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3. Aquatic Locomotion

The energetic cost of locomotion by mammals is expensive and therefore represents a major deficit to the available energy resources. For locomotion in water, the energetic demands and swimming performance of mammals are affected by the water-flow patterns around the swimmer dictated by the high density and viscosity of the aquatic medium (Daniel and Webb, 1987; Schmidt-Nielsen, 1972; Williams, 1987). The generation of propulsive forces (thrust) opposes resistive forces (drag) that increase the locomotor effort. In addition, energy expenditure for locomotion is hampered by periods of apnea during underwater swimming (Hochachka, 1980; Kooyman, 1985) and by a high thermal conductivity of the aquatic medium that potentially necessitates increased thermoregulatory demands (Fish, 1983; Hart and Fisher, 1964; Irving 1971; Nadel, 1977; Whittow, 1987). The large energetic demands of swimming mammals promoted the evolution of physiological, morphological, and behavioral adaptations that reduce energy consumption while allowing for effective locomotion. If aquatic mammals are adapted to swim in such a manner so as to minimize energy expenditure, there should be distinct metabolic and hydrodynamic advantages to swimming modes and morphologies employed by the most aquatically derived species. At varying times, mammals, such as cetaceans, sirenians, and pinnipeds, that spend all or most of their time inhabiting and locomoting in water, must generate adequate thrust for migration, high-speed swimming, and maneuverability. The evolution of such aquatic mammals represents the cul-

mination of a sequence of transitional stages from terrestrial quadrupeds to fully aquatic piscine-like morphologies and propulsive modes of high energetic efficiency (Barnes et al., 1985; Fish et al., 1988; Gaskin, 1982; Gingerich et al., 1983; Tedford, 1976). However, semiaquatic mammals must contend with swimming modes having metabolic and mechanical inefficiencies attributable to morphologies constrained by a compromise between movement on both land and water (Fish, 1984).

In this chapter, I discuss the energetics of swimming by mammals with particular regard to swimming modes and swimming strategies. Metabolic studies that estimate power input provide an indication of the energy potentially available for aquatic propulsion (Davis et al., 1985; DiPrampero et al., 1974; Fish, 1982, 1983; Williams, 1983a). However, because external work is performed in moving the body through a fluid, a full examination of the dynamics of swimming requires an estimate of the power output as the realized rate of energy use contributing to the performance of work (Fish, 1982). External work is manifest as a transfer of momentum between the animal and its environment (Daniel and Webb, 1987) resulting in a thrust force causing movement by the animal through the water. Therefore, studies concerning the energetics of swimming mammals should include examinations of hydrodynamics and biomechanics of the various locomotor modes to estimate power output as the rate of energy expended to produce thrust in addition to metabolic determinations of power input. Use of physiological, morphological, and hydrodynamic studies allows for an integrated approach to elucidate the dynamics of swimming by mammals.

Aquatic Mammal Diversity and Swimming Modes

The majority of mammalian orders have representatives that can be classified as semiaquatic or fully aquatic (Howell, 1930). With the possible exceptions of the giraffe and apes, all mammals have the ability to swim regardless of any specific adaptations for an aquatic existence (Dagg and Windsor, 1972). Perusal of the literature shows that cursorial (Bryant, 1919; Fregin and Nicholl, 1977), fossorial (Best and Hart, 1976; Hickman, 1983, 1984; Talmage and Buchanan, 1954), arboreal (Cole, 1922), and even aerial (Craft et al., 1958) mammals can swim.

TABLE 3.1
Mammalian swimming modes

Swimming mode	Principal appendage	Example	Reference
Drag-based oscillatory	Quadrupedal	Mink	Williams, 1983a
		Mole	Hickman, 1984
	Pectoral	Opossum Polar bear	Fish, 1987 Flyger & Townsend, 1968
Lift-based oscillatory	Pelvic	Muskrat	Fish, 1984
		Water opossum	Fish, 1987; Stein, 1981
		River otter	Tarasoff et al., 1972
Lift-based undulatory	Pectoral	Sea lion	English, 1976; Feldkamp, 1987b
		Phocid seal	Fish et al., 1988; Tarasoff et al., 1972
Lift-based undulatory	Pelvic	Sea otter	Tarasoff et al., 1972
		Walrus	Gordon, 1981
		Dolphin	Lang, 1966; Parry, 1949
	Caudal	Manatee	Hartman, 1979

Terrestrial and semiaquatic mammals swim using mainly oscillatory propulsors (Table 3.1), which are either paired appendages that function as paddles or winglike hydrofoils (Webb and Blake, 1985). Paddling is associated with slow swimming and precise maneuverability (Webb, 1984) and generally is used in surface swimming. The paddling stroke cycle is composed of a power phase and a recovery phase. During the power phase, the paddle pushes posteriorly on the water, generating a drag force to its movement that produces thrust for the whole organism in the direction opposite the paddle movement (Fig. 3.1; Fish, 1984; Webb and Blake, 1985). The paddle is repositioned during the recovery phase without the generation of thrust.

The foreflippers, used by the Otariidae, act as oscillatory hydrofoils that generate thrust by the lifting-wing principle (Fig. 3.1; Webb and Blake, 1985) throughout the stroke cycle (Feldkamp, 1987b). This mechanism provides effective aquatic propulsion for otariid seals, which spend considerable amounts of time in the water foraging for food and undertaking long oceanic migrations (Ridgeway and Harrison, 1981), while maintaining a flipper structure that is adept at locomoting on land (English, 1976; Feldkamp, 1987a, 1987b).

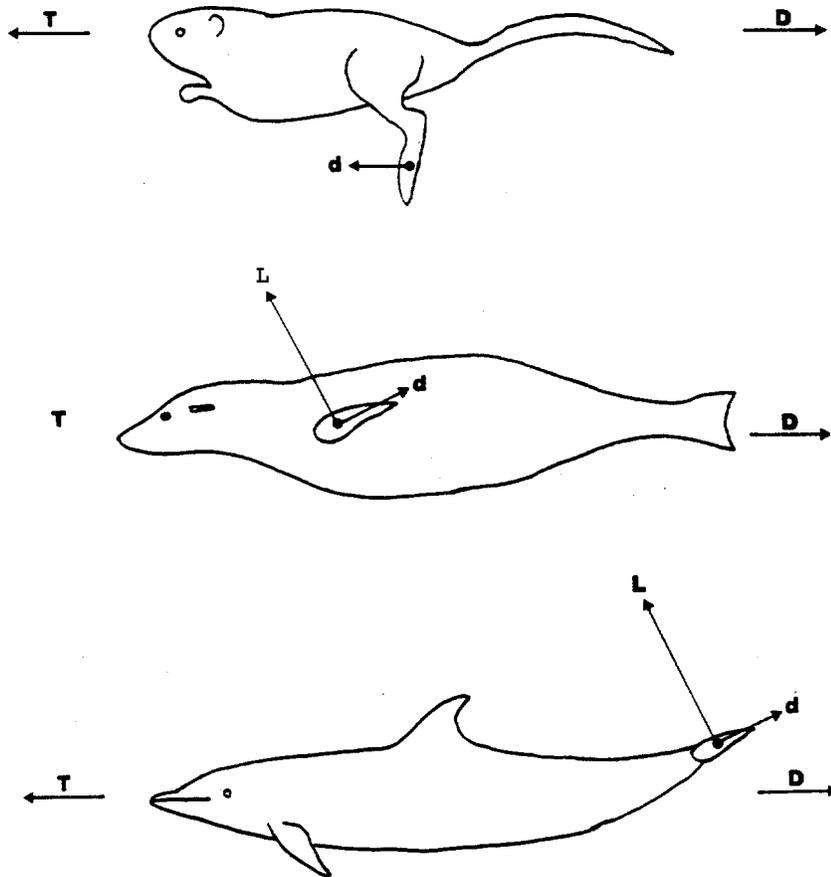


Fig. 3.1. Major forces associated with swimming, including (top) paddling (muskrat), (middle) lift-based oscillation (sea lion), and (bottom) lift-based undulation (dolphin). For each animal swimming in water, drag force (D) resists forward motion of the body and is opposed by an equal thrust force (T) generated by the propulsive appendages. The posterior movement of the hind feet of the muskrat acts as a paddle to generate a drag force on the appendage (d) that contributes to T . The foreflippers of the sea lion and the caudal fluke of the dolphin act as hydrofoils that produce an anteriorly directed lift force (L) that can be resolved to generate T .

The undulatory propulsive mechanism passes waves along the body or caudal fluke and is used by those mammals that are most restricted to the aquatic environment. Cetaceans and sirenians undulate the caudal fluke in a dorsoventral plane to effect propulsion (Hartman, 1979; Lang and Daybell, 1963; Nishiwaki and Marsh, 1985; Parry, 1949; Peterson, 1925; Slijper, 1961; Videler and Kamermans, 1985). Except for the orientation of propulsive movements and the asymmetry of the propulsive musculature, these mammals reflect the typical swimming

pattern observed in many fish. Periodic motion of the caudal fluke generates thrust as a component of an anteriorly inclined lifting force (Fig. 3.1). The Phocidae and Odobenidae laterally undulate the posterior body to move the paired hind flippers in the horizontal plane, effecting a fishlike movement (Backhouse, 1961; Fish et al., 1988; Gordon, 1981; Ray, 1963; Tarasoff et al., 1972). By laterally undulating its compressed tail, the otter shrew (*Potamogale* spp.) may produce propulsion with the nonwebbed feet pressed against the body (Walker, 1975). In addition, fast, submerged swimming by otters is accomplished by the undulatory mode (Chanin, 1985; Kenyon, 1969; Tarasoff et al., 1972).

Undulatory swimming is a rapid and relatively high-powered propulsive mode (Webb, 1984). This mode is used for swimming durations from several seconds to weeks, as involved in cruising, sprints, patrolling, station holding, and migrations.

Swimming Speed

Reports on swimming speeds of various aquatic mammals have in many instances been anecdotal and often unreliable. The reason for questioning these reports is that estimates of swimming speeds based on observations from ships, airplanes, or shorelines have often been made without fixed reference points, information on currents, or accurate timing instruments. These observations have led to erroneous conclusions regarding swimming performance as exemplified for dolphins by Gray's Paradox (Gray, 1936; Parry, 1949). In this case, power output calculated from a simple hydrodynamic model for a dolphin swimming at 10 m/s for 7 s was greater than the power that was assumed to be developed by the muscles (Gray, 1936). The paradox is resolved when one considers that the dolphin was demonstrating a burst performance (Kooyman, 1989; Lang and Daybell, 1963), and the muscle power output used as a standard was based on the sustained performance of the dog and humans (Gray, 1936). Although controlled laboratory studies do allow for measurements of precise swimming speeds, these speeds may not reflect ecologically relevant levels of performance. The future use of microprocessors carried by freely swimming and diving mammals should provide accurate swimming speeds, as has already been done for otariids (Ponganis et al., 1990).

The range of swimming speeds varies markedly. Differences in swim-

ming speeds of mammals are related to body size, swimming mode, and relation to the water surface. Large animals have higher cruising and maximum sprint speeds than smaller swimmers (Aleyev, 1977; Kooyman, 1989). This relationship holds up to a body length of 4.5 m and is due to allometric differences. Body surface area and resistance to movement in water are proportional to the square of body length, whereas muscle mass and power that may be developed for swimming are proportional to the cube of body length. Consideration of length-specific swimming speeds, however, shows that large mammals demonstrate lower performance levels, as exemplified by cetaceans (Webb, 1975a). Mammals that paddle are slower than either undulatory swimmers or lift-based oscillators. This pattern is most likely due to decreased net thrust production and efficiency of paddling compared with the other propulsive modes (see below). In addition, paddling mammals are usually surface swimmers whose speed is limited by interference from surface waves (Fish, 1982, 1984; Williams, 1983a, 1989). Paddlers, such as the muskrat (*Ondatra zibethicus*) and rice rat (*Oryzomys palustris*), maintain routine swimming speeds at or below the predicted speed of maximum wave resistance (Fish, 1984). Sea otters (*Enhydra lutris*) are restricted to sustained surface swimming speeds less than 0.8 m/s, but when submerged can swim at speeds from 0.6 to 1.39 m/s by undulation (Williams, 1989).

Hydrodynamic Drag

To propel itself through water at a constant velocity (U), a mammal needs to generate a thrust force (T) at the expense of metabolic energy that is equal to the sum of resistive drag forces (D), so that:

$$\eta M = TU = DU \quad (1)$$

where η is a dimensionless overall efficiency, M is the metabolic rate, and TU and DU represent thrust and drag power outputs, respectively. Because the rate of energy expended to overcome drag is related to the thrust power output and ultimately to the rate of metabolic energy expenditure, investigators have used estimates of drag in studies of swimming energetics. Complete explanations of hydrodynamics in biological systems can be found in publications by Webb (1975a), Vogel (1981), and Blake (1983b).

Drag consists of frictional and pressure force components that arise from the flow regime about the body (Blake, 1983b; Webb, 1978; Yates, 1983). The flow is divided into two regions: boundary layer and outer flow. The boundary layer arises as the result of water viscosity. Water particles adhere to the body surface, so there is no relative velocity difference, resulting in the no-slip condition. At a short distance from the body, water velocity approximates the outer flow. The velocity gradient between the body surface and outer flow develops because of shear stresses in the boundary layer caused by the fluid viscosity and accounts for the frictional drag component. The pressure component of drag arises from distortion of fluid around the body in the outer flow (Webb, 1978). Deflection of the outer flow due to the shape of the body produces a pressure gradient from varying flow velocities interacting with the boundary layer separating it from the body. This interaction translates into a wake where kinetic energy is lost in addition to a net pressure force that acts in opposition to forward motion (Webb, 1978).

The type of flows within the boundary layer and outer flow also influences frictional and pressure components of drag. Flows may be laminar, turbulent, or transitional. Flow type is determined by the size and speed of the animal and by the density and viscosity of the fluid medium. The influence of these parameters is represented by the non-dimensional Reynolds number:

$$\text{Re} = \frac{UL}{\nu} \quad (2)$$

where Re is the Reynolds number, L is body length, and ν is the kinematic viscosity of water (Blake, 1983b; Webb, 1978). Boundary flow about a submerged, rigid streamlined body is laminar up to a Re of approximately 5×10^5 , turbulent above a Re of 5×10^6 , and transitional between those values (Webb, 1975a; William, 1987). The onset of transitional flow that is partly laminar and partly turbulent occurs at the critical Re, which is influenced by disturbances in the outer flow, surface roughness, and pressure gradients opposite to the direction of flow (Webb, 1975a). The large size and high swimming speed of marine mammals in particular indicate a high Re of greater than 10^6 (e.g., *Enhydra lutris*, $\text{Re} = 1.7 \times 10^6$; Williams, 1989; *Zalophus californianus*, $\text{Re} = 8.4 \times 10^6$; Kooyman, 1989; *Lagenorhynchus obliquidens*, $\text{Re} = 1.5 \times 10^7$; Lang and Daybell, 1963) and thus a transitional or fully turbulent boundary layer.

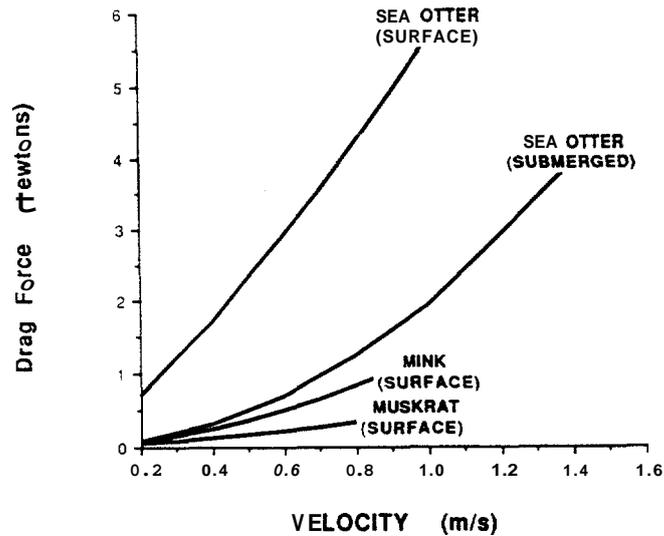


Fig. 3.2. Plot of drag force as a function of velocity (U) from measurements of dead-drag on muskrat (Fish, 1984), mink (Williams, 1983a), and sea otter (Williams, 1989). Drag measurements were obtained on muskrat, mink, and sea otter at the water surface and also on the sea otter in a submerged position.

Thrust and power output based on drag determinations were estimated for a variety of aquatic mammals by use of standard hydrodynamic equations (Au and Weihs, 1980; Gray, 1936; Hui, 1987; Parry, 1949), models (Aleyev, 1977; Purves et al., 1975), dead animals (Fish, 1984; Williams, 1983a, 1989), and towing or coasting (Feldkamp, 1987a; Innes, 1984; Lang and Daybell, 1963; Lang and Pryor, 1966; Williams and Kooyman, 1985). In all cases the bodies are rigid or assumed to be analogous to a flat plate with an equivalent surface area. These rigid-body analogies for aquatic mammals demonstrate that drag and power output increase curvilinearly with increasing velocity (Fig. 3.2), but the magnitude of the drag force differs with the size of the animal. Because swimming speed varies with the size of the animal, comparisons of the energetics of aquatic mammals over a 10^7 -fold range of body mass are difficult.

A convenient method of estimating the resistance of a body moving through water is by computation of the dimensionless drag coefficient, C_D :

$$C_D = \frac{D}{0.5\rho S U^2} \quad (3)$$

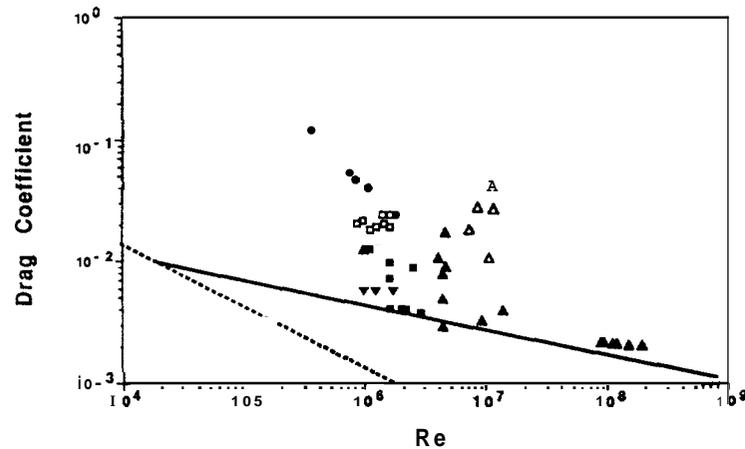


Fig. 3.3. Plot of the drag coefficient (C_D) as a function of the Reynolds number (Re). Symbols represent cetaceans (A and Δ : Aleyev, 1977; Kermack, 1948; Lang and Daybell, 1963; Purves et al., 1975; Videler and Kamermans, 1985; Webb, 1975a; Yates, 1983), pinnipeds (\blacksquare and \square : Feldkamp, 1987a; Fish et al., 1988; Williams and Kooyman, 1985), sea otter (\blacktriangledown : Williams, 1989), beaver (\bullet : Kurbatov and Mordvinov, 1974), and human (\blacklozenge : Williams and Kooyman, 1985). Closed symbols represent estimates of C_D based on rigid-body analogies; open symbols represent values determined from hydrodynamic thrust-based models. The solid line represents the minimum C_D assuming turbulent boundary conditions; the broken line is for C_D assuming laminar conditions.

where ρ is water density, S is wetted surface area, and U is velocity. C_D depends on Re and the flow conditions about the body (Webb, 1978); C_D is positively related to drag force, which is best measured directly from animals (Williams, 1987). In addition, C_D can be compared with a reference drag coefficient representing the theoretical minimum based on a flat plate with equivalent surface area and Re (Fish et al., 1988).

C_D s computed from gliding and towing drag measurements for submerged otariid and phocid seals and odontocete cetaceans range from 0.003 to 0.018 at Re of 10^6 – 10^7 (Feldkamp, 1987a; Lang and Daybell, 1963; Mordvinov and Kurbatov, 1972; Videler and Kamermans, 1985; Williams and Kooyman, 1985). The values of C_D for these marine mammals is greater or equivalent to the minimum drag coefficient for a turbulent boundary layer (Fig. 3.3). The blue whale (*Balaenoptera musculus*) has the lowest calculated value of C_D at 0.0022 for $Re = 1.9 \times 10^8$, assuming a turbulent boundary layer (Kermack, 1948). Although C_D for the blue whale is low, the whale's large surface area and high swimming speed result in the largest drag force reported for a swimming mammal. Calculated power output for the blue whale

is 4×10^5 W (Kermack, 1948), which is 88.3 times as great as the highest power output measured for a dolphin (Lang and Pryor, 1966).

Values of C_D for aquatic mammals indicating turbulent boundary conditions contradict the assertion of drag reduction by maintenance of a laminar boundary layer as an answer to Gray's Paradox (Gray, 1936; Parry, 1949). On the basis of the calculated drag of a dolphin swimming with a turbulent boundary layer, Gray (1936) predicted a higher power output than could be developed by the locomotor muscle mass. Although Gray (1936) underestimated the power generated by a dolphin swimming at burst speed by assuming equivalence with estimates of muscle power output of sustained activity, drag on the dolphin was believed to be reduced by maintenance of laminar flow within the boundary layer.

Attempts to reconcile Gray's Paradox by a mechanism that maintains a laminar boundary layer have focused on hydrodynamic characteristics of the integument of marine mammals. A compliant skin that could dampen turbulence and maintain laminar boundary conditions by active or passive mechanisms was viewed as a possible resolution to the paradox (Kramer, 1960a, 1960b, 1965; Sokolov, 1962). The structure of cetacean skin is similar to humanmade compliant surfaces (Kramer, 1960b, 1965; Yurchenko and Babenko, 1980). Mobile skin folds observed on swimming dolphins (Essapian, 1955) were thought to absorb energy through elastic deformation and to dampen turbulence in the boundary layer, resulting in a reduction of the total drag (Aleyev, 1977; Kramer, 1965; Sokolov, 1960; Yurchenko and Babenko, 1980). In addition, dermal ridges in the skin, the infusion of desquamated epidermal cells into the boundary layer, secretions from the dolphin eye, and heating by the skin to change boundary layer viscosity were hypothesized to retain laminar flow and reduce drag (Lang, 1966; Purves, 1963; Sokolov et al., 1969).

Mordvinov and Kurbatov (1972) reported that the body hair of phocid seals dampens turbulent eddies, thus reducing drag. Most studies on swimming mammals, however, have found little evidence promoting a drag reduction mechanism by laminarization of boundary flow due to properties of the integument. Experiments using naked women towed through water as analogues to swimming dolphins show that mobile skin folds represent a parasitic feature that does not improve drag reduction (Aleyev, 1977). Results reported by Lang and Daybell (1963) refute the assumption of drag reduction by a laminar boundary layer in dolphins. In a study on a live dolphin in which turbulence was

induced over its surface, the drag was the same as when no turbulence was induced, indicating a normally turbulent flow (Lang and Daybell, 1963; Webb, 1975a). Flow visualization experiments in mammals show that the majority of the body surface has turbulent flow conditions (Fish, 1984; Kurbatov and Mordvinov, 1974; Mordvinov, 1974; Purves et al., 1975; Rosen, 1963; Williams and Kooyman, 1985). Although it produces a higher frictional drag component than laminar flow, a turbulent boundary layer will generate a smaller pressure drag (Webb, 1975a). The difference in magnitudes of drag components ultimately produces a smaller total drag for an animal with turbulent flow compared with laminar boundary conditions. The high energy content of the turbulent boundary layer prevents separation of the boundary layer from the body into the outer flow. Separation results in increased pressure and total drag.

Significant drag reduction in aquatic mammals is largely dependent on body shape. Highly aquatic mammals, such as cetaceans and pinnipeds, have streamlined bodies and appendages that incur low drag (Williamson, 1972; Feldkamp, 1977a; Fish et al., 1988). In comparison, less-aquatic mammals, such as humans and beavers, have high values of C_D (Kurbatov and Mordvinov, 1974; Williams and Kooyman, 1985), which are at least 75% as great as the minimum turbulent C_D at equivalent Re (Fig. 3.3).

The fineness ratio ($FR = \text{body length}/\text{maximum body diameter}$), which serves as a crude indicator of the streamlining of a body (Williams, 1987), has an optimal value of 4.5 for the lowest drag, where volume is maximized for a minimum surface area (Hertel, 1966; Webb, 1975a). Cetaceans and phocids maintain a range of FR (3.2–5.6) that spans the optimal FR (Aleyev, 1977; Fish et al., 1988; Hertel, 1966; Mordvinov, 1972; Williams and Kooyman, 1985), although phocids are represented at the lower end of this range. The sea lion (*Zalophus californianus*) and sea otter (*Enhydra lutris*) have moderately elongate body forms with FR s of 5.5 (Feldkamp, 1987a) and 5.8 (Williams, 1989), respectively. Extremes of FR that indicate increased pressure drag are displayed by semiaquatic paddlers: muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*) have relatively nonstreamlined bodies with FR values of 2.5 and 3.0, respectively (Kurbatov and Mordvinov, 1974), while the FR of mink (*Mustela vison*) is 9.1 (Williams, 1983a).

Increased drag and energy loss from surface swimming result from the formation of waves that augment drag up to five times (Hertel, 1966), increasing metabolic expenditure and limiting swimming speed

when compared with submerged swimming (Fish, 1984). The effect of surface waves is negated when the animal is submerged below a depth of three times the body diameter (Hertel, 1966). Periods of submerged swimming by wild minks and sea otters indicate a behavioral strategy to reduce drag (Williams, 1983a, 1989). Dolphins, however, utilize the pressure field of surface waves in bow riding to minimize their locomotor effort (see review in Hertel, 1969). It has been suggested recently that even large whales can save energy by extracting up to 33% of their propulsive power from ocean waves (Bose and Lien, 1990).

Although submerged swimming reduces drag compared with surface swimming, air-breathing mammals can not indefinitely avoid the water surface and its enhanced drag. An alternate strategy is to leap from the water and become airborne. Porpoising consists of serial leaps in which the animal leaves the water and thus reduces drag and energy cost (Au, 1980; Au and Weihs, 1980; Blake 1983a, 1983b). At high swimming speeds, the energy required to leap a given distance is less than the energy to swim an equivalent distance at the water surface. Williams (1987) observed the minimum porpoising speed for adult harbor seals ranged from 2.5 to 3.0 m/s, which agreed with the predicted porpoising speed based on Blake's (1983a) model. This behavior for energy savings may be limited in harbor seals, because porpoising is mainly confined to excited males during the mating season (King, 1983). In addition, Hui (1989) found the emergence angle of 36.9° for free-ranging dolphins (*Delphinus delphis* and *Stenella attenuata*) when porpoising was not the angle predicted for maximum energy savings. Porpoising for energy conservation predicts an emergence angle of 45° for maximum leap distance (Au and Weihs, 1980; Blake, 1983a) or an angle of 30° as a compromise for maximum leap distance and maximum forward speed (Gordon, 1980).

Thrust-based Models

Power outputs based on drag measurements from rigid-body analogues provide only a minimum estimate of the energy expenditure of swimming, because such models do not account for movements of the body or appendages, gross flow effects, interactions, and drag-reducing mechanisms (Webb, 1975a). The propulsive undulatory and oscillatory movements of the body and appendages incur increased energy loss due to increased drag and inertial forces from accelerations of the pro-

pulsor and the water (Daniel, 1984; Fish, 1984; Fish et al., 1988; Lighthill, 1971). Consequently, hydrodynamic models based on thrust calculated from the kinematics of swimming mammals provide a better estimate of power output than drag determinations. Calculated estimates of power output from such models are **3–16** times greater than values calculated for equivalent rigid bodies (Fish, 1984; Fish et al., 1988; Webb, 1975a; Yates, 1983). A further benefit of hydrodynamic models is that comparisons of thrust generation and mechanical efficiency can be evaluated for the different swimming modes used by mammals.

A model to examine paddling locomotion was developed by Blake (1979, 1980) and employed by Fish (1984, 1985) to investigate the energetics of surface-swimming semiaquatic rodents. The power phase of the paddling stroke of the muskrat and rice rat is characterized by a posterior acceleration of the hindfoot generating a thrust force due to the drag on the foot (Figs. 3.1, 3.4; Fish, 1984). Maximum thrust is realized when the hindfoot is oriented **90°** to the horizontally inclined body (Fish, 1984). The jointed hindlimbs of the muskrat allow a paddle angle close to **90°** for a large portion of the power phase (Webb and Blake, 1985). Thrust production is enhanced by an increase in plantar

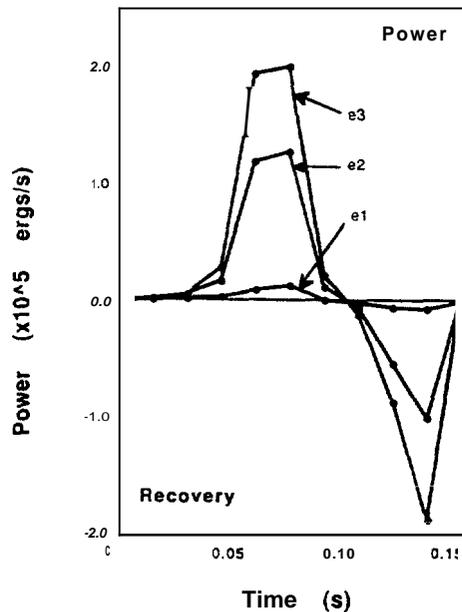


Fig. 3.4. Power output during a complete paddling cycle for the rice rat (*Oryzomys palustris*). Thrust power generated during the power phase and drag power expended during the recovery phase were computed from the model by Blake (1979, 1980). Power produced was determined for proximal (e1), middle (e2), and distal (e3) segments of the paddling hindfoot.

surface area of the feet by elongation of bony elements and addition of lateral fringe hairs on each digit or interdigital webbing (Fish, 1984; Howell, 1930; Mordvinov, 1976). The increase in effective surface area of the feet provides an economical generation of thrust, because the mass of water being worked on is also increased (Alexander, 1983). Mink, which have relatively unmodified feet for a semiaquatic mammal, compensate for deficiencies in thrust production by using long stroke lengths, high stroke frequencies, and quadrupedal swimming (Williams, 1983a). Long stroke lengths and high frequencies, however, are not economical; it is more economical to generate thrust by accelerating a large fluid mass to a small velocity than the converse (Alexander, 1983).

In contrast to the power phase, drag on the foot during the recovery phase is minimized. This action prevents a reduction of net thrust production as the foot is repositioned. In the muskrat, mean power loss attributed to the recovery phase represents 20–39% of thrust power generated during the power phase (Fish, 1984). This small power loss is accomplished by configural changes that reduce foot area by 55% and temporal changes that reduce the relative velocity, thereby minimizing the drag on the foot.

Additional energy losses accrue from paddling because of inertial effects of accelerating and decelerating the mass of the paddle and the added mass (Blake, 1979; Fish, 1984). The added mass is the mass of water entrained with the paddle as it moves (Blake, 1983b). Inertial effects are a major source of energy loss, particularly in small paddlers (Fish, 1984, 1985). In rice rats, acceleration of the paddle and added mass accounts for 31–53% of the total energy necessary for paddling.

Because of large energy expenditures incurred from the recovery phase and inertial effects, efficiency of the paddling mode is low (Webb and Blake, 1985). Mechanical or propeller efficiency (η_p) is calculated as the ratio of the energy utilized for thrust generation to the total energy expended during the paddling stroke. Maximum η_p values for paddling by muskrats and rice rats are 0.33 and 0.25, respectively (Fish, 1984, 1985). The higher η_p for the muskrat is due to enhanced thrust production by its modified hindfeet.

Unlike paddling mammals, which use the drag-based mechanism, otariids, cetaceans, and phocids use lift-based mechanisms to effect propulsion (Feldkamp, 1987a, 1987b; Fish et al., 1988; Lighthill, 1969; Webb, 1975a; Yates, 1983). This mechanism generates a large thrust force as a component of a lift force (Fig. 3.1) produced from the

oscillatory movements of the hydrofoil (i.e., pectoral and pelvic flippers, caudal flukes). Shape and movements of the hydrofoil provide increased efficiency due to a high lift-to-drag ratio and continual generation of thrust throughout the entire stroke cycle.

Power output of the lift-based oscillatory swimming in mammals has not been computed by hydrodynamic models, but the kinematics and efficiency of the swimming mode for sea lions have been examined (English, 1976; Feldkamp, 1987a, 1987b; Godfrey, 1985). Feldkamp (1987b) found that *Zalophus* uses a combination of paddling and lift-based propulsion. The paddling component of the stroke occurs at the beginning of the recovery phase with the winglike, high aspect ratio ($AR = \text{span/chord}$) foreflippers. The remainder of the recovery phase (upstroke) and the power phase (downstroke) generate forces that resolve into downward and upward lift forces and anteriorly directed thrust forces. This mechanism has been likened to the stroke of flying birds (Feldkamp, 1987b).

Although up- and downstrokes produce thrust and represent the majority of the stroke cycle of sea lions, the paddling phase generates the greatest amount of thrust (Feldkamp, 1987b). Therefore, the three-phase system generates a large thrust force by paddling that is enhanced by winglike movements that incur less drag in a recovery phase. Additional drag reduction is affected by the morphology of the foreflippers. The high aspect ratio ($AR = 7.9$) reduces the formation of vortices, reducing the induced drag component caused by movements of the foreflippers (Feldkamp, 1987b). Consequently, the lift-to-drag ratio is improved, and thrust is generated more efficiently. Feldkamp (1987a) calculated a maximum η_p of 0.80 for the lift-based mode of the sea lion when swimming at the highest speeds.

In the undulatory lift-based mode of cetaceans and phocid seals, thrust is generated solely by a caudal hydrofoil represented by a caudal fluke or alternating hind flippers. The swimming motions of cetaceans and phocids are analogous to the thunniform mode of fish (Aleyev, 1977; Fish et al., 1988; Lindsey, 1978; Webb, 1975a), which use "lunate tail" propulsion (Lighthill, 1969). As in the thunniform mode, the presence of a double-jointed system at the hydrofoil base allows the angle of inclination of the hydrofoil to be adjusted throughout the stroke cycle, maintaining nearly continuous maximum thrust (Fish et al., 1988; Lindsey, 1978). In addition, moderate to high aspect ratio ($AR = 3.4-5.5$), low sweep-back angle, and flexibility of the hydrofoil enhance reduced drag with high thrust and efficiency.

Parry (1949) developed a model of undulatory swimming for dolphins based on quasistatic flow (Webb, 1975a). Using this model and data from Norris and Prescott (1961) and Lang and Daybell (1963), Webb (1975a) calculated the thrust power for three species of dolphin. The model thrust power was 6.3–16.0 times greater than the theoretical frictional drag power assuming turbulent conditions (Fig. 3.3). Webb (1975a) assumed that the calculated thrust power was not unreasonable if the dolphins were swimming near the surface, where drag is high.

A model developed by Lighthill (1970) uses unsteady wing theory to calculate the total thrust and power output by a rigid hydrofoil. Lighthill's (1970) model was used by Webb (1975a) to calculate a thrust power of 4030 W for a dolphin (*Lagenorhynchus obliquidens*) swimming at 5.5 m/s (Lang and Daybell, 1963). This value is 65% of the thrust power for the same dolphin calculated from Parry's (1949) model and 10.2 times the theoretical frictional drag power (Webb, 1975a). A revision of Lighthill's model (Chopra and Kambe, 1977) used for the dolphin (Chopra and Kambe, 1977; Yates, 1983) and phocids (Fish et al., 1988) also predicts thrust power greater than drag power at equivalent Re (Fig. 3.3).

Mechanical efficiencies of lunate tail propulsion are the highest for any swimming mode in mammals. Under optimal conditions, efficiency may be as high as 99% (Wu, 1971). For the dolphin, Webb (1975a) and Yates (1983) calculated efficiencies of 0.77 and 0.92, respectively, whereas phocids have efficiencies of 0.85 (Fish et al., 1988).

Power Input

Power input represents the rate of energy use that is potentially available to do work; it is limited proximately by metabolic capacities and ultimately by the availability of food resources (Hui, 1987). Power input for swimming mammals can be determined from estimates of metabolic rate and therefore is related to thrust and drag power outputs by Equation 1. Williams (1987) has reviewed the methodology for measuring swimming metabolism.

Active metabolic rates have been determined from measurements of oxygen consumption for both oscillatory and undulatory swimming mammals including muskrat (Fish, 1982; 1983), mink (Williams, 1983a), sea otter (Williams, 1989), sea lion (Costello and Whittow,

1975; Feldkamp, 1987a; Kruse, 1975), phocid seal (Craig and Pasche, 1980; Davis et al., 1985; Innes, 1984; Øritsland and Ronald, 1975; Williams et al., 1991), cetaceans (T.M. Williams, pers. comm., 1991; Worthy et al., 1987), and human (DiPrampo et al., 1974; Holmer, 1972; Nadel et al., 1974). Metabolic rate is directly related to swimming speed and increases linearly (Fish, 1982; Innes, 1984; Nadel et al., 1974) or curvilinearly (Davis, et al., 1985; Feldkamp, 1987a; Holmer, 1972; Nadel et al., 1974; Williams, 1983a). A steep increase in metabolic rate with swimming speed is associated with the high resistance caused by drag, because drag power output increases as U^3 .

Feldkamp (1987a) noted that the cost of swimming for sea lions was less than for comparatively sized mammalian runners at the same speeds. He argued the reduced cost of swimming was attributed to the buoyant effect of water, which removed any energy expenditure for maintaining posture. However, metabolic studies of running and swimming mink showed the converse (Williams, 1983a, 1983b). At equivalent speeds of 0.7 m/s, the mass-specific metabolic rate for swimming mink was 1.6 times that for running and represented the maximum metabolic rate. Running mink attained the maximum rate at a speed nearly 1.0 m/s faster than swimming. This difference is not unexpected, because, despite their aquatic habits, mink are mainly terrestrial in design. Surface paddling by mink, as a compromise for amphibious behaviors, has limitations because of substantial energy losses due to surface effects (see below) and inefficiencies of the propulsive mode (Williams, 1983a).

Increased metabolic effort by anaerobic mechanisms above the aerobic capacity in swimming mammals has been suggested, although information on these mechanisms has been gathered only in experiments on diving (Kooyman, 1987, 1989). Fish (1982) suggested that increased power input to generate thrust at high surface speeds is supplied by anaerobic metabolism. Hui (1987) estimated that an 11 m/s burst of less than 2 s by a dolphin represents a 166-fold increase of the metabolism over resting rates when including the anaerobic contribution.

Extra energy expenditures are required during swimming to cope with thermoregulatory demands (Fish, 1983; MacArthur, 1984; Nadel et al., 1974). For muskrat, a 5°C decrease in water temperature below thermoneutrality can account for a 22% higher metabolic rate at the same swimming speed (Fish, 1983). Such an increase is due to the interaction of the conductivity of the water and convective effect from the velocity. Williams (1986) found the thermal conductance of the mink

to increase with increasing swimming speed that resulted in heat loss exceeding metabolic heat production and a drop in core body temperature. A decrease in body temperature by as much as 3.1°C in free-swimming Weddell seals during both short-duration and long, exploratory dives (Kooyman, 1989) may indicate that heat loss to the water increases because of convection (Whittow, 1987). An elevated metabolic rate has been suggested as a mechanism to maintain homeothermy in aquatic mammals (Hampton and Whittow, 1976; Irving, 1971; Kanwisher and Sundnes, 1966; Whittow, 1987), but this assertion recently has been disputed. Seals and whales have been reported to have basal metabolic rates equivalent to rates predicted for terrestrial mammals (Lavigne et al., 1986; Worthy and Edwards, 1990; Yasui and Gaskin, 1986). The blubber layer provides sufficient insulation for homeothermy in water without an elevated metabolism. Indeed, overheating may be more of a problem in highly active large cetaceans (Brodie, 1975; Worthy and Edwards, 1990).

The conflicting energetic demands of diving with anoxic conditions and exercise suggest metabolic adjustments. Physiological responses by seals are graded according to dive mode (Guppy et al., 1986; Kooyman, 1987). Short feeding dives are considered to be aerobic, whereas longer exploratory dives display the classical dive response of energy conservation and anaerobic metabolism (Castellini et al., 1985; Guppy et al., 1986; Hochachka and Guppy, 1987). Typical dives are short in duration, so that aquatic mammals are within the aerobic dive limits (Dolphin, 1987; Estes, 1989; Feldkamp et al., 1989; LeBoeuf et al., 1986). This behavior comes into conflict during active swimming in that swimming near the surface encumbers increased drag and energy requirements (see above). Harbor seals can stay within their aerobic dive limits, remaining submerged for 82–92% of the time, when swimming under 1.2 m/s (Williams et al., 1991), but they decrease their submergence time during higher and more strenuous swimming speeds to maintain an aerobic, fat-based metabolism (Davis et al., 1991; Williams et al., 1991).

During diving, submerged swimming may be very energy-efficient when compared with surface swimming (Castellini, 1988; Hochachka and Guppy, 1987; Kooyman et al., 1973; Whittow, 1987). Field and laboratory studies of diving seals show depressed oxygen consumption rates compared with sustained exercise (Castellini et al., 1985). Low metabolic rates allow diving mammals to increase their dive time (Fedak et al., 1988; Kooyman et al., 1981). Costello and Whittow

(1975) concluded that the need to conserve oxygen during diving was larger than the high energetic demands of swimming. **Although** the sea otter displays an oxygen consumption during submerged swimming that is **41%** lower than when surface swimming, hypometabolism is unlikely because these animals maintain their metabolism with oxygen supplied from the enlarged lungs without initiating the diving response (Kooyman, 1973; Williams, **1989**). The lower metabolism of diving marine mammals differs from semiaquatic mammals such as the muskrat in which diving and underwater exercise incur an increase in the energetic expenditure above the resting metabolic rate and approach the energy expended during surface swimming (MacArthur and Krause, **1989**).

The metabolic demands of swimming have been calculated using estimates of the hydrodynamic power output. Hui (**1987**) computed the total power input for a dolphin of the *Stenelfa-Delphinus* morphology based on the assumptions of a rigid-body analogy. **His** estimates of dolphin power input for routine and maximum swimming speeds were **1.0–3.4** and **13.4** times the resting metabolic rate, respectively. This result compares favorably with activity levels of aquatic and terrestrial mammals. However, similar calculations for phocid and otariid seals underestimated the power input when compared with measurements of oxygen consumption (Lavigne et al., **1982**).

Association between metabolic rate and swimming speed is important in consideration of the ecology of aquatic mammals. Limitations due to hydrodynamics and energy metabolism will influence the swimming performance and behavior of the animal. Muskrats reach a limit in their aerobic capacity at **0.6** m/s and routinely swim at a slightly lower velocity (Fish, **1982**). This behavior ensures that the muskrat can economically locomote without invoking an anaerobic metabolism and its associated oxygen debt. The low metabolic effort for harbor seals at routine swimming speed (**1.4** m/s) would be advantageous during diving when energy conservation is critical, whereas the more economical but higher maximum range speed (**2.2–2.3** m/s) is believed to be used in migrations or movement to food patches (Williams, **1987**).

Aerobic Efficiency and Cost of Transport

Aerobic efficiency (η_a) is calculated as the ratio of power output to aerobically supplied power input and relates the thrust power to the

active metabolic rate of a swimming animal. The η_a for swimming mammals is lower than the maximum value of 0.22 reported for fish (Webb, 1975b). Both otariid and phocid seals have the highest values of aerobic efficiency (0.12–0.30) for aquatic mammals, probably because of the streamlined pinniped body form and swimming modes (Feldkamp, 1987a; Innes, 1984; Williams et al., 1991). Because η_a , however, was computed using drag estimates that represent the minimum thrust required, values for seals could be higher if the power output was measured using thrust-based models. Peak values of η_a for surface paddlers show these animals to be less efficient than the submerged lift-based propulsion of seals. The η_a for muskrats (Fish, 1984), minks (Williams, 1983a), and humans (DiPrampero et al., 1974) are **0.046**, 0.014, and 0.052, respectively.

The cost of transport (CT) is also used as a means of assessing the metabolic efficiency of locomotion (Schmidt-Nielsen, 1972; Tucker, 1970). CT is defined as the metabolic energy required to transport a unit mass a unit distance. Figure 3.5 shows minimum CT for various aquatic mammals as a function of body mass. The values of mammalian CT are compared with the regression for fish, which represents the lowest minimum CT for any animal or method of locomotion.

All aquatic mammals have values of minimum CT that are higher than for fish of equivalent sizes. Although higher maintenance costs associated with homeothermy could account for the difference of CT, high drag due to surface swimming and locomotory modes additionally would produce an elevated CT (Fish, 1982).

Surface-paddling muskrats (Fish, 1982), mink (Williams, 1983a), sea otters (Williams, 1989), and humans (P. E. DiPrampero, pers. comm., 1979) have the highest minimum CT for swimming mammals at 10–25 times the CT of fish of equivalent sizes. A lower minimum CT is attained by mammals that swim submerged and use more-efficient propulsive modes. The amount of oxygen used by humans to swim a unit distance is six to nine times that used by harbor seals (Craig and Pasche, 1980). The sea otter has a 40% lower minimum CT when swimming in a submerged undulatory mode than when surface paddling (Williams, 1989). Further decreases in the minimum CT are attained for lift-based oscillators and undulators that are only 1.9–4.6 times the minimum CT for a similar-sized fish (Costello and Whittow, 1975; Davis et al., 1985; Feldkamp, 1987a; Innes, 1984; Kruse, 1975). Schmidt-Nielsen (1972) predicted from hydrodynamic data and estimates of muscular efficiency that the minimum CT for a dolphin

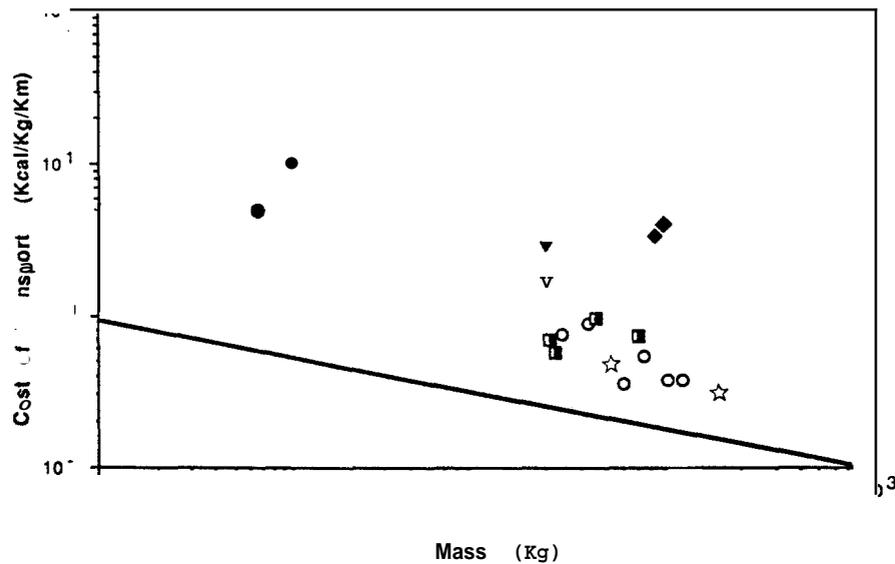


Fig. 3.5. Comparison of the minimum cost of transport over a range of body masses. Symbols represent mink (■; Williams, 1983), muskrat (●; Fish, 1982), sea otter (▼ and V; Williams, 1984), human (◆; P. E. DiPrampo, pers. comm., 1979), sea lion (■; Costello and Whittow, 1975; Feldkamp, 1987a; Kruse, 1975), phocid seals (○; Davis et al., 1985; Innes, 1984), and dolphins (☆; T. M. Williams, pers. comm., 1991; Worthy et al., 1987). Closed symbols represent surface paddlers, open symbols represent submerged undulatory propulsors, and half symbols represent lift-based oscillators. The solid line is the minimum cost of transport extrapolated from data on fish (Davis et al., 1985).

should fall on the line for fish. However, there has been no controlled study that confirms this assertion. The CT calculated from the average metabolic rate of a 41.5-kg harbor porpoise swimming at approximately 2 m/s (Worthy et al., 1987) is still 2.5 times the minimum value, although the single estimate may not reflect the minimum CT of the porpoise. A similar assertion of low minimum CT for the sea lion (Lavigne et al., 1982; Luecke et al., 1975) also represents an underestimate from the metabolically derived CT (Feldkamp, 1987a).

Regardless of swimming mode, the minimum CT for many aquatic mammals has been found to coincide with their routine swimming speeds. During foraging bouts or migrations, this behavior would be economically advantageous because it minimizes energy expenditure while maximizing distance traveled. Fish (1982) found that muskrats swim at a speed within aerobic limits at the minimum CT. Dive velocities of otariids were observed to be equal to or less than the minimum CT velocity (Ponganis et al., 1990). Thus, for the available oxygen

stores fur seals and sea lions are able to cover the greatest distance during the foraging dives and remain within the aerobic dive limits. Migrating gray whales (*Eschrichtius robustus*) have a minimum CT based on breathing rate that occurs at the mean velocity of 2.0 m/s (Sumich, 1983). Economical travel would be paramount for extending the stored energy reserves over a migration of 15,000–20,000 km, during which the whales fast.

Conclusions

Swimming performance (speed, acceleration, and endurance) is directly related to the ability to effectively use available energy resources in response to hydrodynamic requirements in the balance of thrust and drag (Weihs and Webb, 1983). For mammals, the evolutionary transition from terrestrial to semiaquatic and ultimately fully aquatic habits has allowed for increased swimming performance by abandoning the water surface and adopting low-drag body forms with changes in propulsive mode (Fig. 3.6). Metabolic and biomechanic studies of swimming show lift-based modes to have higher efficiency and higher performance levels than the paddling mode. The semiaquatic nature of most paddlers restricts the development of aquatic specialization for increased efficiency and performance. The vastly different environments for these mammals dictates concessions of locomotor agility. Highly aquatic mammals use efficient lift-based modes, which reduce drag and increase thrust. The oscillatory pectoral mode of otariids affords these animals greater high-speed maneuverability with a constant generation of thrust throughout the stroke cycle. Although different in orientation, the undulatory modes of cetaceans and phocids are analogous to the modes of piscine vertebrates for high efficiency, rapid propulsion. The convergence of swimming mode and low-drag body form indicate the importance of energetics in highly aquatic mammals. However, ecological and historical constraints limit the evolution of optimal designs, so that aquatic mammals represent compromises between form, function, and phylogeny.

The above review on swimming mammals, although demonstrating the energy relationship between active metabolic rate and power output for mammals and elucidating the physical causations of energy loss, reflects a largely incomplete picture. The size of most aquatic mammals, their availability, and problems associated with data collec-

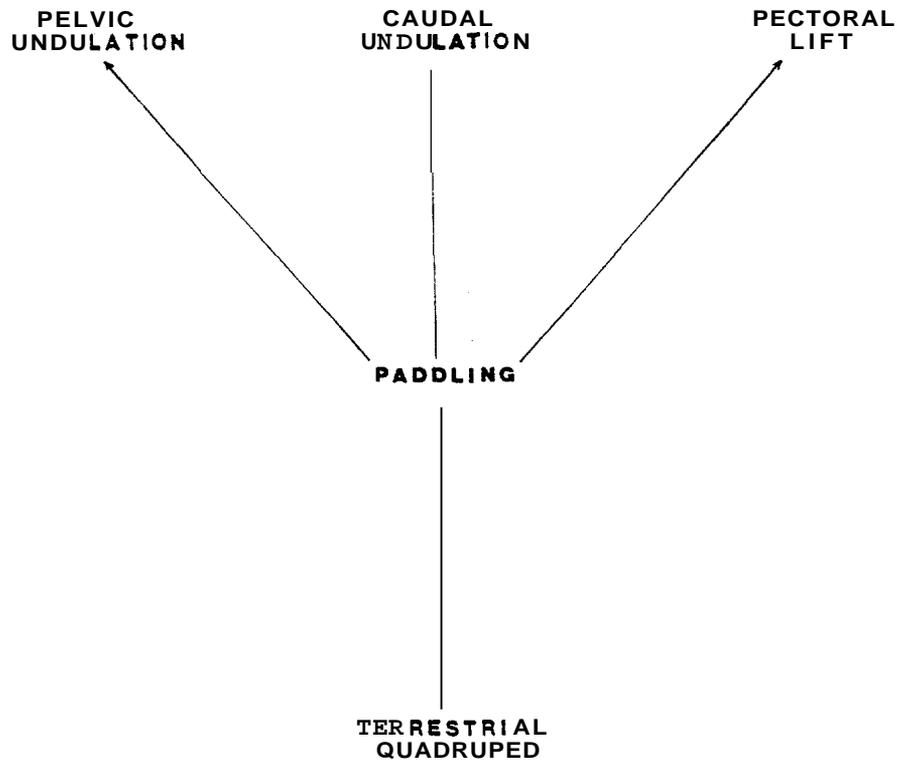


Fig. 3.6. A possible evolutionary relationship of mammalian swimming modes.

tion in water both in the field and laboratory have prevented a full examination of the evolutionary and ecological diversity over a complete range of performance levels. The basis for all future studies on swimming mammals must be reliable measurements and observations of performance, including speeds, accelerations, and maneuverability. Ecological and evolutionary questions can be addressed by examining a greater diversity of aquatic mammals than has previously been investigated. This diversity should include considerations of size, swimming mode, population variation, and variation between closely related species. Specifically, the cetaceans and sirenians should be targeted for examination because of their importance as highly derived aquatic mammals and the paucity of information on their active metabolism and mechanism of thrust production. The convergence of similar body designs, despite different activity levels and diets, may provide an understanding of similar physical constraints and evolutionary pathways of these two phylogenetically different groups. Finally, investigations of

the evolutionary transition from terrestrial to semiaquatic to fully aquatic mammals should employ an experimental design in which direct comparisons of performance are measured in terrestrial and aquatic situations. Examinations of this type would provide insight to the compromises inherent in physiological and morphological adaptations that operate in **two** different physical environments.

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Literature Cited

- Alexander, R. McN. **1983**. *Animal Mechanics*. Blackwell, Oxford. **301** pp.
- Aleyev, Yu. G. **1977**. *Nekton*. Junk, The Hague. **435** pp.
- Au, D. **1980**. Leaping dolphins. Letter to the editor. *Nature*, **287:759**.
- Au, D., and D. Weihs. **1980**. At high speeds dolphins save energy by leaping. *Nature*, **284:548–550**.
- Backhouse, K. M. **1961**. Locomotion of seals with particular reference to the forelimb. *Symp. Zool. Soc. Lond.*, **5:59–75**.
- Barnes, L. G., D. P. Domning, and C. E. Ray. **1985**. Status of studies on fossil marine mammals. *Mar. Mamm. Sci.*, **1:15–53**.
- Best, T. L., and E. B. Hart. **1976**. Swimming ability of pocket gophers (Geomyidae). *Tex. J. Sci.*, **27:361–366**.
- Blake, R. W. **1979**. The mechanics of labriform locomotion. I. Labriform locomotion in the angelfish (*Pterophyllum eimekei*): an analysis of the power stroke. *J. Exp. Biol.*, **82:255–271**.
- . **1980**. The mechanics of labriform locomotion. II. An analysis of the recovery stroke and the overall fin-beat cycle propulsive efficiency in the angelfish. *J. Exp. Biol.*, **85:337–342**.
- . **1983a**. Energetics of leaping dolphins and other aquatic animals. *J. Mar. Biol. Assoc. U.K.*, **63:61–70**.
- . **1983b**. *Fish locomotion*. Cambridge University Press, London. **208** pp.
- Bose, N., and J. Lien. **1990**. Energy absorption from ocean waves: a free ride for cetaceans. *Proc. R. Soc. Lond. B*, **240:591–605**.
- Brodie, P. F. **1975**. Cetacean energetics, an overview of intraspecific size variation. *Ecology*, **56:152–161**.
- Bryant, H. C. **1919**. The coyote not afraid of water. *J. Mammal*, **1:87–88**.
- Castellini, M. A. **1988**. Visualizing metabolic transitions in aquatic mammals: does apnea plus swimming equal “diving”? *Can. J. Zool.*, **66:40–44**.
- Castellini, M. A., B. J. Murphy, M. Fedak, K. Ronald, N. Gofton, and P. W. Hochachka. **1985**. Potentially conflicting metabolic demands of diving and exercise in seals. *J. Appl. Physiol.*, **58:392–399**.

- Chanin, P. **1985**. The Natural History of Otters. Facts on File Publ., New York. 179 pp.
- Chopra, M. G., and T. Kambe. **1977**. Hydrodynamics of lunate-tail swimming propulsion. Part 2. *J. Fluid Mech.*, **79**:49–69.
- Cole, L. J. **1922**. Red squirrels swimming a lake. *J. Mammal.*, **3**:53–54.
- 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. Edmondson, 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. Pasche. **1980**. Respiratory physiology of freely diving harbor seals (*Phoca 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. **1984**. Unsteady aspects of aquatic locomotion. *Am. Zool.*, **24**:121–134.
- Daniel, T. L., and P. W. Webb. **1987**. Physical determinants of locomotion. Pp. 343–369 in *Comparative Physiology: Life in Water and on Land* (P. Dejours, L. Bolis, C. R. Taylor, and E. R. Weibel, eds.). Liviana Press, New York. 556 pp.
- Davis, R. W., M. A. Castellini, T. M. Williams, and G. L. Kooyman. **1991**. Fuel homeostasis in the harbor seal during submerged swimming. *J. Comp. Physiol. B*, **160**:627–635.
- 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.
- DiPrampo, P. E., D. R. Pendergast, D. W. Wilson, and D. W. Hennie. **1974**. Energetics of swimming in man. *J. Appl. Physiol.*, **37**:1–5.
- Dolphin, W. F. **1987**. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. *Can. J. Zool.*, **65**:354–362.
- English, A. W. **1976**. Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). *J. Zool. (Lond.)*, **178**:341–364.
- Essapian, F. S. **1955**. Speed-induced skin folds in the bottle-nosed porpoise, *Tursiops truncatus*. *Breviora Mus. Comp. Zool.*, **43**:1–4.
- Estes, J. A. **1989**. Adaptations for aquatic living by carnivores. Pp. 242–282 in *Carnivore Behavior, Ecology, and Evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York. 624 pp.
- Fedak, M. A., M. R. Pullen, and J. Kanwisher. **1988**. Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. *Can. J. Zool.*, **66**:53–60.
- Feidkamp, S. D. **1987a**. Swimming in the California sea lion: Morphometrics, drag and energetics. *J. Exp. Biol.*, **131**:117–135.
- . **1987b**. Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool. (Lond.)*, **212**:43–57.
- Feldkamp, S. D., R. L. DeLong, and G. A. Antonelis. **1989**. Diving patterns of California sea lions, *Zalophus californianus*. *Can. J. Zool.*, **67**:872–883.
- Fish, F. E. **1982**. Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.*, **55**:180–189.
- . **1983**. Metabolic effects of swimming velocity and water temperature in the muskrat (*Ondatra zibethicus*). *Comp. Biochem. Physiol.*, **75**:397–400.
- . **1984**. Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). *J. Exp. Biol.*, **110**:183–201.
- . **1985**. Swimming dynamics of a small semi-aquatic mammal. *Am. Zool.*, **25**:13A.
- . **1987**. Swimming mode changes associated with terrestrial-semiaquatic transition in mammals. *Am. Zool.*, **27**:86A.
- 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.

- Flyger, V., and M. R. Townsend. 1968. The migration of polar bears. *Sci. Am.*, 218:108–116.
- Fregin, G. F., and T. Nicholl. 1977. Swimming: its influences on heart rate, respiration rate, and some hematological values in the horse. *J. Equine Med. Surg.*, 1:288–293.
- Gaskin, D. E. 1982. *The Ecology of Whales and Dolphins*. Heinemann, London. 459 pp.
- Gingerich, P. D., N. A. Wells, D. E. Russell, and S. M. I. Shah. 1983. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan. *Science*, 220:403–406.
- Godfrey, S. J. 1985. Additional observations of subaqueous locomotion in the California sea lion (*Zalophus californianus*). *Aquat. Mamm.*, 11:53–57.
- Gordon, C. N. 1980. Leaping dolphins. Letter to the editor. *Nature*, 287:759.
- Gordon, K. R. 1981. Locomotor behaviour of the walrus (*Odobenus*). *J. Zool. (Lond.)*, 195:349–367.
- Gray, J. 1936. Studies in animal locomotion. VI. The propulsive powers of the dolphin. *J. Exp. Biol.*, 13:192–199.
- Guppy, M., R. D. Hill, R. C. Schneider, J. Qvist, G. C. Liggins, W. M. Zapol, and P. W. Hochachka. 1986. Microcomputer-assisted metabolic studies of voluntary diving of Weddell seals. *Am. J. Physiol.*, 250:R175–R187.
- Hampton, I. F. G., and G. C. Whittow. 1976. Body temperature and heat exchange in the Hawaiian spinner dolphin, *Stenella longirostris*. *Comp. Biochem. Physiol.*, 55A:195–197.
- Hart, J. S., and H. D. Fisher. 1964. The question of adaptations to polar environments in marine mammals. *Fed. Proc.*, 23:1207–1214.
- Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. *Spec. Publ. Am. Soc. Mammal.* No. 5. 153 pp.
- Hertel, H. 1966. *Structure, Form, Movement*. Reinhold, New York. 251 pp.
- . 1969. Hydrodynamics of swimming and wave-riding dolphins. Pp. 31–63, in *The Biology of Marine Mammals* (H. T. Andersen, ed.). Academic Press, New York. 511 pp.
- Hickman, G. C. 1983. Burrows, surface movement, and swimming of *Tachyoryctes splendens* (Rodentia: Rhizomyidae) during flood conditions in Kenya. *J. Zool. (Lond.)*, 200:71–82.
- . 1984. Swimming ability of talpid moles, with particular reference to the semi-aquatic *Condylura cristata*. *Mammalia*, 43:505–513.
- Hochachka, P. W. 1980. *Living without oxygen*. Harvard University Press, Cambridge. 181 pp.
- Hochachka, P. W., and M. Guppy. 1987. Diving mammals and birds. Pp. 36–56 in *Metabolic Arrest and the Control of Biological Time* (P. W. Hochachka and M. Guppy, eds.). Harvard University Press, Cambridge. 227 pp.
- Holmer, I. 1972. Oxygen uptake during swimming in man. *J. Appl. Physiol.*, 33:502–509.
- Howell, A. B. 1930. *Aquatic Mammals*. Charles C Thomas, Springfield, Ill. 338 pp.
- Hui, C. 1987. Power and speed of swimming dolphins. *J. Mammal*, 68:126–132.
- . 1989. Surface 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. Ph.D. dissertation, University of Guelph, Ontario.
- Irving, L. 1971. Aquatic mammals. Pp. 47–96 in *Comparative Physiology of Thermoregulation*. Vol. 3 (G. C. Whittow, ed.). Academic Press, New York. 278 pp.
- Kanwisher, J., and G. Sundnes. 1966. Thermal regulation in cetaceans. Pp. 397–407 in *Whales, Dolphins and Porpoises* (K. S. Norris, ed.). University of California Press, Berkeley. 789 pp.

- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *N. Am. Fauna*, **68**:1–352.
- Kermack, K. A. 1948. The propulsive powers of blue and fin whales. *J. Exp. Biol.*, **25**:237–240.
- King, J. E. 1983. *Seals of the World*. Cornell University Press, Ithaca. 240 pp.
- Kooyman, G. L. 1973. Respiratory adaptations of marine mammals. *Am. Zool.*, **13**:457–468.
- . 1985. Physiology without restraint in diving mammals. *Mar. Mamm. Sci.*, **1**:166–178.
- . 1987. A reappraisal of diving physiology: seals and penguins. Pp. 459–469 in *Comparative Physiology: Life in Water and on Land*. Vol. 9 (P. Dejours, L. Bolis, C. R. Taylor, E. R. Weibel, eds.). Fidia Research Series, Liviana Press, Padova. 556 pp.
- . 1989. *Diverse Divers*. Springer-Verlag, Berlin. 200 pp.
- Kooyman, G. L., M. A. Castellini, and R. W. Davis. 1981. Physiology of diving in marine mammals. *Annu. Rev. Physiol.*, **43**:343–356.
- Kooyman, G. L., D. H. Kerem, W. B. Campbell, and J. J. Wright. 1973. Pulmonary gas exchange in freely diving Weddell seals (*Leptonychotes weddelli*). *Respir. Physiol.*, **17**:283–290.
- Kramer, M. O. 1960a. Boundary layer stabilization by distributing damping. *J. Am. Soc. Nav. Eng.*, **72**:25–33.
- . 1960b. The dolphin's secret. *New Sci.*, **7**:1118–1120.
- . 1965. Hydrodynamics of the dolphin. Pp. 111–130 in *Advances in Hydroscience*. Vol. 2 (V. T. Chow, ed.). Academic Press, New York.
- Kruse, D. H. 1975. Swimming metabolism of California sea lions, *Zalophus californianus*. M.S. thesis, San Diego State University.
- Kurbatov, B. V., and Yu. E. Mordvinov. 1974. Hydrodynamic resistance of semiaquatic mammals. *Zool. Zh.*, **53**:104–110.
- Lang, T. G. 1966. Hydrodynamic analysis of cetacean performance. Pp. 410–432 in *Whales, Dolphins and Porpoises* (K. S. Norris, ed.). University of California Press, Berkeley. 789 pp.
- Lang, T. G., and D. A. Daybell. 1963. Porpoise performance tests in a seawater tank. *Nav. Ord. Test Sm.*, China Lake, Calif. NAVWEPS Rept. 8060. NOTS Tech. Publ. 3063.
- Lang, T. G., and K. Pryor. 1966. Hydrodynamic performance of porpoises (*Stenella attenuata*). *Science*, **152**:531–533.
- Lavigne, D. M., W. Barchard, S. Innes, and N. A. Oritsland. 1982. Pinniped bioenergetics. FOA Fisheries Series No. 5, *Mammals in Seas*, **4**:191–235.
- Lavigne, D. M., S. Innes, G. A. J. Worthy, K. M. Kovacs, O. J. Schmitz, and J. P. Hickie. 1986. Metabolic rates of seals and whales. *Can. J. Zool.*, **64**:279–284.
- LeBoeuf, B. J., D. P. Costa, A. C. Huntley, G. L. Kooyman, and R. W. Davis. 1986. Pattern and depth of dives in Northern elephant seals, *Mirounga angustirostris*. *J. Zool. (Lond.)*, **208**:1–7.
- Lighthill, M. J. 1969. Hydrodynamics of aquatic animal propulsion. *Annu. Rev. Fluid Mech.*, **1**:413–446.
- . 1970. Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid Mech.*, **44**:265–301.
- . 1971. Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. Ser. B. Biol. Sci.*, **179**:125–138.
- Lindsey, C. C. 1978. Form, function, and locomotory habits in fish. Pp. 1–100 in *Fish Physiology: Locomotion*. Vol. 7 (W. S. Hoar and D. J. Randall, eds.). Academic Press, New York. 576 pp.
- Luecke, R. H., V. Natarajan, and F. E. South. 1975. A mathematical biothermal model of the California sea lion. *J. Therm. Biol.*, **1**:35–45.

- MacArthur, R. A. 1984. Aquatic thermoregulation in the muskrat (*Ondatrazibethicus*): energy demands of swimming and diving. *Can. J. Zool.*, **62**:241–248.
- MacArthur, R. A., and R. E. Krause. 1989. Energy requirements of freely diving muskrats (*Ondatrazibethicus*). *Can. J. Zool.*, **67**:2194–2200.
- Mordvinov, Yu. E. 1972. Some hydrodynamic parameters of body shape in Pinnipedia. *Hydrobiol. J.* **8**:81–84.
- . 1974. The character of boundary layer in the process of swimming in the muskrat (*Ondatrazibethica*) and mink (*Mustelalutreola*). *Zool. Zh.*, **53**:430–435.
- . 1976. Locomotion in water and the indices of effectiveness of propelling systems for some aquatic mammals. *Zool. Zh.*, **55**:1375–1382.
- Mordvinov, Yu. E., and B. V. Kurbatov. 1972. Influence of hair cover in some species of Phocidae upon the value of general hydrodynamic resistance. *Zool. Zh.*, **51**:242–247.
- Nadel, E. R. 1977. Thermal and energetic exchanges during swimming. Pp. 91–119 in *Problems with Temperature Regulation during Exercise* (E. R. Nadel, ed.). Academic Press, New York. 141 pp.
- Nadel, E. R., I. Holmer, U. Bergh, P. O. Astrand, and A. J. A. Stolwijk. 1974. Energy exchanges of swimming man. *J. Appl. Physiol.*, **36**:465–471.
- Nishiwaki, M., and H. Marsh. 1985. Dugong. Pp. 1–31 in *Handbook of Marine Mammals*. Vol. 3 (S. H. Ridgeway and R. Harrison, eds.). Academic Press, New York. 362 pp.
- Norris, K. S., and J. H. Prescott. 1961. Observations on Pacific cetaceans of California and Mexican waters. *Univ. Calif. Publ. Zool.*, **63**:291–402.
- Øritsland, N. A., and K. Ronald. 1975. Energetics of the free diving harp seal (*Pagophilus groenlandicus*). *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.*, **169**:451–454.
- Parry, D. A. 1949. The swimming of whales and a discussion of Gray's paradox. *J. Exp. Biol.*, **26**:24–34.
- Petersen, C. G. J. 1925. The motion of whales during swimming. *Nature*, **116**:327–329.
- Ponganis, P. J., E. P. Ponganis, K. V. Ponganis, G. L. Kooyman, R. L. Gentry, and F. Trillmich. 1990. Swimming velocities in otariids. *Can. J. Zool.*, **68**:2105–2112.
- Purves, P. E. 1963. Locomotion in whales. *Nature*, **197**:334–337.
- Purves, P. E., W. H. Dudok van Heel, and A. Jonk. 1975. Locomotion in dolphins. Part I. Hydrodynamic experiments on a model of the bottle-nosed dolphin, *Tursiops truncatus*, (Mont.). *Aquat. Mamm.*, **35**–31.
- Ray, G. C. 1963. Locomotion in pinnipeds. *Nat. Hist. (N.Y.)*, **72**:10–21.
- Ridgeway, S. H., and R. J. Harrison. 1981. *Handbook of Marine Mammals*. Vol. 1. The walrus, sea lions, fur seals and sea otter. Academic Press, London. 235 pp.
- Rosen, M. W. 1963. Flow visualization experiments with a dolphin. *Nav. Ord. Test. Sm., China Lake, Calif. NAVWEPS Rept.* **8062**, NOTS Tech. Publ. **3065**.
- Schmidt-Nielsen, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science*, **117**:222–228.
- Slijper, E. J. 1961. Locomotion and locomotory organs in whales and dolphins (Cetacea). *Symp. Zool. Soc. Lond.*, **5**:77–94.
- Sokolov, V. 1960. Some similarities and dissimilarities in the structure of the skin among the members of the suborders Odontoceti and Mysticoceti (Cetacea). *Nature*, **185**:745–747.
- . 1962. Adaptations of the mammalian skin to the aquatic mode of life. *Nature*, **195**:464–466.
- Sokolov, V., I. Bulina, and V. Rodionov. 1969. Interaction of dolphin epidermis with flow boundary layer. *Nature* **222**:267–268.

- Stein, B. R. **1981**. Comparative limb myology of two opossums, *Didelphis* and *Chironectes*. *J. Morphol.*, **169**:113–140.
- 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.
- Talmage, R. V., and G. D. Buchanan. **1954**. The armadillo (*Dasypus novemcinctus*). A review of its natural history, ecology, anatomy and reproductive physiology. Rice Inst. Pamph. Monogr. Biol., **41**:1–135.
- Tarasoff, F. J., A. Bisailon, 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.
- Tedford, R. H. **1976**. Relationship of pinnipeds to other carnivores (Mammalia). *Syst. Zool.*, **25**:363–374.
- Tucker, V. A. **1970**. Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.*, **34**:841–846.
- Videler, J., and P. Kamermans. **1985**. Differences between upstroke and downstroke in swimming dolphins. *J. Exp. Biol.*, **119**:265–274.
- Vogel, S. **1981**. *Life in Moving Fluids*. Willard Grant Press, Boston. 352 pp.
- Walker, E. P. **1975**. *Mammals of the World*. Johns Hopkins University Press, Baltimore. 1500 pp.
- Webb, P. W. **1975a**. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.*, **190**:1–159.
- . **1975b**. Efficiency of pectoral-fin propulsion of *Cymatogaster aggregata*. Pp. 573–584 in *Swimming and Flying in Nature*, Vol. 2 (T. Y. Wu, C. J. Brokaw, and C. Brennen, eds.). Plenum Press, New York. 1005 pp.
- . **1978**. Hydrodynamics: nonscombrid fish. Pp. 189–237 in *Fish Physiology: Locomotion*. Vol. 7 (W. S. Hoar and D. J. Randall, eds.). Academic Press, New York. 576 pp.
- . **1984**. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.*, **24**:107–120.
- Webb, P. W., and R. W. Blake. **1985**. Swimming. Pp. 110–128 in *Functional Vertebrate Morphology* (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Harvard University Press, Cambridge. 429 pp.
- Weihs, D., and P. W. Webb. **1983**. Optimization of locomotion. Pp. 339–371 in *Fish Biomechanics* (P. W. Webb and D. Weihs, eds.). Praeger, New York. 398 pp.
- Whittow, G. C. **1987**. Thermoregulatory adaptations in marine mammals: interacting effects of exercise and body mass. A review. *Mar. Mamm. Sci.*, **3**:220–241.
- Williams, T. M. **1983a**. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. Exp. Biol.*, **103**:155–168.
- . **1983b**. Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body on running energetics and gait patterns. *J. Exp. Biol.*, **105**:283–295.
- . **1986**. Thermoregulation of the North American mink during rest and activity in the aquatic environment. *Physiol. Zool.*, **59**:293–305.
- . **1987**. Approaches for the study of exercise physiology and hydrodynamics in marine mammals. Pp. 127–145 in *Approaches to Marine Mammal Energetics* (A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini, eds.). Spec. Publ. Soc. Mar. Mammal., **1**:1–253.
- . **1989**. Swimming by sea otters: adaptations for low energetic cost locomotion. *J. Comp. Physiol. A*, **164**:815–824.
- Williams, T. M., and G. I. 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. B*, **160**:637–644.
- Williamson, G. R. **1972**. The true body shape of rorqual whales. *J. Zool. (Lond.)*, **167**:277–286.
- Worthy, G. A., and E. F. Edwards. **1990**. Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoenaphocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiol. Zool.*, **63**:432–442.
- 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 *Approaches to Marine Mammal Energetics* (A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini, eds.). *Spec. Publ. Soc. Mar. Mammal.*, **1**:1–253.
- Wu, T. Y. **1971**. Hydrodynamics of swimming propulsion. Part 2. Some optimum shape problems. *J. Fluid Mech.*, **46**:521–544.
- Yasui, W. Y., and D. E. Gaskin. **1986**. Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). *Ophelia*, **25**:183–197.
- Yates, G. T. **1983**. Hydromechanics of body and caudal fin propulsion. Pp. **177–213** in *Fish Biomechanics* (P. W. Webb and D. Weihs, eds.). Praeger, New York, **398** pp.
- Yurchenko, N. F., and V. V. Babenko. **1980**. Stabilization of the longitudinal vortices by skin integuments of dolphins. *Biophysics*, **25**:309–315.