

Influence of Hydrodynamic Design and Propulsive Mode on Mammalian Swimming Energetics

Frank E. Fish

Department of Biology, West Chester University,
West Chester, PA 19383, USA.

Abstract

Optimisation of energy by aquatic mammals requires adaptations that reduce drag, and improve thrust production and efficiency. Drag is minimised by streamlining the body and appendages. Highly derived aquatic mammals have body shapes close to the optimal hydrodynamic design for drag reduction. There is no conclusive evidence for specialised drag reduction mechanisms, although decreasing hair density is associated with reduced drag. Improvement in thrust production and efficiency is accomplished by changes in propulsive mode and appendage design. Semiaquatic mammals employ drag-based propulsion using paddles, whereas fully aquatic mammals use lift-based propulsion with hydrofoils. Because paddling generates thrust through half the stroke cycle, propulsive efficiency is low and energetic cost is high compared with that for mammals using hydrofoils. Lift-based swimming is a rapid and high-powered propulsive mode. Oscillations of the hydrofoil generate thrust throughout the stroke cycle. For cetaceans and pinnipeds, propulsive efficiency is approximately 80%, and transport cost is below that of semiaquatic mammals. Behavioural adaptations help minimise energy expenditure by swimming mammals. Submerged swimming avoids increased drag from energy lost in formation of surface waves. Porpoising and wave riding, characteristic of dolphins, can reduce the transport costs, allowing for longer-duration swimming at high speeds.

Introduction

Design is acknowledged to have a major impact on the ecological performance of organisms (Liem 1990). The similarity with fish that is displayed in body design and propulsive mode of aquatic mammals, such as cetaceans, is considered the quintessential example of evolutionary convergence (Howell 1930). Such convergence is associated with constraints imposed on animals by the physical environment and with selection for morphological, physiological and behavioural adaptations for swimming that maximise efficiency (Daniel and Webb 1987; Blake 1991). Because swimming is an integral behaviour to mammals that forage, mate, escape predation, disperse, and migrate in water, constraints on performance promoted adaptations for effective locomotion by aquatic mammals (Fish 1992b). Evolution of highly derived aquatic morphologies and swimming modes represents the culmination of a sequence of transitional stages displayed by terrestrial quadrupeds to fully aquatic mammals (Howell 1930; Gingerich *et al.* 1990; Fish 1992b).

However, the study of swimming performance and its influence on the evolution of aquatic mammals cannot be easily examined. Within any clade of extant mammalian species, there is no complete sequence of transitional stages with respect to design and swimming mode from terrestrial to fully aquatic habits. Mustelids exhibit the broadest gradient of transitional stages (Fish and Stein 1991), although sea otters (*Enhydra lutris*) are not fully independent of the land (Kenyon 1969; Chanin 1985; Estes 1989). Those clades that are most aquatic

i.e. Cetacea, Pinnipedia, Sirenia) are morphologically disjunct from their ancestral groups (i.e. cetaceans are related to artiodactyls and evolved from mesonychid Condylarthra; Van Valen 1966; Wyss 1990). The fossil record rarely shows intermediate forms for these clades and postcranial material is often missing (Gingerich *et al.* 1983, 1990; Barnes *et al.* 1985). In addition, arguments concerning monophyly versus polyphyly with regard to cetacean and pinniped phylogenies have questioned the origins of these orders (Barnes *et al.* 1985; Wyss 1989).

In general, aquatic mammals display a wide variety of adaptations due to their diverse evolutionary histories and performance requirements (Table 1). Cetaceans and sirenians totally abandoned the terrestrial environment and swim by undulation of the body and tail in concert with caudal flukes. Pinnipeds maintain their link with the land, although extremely limited, and swim using paired limbs that are modified as flippers. These highly derived aquatic mammals are regarded as accomplished swimmers and divers that operate throughout the expanse of the marine environment. In comparison, semiaquatic mammals appear slow and inefficient in water and are restricted to shallow freshwater bodies and near-shore environments. Semiaquatic mammals must compromise form and function to operate in the vastly different environments of water and land (Fish 1982*b*, 1984; Williams 1983). These mammals employ paddle propulsion that has been modified from terrestrial gait patterns (Fish 1992*b*, 1993).

Table 1. Mammalian diversity with regard to swimming mode and aquatic habits

Order	Representative	Propulsion	Habits
Monotremata	<i>Ornithorynchus</i>	pectoral paddling	semiaquatic
Marsupialia	<i>Chironectes</i>	pelvic paddling	semiaquatic
Insectivora	<i>Desmana</i>	pelvic paddling	semiaquatic
	<i>Potomogale</i>	caudal undulation	semiaquatic
	<i>Sorex</i>	pelvic paddling	semiaquatic
	<i>Thalarchos</i>	pectoral paddling	semiaquatic
Carnivora	<i>Mustela</i>	quadrupedal paddling	semiaquatic
	<i>Lutra</i>	pelvic paddling and undulation	semiaquatic
	<i>Enhydra</i>	pelvic paddling and undulation	aquatic
	<i>Phoca</i>	pelvic oscillation	aquatic
Pinnipedia	<i>Zalophus</i>	pectoral oscillation	aquatic
	<i>Odobenus</i>	pelvic oscillation	aquatic
	<i>Trichechus</i>	caudal oscillation	aquatic
	<i>Hippopotamus</i>	quadrupedal paddling	semiaquatic
Cetacea	<i>Tursiops</i>	caudal oscillation	aquatic
	<i>Balaenoptera</i>	caudal oscillation	aquatic
Rodentia	<i>Castor</i>	pelvic paddling	semiaquatic
	<i>Ondatra</i>	pelvic paddling	semiaquatic
	<i>Hydrochoerus</i>	quadrupedal paddling	semiaquatic
Lagomorpha	<i>Sylvilagus</i>	quadrupedal paddling	semiaquatic

To understand the performance limits and the evolutionary transition associated with increasing aquatic habits by mammals, the energetics of swimming can be examined with regard to the propulsive modes and morphologies of extant species. If aquatic mammals are adapted to swim in a manner that minimises energy expenditure, there should be distinct metabolic and hydrodynamic advantages to morphological designs and propulsive modes employed by the most derived species. Analysis of swimming mechanics and energetics may thus elucidate physical and biological constraints that may have influenced the transitional stages of aquatic mammals.

Physical Characteristics of Water affecting Swimming Performance

The energetic cost of swimming by mammals is affected by water-flow patterns around the swimmer as dictated by physical properties of the aquatic medium (Daniel and Webb 1987; Webb 1988). Most important are density and viscosity (Daniel and Webb 1987). Density affects inertial and pressure forces within a fluid whereas viscosity is the internal resistance to distortion and produces fluid friction (Webb 1988). Water is over 800 times denser than air, and at least 30 times more viscous. Thus, the resistance of moving through water is greater than in air. An additional disadvantage of moving through water is that it yields when pushed against (Lindsey 1978). Energy is lost to eddy formation as the water is pushed on by an animal to effect propulsion. As a consequence of the physical characteristics of the medium, movement through water imposes severe limitations on speed and energetic performance for swimming mammals.

Despite these limitations, there are advantages to moving in water. Aquatic locomotion can be the most economical form of transport (Schmidt-Nielsen 1972). Because the density of the tissues are close to that of water, a swimmer is neutrally buoyant. Swimmers do not expend energy to support the body during locomotion as do terrestrial animals and flyers (Rayner 1986; Withers 1992). The power required for swimming is determined by speed and stress developed in muscles, but is not affected by gravity (Pennycuik 1992). This allowed aquatic mammals to display over a ten-million-fold range in body mass from a 12-g water shrew (*Sorex palustris*) to a 150-ton blue whale (*Balaenoptera musculus*). Swimming is also relatively economical, because propulsive forces are easy to generate in water (Rayner 1985, 1986).

Energy Balance

A swimming mammal expends mechanical and metabolic energy to generate a propulsive force, thrust, that is opposed equally by a resistive force, drag. When swimming at constant velocity (U), thrust (T) and drag (D) are equal. The rate of energy use during swimming is given by

$$M\eta_a = P\eta_p = TU = DU \quad (1)$$

where M is metabolic rate, η_a is aerobic efficiency, P is total power output, η_p is propulsive efficiency, and TU and DU represent thrust and drag power outputs, respectively. Power output is the rate of energy use to perform work.

Metabolic rate represents power input and indicates the potential energy available by an animal to do work. Metabolic rate is measured typically by oxygen consumption (Williams 1987), assuming no significant anaerobic contribution to metabolism (Fish 1992b). Compared with studies of metabolic effort during terrestrial locomotion (Taylor *et al.* 1982), there have been relatively few metabolic studies on mammalian swimming. The paucity of information is due primarily to the difficulty in obtaining many aquatic mammals, which are cumbersome in size and require large and specialised facilities for study. Even so, aerobic metabolism for mammals when swimming has been examined for a wide diversity of functional and taxonomic groups, including cetaceans (Worthy *et al.* 1987), humans (Holmer 1972; DiPrampo *et al.* 1974; Nadel 1977; Chatard *et al.* 1991), mustelids (Williams 1983, 1989), otariid seals (Costello and Whittow 1975; Kruse 1975; Feldkamp 1987a; Butler *et al.* 1992), phocid seals (Øritsland and Ronald 1975; Craig and Pasche 1980; Innes 1984; Davis *et al.* 1985, 1991; Williams *et al.* 1991; Markussen *et al.* 1992), and rodents (Fish 1982b, 1983). Other methods have been employed to estimate the metabolic increase associated with swimming, including correlation of heart rate and oxygen consumption (Williams *et al.* 1992), breathing rate (Sumich 1983), estimates of food consumption (Edwards 1992), and hydrodynamic models (Schmidt-Nielsen 1972; Kawamura 1975; Yasui 1980; Lavigne *et al.* 1982; Hui 1987; Kshatriya and Blake 1988). These alternative methods may not be

accurate because of the assumptions that were adopted for the metabolic determination. Such inaccuracies are particularly prevalent when using hydrodynamic models, because of optimistic estimates of drag reduction and muscle efficiency (Gray 1936; Fish and Hui 1991).

Total power output, P , is the rate of energy usage required to perform work by the portion of the body that effects locomotion (Lighthill 1975). Some of P is used to generate thrust, while the remainder of P is lost to the wake. Energy is lost in transferring momentum to the water. Additional losses may come from energy required to move the mass of the propulsive structure (i.e. flippers, paddles) and energy lost to the acceleration reaction from unsteady motion (Blake 1979; Daniel 1984; Fish 1984). The acceleration reaction results from acceleration or deceleration of the body that changes the kinetic energy of the water (Webb 1988).

Efficiency, η_a or η_p , provides a measure of performance for swimming mammals. The η_a is the ratio of thrust power to aerobically derived metabolic rate. The η_a is determined by the efficiency of hydrolysing ATP for work by muscles, work that moves water, and the fraction of work going into thrust (Daniel 1991). The third determinate of η_a is propulsive efficiency, η_p . Although efficiency may not be directly acted on by selection, biological processes that minimise energy input and maximise performance should be positively selected (Blake 1991). Such circumstances whereby energy is optimised are often associated with behaviours and morphologies of high efficiency (Weihs and Webb 1983; Blake 1991). High propulsive efficiency allows active predators to cruise economically in search of prey. Optimisation of energy use while swimming requires adaptations that reduce drag, and improve thrust production and efficiency (Weihs and Webb 1983).

Drag Reduction

Components of Drag

The total drag experienced by a steadily swimming mammal consists of frictional (D_f), pressure (D_p), wave (D_w), and induced (D_i) drag components, namely:

$$D = D_f + D_p + D_w + D_i \quad (2)$$

where subscripts denote the component drags, respectively. Frictional or viscous drag originates from fluid viscosity and 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 the wetted surface area of the body and flow conditions within the boundary layer (Webb 1975). Boundary flow can be laminar, turbulent, or transitional. A boundary layer with turbulent flow produces the highest frictional drag.

Flow conditions are determined by the size and speed of the swimming animal and by the density and viscosity of water. Interaction of these parameters is represented by the non-dimensional Reynolds number:

$$Re = UL\rho/\mu = UL/\nu \quad (3)$$

where L is body length, ρ is density, μ is viscosity, and ν is ratio of ρ and μ called the kinematic viscosity (Webb 1975). Boundary flow for a submerged, rigid streamline body is laminar up to Re of approximately 5×10^5 , turbulent above Re of 5×10^6 , and transitional between those values (Webb 1975; Blake 1983a; Fish 1992b).

Pressure or form drag arises as a result of distortion of flow outside of the boundary layer. 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 force (Webb 1975). Increased drag forces are realised as a result of the interaction of the boundary layer and pressure gradients with a resulting separation

of the boundary layer from the body. This interaction translates into a wake where kinetic energy is lost in addition to the net pressure force that acts in opposition to forward motion. Broad wakes indicate greater energy losses and a higher pressure drag component than narrow wakes (Blake 1983a).

When swimming submerged, frictional and pressure components dominate. However, as a mammal swims at or near the water surface, the animal experiences increased resistance from production of surface waves. Kinetic energy from the animal motion is lost as it is changed into potential energy in the formation of waves. This wave drag reaches a maximum of five times frictional drag (Hertel 1966). The maximum occurs when the body is just submerged at a relative depth of 0.5 of maximum body diameter. Wave drag falls off with positive and negative submergence depths and becomes unimportant at depths more than three times body diameter or when the animal becomes airborne. Surface drag on towed harbor seals (*Phoca vitulina*) was 2.5 times the submerged value at the identical velocity (Williams and Kooyman 1985), and drag on mink (*Mustela vison*) carcasses at the water surface was 7–10 times more than calculated drag when submerged (Williams 1983).

Hydrofoils (e.g. fins, flippers, flukes), used by aquatic mammals for propulsion and manoeuvres, produce an induced drag component. As the hydrofoil is canted at an angle to the water flow (i.e. angle of attack), a lift force is generated due to deflection of the fluid and pressure differences between the two hydrofoil surfaces (Webb 1975; Blake 1983a). The pressure difference produces flow around the hydrofoil tip. Tip vortices result with energy lost as the induced drag (Fig. 1). Induced drag is directly proportional to lift squared (Blake 1983a). Oscillation of the hydrofoil for propulsion produces vorticity from the trailing edge that dissipates energy into the wake, adding to drag (Fig. 1).

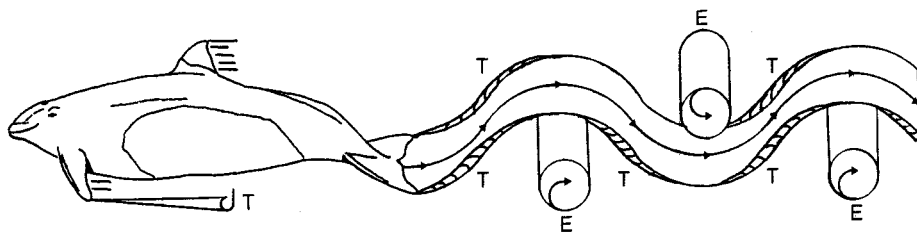


Fig. 1. Pattern of vorticity shed in wake of a dolphin. Tip vortices (T) generated from the flippers and flukes and trailing edge vortices (E) generated from the flukes are shown. Adapted from Prandtl and Tietjens (1934), Lighthill (1975) and Magnuson (1978).

Mechanisms for Drag Minimisation

Drag is minimised primarily by streamlining the shape of the body and the appendages. The streamlined profile of these structures is characterised by a rounded leading edge, slowly tapering tail, and a Fineness Ratio (FR = maximum length to maximum thickness) of 3–7 (Webb 1975; Blake 1983a). The optimal FR, which provides the minimum drag for the maximum volume, is 4.5 (von Mises 1945). Streamlining reduces the magnitude of the pressure gradient over the body surface and delays separation of the boundary layer from the body. Separation occurs closer to the trailing edge, resulting in a smaller wake and reduced D_p . In addition, posterior displacement of the maximum thickness is important because this is where transition to turbulent flow and boundary-layer separation is likely to develop (Blake 1983a).

Highly derived aquatic mammals are well streamlined with body dimensions within the optimal range of FR (Figs 2, 3). In general, cetaceans, pinnipeds and sirenians have body shapes with FRs between 3.3 and 8.0 (Fig. 2). The notable exception for cetaceans is the

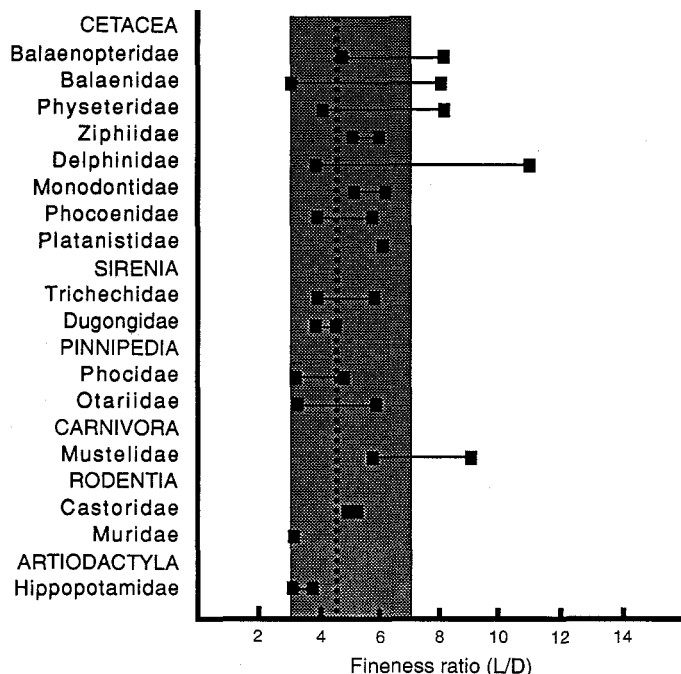


Fig. 2. Comparison of ranges of Fineness Ratio (FR) for various mammalian families. The dashed line indicates the optimal FR of 4.5 whereby a body has the least drag for the maximum volume (von Mises 1945). The shaded area represents the range of FR in which drag increases by 10% above the optimum value. Sources: Hertel (1966); Mordvinov (1972); Spain and Heinsohn (1975); Alejev (1977); Buijs and Dudok van Heel (1979); Yasui (1980); Cummings (1985); Reeves and Leatherwood (1985); Williams and Kooyman (1985); Lockyer and Waters (1986); Feldkamp (1987a); Fish *et al.* (1988); Bose *et al.* (1990); Read (1990); Domning and Buffrenil (1991); Curren (1992); Reynolds (1993); D. P. Domning, personal communication; F. E. Fish, unpublished data.

northern right whale dolphin (*Lissodelphis borealis*) or 'snake porpoise' (Perrin 1991) that can have a FR up to 10.9 (Leatherwood and Walker 1979). Despite their bulk and specialisation of the head for filter feeding, the mysticete whales are well streamlined (Fig. 3). FRs for the Balaenopteridae range from 4.8 to 8.1 (Alejev 1977; Lockyer and Waters 1986; Bose *et al.* 1990) and for the Balaenidae range from 3.3 to 8.0 (Alejev 1977; Cummings 1985; Reeves and Leatherwood 1985).

The position of the maximum thickness in the most rapidly swimming aquatic mammals is similar to engineered 'laminar' profiles (Hertel 1966), which reduce drag by maintenance of laminar boundary flow (Webb 1975). The maximum thickness of dolphins is located 0.34–0.45 of the body length from the beak (Fish and Hui 1991). Separation of the boundary layer behind the maximum thickness has been observed in tests on a model bottlenose dolphin (*Tursiops truncatus*) (Purves *et al.* 1975). The position of maximum thickness is located at 0.4 body length for otariid seals (Feldkamp 1987a) and 0.5–0.6 body length for phocid seals (Alejev 1977; Innes 1984). However, the position can be varied by an individual seal, because the neck is capable of being retracted and extended (King 1983). Extension of the neck during rapid swimming could modify the flow over the anterior of the seal and reduce drag by extending the region of laminar flow. Such a drag reduction could aid seals in catching fast-swimming, elusive prey.

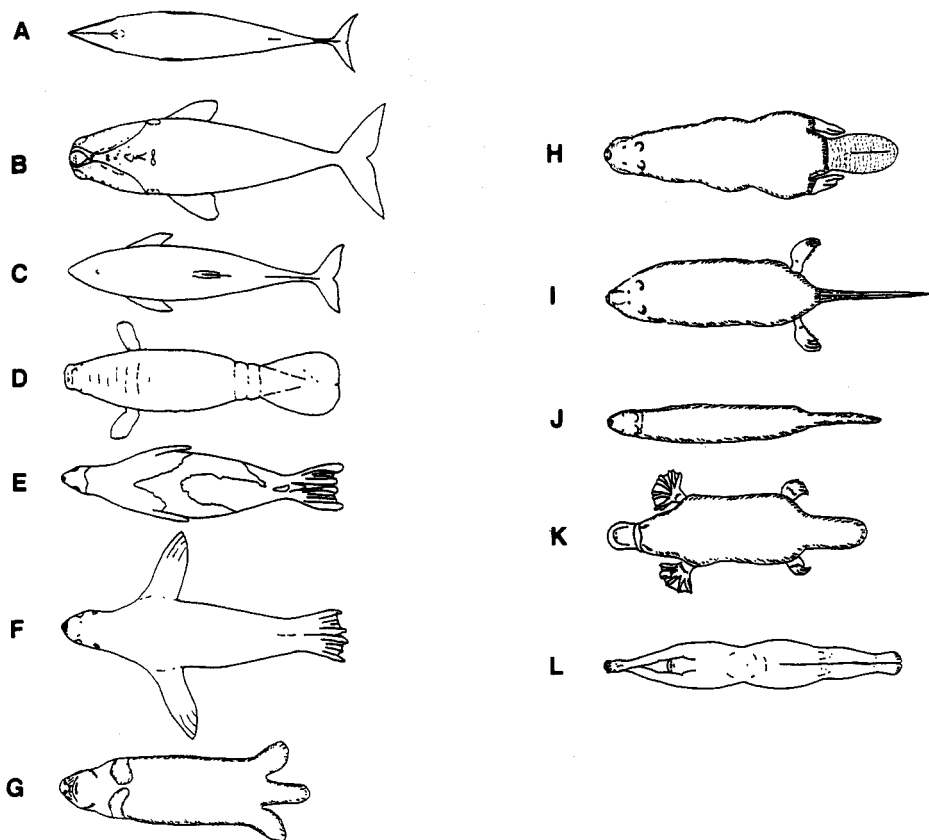


Fig. 3. Body shape variation. Marine mammals (A–G) display better streamlining and more sophisticated propulsive structures than terrestrial and semiaquatic mammals (H–L). A, minke whale (*Balaenoptera acutorostrata*); B, right whale (*Eubalaena glacialis*); C, harbor porpoise (*Phocoena phocoena*); D, Florida manatee (*Trichechus manatus*); E, harp seal (*Phoca groenlandica*); F, California sea lion (*Zalophus californianus*); G, sea otter (*Enhydra lutris*); H, beaver (*Castor canadensis*); I, muskrat (*Ondatra zibethicus*); J, mink (*Mustela vison*); K, platypus (*Ornithorhynchus anatinus*); L, human (*Homo sapiens*).

High swimming speeds require a body design to minimise drag such as that associated with pursuit-type predators like seals and dolphins (Williams and Kooyman 1985; Fish *et al.* 1988; Fish and Hui 1991). Less apparent is the near optimum body design for the sirenians (Figs 2, 3). Dugongs (*Dugong dugon*) and manatees (*Trichechus* sp.) are considered to swim in a leisurely manner ($0.6\text{--}0.8\text{ m s}^{-1}$) (Hartman 1979; Nishiwaki and Marsh 1985). As herbivores, sirenians do not require speed and rapid acceleration to catch prey. Low-speed swimming allows for precise manoeuvrability and can release the animal from the morphological constraints associated with a streamlined body. However, sirenians will migrate and cruise at speeds of $0.8\text{--}1.9\text{ m s}^{-1}$ (Hartman 1979). Furthermore, sprints of over 6 m s^{-1} reported for sirenians (Hartman 1979; Nishiwaki and Marsh 1985) would aid in escape from predators such as crocodilians and sharks (Reynolds and Odell 1991). Alternately, a FR near the optimal value would aid in thermoregulation by limiting surface area and heat loss in the thermal-sensitive sirenians.

Semiaquatic mammals deviate from the optimal design to minimise drag (Fig. 3). These animals do not show the teardrop, fusiform shape of the highly derived aquatic mammals. With the exception of sea otter, aquatic mustelids are elongate, displaying FRs above 7 (Fig. 2). An elongate body form is characteristic of the Mustelidae, but is advantageous in the acrobatic swimming pattern displayed by river otters (e.g. *Lutra*, *Pteroneura*). Although semiaquatic rodents have FRs within the optimal range (Fig. 2), these values were based on body length without consideration of the tail. Because the rodent tail is delineated strongly from the body, the tail will have little influence on pressure drag derived from flow around the body and in the wake. However, Fish (1982a) demonstrated that undulations of the laterally compressed tail of muskrat (*Ondatra zibethicus*) reduced drag by counteracting yawing motions generated from alternate paddling of the hind feet.

Comparison of body shape for swimming mammals can be made by examining the dimensionless coefficient of drag, C_D , which is related positively to the drag force as expressed by the equation

$$C_D = D / 0.5 \rho S U^2 \quad (4)$$

where S is wetted surface area. C_D is a function of Re and accounts for peculiarities in the behaviour of drag (Vogel 1981). Data from hydrodynamic estimates of C_D and gliding and towing drag measurements (Fig. 4) show that body forms of less-aquatic mammals, such as

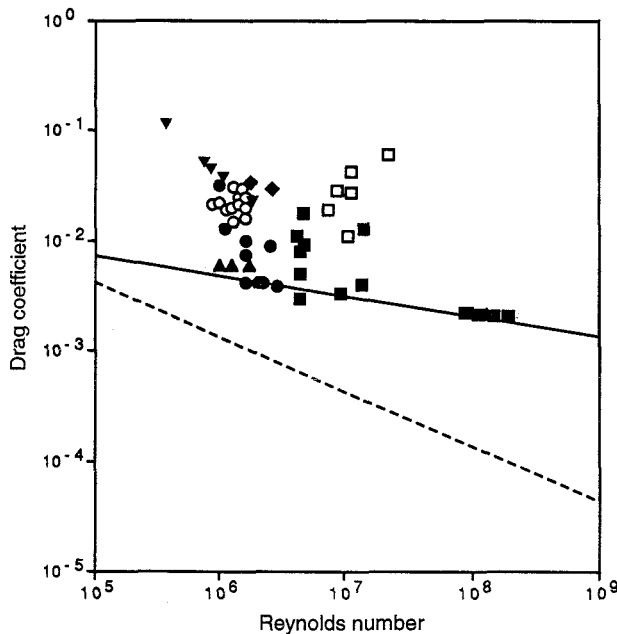


Fig. 4. Relationship between drag coefficient (C_D) and Reynolds Number (Re). ■, □, cetaceans (Kermack 1948; Lang and Daybell 1963; Purves *et al.* 1975; Webb 1975; Alejev 1977; Yates 1983; Videler and Kamermans 1985); ●, ○, pinnipeds (Williams and Kooyman 1985; Feldkamp 1987a; Fish *et al.* 1988); ▲, sea otter (Williams 1989); ▼, beaver (Kurbatov and Mordvinov 1974); ◆, human (Williams and Kooyman 1985). Open symbols represent estimates of C_D determined from hydrodynamic thrust-based models; closed symbols represent values of C_D determined from tow and gliding experiments and from calculations assuming rigid-body analogies. Theoretical frictional drag coefficients are displayed as functions of Re for laminar (broken line) and turbulent (solid line) boundary layer conditions.

beaver and humans, have high values of C_D (Kurbatov and Mordvinov 1974; Williams and Kooyman 1985). Highly aquatic mammals, such as cetaceans, pinnipeds and sea otter, incur low drag (Kermack 1948; Lang and Daybell 1963; Purves *et al.* 1975; Aleyev 1977; Videler and Kamermans 1985; Williams and Kooyman 1985; Feldkamp 1987a; Williams 1989).

Low C_D values and high swimming speeds attained by many marine mammals have directed some research toward specialised drag reduction mechanisms. The search for such mechanisms has been confined mainly to dolphins (Gray 1936; Kramer 1960; Fish and Hui 1991). In what is known as Gray's Paradox (Gray 1936; Parry 1949), hydrodynamic estimates of dolphin power output at high Re were inferred to be greater than the power that could be developed for the mass of muscle available for swimming. Resolution of the paradox was believed only possible if the drag was reduced by maintaining laminar flow within the boundary layer (Gray 1936) despite a high Re dictating a turbulent boundary flow with increased frictional drag. While the idea of a special drag reduction mechanism in dolphins has been irresistible, direct evidence of its existence has been elusive. No conclusive evidence has been found of laminar boundary flow in dolphins by mechanisms including compliant skin dampening, secretions, skin sloughing, infusion of long-chain polymers into the boundary layer, boundary-layer heating, skin folds, and boundary-layer entrainment (see review by Fish and Hui 1991). Special drag reduction mechanisms are unnecessary to explain Gray's Paradox, which is reconciled when one considers that the calculations of power output were based on burst swimming (10 m s^{-1} for 7 s) and muscle power output was an underestimate based on sustained performance of dogs and humans (Gray 1936; Fish 1992b).

Estimates of C_D from towing and gliding experiments indicate that turbulent boundary condition predominate (Fig. 4). These results are supported by flow visualisation studies in mammals that show that the majority of the body surface has turbulent boundary conditions (Rosen 1963; Kurbatov and Mordvinov 1974; Mordvinov 1974; Purves *et al.* 1975; Fish 1984; Williams and Kooyman 1985). Although a turbulent boundary layer produces a higher D_f than when laminar conditions exist, the total drag force will be lower with turbulent boundary flow (Fig. 5). The high energy content of a turbulent boundary layer prevents separation of the boundary layer from the body. Separation results in increased D_p and total drag and will occur at a lower Re with laminar boundary conditions (Webb 1975). In addition, actual drags for swimming mammals will be higher than values obtained from towing and gliding experiments or models that assume a rigid body (Fish 1992b). Propulsive movements of the body and appendages are expected to increase C_D by a factor of 3–5 (Lighthill 1975). Comparative C_D s based on thrust-based models (Fish 1992b) are greater than C_D s from rigid bodies (Fig. 5).

The properties of the hair of aquatic mammals were noted to reduce drag by aiding in streamlining of the body (Mordvinov and Kurbatov 1972; Tarasoff 1972). The lack of arrector pili muscles in seals and sea otter permits the pelage to lie flat in water, minimising resistance to swimming (Ling 1970). The semiaquatic muskrat, however, has arrector pili muscles, which will be of benefit for insulation when out of the water. When models of a seal with and without hair covering were compared, a reduction of the drag with the hair covering was reported for flow velocities of $8\text{--}10 \text{ m s}^{-1}$ (Romanenko *et al.* 1973). However, Kooyman (1989) noted that these results may not be ecologically relevant, because seals normally swim at lower speeds (Williams and Kooyman 1985; Ponganis *et al.* 1990; LeBoeuf *et al.* 1972). Decreased hair density appears to be associated with drag reduction. High swimming speeds and low drag are typified by dolphins, which possess a naked skin (Fish and Hui 1991).

Drag reduction by streamlining also is fostered by means of buoyancy control. Compared with the centre of gravity, the centre of buoyancy is closer to the head for terrestrial mammals in water (Slipper 1976). This relationship produces a torque that causes the body to float at an angle to the horizontal. This orientation would increase drag during swimming by presenting a greater frontal surface area to the water flow and decrease streamlining

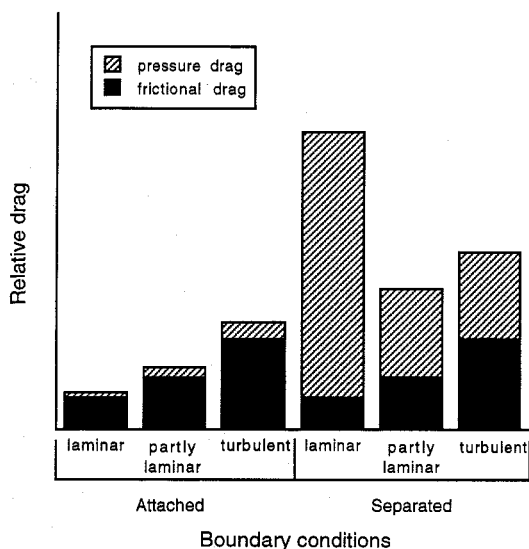


Fig. 5. Relative drags for attached and separated flow with laminar, partly laminar, and turbulent boundary layer flow (modified from Webb 1975).

(Vogel 1981; Fish 1993). Internal and external modifications for buoyancy control provide aquatic mammals with longitudinal trim for better streamlining (Domning and Buffrenil 1991; Fish 1993). For semiaquatic mammals, non-wettable fur provides buoyancy by an entrapped layer of air (Johansen 1962; Ling 1970; Dagg and Windsor 1972; Esher *et al.* 1978; Fish and Stein 1991). With its non-wettable fur, the semiaquatic opossum *Chironectes minimus* maintains a nearly horizontal body orientation when swimming, while its close terrestrial relative, *Didelphis virginiana*, can maintain little buoyancy with its saturated fur and swims with its body canted at an angle to the water surface (Fish 1993). The elongate shape of the lungs of marine mammals helps to displace the centre of buoyancy posteriorly. This arrangement is possible because the diaphragm of marine mammals is oriented obliquely to almost parallel to the spine (Howell 1930; King 1983; Domning and Buffrenil 1991). Modification of bone to act as hydrostatic ballast also has been suggested as an adaptation to maintain trim (Domning and Buffrenil 1991; Fish and Stein 1991). The condition of pachyosteosclerosis in the bones of sirenians distributes the skeletal weight appropriately for horizontal trim (Domning and Buffrenil 1991). Cetaceans show the opposite condition by reducing skeletal mass to reduce body inertia for improved acceleration performance (Webb and Buffrenil 1990).

Also important to body design for drag reduction is the design of the appendages. Even for highly adapted aquatic mammals, drag on the appendages can be a major component of the total drag on the animal. Lang and Pryor (1966) estimated drag from the appendages (i.e. flukes, flippers fin) of a dolphin *Stenella attenuata* to account for 28% of total drag, while Yasui (1980) estimated the drag contribution from the appendages of the harbor porpoise (*Phocoena phocoena*) to be 36% of total drag. For cetaceans and pinnipeds, the appendages are well streamlined with the FR ranging from 3.2 to 6.6 (Lang 1966a; Feldkamp 1987b; Bose *et al.* 1990; Battle and Fish 1993). The ends of appendages taper to a point, which reduces tip vorticity (Fig. 1) and minimises the D_i component (Rayner 1985). For semiaquatic mammals that swim by paddling, the appendages are designed to maximise drag for thrust production (see Swimming Modes section below).

Thrust Generation and Propulsive Efficiency

Swimming Modes

For swimming mammals, thrust is generated by oscillatory or undulatory motions of the

propulsive appendages (Webb 1988). Each mode is associated with particular appendicular morphologies and lifestyles.

A diverse assemblage of terrestrial and semiaquatic mammals swim by paddle propulsion (Howell 1930; Fish 1992b). Paddling is associated with slow surface swimming and precise manoeuvrability. This swimming mode is primitive, representing a modification of a terrestrial gait (Williams 1983; Rayner 1985; Fish 1992b, 1993). Thrust is generated by alternate strokes of the paired appendages. Combinations of fore feet, hind feet, or all four feet, are used (Tarasoff *et al.* 1972; Fish 1984, 1992b, 1993; Williams 1983, 1989). The paddling stroke cycle is composed of power and recovery phases (Fish 1984). During the power phase, posterior motion of the foot generates a drag force (Fig. 6). This rearward resistance is translated into forward thrust for the organism (Fish 1984; Weihs and Webb 1983). The feet are unstreamlined and have a triangular design with a broad distal end and interdigital webbing or fringe hairs to increase to paddle area (Howell 1930; Fish 1984), thereby increasing propulsive efficiency by affecting a large mass of water (Alexander 1983; Blake 1983a). In addition, the narrow attachment of the triangular paddle with the body reduces drag due to interference between body and propulsor. The recovery phase is used to reposition the foot without generation of thrust. During recovery, effective paddle area is reduced by adduction and plantarflexion or by feathering the limb. This configurational change minimises energy lost in repositioning the paddle (Fig. 7). Configurational changes of hind feet of muskrats during recovery reduced paddle area by 55% and drag by 33% (Fish 1984).

The paddling mode is abandoned by otters when performing rapid, submerged swimming; instead, otters swim by dorsoventral undulation of the body and tail with assistance from the hind feet (Kenyon 1969; Tarasoff *et al.* 1972; Williams 1989). Changing from paddling to undulation may represent a gait change for improved swimming performance (Williams 1989). Tarasoff *et al.* (1972) described the undulatory mode of *Lutra* as carangiform, indicating analogous swimming movements with generalised teleost fishes. This mode is less specialised and provides lower performance than lift-based oscillatory modes, but improved performance compared with drag-based paddling (Webb 1975; Fish 1992b). In the undulatory mode thrust is generated by accelerating a mass of water that is adjacent to the body (acceleration reaction). However, for river otters (*Lutra* sp.), the distal tapering of the tail should reduce propulsive efficiency, because progressively less momentum is transferred to the water toward the tip of the tail. Like fish that developed an expanded caudal fin to affect a larger mass of fluid, the broad compressed tail of the giant river otter (*Pteronura brasiliensis*) and broad hind feet of the sea otter (Howell 1930) may be adaptations to maximise thrust production while undulating. Further examination of undulatory swimming by mammals is necessary to determine the effectiveness of this mode with regard to energetic performance.

Highly derived aquatic mammals oscillate the appendages for rapid and relatively high-powered propulsive modes which employ hydrodynamic lift-based momentum exchange (Webb 1984; Webb and Buffrenil 1990). Thrust is generated from appendages modified as hydrofoils that move while oriented at a small angle to their pathway (angle of attack) (Weihs and Webb 1983). The hydrofoils produce a lift force perpendicular to the pathway, which is resolved into an anteriorly directed thrust force (Fig. 6). To maximise lift and thrust, the hydrofoil should have a crescent, winglike design with high aspect ratio (S^2/A , where S is the span and A is the area) (Lighthill 1975; Webb 1984; van Dam 1987). This shape provides the hydrofoil with a high lift-to-drag ratio and high propulsive efficiency (Weihs and Webb 1983).

The fore flippers, used by the Otariidae, act as oscillatory hydrofoils (Feldkamp 1987a). Lift-based oscillations also generate thrust from dorsoventral movements by the caudal flukes of cetaceans and sirenians (Parry 1949; Lang and Daybell 1963; Hartman 1979; Nishiwaki and Marsh 1985; Videler and Kamermans 1985) or from lateral movements of the paired hind flippers by the Phocidae and Odobenidae (Backhouse 1961; Ray 1963; Tarasoff *et al.* 1972; Gordon 1981; Fish *et al.* 1988). Lift-based oscillation, exclusive of the otariid

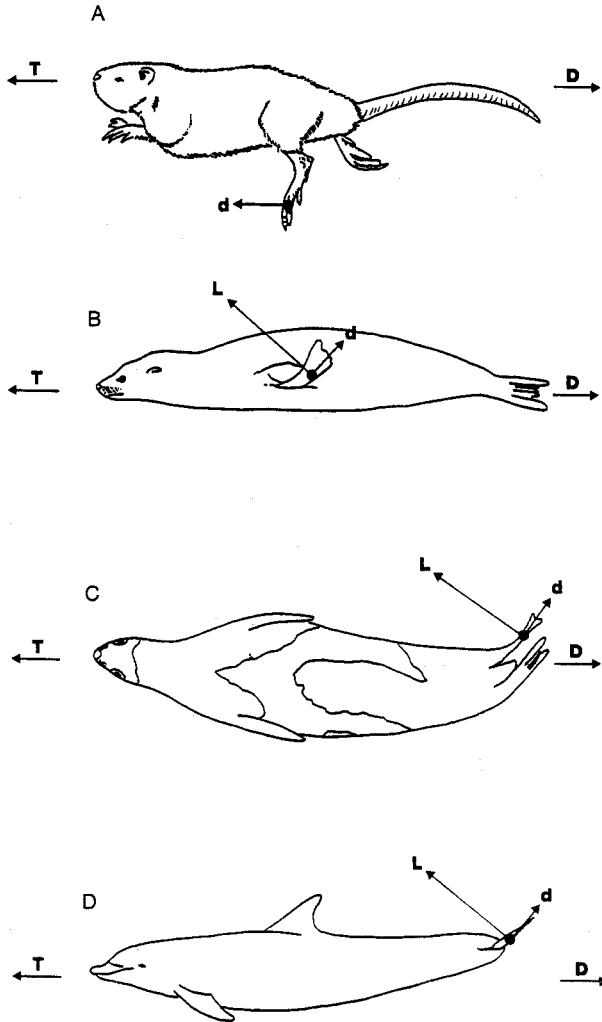


Fig. 6. Major forces associated with propulsive modes. *A*, muskrat (*Ondatra zibethicus*), paddling; *B*, sea lion (*Zalophus californianus*), pectoral oscillation; *C*, harp seal (*Phoca groenlandica*), pelvic oscillation; *D*, bottlenose dolphin (*Tursiops truncatus*), caudal oscillation. To swim at a constant velocity, an animal must generate a thrust force (T) equal and opposite to a drag force (D). Paddling is a drag-based swimming mode. The posterior sweep of the hind feet of the muskrat generates a drag force (d) which contributes to T . Using lift-based propulsive modes, the foreflippers of the sea lion, hind flippers of the harp seal, and caudal flukes of the dolphin act as hydrofoils to generate T . Lift derived from movement of the hydrofoil is resolved into an anteriorly directed thrust force. The drag associated with the hydrofoil (d) is produced mainly from frictional and induced drag components and is small relative to the lift force. (Adapted from Fish 1992b.)

pinnipeds, is analogous to the thunniform mode of fishes, which represents the advanced end of a continuum of undulatory modes (Webb 1975; Lindsey 1978). In this mode, undulations of the body are transmitted to the oscillatory hydrofoil through mobile joints. These joints control the angle of attack of the hydrofoil to maintain lift and thrust throughout the stroke cycle (Webb 1975; Fish *et al.* 1988).

Efficiency and Mode

Maximisation of thrust production and increased propulsive efficiency are highly associated with swimming modes employed by mammals (Rayner 1985; Fish 1992*b*). More energy is required to produce the same force by paddling than by lift-based propulsion (Weihs and Webb 1983). The large energy expenditure for paddling occurs because thrust is generated through only half of the stroke cycle. Energy is lost in repositioning the limb during recovery and in accelerating the paddle mass and fluid adjacent to the limb (Fig. 7). As a result, η_p is low for paddle propulsion (i.e. < 40%; Fig. 8). However, at low speeds, paddling will work at higher η_p than swimming modes employing body and tail motions (Webb 1984).

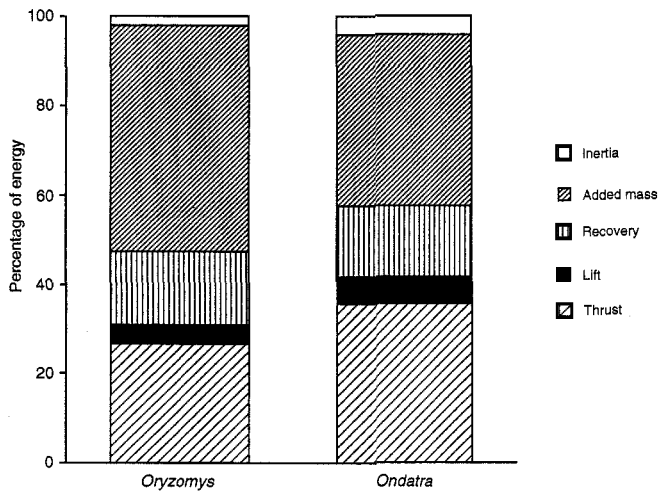


Fig. 7. Percentage of energy used during the paddling stroke cycle for the rice rat (*Oryzomys palustris*) and muskrat (*Ondatra zibethicus*). Energy is used for propulsion to generate thrust, and energy is lost to generation of lift, drag in repositioning the limb during recovery, acceleration forces to overcome added mass and limb inertia. Data from Fish (1984, 1985).

Thrust production and η_p for dolphins and seals swimming in the thunniform mode have been computed using unsteady lifting-wing theory (Lighthill 1975; Webb 1975; Chopra and Kambe 1977; Yates 1983; Fish *et al.* 1988). In lift-based modes, oscillations of the hydrofoil generate thrust throughout the stroke cycle, providing higher values of η_p than paddling (Feldkamp 1987*b*; Fish *et al.* 1988; Fish and Hui 1991). In addition, the design of the hydrofoil generates large thrust forces with low drag. For cetaceans and pinnipeds, η_p is approximately 80% (Fig. 8).

Differences in values of aerobic efficiency also correspond to swimming mode (Fig. 9). Life-based modes used by pinnipeds have maximum aerobic efficiencies of approximately 0.3 (Feldkamp 1987*a*; Williams *et al.* 1991). However, η_a for drag-based paddlers is low, ranging from 0.014 to 0.052 (DiPrampero *et al.* 1974; Williams 1983, 1989; Fish 1984).

Cost of Transport

The Cost of Transport (CT) can be used also to assess the efficiency of different swimming modes (Schmidt-Nielsen 1972; Williams 1987; Fish 1992*b*). CT is defined as the metabolic cost needed to move a unit body mass a unit distance, and CT is inversely proportional to η_a (Tucker 1970). Because CT is computed by dividing mass-specific metabolic rate by U , it is unnecessary to determine drag or thrust, as a measure of power

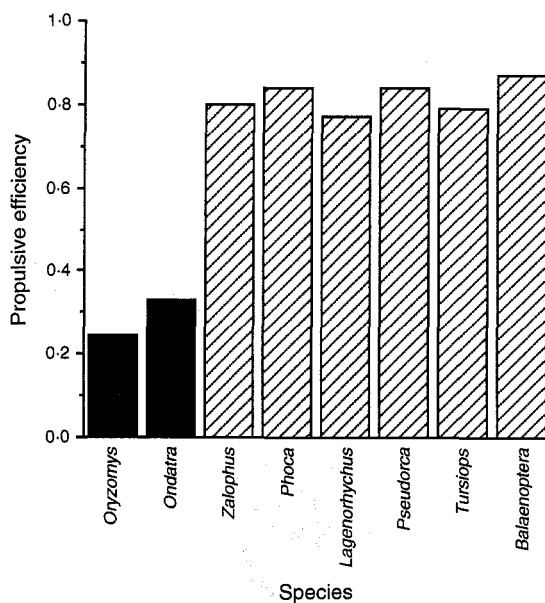


Fig. 8. Comparison of propulsive efficiencies, η_p , between drag-based (black bars) and lift-based (hatched bars) swimming modes for *Oryzomys* (Fish 1985), *Ondatra* (Fish 1984), *Zalophus* (Feldkamp 1987a), *Phoca* (Fish *et al.* 1988), *Lagenorhynchus* (Webb 1975), *Pseudorca* (Fish 1992a), *Tursiops* (Fish 1992a), and *Balaenoptera* (Bose and Lien 1989). Drag-based paddling has low η_p (< 33%), whereas lift-based modes have high η_p s (> 79%).

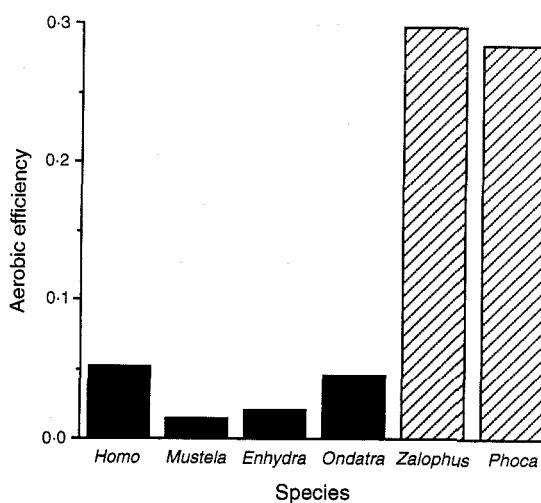


Fig. 9. Comparison of aerobic efficiencies, η_a , between drag-based (black bars) and lift-based (hatched bars) swimming modes for *Homo* (DiPrampo *et al.* 1974), *Mustela* (Williams 1983), *Enhydra* (Williams 1989), *Ondatra* (Fish 1984), *Zalophus* (Feldkamp 1987a), *Phoca* (Williams *et al.* 1991).

output, to evaluate efficiency. The minimum CT indicates the velocity used by an animal to travel the greatest distance most economically and occurs in the mid-range of swimming speeds for animals (Williams 1987).

Swimming mammals have CTs higher than the CT for fish (Fig. 10), which represents the lowest minimum CT for any vertebrate animal and locomotor mode (Fish 1992*b*). Mammals that use the paddling mode have a higher minimum CT than those that use lift-based swimming (Fig. 10). The CT for muskrat, mink, sea otter and human is 10–25 times the CT for fish of equivalent sizes (Fish 1982*b*; Williams 1983, 1989; P. E. DiPrampo, personal communication). However, for lift-based propulsion by pinnipeds and cetaceans, CT is only 1.9–4.6 times higher than similarly sized fish (Costello and Whittow 1975; Kruse 1975; Innes 1984; Davis *et al.* 1985; Øritsland and Ronald 1975; Feldkamp 1987*a*; Worthy *et al.* 1987; Williams *et al.* 1992).

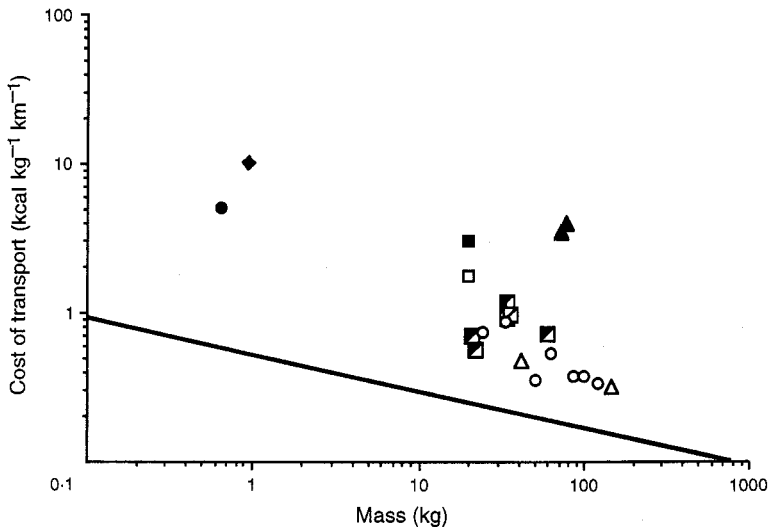


Fig. 10. Relationship between Cost of Transport (CT) and body mass. Δ , cetaceans (Worthy *et al.* 1987; Williams *et al.* 1992); \blacktriangle , human (P. E. DiPrampo, personal communication, 1979); \blacklozenge , mink (Williams 1983); \bullet , muskrat (Fish 1982); \circ , phocid seals (Øritsland and Ronald 1975; Innes 1984; Davis *et al.* 1985); \blacksquare , sea lions (Costello and Whittow 1975; Kruse 1975; Feldkamp 1987*a*); \blacksquare , \square , sea otter (Williams 1989). Closed symbols represent mammals swimming at the water surface using the paddling mode. Submerged swimming is represented by open (pelvic and caudal oscillators) and half (pectoral oscillators) symbols. The solid line represents the extrapolated minimum CT for fish (Davis *et al.* 1985).

The comparatively higher CT for paddlers may be inflated because these animals typically swim at the water surface, where they encounter increased resistance due to wave drag. The sea otter presumably lowers its CT by 40% by submerged swimming (Fig. 10; Williams 1989); however, this mammal also changes from paddling to the more efficient undulatory mode when submerged. Submerged swimming also can affect CT by adjustments in metabolism. The need to conserve oxygen during diving is considered greater than the energetic demands of swimming (Costello and Whittow 1975). Lowered CT values for highly derived aquatic mammals may result from hypometabolism due to diving (Castellini *et al.* 1985). A low CT would allow for increased submergence time and foraging distance for divers.

Behavioural Strategies for Energy Economy

It is reasonable to assume that the evolution of a suite of adaptations that increase energy economy and locomotor performance would include behavioural strategies. Although there exists much speculation on the energetic advantages of various swimming behaviours, there is little empirical evidence to validate such behavioural adaptations.

Swimming Speed

The simplest behavioural parameter that can be controlled is swimming speed (Weihs and Webb 1983). High speeds allow for increased foraging and active pursuit, but require large energy expenditures because thrust power is directly related to the cube of velocity. Low swimming speeds observed for marine mammals, while foraging and migrating (Hartman 1979; Sumich 1983; Lockyer and Morris 1987; Ponganis *et al.* 1990; Fish and Hui 1991; LeBoeuf *et al.* 1992), would minimise the CT and maximise the distance travelled for the work performed (Williams 1987).

Swimming speed is more severely affected at the water surface to which all aquatic mammals are bound unremittingly in their need to exchange respiratory gases. At the water surface, aquatic mammals experience increased resistance from wave drag. The increased drag limits the maximum speed, known as hull speed, which is attainable during surface swimming (Fish 1982b; Williams 1989). Hull speed is due to constructive interference from bow and stern waves, which traps the animal in a wave trough (Vogel 1988). To swim at a speed greater than hull speed, the animal would have to swim uphill, expending a large amount of energy in the process. Muskrats were reported to swim on average just below their hull speed (Fish 1982b), whereby muskrats minimise CT and avoid oxygen debt by surface swimming lower than hull speed.

Increased swimming performance in the evolution of aquatic mammals necessitated the abandonment of surface swimming (Williams 1989; Fish 1992b). Thrust is produced more effectively by lift-based swimming modes when submerged than at the surface (Baudinette and Gill 1985; Webb *et al.* 1991). Swimming below the water surface minimises or obviates the increased energy expenditure and speed limitations imposed from wave drag (Lang and Daybell 1963; Hartel 1966). Sea otters can decrease metabolic rate by 41% (Fig. 10) and travel at higher speeds when swimming submerged than at the surface (Williams 1989). Dolphins were found to swim at faster speeds in deep water (> 10 m) than in shallow water (Wursig and Wursig 1978). Hui (1989) postulated that dolphins could gain large energy benefits by swimming for long distances between breaths as long as the dolphins swam at depths greater than one-half of one body length. Energy saved by swimming away from the surface would offset increased energy expended in coming to the surface to breathe.

Porpoising and Free-riding

Porpoising has been hypothesised as a strategy for energy economy. This behaviour is performed by the fastest mammalian swimmers (Peterson and Bartholomew 1967; Williams 1987; Fish and Hui 1991) and consists of rhythmic, serial leaping (Fish and Hui 1991). Au and Weihs (1980a, 1980b) and Blake (1983b) proposed models that showed that the energy to swim a given distance increases with swimming speed faster than the energy to leap that distance. Therefore, above a critical swimming speed where the energies converge, there is an energetic advantage to swimming by porpoising. However, Hui (1989) considered porpoising to be primarily an energy conservation behaviour directed more to economical breathing than swimming. He is supported by observations of porpoising dolphins that swim twice the distance they leap (Au *et al.* 1988). Furthermore, emergence angle of leaps by dolphins were lower than a 45° angle predicted for maximum leap distance (Au and Weihs 1980a; Hui 1989).

The greatest economy for swimming will occur by means of free-riding behaviour. In free-riding, kinetic energy from the environment is used by the animal to effect

locomotion. Rather than increasing energy demands of surface swimmers, wave energy can be used to reduce swimming effort. Dolphins are often observed to ride the pressure wave associated with the bows of ships (Woodcock 1948; Fejer and Backus 1960; Norris and Prescott 1961). This behaviour is complex, with any energy savings to the dolphin related to bow design, swimming depth, and distance from the ship (Fish and Hui 1991). Williams *et al.* (1992) demonstrated that a bottlenose dolphin could reduce its CT with increased speed by swimming within a boat's stern wave.

Wind-wave riding and surf-wave riding also may reduce the energy of surface swimming (Caldwell and Fields 1959). These wave-riding behaviours differ from bow-wave riding because they use the interaction of the dolphin's weight and slope of the wave front to effect movement analogous to human surfers (Hayes 1953; Fejer and Backus 1960; Perry *et al.* 1961). Sea lions *Zalophus californianus* 'body-surf' down the front of waves to obtain a free-ride onto the beach (Peterson and Bartholomew 1967). Wind-generated ocean waves have been hypothesised to provide large whales with an energy savings of over 30% (Bose and Lien 1990). By synchronising the motion of the wave with the motion of the flukes, large whales could theoretically increase the relative velocity experienced by the flukes and thereby increase the lift and thrust generated.

The occurrence of highly organised formations by marine animals has been suggested as an adaptation for energy economy (Lang 1966b; Brodie 1977). Formation swimmers influence water flow around adjacent individuals, resulting in decreased drag with a concomitant decrease in overall energy cost of locomotion (Weihs 1973).

The simplest formation for energy economy is a single-file formation. In this formation, the pattern and rotation of vortices shed from the non-oscillating body of the leading swimmer induces a water velocity relative to the vortices that is in the same direction as the swimming direction. A trailing swimmer will experience a decreased relative velocity with reduced drag and swimming effort (Weihs 1973). Single-file formations were observed for sea lions (Peterson and Bartholomew 1967). Because swimming motions are confined to oscillations of the pectoral flippers, the vorticity pattern shed from the body of a leading sea lion could benefit trailing animals in the formation.

Cetaceans should not swim in single-file formations as it would increase swimming effort. Rotation of vortices shed from oscillations of a caudal propulsor is opposite the rotation found for a non-oscillating body (Fig. 1; Weihs 1973). An animal swimming directly behind another would experience an increased relative velocity, whereas in the diagonal position relative velocity and swimming effort would be reduced. Weihs (1973) developed a hydro-mechanical model that predicted the optimal formation design for energy saving by schooling fish. With consideration to the differences in orientation of fish and cetacean caudal propulsors and vortex patterns, cetaceans should arrange themselves vertically in a diamond formation and horizontally abreast (Weihs 1973). Large groups of dolphins were observed in side-by-side and echelon formations (Norris and Prescott 1961; Leatherwood and Walker 1979). Smaller cetaceans often position themselves beside and slightly behind the maximum diameter of a larger animal (Norris and Prescott 1961). While the larger whale will experience increased drag, the smaller gains an energetic benefit (Kelly 1959; Lang 1966b). This effect is beneficial particularly for young whales in order to maintain speed with their mothers. The ultimate in such free-riding by young is observed in capybaras (*Hydrochoerus hydrochaeris*) in which infants are carried on the mother's back (MacDonald 1981).

Conclusions

At the beginning of this discussion, I stated that the secondary radiation of mammals into the aquatic habitat provides us with a unique opportunity to examine the relationship between behavioural, physiological and morphological adaptations with regard to energy use. The interaction between the habits of mammalian swimmers and the aqueous environment has produced various morphological designs and propulsive modes for effective aquatic

locomotion. Efficient use of energy by highly derived aquatic mammals is associated with adaptations that simultaneously promote drag reduction and thrust maximisation. Key among these adaptations are streamlined body forms and lift-based propulsive modes in addition to behaviours that enhance energy economy. For semiaquatic mammals, paddling is less efficient than the lift-based modes, but has the great advantage of allowing for adequate aquatic performance with minimal compromise to terrestrial movement (Rayner 1985). It is suggested that evolutionary transition from terrestrial to fully aquatic habits by mammals was accompanied through increased swimming performance by submerged swimming, low-drag body designs, and high-thrust, high-efficiency propulsive modes.

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