

TOPICAL REVIEW

The myth and reality of Gray's paradox: implication of dolphin drag reduction for technology

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Abstract

The inconsistency for the calculated high drag on an actively swimming dolphin and underestimated muscle power available resulted in what has been termed Gray's paradox. Although Gray's paradox was flawed, it has been the inspiration for a variety of drag reduction mechanisms. This review examines the present state of knowledge of drag reduction specific to dolphins. Streamlining and special behaviors provide the greatest drag reduction for dolphins. Mechanisms to control flow by maintaining a completely laminar boundary layer over the body have not been demonstrated for dolphins.

1. Introduction

Movement through water is difficult due to the density and viscosity of the medium. The consequences for both aquatic animals and marine vessels are large energy demands for travel and limitations on speed. Hydrodynamic mechanisms for increased thrust production or decreased drag, therefore, can benefit animal and machine by enhancing locomotor performance. Inspiration from biology by engineers for economical high-speed transport has focused primarily on drag reduction.

The high-speed swimming performance of dolphins (order *Cetacea*) has been noted throughout much of recorded history. The earliest account of the swimming ability of dolphins comes from Aristotle (*Historia Animalium*). He considered dolphins to be the fastest of all animals and capable of leaping over the masts of large boats. Such perceptions of the dolphin's swimming ability remain to the present day and fuel speculation of special mechanisms to reduce drag (Gray 1936, Kramer 1960a, Fish and Hui 1991, Carpenter *et al* 2000, Babenko and Carpenter 2002). Aquatic animals are considered superior in their capabilities to technologies produced from nautical engineering (Triantafyllou and Triantafyllou 1995). Speeds over 11 m s^{-1} ($>21 \text{ kts}$) were observed for dolphins

(Fish and Rohr 1999). Such high levels of performance were assumed to be dependent on adaptations that reduced drag.

This review will examine drag reduction mechanisms and their associated hydrodynamics for dolphins. Specialized adaptations used by dolphins to reduce drag and decrease the energetic cost of swimming will be explored. An understanding of these adaptations may provide insight for the design of analogous engineered systems.

2. Gray's paradox

With respect to all the information regarding dolphin swimming, by far, arguments surrounding the investigation and application of special mechanisms for drag reduction by dolphins are the most contentious (Gray 1936, Fish and Hui 1991, Vogel 1994, Fein 1998). The controversy, known as 'Gray's paradox', was the result of the first attempt to evaluate swimming energetics in animals (Gray 1936, Webb 1975). Gray (1936) used a simple hydrodynamic model based on a rigid body to calculate drag power. He applied this model to a dolphin and a porpoise swimming at speeds of 10.1 and 7.6 m s^{-1} , respectively. For his calculations, Gray assumed that turbulent boundary flow conditions existed in the boundary

layer, because of the speed and size of the animals. The results of the calculations indicated that the estimated drag power could not be reconciled with the available power generated by the muscles.

Gray's resolution to the problem was that the drag on the dolphin would be lower by maintenance of a fully laminar boundary layer. Gray proposed a mechanism to laminarize the boundary layer by accelerating the flow over the posterior half of the body. This mechanism was largely ignored in subsequent work, whereas, the basic premise that dolphins maintained laminar boundary conditions became the focus and justification of much of the work on dolphin hydrodynamics for the next 60 years (Kramer 1960a, 1960b, Webb 1975, Aleyev 1977, Fish and Hui 1991, Fish and Rohr 1999).

The basic premise of Gray's paradox was flawed, because of potential errors in the estimation of swimming speed and inconsistencies between dolphin swimming performance and data on muscle power outputs. Gray (1936) used a shipboard observation of a dolphin swimming along the side of the ship. The dolphin was reported to swim from stern to bow in 7 s. If the dolphin was swimming close enough to utilize the wave system of the ship, its speed may have been artificially enhanced and energetic effort reduced due to free-riding behaviors (Williams *et al* 1992, Weihs 2004).

More important than the actual speed, the observation of the dolphin swimming speeds was for a sprint. Gray used measurements for muscle power output of sustained performance (3–5 min) by human oarsmen (Henderson and Haggard 1925). Muscle performance is a function of the type of muscle fibers stimulated during an activity. Fast glycolytic (FG) fibers are adapted for short burst activities with high power output and very high intrinsic speed of shortening; whereas, slow oxidative (SO) fibers are slow contracting and are suitable for slow, sustained activity (Alexander and Goldspink 1977). The peak power outputs of FG fibers are 2.6–3 times greater than SO fibers (Barclay *et al* 1993, Askew and Marsh 1997). Both FG and SO fibers are found in the musculature of cetaceans (Ponganis and Pierce 1978, Bello *et al* 1985, Suzuki *et al* 1983). FG fibers are fueled primarily by anaerobic metabolism and SO fibers use primarily aerobic metabolism. Freed from direct cardiovascular limitations, anaerobic metabolism has a maximum metabolic power output 2–17 times greater than aerobic metabolism (Hochachka 1991).

The short duration of activity of the swimming dolphin, which was reported by Gray, would indicate the use of FG fibers and higher power outputs (Fish and Hui 1991). Gray (1936) calculated muscle power outputs of 14 W kg^{-1} for a dolphin with a low-drag laminar boundary layer and 122 W kg^{-1} with a high-drag turbulent boundary layer, respectively. With anaerobic contributions, a dolphin could generate an estimated 110 W kg^{-1} (Weis-Fogh and Alexander 1977).

Turbulent boundary flow conditions delay separation of the boundary layer from the dolphin's skin surface (Webb 1975, Fish 1998). These conditions result in a narrow wake and reduced pressure drag (Webb 1975). Separation is more likely to occur with laminar boundary conditions, producing

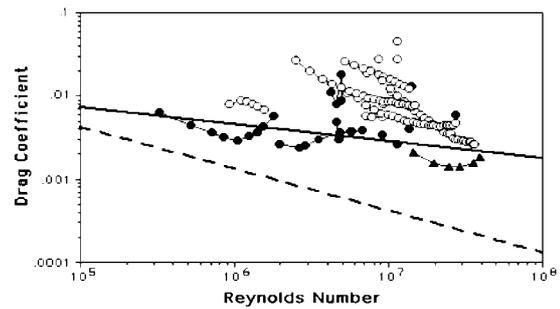


Figure 1. Drag coefficient plotted against Reynolds number for dolphins. Data were obtained from experiments on rigid models, towed bodies and gliding animals (closed circles) and from hydrodynamic models based on swimming kinematics (open circles). The upper solid line represents the drag coefficient for a flat plate with a turbulent boundary layer and the lower dashed line is for a flat plate with laminar boundary flow. Solid triangles are drag coefficients for a rigid solid of revolution of the NACA 66 series. Figure from Fish and Rohr (1999).

a greater drag penalty (Webb 1975, Gad-el-Hak and Bushnell 1991). In effect, the dolphin is capable of swimming at high speeds for short durations, while maintaining a fully attached turbulent boundary layer.

Drag coefficients (C_D) for dolphins indicated full turbulent or transition boundary conditions (Fish and Rohr 1999). In general, data obtained from hydrodynamic models of actively swimming animals are higher than values from towing or gliding experiments and higher than theoretical frictional drag coefficients with turbulent boundary conditions (figure 1, Fish 1998). Studies using towed models and gliding dolphins gave mixed results with some values of C_D below fully turbulent conditions (Kayan 1974). However as Reynolds number (Re) increased, C_D climbed into the turbulent regime.

For actively swimming dolphins, high C_D is expected, because the oscillating motions of the flukes and body will produce 'boundary layer thinning' (Lighthill 1971). Lighthill (1971) estimated that skin friction could increase up to a factor of five. This effect was confirmed using computational fluid dynamics (Liu *et al* 1997, Fish 1998). In addition, the pressure component of drag will increase because the propulsive motions produce a deviation from a streamlined body (Fish 1993). Indeed, behavioral patterns by diving mammals and birds demonstrate energetic savings by passive gliding over active swimming (Williams *et al* 2000).

3. Body and appendage shape

Streamlining of the body and the appendages minimizes drag (figure 2). The potential for drag reduction due to body shape came under the early scrutiny of engineers. Cayley (circa 1800) examined the dolphin body as a solid of least resistance design (Gibbs-Smith 1962). Modern submarines, since the development of the USS Albacore in 1953, utilized a fusiform body analogous to dolphins, although this similarity was independently developed.

A rounded leading edge and a slowly tapering tail characterize the streamlined profile of the dolphin (figure 2).

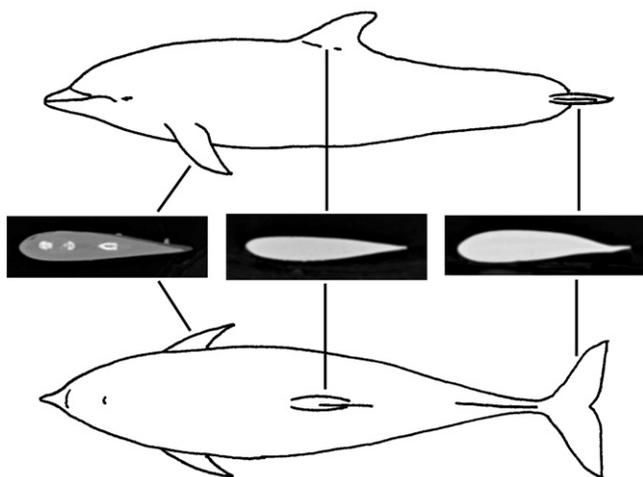


Figure 2. Lateral and dorsal body shapes and cross-sectional shapes of control surfaces (flipper, dorsal fin, flukes) for a bottlenose dolphin (*Tursiops truncatus*). Cross sections are from mid-span sections of medical CT-scans (computer tomography).

This design delays separation, which occurs closer to the trailing edge. An indication of the streamlining of a body is the fineness ratio (FR , ratio of maximum length to maximum thickness) (Webb 1975). Bodies of rotation demonstrate minimum drag in a range of FR of 3–7 (von Mises 1945, Hertel 1966, Hess 1976). Based on airship design, the optimal FR is 4.5. This optimal FR provides the minimum drag for the maximum volume (von Mises 1945). However, analysis of streamlined bodies of revolution based on mathematically related model hulls demonstrated minimum resistance at FR of 7.0 (Gertler 1950). In general, dolphins and whales are well streamlined with FR values between 3.3 and 8.0 (Fish 1993).

The position of the maximum thickness in dolphins is similar to engineered ‘laminar’ profiles (Hertel 1966, Fish 1993). The maximum thickness of dolphins is located at 34–45% of the body length from the tip of the beak (Fish and Hui 1991). This position reduces drag by maintenance of an extended favorable pressure gradient and laminar boundary flow (Webb 1975). Separation of the boundary layer was observed downstream of the maximum thickness in tests on a model bottlenose dolphin (*Tursiops truncatus*) (Purves *et al* 1975). Tests on a live dolphin swimming in a bioluminescent sea indicated no major flow separation from the body (Rohr *et al* 1998).

Abrupt departures from a streamlined shape are avoided through use of integumentary structures. Blubber contours the body of marine mammals along their longitudinal axis (Fish 1993). In addition, blubber streamlines the caudal peduncle in dolphins to reduce its drag in the flukes’ plane of oscillation (Fish and Hui 1991).

The cross-sectional shape of the appendages (e.g., fins, flukes, flippers) has a streamlined profile (Felts 1966, Lang 1966a, Purves 1969, Pavlov 2003, Fish *et al* 2006). This streamlined shape reduces pressure drag and induced drag. The induced drag component is produced from vorticity generated by lifting hydrofoils. When a hydrofoil is canted at

an angle to the incident water flow (i.e., angle of attack), lift is generated as a reaction to deflection of the fluid and pressure difference between the two surfaces of the hydrofoil (Webb 1975, Bushnell and Moore 1991). The pressure difference induces the formation of longitudinal tip vortices, resulting in energy dissipation (Webb 1975, Vogel 1994). Well-performing appendages maximize the ratio of lift (L) to drag (D) (Webb 1975). An increase in the maximum L/D with increasing size is achieved by increasing span more rapidly than the square-root of planar area, thereby increasing the aspect ratio ($AR = \text{span}^2/\text{area}$) (von Mises 1945, Lighthill 1977, van Dam 1987, Bose *et al* 1990). High AR and tapering of the appendages reduces tip vorticity and induced drag (Webb 1975, Rayner 1985, Webb and de Buffrénil 1990). Dolphins and whales have flukes with AR ranging from 2.0 to 6.2 (Fish and Rohr 1999).

Induced drag is limited also by the sweepback of the appendage. A tapered wing with sweptback or crescent design could reduce the induced drag by 8.8% compared to a wing with an elliptical planform (van Dam 1987). Induced drag can be reduced with a swept wing planform with a root chord greater than the chord at the tips giving a triangular shape (Küchemann 1953, Ashenberg and Weihs 1984). This optimal shape approximates the planforms of the appendages of dolphins (Fish and Rohr 1999).

4. Viscous damping

The idea that laminar flow in the boundary layer could be maintained over the entire body of the dolphin to reduce drag was provided by a mechanism by Kramer (1960a, 1960b). Kramer claimed that the dolphin’s smooth, compliant skin was the means to achieve a laminar boundary layer without separation. The skin was proposed to deform and reduce drag by the process of viscous damping. In viscous damping, the compliance of the skin due to its viscoelastic properties would absorb energy from pressure oscillations and damp turbulence-forming perturbations of the Tollmien–Schlichting wave type to maintain laminar flow (Pershin 1988).

Kramer (1960a, 1960b) constructed a torpedo with an artificial skin. The artificial skin was based on the structure of the dolphin’s epidermis and dermis. Drag reduction was to be implemented by the skin’s passive viscoelastic properties. When tested in open water the torpedo with the artificial skin was reported to produce a 59% reduction in drag when compared to a reference model with fully turbulent flow (Kramer 1960a, 1960b). Replication of Kramer’s experiments was not successful using a compliant surface which was modeled after the dolphin’s skin. The structure of the skin and blubber layer of dolphins is highly organized and complex (Parry 1949, Sokolov 1960, Aleyev 1977, Pershin 1988, Hamilton *et al* 2004); thus, the analogy with the compliant skin proposed by Kramer may be only superficial and have little functional significance. Some limited success in reducing skin friction has been possible with other compliant coatings (Landahl 1962, Gad-el-Hak 1987, Riley *et al* 1988, Carpenter 1990, Carpenter 1998, Carpenter *et al* 2000, Bandyopadhyay *et al* 2005). Dixon *et al* (1994) were able to measure a 2.5- and

5-fold transition delay for single- and double-layer viscoelastic walls, respectively, when compared to a rigid wall. A delay in laminar-turbulent transition is possible by using a series of multiple compliant panels, which are tuned to local Reynolds numbers (Carpenter *et al* 2000).

The dolphin skin's elasticity is due to large amounts of organized collagen and elastic fibers (Pershin 1988, Hamilton *et al* 2004). Kramer (1965) reported a modulus of elasticity (E) of $1 \times 10^8 \text{ N m}^{-2}$ for a dolphin skin sample. This value was considered high due to an artifact of testing preserved tissue (Babenko 1979). A high value of E indicates a stiff material. Measurements of E on live dolphins were $1.7\text{--}2.0 \times 10^4 \text{ N m}^{-2}$ (Babenko 1979). E varies with species, position on the body, degree of training and physical condition (Babenko 1979, Babenko *et al* 1982). The elastic properties of the integument are dependent particularly on the deeper layer of thick blubber. The blubber layer is highly resilient with E similar to biological rubbers (Pabst *et al* 1995). Elasticity of the skin and underlying blubber may absorb pressure pulsations due to flow perturbations and thus maintain a favorable pressure gradient to stabilize the boundary layer (Kramer 1960a, 1960b, Babenko 1979, Babenko *et al* 1982).

The skin of live dolphins has a maximum 95% absorption of perturbation energy, corresponding to the order of energy of turbulent pulsations in the boundary layer (Babenko 1998). Madigosky *et al* (1986) examined the velocity and absorption of acoustic surfaces on live dolphins and concluded that the lower hypodermis with its associated blubber played an important role in determining the compliant response to hydrodynamic disturbances. Shear compliance of blubber is intermediate between soft-compliant coatings, which increase drag and harder compliant coatings, which have no effect on drag (Fitzgerald *et al* 1995).

Changes in compliance were envisioned by regulating blood pressure within the blood vessels of the skin (Babenko *et al* 1982, Koslov and Pershin 1983). For a rapidly swimming dolphin, the reduction in hydrodynamic pressure over the maximum thickness of the body would foster increased peripheral capillary profusion causing distention of the skin surface (Babenko *et al* 1982). Experiments demonstrating changes in capillary profusion with varying atmospheric pressure were performed on humans with a thinner integument than dolphins. Evidence against this mechanism for control of boundary layer turbulence was supplied by pressure measurements on swimming dolphins, where turbulence occurs at the position posterior of the maximum thickness and pressure is reduced (Romanenko 1995).

An active mechanism of turbulence damping was hypothesized by changing skin compliance with muscular control by microvibrations (Haider and Lindsley 1964, Babenko *et al* 1982, Koslov and Pershin 1983, Ridgway and Carder 1993). This mechanism relies upon a sensory input of pressure pulsations from the richly innervated skin. Microvibrations are small tremor-like vibrations (1–5 mm; 7–13 Hz) that occur at all times over the entire body of warm-blooded animals (Haider and Lindsley 1964, Ridgway and Carder 1993). Dolphin skin generates microvibrations with amplitude 3–4 times higher than for humans. It was

suggested that the dolphin skin could move or vibrate to improve hydrodynamic performance (Ridgway and Carder 1993). Drag could be decreased by the skin actively flexing away from areas of higher pressure toward areas of lower pressures and thus decrease the pressure gradient.

The presumption of both active and passive compliance appears inconsistent with dolphin swimming patterns. The results of live dolphin studies indicated a turbulent boundary layer flow when gliding, but an incomplete turbulent layer when swimming (Romanenko and Yanov 1973, Romanenko 1981). Drag minimization would be equally important for gliding and active swimming. There is no reason to expect that either passive or active mechanisms are switched on or off depending on the activity state. Both mechanisms invoke properties of the skin that are uncoupled from activation of the propulsive musculature.

5. Dermal ridges and skin folds

The skin of cetaceans is generally described as smooth (Shoemaker and Ridgway 1991). However, cutaneous ridges are present at the surface of the skin in many dolphins. The ridges are formed from the dermal crests and papillae (Sokolov 1960, Purves 1963, 1969, Purves *et al* 1975, Aleyev 1977, Pershin 1988). A survey of ridges in seven species of cetaceans showed that the ridges were spaced 0.41–2.35 mm apart and were 7–114 mm in height (Shoemaker and Ridgway 1991).

The orientation of the ridges is crucial for considerations of drag reduction. A longitudinal orientation would be analogous to riblets. Riblets are streamwise microgrooves that act as fences to break up cross-flow vortices, and reduce surface shear stress and momentum loss from the boundary layer (Yurchenko and Babenko 1980, Walsh 1990). A 7–9% drag reduction is possible with riblets (Walsh 1990, Reidy 1987). However, the ridge dimensions are greater for dolphins than the dimensions for riblets to achieve drag reduction (Walsh 1990).

The literature presents a contradictory picture of the orientation of the cutaneous ridges. Sokolov and his colleagues noted a streamwise arrangement for dolphins as summarized by Aleyev (1977). Purves (1963) and Pilleri (1976) described the ridge direction as oblique, not lengthwise, to the longitudinal axis. Finally, Shoemaker and Ridgway (1991) noted that the ridges were oriented perpendicular to the longitudinal axis of the body. The ridges ran circumferentially around the body from the eye to the base of the dorsal fin (Ridgway and Carder 1993). Posterior of the dorsal fin, the ridges ran obliquely.

The ridge orientation described by Shoemaker and Ridgway (1991) would not function for drag reduction like riblets. In addition, dolphin dermal ridges do not have sharp edges as do the engineered forms (Fish and Hui 1991). Indeed, the effects for drag reduction have never been demonstrated for dermal ridges.

The dense packing of dermal papillae associated with the cutaneous ridges suggests a sensory function (Palmer and Weddell 1964, Khomenko and Khadzhinskiy 1974). The dermal papillae contain blood vessels and a rich supply of

nerve bundles. The highly innervated skin has a threshold sensitivity of $10\text{--}40\text{ mg mm}^{-2}$, which is close to the most sensitive skin areas (i.e., fingertips, lips, eyelids) in humans (Ridgway and Carder 1993). Dolphins are sensitive to vibrations and small pressure changes. The skin, therefore, could function in the detection of flow velocities and flow disruptions. Sensory feedback would be more important in detecting boundary layer separation, which would more severely impact drag rather than boundary layer transition.

Mobile skin folds were observed on accelerating dolphins (Essapian 1955, Backhouse 1960, Pershin 1988). These folds were believed to result from vorticity along the body surface. The vorticity creates pressure differences, which could deform the flexible skin (Backhouse 1960, Aleyev 1977). It has also been suggested that folds may be generated from active control by muscles (Sokolov *et al* 1969). Hydrodynamically generated folds move posteriorly in a wavelike manner perpendicular to direction of the dolphin's movement (Essapian 1955). It was hypothesized that the folds were a mechanism to damp turbulence (Sokolov *et al* 1969, Babenko and Surkina 1969, Carpenter *et al* 2000). Carpenter *et al* (2000) argued that hydrodynamic benefits would occur when the folds moved at 0.7 of the free stream velocity. The velocity of folds on live dolphins was measured as 6.5 m s^{-1} (Madigosky *et al* 1986), which indicated an advantage at a swimming speed of 9 m s^{-1} (Carpenter *et al* 2000). However, measurements of the velocity of the folds were made in air on resting animals (Madigosky *et al* 1986) and a predicted speed of 9 m s^{-1} is only used for quick bursts (Fish and Rohr 1999).

Skin folds, similar to those on dolphins, developed passively on the bodies of naked human subjects towed through the water at $2\text{--}4\text{ m s}^{-1}$ (Aleyev 1977). The speed of the posterior movement of the folds was 10% lower than the towing speed. The folds increased the drag on the body. When subjects were tested while wearing a swimsuit to suppress the formation of skin folds, the drag decreased 6.1% compared to nude subjects (Aleyev 1977).

Rather than have the compliant skin of dolphins maintain a laminar boundary layer, drag reduction is possible by matching a compliant surface with a turbulent flow. Choi *et al* (1997) found that a 7% drag reduction was realized with a compliant surface with a turbulent boundary layer. Given the turbulent nature of the ocean environment, turbulence control would be advantageous for drag reduction by dolphins.

6. Secretions

The addition of dilute solutions of long-chain polymers into flow is well established as a means of drag reduction (Rosen and Cornford 1971, Hoyt 1975, Daniel 1981). Non-Newtonian additives move the region of maximum shear stress away from a rigid surface into the region of low velocity gradient, reducing turbulence (Baier *et al* 1985). The epidermal cells of dolphins contain masses of tonofilaments and lipid droplets (Harrison and Thurley 1972). Epidermal cell production in *Tursiops truncatus* occurs at a rate 250–290 times that of humans (Palmer and Weddell 1964). This high rate is associated with an extensive germinative skin layer (Brown *et al* 1983) and

increased skin sloughing. However, cells that are shed from the epidermis have a negligible effect on hydrodynamic drag (Sokolov *et al* 1969). Nagamine *et al* (2004) determined by numerical simulation that the combination of a shedding epidermis and compliant wall decreases shear stress and potentially drag.

The surface chemical/physical properties of the skin in conjunction with its high rate of sloughing may help to maintain low drag characteristics by preventing fouling by encrusting organisms on the dolphin's surface (Fish and Hui 1991). Biofouling consisting of slime and barnacles can cause a four-fold increase in resistance (Swain 1998). The skin of dolphins has similarities to the oral mucosa, which is self-cleaning and resists fouling (Baier *et al* 1985).

Secretions from the dolphin eye are highly viscous complexes of proteins and polysaccharides (Uskova *et al* 1983). Sokolov *et al* (1969) found no effect on drag characteristics from these secretions. Uskova *et al* (1983) demonstrated that the eye secretions could reduce water viscosity and concluded that the secretions had a hydrodynamic function. Although the secretions may fill in any disruptions in skin contour around the eyes, the area covered by the secretions is generally too small to aid in any significant drag reduction for the body.

7. Boundary layer heating

Increasing the temperature of water will lower its viscosity (Webb 1975), thereby decreasing drag. Walters (1962) and Lang (1966b) suggested that heating the boundary layer would decrease the drag over a warm-bodied swimmer. Schlichting (1960) proposed reducing the viscosity of the inner region of the boundary layer to modify its velocity profile and make it stable. Stabilization of laminar flow is caused by increasing the critical Reynolds number. Warm-bodied cetaceans have the potential to use heat conducted from the body surface to decrease water viscosity (Fish and Hui 1991). The surface temperatures of dolphins were reported to be higher than the water temperature by as much as $9\text{ }^{\circ}\text{C}$ (McGinnis *et al* 1972, Hampton and Whittow 1976). In water at $27\text{ }^{\circ}\text{C}$, a reduction in viscosity of only 11% would be realized (Fish and Hui 1991). The viscosity reduction would result in drag reduction only if the water were instantaneously heated along the surface of the body. The swimming speed of the animal precludes sufficient contact between the skin and the water for effective heating. In addition, heat from the body is convected to the water through thermal windows via the extensive circulatory network in the appendages (Scholander and Schevill 1955, Pabst *et al* 1995). The effectiveness of heating is considered limited (Lang and Daybell 1963) or insignificant (Webb 1975) as a drag reduction mechanism.

8. Boundary layer acceleration

As originally proposed by Gray (1936), propulsive fluke movements could re-laminarize the boundary layer to reduce the drag on a dolphin by acceleration of the boundary layer. Drag reduction by oscillating-foil action was demonstrated

for robotic tuna (Triantafyllou *et al* 1996, Barrett *et al* 1999). Oscillations of the flukes generate unsteady velocity and pressure gradients by accelerating water over the body (Gray 1936, Romanenko 1995). Delay of transition is possible by injection of high momentum fluid into the boundary layer. However, the generally high drag values for actively swimming dolphins indicate turbulence within at least a significant portion of the boundary layer (figure 1).

Accelerated flow could prevent separation and account for the results of flow visualization and pressure studies (Steven 1950, Rosen 1961, 1963, Romanenko and Yanov 1973, Wood 1973, Purves *et al* 1975, Romanenko 1981). Boundary layer separation behind the dorsal fin was noted for rigid dolphin models in a flow (Purves *et al* 1975); whereas, actively swimming dolphins exhibited separation further downstream at the flukes (Steven 1950, Rosen 1961, 1963, Wood 1973). For a model, an adverse pressure gradient fostering separation is expected to develop as the flow over the body decelerates posterior of the maximum thickness.

Suppression of boundary layer separation was achieved under conditions of high oscillatory frequency and/or large chord lengths for flapping-foil propellers (Platzer *et al* 1998). Acceleration of boundary flow along with fluid accelerated by the flukes into the propulsive wake would delay separation by reducing the pressure gradient. From Bernoulli's theorem, the pressure in the wake will be slightly lower than pressure in the free stream as fluid is discharged into the wake at a velocity greater than the free stream (Webb 1975). This action reduces the pressure gradient over the posterior portion of the body. Calculations of the dynamic pressure distribution over an actively swimming dolphin indicated the extension of a favorable pressure gradient over the total body with a steep pressure reduction in the region of the peduncle and flukes (Romanenko 1981, 1995).

9. Behavioral mechanisms for drag reduction

The need to breathe gaseous oxygen to fulfill metabolic demands incurs a potentially high drag at the water surface for cetaceans. When swimming near or at the surface, the animal experiences increased resistance from production of surface waves (Lang and Daybell 1963, Hoerner 1965, Hertel 1966). Wave drag estimates (based on a towed body: NACA 60-018 profile) suggest that wave drag becomes important when the animal is within three body depths of the surface. Wave drag is at a maximum of five times the frictional drag for a body just under the surface (Hertel 1966). The locomotor strategy of submerged swimming can result in reduction of drag (Williams 1989). Energy saved by prolonged swimming away from the surface would offset increased energy expended in coming to the surface to breathe. 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. Furthermore to prevent increased energy cost when coming to the surface to breathe, these animals limit such times and quickly ventilate the lungs before submerging.

An alternate behavior is porpoising to prolong ventilation time while reducing drag (Au and Weihs 1980, Hui 1989, Fish and Hui 1991). Porpoising consists of rhythmic, serial leaps in which the animal leaves and re-enters the water during continuous swimming. Models of porpoising predict that at high velocities the energy to leap a given distance is lower than the energy to swim (Au and Weihs 1980, Weihs 2002). The energy savings comes from a reduction in drag during the aerial phase compared to swimming in water just beneath the surface.

A substantial amount of time during swimming may be occupied by gliding when low drag would be beneficial (Lighthill 1970, Williams *et al* 1996, 2000). Gliding is performed during surfacing for respiratory exchange (Amundin 1974). During deep dives, dolphins can reduce energy costs by approximately 20% when transiting to the bottom by using intermittent swimming behaviors (Williams *et al* 1996). Diving dolphins glide to reduce locomotor energy costs (Skrovan *et al* 1999). When diving deeply (>20 m), lung collapse reduces the net buoyant force causing the animal to sink (Ridgway *et al* 1969, Ridgway and Howard 1979). The dolphin can descend using its negative buoyancy to glide, thus saving energy over active swimming. During ascent, the reverse occurs and the dolphin accelerates by actively swimming until its lungs re-inflate sufficiently to provide positive buoyancy (Skrovan *et al* 1999). By allowing the body to be neutrally or slightly negatively buoyant an animal foraging on the bottom can conserve its oxygen reserves and increase its dive time.

Drafting is the transfer of forces between individuals by using the flow structure of the individuals (Weihs 2004). Drafting is beneficial for young dolphins in order to maintain speed with their mothers. By swimming next to the mid-section or near the genital region of the mother, young dolphins can realize energy savings of up to 60% (Weihs 2004).

10. Conclusions

The idea that dolphins have special mechanisms to reduce drag has been tantalizing, although elusive. Evidence to support drag reduction by mechanisms associated with Gray's paradox has been lacking and the assumptions used in Gray's (1936) calculations were flawed. Maintenance of a laminar boundary layer for drag reduction has technological application by compliant surfaces, polymer additives, riblets, boundary layer heating and boundary layer acceleration, but these mechanisms have not been demonstrated for dolphins. The evidence indicates a turbulent boundary layer for dolphins that reduces the likelihood of separation and minimizes drag. Drag reduction for dolphins is primarily due to streamlining of the body and appendages and by behavioral mechanisms.

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