Oikos 45:365–373.

Worthy G.A.J., S. Innes, B.M. Braune, and R.E.A. Stewart. 1987. Rapid acclimation of cetaceans to an open-system respirometer. Pp. 115–126 in A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. Approaches to Marine Mammal Energetics. Special Publication no. 1. Society for Marine Mammology, Lawrence, Kans.

Zimmer C. 1998. At the Water's Edge: Macroevolution and the Transformation of Life. Free Press, New York.