

Imaginative solutions by marine organisms for drag reduction

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Both machines and animals must contend with the same physical laws that regulate their design and behavior. Many animals demonstrate high levels of performance with respect to movement through water, and therefore, may be useful as model systems to analyze novel mechanisms for drag reduction that are superior to engineered solutions. A survey of various animals demonstrates that they have evolved a number of morphological and behavioral drag-reducing mechanisms. Although more complex, these mechanisms act similarly to analogous engineered solutions for movement when submerged and across the air-water interface.

We were lying upon the back of a sort of submarine boat, which appeared (as far as I could judge) like a huge fish of steel. (Jules Verne, Twenty Thousand Leagues Under The Sea)

INTRODUCTION

The idea that new technologies can be developed from observation of nature has been long standing. Indeed, nature has served as the inspiration for various technological developments including flight and robotics [1, 2, 3]. Copying nature by the biomimetic approach attempts to seek common solutions from engineering and biology for increased efficiency and specialization [4]. It is no accident that the shape of modern submarines, fish, and marine mammals are so closely matched. Parallels between natural and engineered designs occur because both are selected for a range of performance constrained by the same physical forces.

Analysis of locomotor specializations in animals holds for engineers the possibility that animals can be used as solutions to design problems for reduction in energy input, whether in their construction or in the performance of work. Any mechanism that allows for increased energy economy use can provide an important advantage to the survival of an animal. It is viewed that evolution (descent with modification) through the Darwinian process of "natural selection" has fostered improvements in design which have culminated in adaptations for high speed and efficiency [4, 5]. Because natural selection chooses from a wide range of design and performance possibilities as dictated through the genetic code and functional demand of the environment, a variety of possible solutions to engineering problems may be investigated. The diverse morphological specializations exhibited by animals may be targeted by engineers for technology transfer and effectively reduce the time of development of innovative technological solutions.

However, the use of animal models for design improvements is not without criticism. Strict adherence to biological designs is considered to rarely produce any practical results and can impede the development of engineered systems [6, 7]. Airplanes do not flap their wings like birds for lift and ships do not undulate like fish for propulsion. The reason that the duplication of biological systems has been limited is due to evolutionary and material constraints.

Animals are functionally multifaceted (i. e., they move, feed, reproduce) and must compromise optimal solutions for specialized functions to perform adequately rather than maximally [8, 9]. The biotic and abiotic environments of the time that a new design evolves dictates its selection without anticipation for potential future purpose and effectiveness. Both superior and poor designs with respect to present time may be lost if they did not function adequately in past environments or if they were accidentally lost due to chance events. In addition, animals have evolved along lines of common descent with shared developmental patterns which restricts possible solutions. Radical redesigns are not permitted to expedite enhancing performance; instead, it is existing designs which are modified. Although swimming in whales would be more efficient if these animals remained submerged like fish (see below), their common evolutionary history with other air-breathing mammals requires that they periodically return to the water surface to fill their lungs despite increased energy cost.

Animals are further limited by the variety of structural materials available. Animals are composed of either fibers, such as collagen, chitin, and keratin, or composites, such as bone and cartilage [10]. Compared to manufactured materials, like metals, ceramics and glasses, biological materials are generally weaker and less stiff. Furthermore, movements are generated through forceful contraction of

the muscles transmitted to a jointed skeleton by tendonous connections. The arrangement of the contractile machinery precludes the use of rotational movements so ubiquitous in engineered systems [8]. Therefore, biological systems suffer lower efficiency due to periodic accelerations over a propulsive cycle.

Despite these concerns, the realization of new and superior designs to reduce drag based on animal systems has been tantalizing, although elusive [7, 11, 12]. Aquatic animals are considered superior in their capabilities to technologies produced from nautical engineering [2]. Speeds over 11 m/s (>21 kts) have been attained by dolphins [13], whereas fish display speeds as high as 20 m/s (39 kts) and can accelerate at 40-50 m/s² [11, 14]. Such high levels of performance were assumed to be dependent on adaptations which reduced drag.

This report explores the specialized adaptations used by aquatic animals for drag reduction. These adaptations are compared with analogous engineered solutions. Comparison of biological and mechanical systems can provide insight into the effectiveness of each system and help direct engineers toward innovative applications of biological systems. For a full appreciation of the topic, this survey includes discussion of mechanisms which are considered valid, fallacious, and speculative.

DRAG COMPONENTS

A previous review of biological drag reduction by Bushnell and Moore [5] examined three types of drag (form drag, skin-friction drag, and drag-due-to-lift) for organisms totally immersed in a fluid, whether air or water. The present review examines how organisms reduce their drag in an aqueous environment for fully submerged bodies and bodies operating at the air-water interface.

The primary component of drag experienced by aquatic animals varies in accordance with (1) flow conditions around the animal and in its boundary layer, (2) proximity to the air-water interface, and (3) the relative predominance of inertial, gravitational, and viscous forces. Because of the interest in rapid motion in water and application of biological designs to large structures, the discussion will focus on conditions encompassing high Reynolds numbers (Re), expressed as:

$$Re = UL / \nu \quad (1)$$

where U is the velocity, L is a characteristic linear distance (e.g., body length), and ν is kinematic viscosity, which is equal to $1.044 \times 10^{-6} \text{ m}^2/\text{s}$ for sea water at 20°C. At high Re, inertial forces predominate over viscous forces. Of particular interest is the range of $Re > 10^5$, where transition from laminar to turbulent flow conditions can occur. Gravitational forces predominate when animals swim near or pierce the water surface. The ratio of inertial forces to gravitational forces experienced by a body moving at or close to a fluid/fluid interface is given by the dimensionless Froude number, F_L , as:

$$F_L = U/(gL_w)^{1/2} \quad (2)$$

where g is the gravitational acceleration, 9.8 m/s², and L_w is the waterline length along the longitudinal axis of the body.

For submerged bodies, minimum drag is associated with purely frictional drag with laminar boundary conditions (Fig. 1). To maintain a laminar boundary layer, the surface of the body should be smooth and the configuration of the body should promote a large favorable (negative) pressure gradient [15]. This gradient occurs when the

pressure is decreasing along the streamline from the leading edge toward the trailing edge by gradually increasing the thickness of the

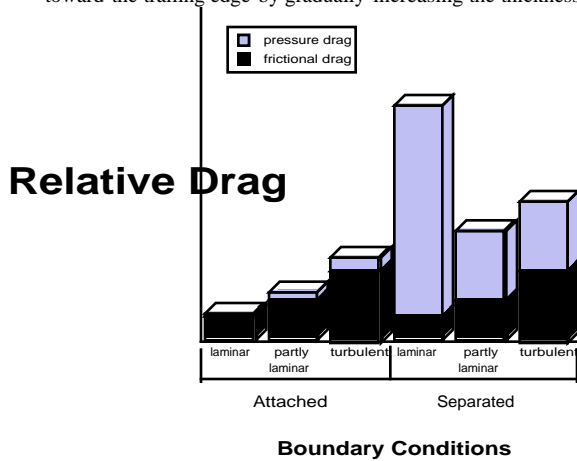


Fig. 1. Relative drag associated with boundary conditions. Redrawn from [11].

body. A large region with a favorable pressure gradient is achieved by positioning the maximum thickness of the body posteriorly. However at high Re ($> 10^5$), transition from laminar to turbulent boundary conditions can occur. The result of this transition is an increase in the frictional drag due to an increase in boundary layer thickness.

Pressure or form drag is produced from pressure difference in the flow outside the boundary layer arising from changing flow velocities around the body. The pressure differential from leading to trailing edges of the body is the source of the force [11]. Streamlining minimizes drag by reducing the magnitude of the pressure gradient over the body [7].

Pressure drag is also dependent on the interaction of the boundary layer and pressure gradient. Boundary layer separation generally occurs in the region posterior of the maximum thickness of the body. In this region an adverse pressure gradient develops with high pressure located posteriorly. At a point along the gradient, fluid in the boundary layer does not have sufficient momentum to overcome the increasing pressure and separation occurs. Premature separation along the body as opposed to near the trailing edge will produce a broad wake with substantial energy loss. Separation is more likely to occur with laminar boundary conditions. This results in higher drag with laminar conditions than with a turbulent boundary layer (Fig. 1). Separation is delayed in a turbulent boundary layer, because momentum is transferred vertically due to increased mixing within the layer [15].

Wave drag occurs when an animal swims at or near the water surface acting as a displacement hull [16, 17, 18]. Kinetic energy from the animal's motion is transferred into potential energy in the upward displacement of water in the formation of surface waves. This energy loss can be substantial at a maximum of five times the frictional drag when the body is at a relative depth of 50% of the maximum diameter of the body and $F_L = 0.5$ [17, 19, 20].

Speed at the water surface is constrained by the formation of surface waves [18, 21, 22]. As an animal swims faster, constructive interference from bow and stern waves trap it in a trough, ultimately limiting further increases in speed [23, 24]. To move faster, the animal would have to literally swim uphill, which is energetically very costly. This effective speed limit for a conventional displacement hull, such as a ship or duck, is called the hull speed, U_h [21]. Hull speed depends on L_w with longer bodies having higher hull speeds. U_h is calculated as:

$$U_h = (g L_w / 2\pi)^{1/2} \quad (3)$$

Spray drag or surface interference drag is created by water piled up along the forebody of a surface-piercing strut or foil and being shot into the air [19]. At high F_L , spray drag is approximately 26% of total drag for a surface-piercing flat plate and 30% for a strut with a blunt trailing edge [19]. The best design to reduce spray drag is a pointed

leading edge and long forebody region relative to the maximum thickness (Fig. 2).

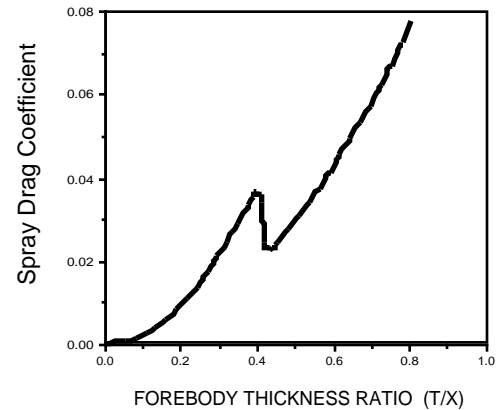


Fig. 2. Relationship between spray drag and forebody thickness ratio based on [19].

The induced drag component is produced from vorticity generated by lifting hydrofoils (e.g., fins, flippers, flukes). When the hydrofoil is canted at an angle to the water flow (i.e., angle of attack), a lift is generated due to deflection of the fluid and pressure difference between the two surfaces of the hydrofoil [5, 11]. The pressure difference induces the formation of longitudinal tip vortices resulting in energy dissipation [7, 11]. The induced drag coefficient (C_{Di}) is determined as:

$$C_{Di} = C_L^2 / \pi AR \quad (4)$$

where C_L is the coefficient of lift and AR is the aspect ratio. AR is an indicator of the geometry of the hydrofoil and is calculated as:

$$AR = S^2 / A = S / C \quad (5)$$

in which S is the hydrofoil span, A is the maximum projected area of the hydrofoil, and C is the chord. As AR increases, the hydrofoil planform becomes long and narrow. Equation 4 suggests that hydrofoils with high AR will experience a low induced drag.

BIOLOGICAL SOLUTIONS FOR DRAG REDUCTION

A variety of engineered solutions and possible animal mechanisms for drag reduction exist for each of the drag components presented above. Animals reduce drag by utilizing secreted materials, anatomical features, and behavioral patterns.

Friction Drag

Mucus

The addition of dilute solutions of long-chain polymers into flow is well established as a means of drag reduction [25]. The conditions necessary are (1) turbulent or pulsed laminar flow in the boundary layer, (2) the polymer is linear and soluble, (3) the polymer has a molecular weight of 50,000 or more, and (4) the density and viscosity of the fluid from the surface outwards must be constant [25, 26]. The mucus secreted by fish over the body surface is considered to meet these conditions. The mucus is a combination mucopolysaccharides, nucleic acids, proteins, and surfactants in the form of lipids, phospholipids and lipoproteins [5].

The undulatory or oscillatory movements of fish during swimming indicates turbulent or pulsed flow for which mucus could be effective in reducing drag [25, 26]. Measurements of dilute solutions of fish mucus in turbulent pipe flow exhibited as much as 66% reduction in friction drag [25, 27]. The mucus is believed to reduce the velocity gradient over the fish and thus decrease viscous shear stress and reduce the rate of momentum transfer from the free-stream flow to the surface of the fish [26]. The mucus also may fill in irregularities to improve streamlining [28]. However, no association was found between amount of drag reduction and species of fish which swim at

high speeds. Even snails, which are not noted for speed, produce a mucus that reduces drag [25].

Secretions from dolphins have been examined also for drag reducing abilities, although with no success. Secretions from the dolphin eye fail to produce any drag-reducing effect [29]. Likewise, the high density of epidermal cells shed from dolphin skin have little effect, although the composition of these cells is considered similar to a mucopolysaccharide [29, 30]. High rates of skin sloughing may aid in minimizing drag by preventing fouling by encrusting organisms [31].

Riblets

The development of riblets to reduce turbulent skin friction came in part from the study of shark scales or dermal denticles [32]. Riblets are streamwise microgrooves that act as fences to break up spanwise vortices, and reduce the surface shear stress and momentum loss. Fast swimming sharks have scales that are different from other sharks. These scales have flat crowns and sharp ridges oriented longitudinally with rounded valleys [33, 34, 35, 36]. Although the ridges are discontinuous due to the distribution of the scales, a 7-8% drag reduction is possibly as measured for continuous riblets [32, 37]. The streamwise surface grooves of scallop shells also indicate the use of riblets [38]. The optimal riblet spacing is present in those scallops demonstrating the greatest swimming ability. Small ridges on the epidermis of dolphins had been hypothesized to stabilize longitudinal vortices [39, 40], but the geometry of the ridges with rounded edges does not suggest an effective analogy with riblets [12].

Viscous dampening

By far, arguments surrounding the investigation and application of mechanisms for viscous dampening by dolphins have been the most contentious [7, 12]. The controversy, known as Gray's Paradox, was the result of an estimation of the power output, based on calculation of drag with turbulent boundary conditions, for a rapidly swimming dolphin. The estimated drag power could not be reconciled with the available power generated by the muscles [41]. Gray's resolution to the problem was that the drag on the dolphin would have had to be lower by maintenance of a fully laminar boundary layer, despite Re above transition. Gray proposed a mechanism to laminarize the boundary layer by accelerating the flow over the posterior half of the body (see boundary layer acceleration below). However, the basic premise of Gray's Paradox was flawed, because the observation of the dolphin swimming speed was for a sprint (7 sec) and Gray used measurements of muscle power output for sustained performance of human oarsmen, which are lower than power outputs for burst activities [12].

Gray's Paradox, however, endured and was invigorated by the work of Max Kramer [42, 43, 44]. Kramer claimed that a laminar boundary layer without separation could be achieved at high Re by coating a torpedo with an artificial skin based on the skin of a dolphin. The dolphin integument is composed of a smooth, hairless epidermal surface forming an elastic membrane [45] and is anchored to the underlying dermis by longitudinal dermal crest with rows of papillae, which penetrate the lower epidermis [29, 40, 43, 44, 45]. Kramer's analogous skin was composed of a heavy rubber diaphragm supported by rubber studs with the intervening spaces filled with a viscous silicone fluid [42]. It was hypothesized that the coating would dampen out perturbations in the flow and prevent or delay transition. When a portion of a towed body anterior of the maximum thickness was coated, a 59% reduction in drag was achieved at $Re=15 \times 10^6$ compared to a rigid reference model with fully turbulent flow. These results suggested the "dolphin's secret" and a resolution to Gray's Paradox [43].

In what has been characterized as "enthusiastic optimism" and "Pentagon and Kremlin paranoia" [7], research on dolphin hydrodynamics and compliant coatings was accelerated during the 1960s [12, 45, 46]. Attempts to verify Kramer's results subsequently failed [46, 47], although some success in reducing skin friction was possible with other compliant coatings [48, 49]. It was suggested that a compliant coating would reduce drag by controlling turbulence in the boundary layer rather than delaying transition [46]. It would be more important in minimizing total drag by delaying separation than to delay transition in the boundary layer.

The structure of the skin and blubber layer of dolphins is highly organized and complex [40, 50]; thus, the analogy with the compliant skin proposed by Kramer may be only superficial and have little functional similarity. When swimming at high speed or for bursts, dolphins exhibit prominent skin folds [51]. Similar speed-induced skin

folds were shown to add to drag when observed on naked women swimming or towed at 2-4 m/s [45]. The possession of a thick skin, which could make the induced folds, is attributed also to turbulent boundary conditions for the beluga whale (*Delphinapterus leucas*) [36].

Drag measurements of gliding dolphins and rigid models indicated that the boundary layer was largely turbulent [13, 16, 36, 39,45, 52]. This was verified by low-speed, flow visualization studies on dolphins using dye or bioluminescence [53, 54, 55]. The fluid layer against the body, inferred to represent the boundary layer, thickened anterior of the dorsal fin. The inferred transition anterior to the dorsal fin corresponded with a local Re of about 3×10^6 , and was confirmed from measurements of turbulent pulsations on a live dolphin [45]. The boundary layer remained attached up to the flukes for gliding animals [55], but separated anterior of the flukes for an actively swimming dolphin [53]. Similar observations were made on seals swimming through bioluminescence [56]. Seals swim in a manner analogous to dolphins [57].

As indicated from flow visualization experiments on dolphins, differences in boundary layer flow occur between actively swimming and gliding animals. This implies that viscous dampening may be under active control when the animal is oscillating its flukes. Experiments using remote pressure sensors in the boundary layer of an actively swimming dolphin indicated that although agitated the boundary layer did not become completely turbulent [58]. Although the degree of turbulence and the pressure were determined to decrease over the posterior portion of the body, these results may not be associated with viscous dampening as has been hypothesized [36, 59]. Indeed there is no evidence to suggest that viscous dampening of the skin should be any more likely when the animal is oscillating its flukes as opposed to gliding [12]. A substantial amount of time during swimming may be occupied by gliding when low drag would be beneficial.

As originally proposed by Gray [41], acceleration of the boundary layer due to propulsive fluke actions could account for the results of flow visualization and pressure studies [53, 58]. Estimates of drag on actively swimming dolphins based on kinematics and hydrodynamic models have indicated turbulence due to high drag values [11, 52, 60, 61]. Such high drags are consistent with estimates for actively swimming animals which can be 2-5 times the greater than drag values of equivalent rigid bodies [62].

Dynamic dampening

The network of subdermal canals and pores in the skin of fish suggests use of a suction mechanism to stabilize the boundary layer and prevent separation [63, 64]. In the trachipterid fish, *Desmodema*, the placement of maximum thickness is at 7% of total length. This will result in a negative pressure gradient over the majority of the body. The pore and canal system is believed to redistribute fluid from high to low pressure regions. Engineered systems using boundary layer suction achieved 66-100% laminar flow [65].

Boundary layer acceleration

Injection of high momentum fluid into the boundary layer has the capacity to delay both transition and separation [11]. The effluent from the gills of fish could potentially introduce kinetic energy into the boundary layer [28, 66]. Flow visualization in fish, however, has shown the pulsed flow during active respiration increases turbulence [45, 66]. The location of the gill slits anterior of the maximum thickness of fish (i.e., position of lowest pressure) would enhance respiratory flow rather than surface flow. During passive or ram ventilation in scombrid fish, the mouth and gill coverings are kept open so that water can continuously flow over the gills without pumping. The constant swimming motion of the fish maintains the flow. Ram ventilation does not prevent turbulence, but it appears to extend the laminar region of the boundary layer by 13-100% [45].

Re-acceleration of the boundary layer as fluid was accelerated from the oscillating flukes of dolphins was proposed originally as the resolution to Gray's Paradox [41]. Calculations of the dynamic pressure distribution over an actively swimming dolphin indicate the extension of a favorable pressure gradient over the total body with a steep pressure reduction in the region of the peduncle and flukes [59]. This mechanism seems to have greater potential for boundary layer stabilization in the dolphin than maintenance of laminar flow with viscous dampening. A similar mechanism may operate in cephalopods (e.g., squid, octopus). Water flowing into the inlet of the mantle cavity

during inhalation and during exhalation through the siphon when jetting could accelerate the boundary layer [45].

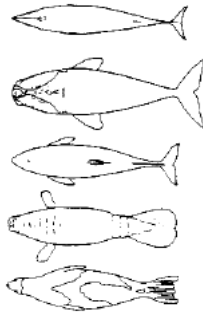


Fig. 3. Representative body shapes of marine mammals. From top to bottom: minke whale (*Balaenoptera acutorostrata*), right whale (*Eubalaena glacialis*), harbor porpoise (*Phocoena phocoena*), Florida manatee (*Trichechus manatus*), and harp seal (*Phoca groenlandica*).

Boundary layer heating

Warm-bodied animals, such as marine mammals, scombrid fishes, and lamnid sharks, have the capacity to use heat conducted from the body surface to decrease water viscosity [66, 67]. Dolphins exhibit a temperature differential between the water and skin surface of 9°C which would reduce viscosity by 11% [12]. A maximum temperature difference of 15°C for tuna would provide a 14% decrease in friction drag as long as the boundary layer was heated instantaneously [11]. Although plausible, this method of drag reduction is unlikely due to the short amount of time (0.1 s) that the water would be in contact with the body [66].

Pressure Drag

Fusiform shape

It is surprising that although G. Cayley (circa 1800) considered the fusiform design of the dolphin to be a body of least resistance, this design was not embraced for submarine hulls until the USS Albacore in 1953. Drag is minimized primarily by streamlining the shape of the body and the appendages. The streamlined profile of these structures is characterized by a rounded leading edge and a slowly tapering tail (Fig. 3). This design delays separation which occurs closer to the trailing edge, resulting in a smaller wake and reduced pressure drag.

An indication of the streamlining of a body is the Fineness Ratio (FR = ratio of maximum length to maximum thickness) [11]. Bodies of rotation demonstrate minimum drag in a range of FR of 3-7 [17, 68, 69]. Based on airship design, the optimal FR is 4.5 which provides the minimum drag for the maximum volume [68]. Fast swimming fishes, penguins and aquatic mammals are well streamlined with body dimensions within the optimal range of FR [11, 57, 70, 71].

In engineered 'laminar' profiles, the position of the maximum thickness is located posteriorly to reduce drag by maintenance of an extended favorable pressure gradient and laminar boundary flow [11]. The shape of a dolphin and a sea lion have been likened to a NACA 66-018 airfoil [17, 72], whereas, tuna display similarities with the NACA 67-021 [17]. Indeed, most rapidly swimming aquatic animals have displaced the maximum thickness posteriorly [17, 45]. The maximum thickness of fast swimming fish and marine mammals is located at 0.3-0.7 of the body length [12, 17, 45, 66, 72].

Abrupt departures from a streamlined shape are avoided through use of integumentary structures. Blubber in marine mammals contours the body along its longitudinal axis [56, 71]. In addition, blubber streamlines the caudal peduncle in dolphins to reduce its drag in the flukes' plane of oscillation [12] and provides a streamlined shape to the appendages [73, 74]. Hair and feathers also can be used with their entrapped air layers to contour the body [70, 75, 76]. The lack of arrector pili muscles in seals and sea otters permits the pelage to lie flat in water, minimizing resistance to swimming [77]. When models of a seal with and without hair covering were compared, a reduction in drag with the hair covering occurred at velocities of 8-10 m/s [78]. However, it was noted that these speeds are not normal for seals and the results may not be ecologically relevant [79].

Despite the presumption of the teardrop, fusiform shape as the optimal design for drag reduction, a number of aquatic animals have anterior projecting beaks, bills, and rostrums. In part, the departure from a smoothly rounded head in these animals may be a function of their feeding morphology requiring grasping jaws. However, the alternating concave and convex profile of the forebody may induce a stepwise, gradual pressure change which can reduce skin friction in animals [70, 80, 81]. The relatively small surface area of the anterior projection in conjunction with a reduced pressure gradient [45,82] can decrease drag.

Redirection of flow about dorsal spines of some sharks would aid in preventing flow separation and increased pressure drag. The spines are found on the leading edge of the dorsal fins. Because there is a gap between the spines and the fins, the combination could act in a manner analogous to slotted wings as the body laterally undulates during swimming, canting the dorsal fins at an angle to the flow [83].

Burst-and-coast swimming is a behavioral strategy that exploits the lower drag of a rigid, non-flexing animal compared to when it is actively swimming [62]. Animals rarely swim steadily. Many animals swim intermittently using a two-phase periodic behavior of alternating accelerations (burst phase) interspersed with periods of glides (coast phase) [84, 85]. Estimates of energy savings were projected from 24% to over 50% for fish using this behavior [86, 87].

Vortex generators

Large-scale vortices can be generated around the bodies and appendages of animals to influence flow and reduce drag [5, 11]. Alternate vortices shed from around the head of swimming fish were postulated to act as rigid pegs [88]. The Vortex Peg Hypothesis suggested that the fish pushed off the vortices reducing swimming effort and that the drag was virtually zero by reclaiming energy from the vortices [11, 53, 88]. This hypothesis was considered unlikely, because the velocity difference between the fish and vortices was too great to make the system efficient [11].

However, anteriorly generated vortices and vortices generated from the undulation of the caudal fin can interfere with each other to increase locomotor efficiency [53, 89, 90]. The opposing rotations of the anterior vortices generated as a Kármán vortex street and the thrust-type vortices (reverse Kármán vortex street) can destructively interfere [90]. This interference produced enhanced efficiency when the sites of vortex generating were optimally spaced.

Leading edge bumps were identified as possible drag reducing devices [5]. Leading edge bumps are found on the head of hammerhead sharks and pectoral flipper of humpback whales, which are used as lifting surfaces during maneuvers [91, 92]. On the humpback whale flipper, the bumps are evenly spaced over the majority of the span [91]. These bumps were hypothesized to generate vorticity to postpone stall at high angles of attack. This function may be analogous to strakes which change the stall characteristics of aircraft wings by generating vorticity [19, 93]. Vortex generators are most effective for increasing lift and reducing drag when the boundary layer has been tripped [94]. Turbulent boundary conditions would be likely for humpback whale flippers which operate near $Re = 2 \times 10^6$ [91].

Turbulizers

Induction of turbulence by roughness and surface projections within the boundary layer can ultimately reduce total drag by delaying boundary layer separation [11]. Sculpturing on the shells of cephalopods (ammonoids and nautiloids) had a positive hydrodynamic effect when immersed in the boundary layer, but sculpturing which extended outside of the boundary layer had a negative effect [95]. For fish, the presence of scales, rough surfaces, and spiny projections has been likened to a tripping device to stabilize the boundary layer [5, 11, 45, 6496]. In mullet, *Mugil saliens*, scale development is correlated with body size and Re [45, 96]. At Re less than 10^3 , the fish has no scales; whereas at 3×10^5 , rough ctenoid scales appear on the body behind the head. The ctenoid scales have a comblike edge. These scales are believed to produce microturbulence. Ctenoid scales are replaced, however, with smoother cycloid scales above 10^6 , where transition would normally occur.

The elongate rostrum of the swordfish, *Xiphias gladius*, has a rough surface with craters and bumps [82]. Because the sword can reach a length of 40-45% of body length, at high swimming speeds, the

critical Re for transition would be reached before the head. Thus, separation would be avoided from the body of the fish, despite the anterior position of the maximum thickness which is just posterior of the head [45, 82].

Drafting

Various animals travel in highly organized formations. This behavior has been hypothesized to reduce drag and enhance locomotor performance of individuals. Formation movement generally is accepted for automotive and cycling competitions [97, 98, 99], which use the techniques of "drafting" or "slipstreaming". Wind tunnel measurements on cars demonstrated a 37-48% reduction in drag when following closely behind another vehicle [97, 100]. Trailing cyclists in a pace line experience a 38% reduction in wind resistance [98] and an energy savings of 62% when drafting behind a more massive body, such as a truck [99].

For animals, formation swimmers influence the flow of water around adjacent individuals. Vorticity generated by anterior individuals provides momentum to the water. If a trailing animal is oriented parallel and is moving in the same direction to the tangential velocity of the vortex, the body will experience a reduction in its relative velocity. Because the drag is directly proportional to the velocity squared, a decrease in the relative velocity can decrease drag and the associated energy expenditure. Vorticity is shed into the wake of a passive body as two rows of counter-rotating vortices (i.e., Kármán vortex street) where the optimal position for drag reduction is directly behind another body [101]. Although similar in pattern to the Kármán vortex street, a thrust-type vortex system has the opposite rotation of the vortices. In this system which is generated by an oscillating foil, the optimal orientation is diagonally [102].

Queues of spiny lobsters (*Panulirus argus*) in water were shown to sustain less drag per individual than a single lobster traveling at the same speed [103]. The reduction in energetic cost per individual in a queue was a direct function of queue size. Ducklings which swim behind the mother in single-file experience a 7.8-43.5% decrease in energy cost with increased savings for larger groups [101]. In addition, the duckling at the end of the formation appears to received the largest energetic savings [104]. Drag reduction in single-file formation is associated with small spacings between individuals (< one body length) [97, 100, 104].

Thrust-type vortices produced by fish provide drag reduction in diamond-shaped formations [86, 102]. Trailing fish experience a relative velocity 40-50% of the free stream velocity and a reduction of the force generated for swimming by a factor of 4 to 6. However, the decrease in relative velocity is not maintained with each successive row of trailing fish due to destructive interference.

Wave Drag

Bow structure

Bulbous bows on displacement hulls reduce wave drag by 60% by canceling most of the wave pattern created at the bow and avoiding energy loss by wave breaking [105, 106]. Semiaquatic mammals (e.g., beaver, muskrat, water opossum) swim on the water surface while holding their forelimbs under the chin [22, 107]. Such a configuration of the limbs may effectively act like a bulbous bow, although this has not been examined.

Hydroplaning

Relatively few animals swim at the water surface for extended periods. As a displacement hull, surface swimming animals encounter high energy costs and limitations to speed from wave drag. Despite the small size of ducklings which places severe limitations on swimming velocity due to hull speed, speeds above hull speed are accomplished by replacing the displacement hull configuration with a planing hull [18]. The motion of a planing hull has been described as "hydroplaning" or "skimming" [108]. With the hull inclined with a positive angle of trim, a positive pressure develops under the hull creating a vertical "dynamic lift" component which at high speeds may be greater than buoyancy [105, 109].

Several factors contribute to the relatively low drag of planing.

(1) The increase in trim angle raises the bow from the water decreasing the amount of wetted surface area reducing skin friction [108, 109]. (2) Above hull speed water does not have time to respond to the pressure disturbance and the water surface is effectively smoothed [105, 108, 110]. (3) Wave drag is largely eliminated by lifting the hull, although spray drag will increase [19, 105, 109].

At $F_L = 0.6-1.0$, a hull is semiplaning such that it is supported by both hydrodynamic (dynamic lift) and hydrostatic (buoyant lift) forces [105, 109]. Above $F_L = 1$, the hull is supported entirely by dynamic lift (planing). Mallard ducklings (*Anas platyrhynchos*) can burst at $F_L > 1$ effectively planing on the water surface [18]. Steamer ducks (*Tachyeres* spp.) include three large, flightless species which hydroplane continuously over distances of 1 km and at speeds up to 6.67 m/s ($F_L = 3$) over the water surface using their feet and wings [18, 111].

Spray Drag

Two bat species (*Noctilio leporinus*, *Pizonyx vivesi*) are adapted for catching and eating fish [112, 113]. The bats use their echolocation to detect fish by ripples or breaks on the water surface and then drag their feet through the water to gaff the fish with their claws. To reduce drag, the toes and claws are laterally compressed with a reversed fusiform cross-section [114]. Although a typical fusiform shape works effectively for fully immersed bodies, this shape should be avoided at the air-water interface [20]. At high Froude numbers ($F_L < 0.5$), spray drag can be a significant proportion of the total drag, whereas wave drag is insignificant [19]. For the fishing bats, where $F_L > 270$, the reversed fusiform design with a long forebody region relative to the claw thickness can reduce spray drag [19, 114]. An analogous design is observed in the lower mandible of the black skimmer (*Rhyncops nigra*), which catches fish at the water surface with its beak [115]. Application of this mechanism, however, is limited to linear motion, because the reversed fusiform design will incur premature separation with increased drag and loss of lift during turning maneuvers.

Induced Drag

The design of the appendages (e.g., fins, flukes, flippers) determines the magnitude of the induced drag. Well-performing appendages maximize the ratio of lift (L) to drag (D) generated by their action [11]. 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 AR [68, 116, 117, 118, 119]. High AR and tapering of the appendages reduces tip vorticity and induced drag [11, 119, 120, 121]. The fastest swimming fish and marine mammals have propulsors with AR ranging from 3.4-8.7 [57]. AR above 8-10 provides little further advantage and may be structurally limited [11].

Induced drag also is limited by the sweep angle 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 [117]. 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 [122, 123]. This optimal shape approximates the planform of animals which swim with a lunate propulsor, including scombrid fishes, laminid sharks, extinct ichthyosaurs, cetaceans, and phocid seals [11, 57, 62, 118].

Flight

A behavioral strategy to minimize drag is to leave the water entirely. Many aquatic animals leap clear of the water to travel through the air to reduce the energy required for locomotion and avoid predation. In certain cases the animals take a ballistic trajectory, such as dolphins, seals, sea lions, penguins, and fish [124, 125, 126], whereas others have modified lifting surfaces to extend the flight over long distances, such as flying squid and flying fish [127, 128].

Porpoising consists of rhythmic, serial leaps in which the animal leaves and re-enters the water nose-first 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 [124, 129]. Below some critical speed, however, the opposite is assumed. As obligate air-breathers, marine mammals and penguins must swim in close proximity to the surface despite increased drag [17, 71]. Porpoising permits these animals to breathe while simultaneously reducing locomotor energy costs [125, 130].

CONCLUDING REMARKS

Progress in technologies concerned with drag reduction comes from the discovery and refinement of new designs. A diversity of drag reducing mechanisms are exhibited by aquatic animals in association with their habits and restrictions on body design. Both machines and

animals must contend with the same physical laws that regulate their design and behavior. Although animal mechanisms have been recognized mainly after an engineered solution was developed, the analogy simply demonstrates functional similarity and close examination of the biological mechanism may indicate possible pathways for improvements in engineered designs. In comparison to engineers who can limit variables in their systems, the problem for biologists has been that the systems they study are complex. More than two hundred years ago, the British philosopher David Hume pondered the complexity of biological organisms as:

All these various machines, and even their most minute parts, are adjusted to each other with an accuracy which ravishes into admiration all men who have ever contemplated them. The curious adapting of means to ends, throughout all nature, resembles exactly, though it much exceeds, the productions of human contrivance.

As matters of energy economy and greater speeds are desired in engineered systems [5], imaginative solutions for drag reduction from nature may serve as the inspiration for new technologies. The union between biologists and engineers and use of modern computational approaches [131, 132] promises an understanding of biological systems and modifications fitted to an engineered application.

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REFERENCES

- Jakab, P. L. 1990. *Visions of a flying machine*. Smithsonian Institution Press, Washington.
- Triantafyllou, G. S. and Triantafyllou, M. S. 1995. An efficient swimming machine. *Sci. Amer.*, 272:64-70.
- Bandyopadhyay, P. R. and Donnelly, M. J. 1997. The swimming hydrodynamics of a pair of flapping foils attached to a rigid body. *Tenth Internat. Symp. Unmanned Untethered Submersible Tech.: Proc. Sp. Ses. Bio-Eng Res. Related to Autonomous Underwater Vehicles*. Pp. 27-43.
- Vincent, J. 1990. *Structural biomaterials*. Princeton Univ. Press, Princeton.
- Bushnell, D. M. and Moore, K. J. 1991. Drag reduction in nature. *Ann. Rev. Fluid Mech.*, 23:65-79.
- Harris, J. S. 1989. An airplane is not a bird. *Invention & Technology*, 5: 18-22.
- Vogel, S. 1994. *Life in moving fluids*. Princeton University Press, Princeton.
- Katz, S. L. and Jordan, C. E. 1997. A case for building integrated models of aquatic locomotion that couple internal and external forces. *Tenth Internat. Symp. Unmanned Untethered Submersible Tech.: Proc. Sp. Ses. Bio-Eng Res. Related to Autonomous Underwater Vehicles*. Pp. 135-152.
- Webb, P. W. 1997. Designs for stability and maneuverability in aquatic vertebrates: What can we learn. *Tenth Internat. Symp. Unmanned Untethered Submersible Tech.: Proc. Sp. Ses. Bio-Eng Res. Related to Autonomous Underwater Vehicles*. Pp. 85-108.
- Alexander, R. McN. 1985. The ideal and the feasible: physical constraints on evolution. *Biol. J. Linn. Soc.*, 26:345-358.
- Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.*, 190:1-158.
- Fish, F. E. and Hui, C. J. 1991. Dolphin swimming - a review. *Mamm. Rev.*, 21:181-195.
- Lang, T. G. 1975. Speed, power, and drag measurements of dolphins and porpoises. In T. Y. Wu, C. J. Brokaw and C. Brennen (eds.), *Swimming and flying in nature*, Vol. 2, pp. 553-571. Plenum Press, New York.
- Magnuson, J. J. 1978. Locomotion by scombrid fishes: hydrodynamics, morphology and behaviour. In W. S. Hoar and D. J. Randall (eds.), *Fish physiology*, vol. 7, pp. 239-313. Academic Press, London.
- Katz, J. and Plotkin, A. 1991. *Low-speed aerodynamics: from wing theory to panel methods*. McGraw-Hill, New York.
- Lang, T. G. and Daybell, D. A. 1963. Porpoise performance tests in a seawater tank. *Nav. Ord. Test Sta. Tech. Rep.* 3063.
- Hertel, H. 1966. *Structure, form, movement*. Reinhold, New York.
- Aigeldinger, T. L. and Fish, F. E. 1995. Hydroplaning by ducklings: Overcoming limitations to swimming at the water surface. *J. Exp. Biol.*, 198:1567-1574.
- Hoerner, S. F. 1965. *Fluid-Dynamic Drag*. Published by author, Brick Town, New Jersey.
- Marchaj, C. A. 1991. *Aero-hydrodynamics of sailing*. International Marine Publishing, Camden, Maine.
- Prange, H. and Schmidt-Nielsen, K. 1970. The metabolic cost of swimming in ducks. *J. Exp. Biol.*, 53:763-777.
- Fish, F. E. 1982. Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.*, 55:180-189.
- Vogel, S. 1988. *Life's devices*. Princeton University Press, Princeton.
- Denny, M. W. 1993. *Air and water*. Princeton University Press, Princeton.
- Hoyt, J. W. 1975. Hydrodynamic drag reduction due to fish slimes. In T. Y. Wu, C. J. Brokaw, and C. Brennen (eds.), *Swimming and flying in nature*, Vol. 2, pp. 653-672. Plenum Press, New York.
- Daniel, T. L. 1981. Fish mucus: In situ measurements of polymer drag reduction. *Biol. Bull.*, 160:376-382.
- Rosen, M. W. and Cornford, N. E. 1971. Fluid friction of fish slimes. *Nature*, 234:49-51.
- Breder, C. M. 1926. The locomotion of fishes. *Zoologica (N.Y.)*, 4:159-256.
- Sokolov, V., Bulina, I. and Rodionov, V. 1969. Interaction of dolphin epidermis with flow boundary layer. *Nature*, 222:267-268.
- Harrison, R. J. and Thurley, K. W. 1972. Fine structural features of delphinid epidermis. *J. Anat.*, 111: 498-499.
- Gucinski, H. and Baier, R. E. 1983. Surface properties of porpoise and killer whale skin *in vivo*. *Amer. Zool.*, 23:959.
- Walsh, M. J. 1990. Riblets. *Prog. Astro. Aero.*, 123:203-261.
- Pershin, S. V., Chernyshov, L. F., Kozlov, L. F., Koval, A. P., and Zayets, V. A. 1976. Patterns in the integuments of fast-swimming fishes. *Bionika*, 10:3-21.
- Reif, W.-E. 1978. Protective and hydrodynamic function of the dermal skeleton of elasmobranchs. *Neues Jahrb. Geol. Paläotol.*, 157:133-141.
- Reif, W.-E. and Dinkelacker, A. 1982. Hydrodynamics of the squamation in fast swimming sharks. *Neues Jahrb. Geol. Paläotol.*, 164:184-187.
- Pershin, S. V. 1988. *Fundamentals of hydrobionics*. Sudostroyeniye Publ., Leningrad.
- Reidy, L. W. 1987. Flat plate drag reduction in a water tunnel using riblets. NOSC Tech. Rep. 1169.
- Anderson, E. J., MacGillivray, P. S., and DeMont, M. E. 1997. Scallop shells exhibit optimization of riblet dimensions for drag reduction. *Biol. Bull.* 192:341-344.
- Purves, P. E., Dudok van Heel, W. H., and Jonk, A. 1975. Locomotion in dolphins Part I: Hydrodynamic experiments on a model of the bottle-nosed dolphin, *Tursiops truncatus*, (Mont.). *Aqu. Mamm.*, 3:5-31.
- Yurchenko, N. F. and Babenko, V. V. 1980. Stabilization of the longitudinal vortices by skin integuments of dolphins. *Biophysics*, 25:309-315.
- Gray, J. 1936. Studies in animal locomotion VI. The propulsive powers of the dolphin. *J. Exp. Biol.*, 13:192-199.
- Kramer, M. O. 1960. Boundary layer stabilization by distributed damping. *J. Amer. Soc. Nav. Eng.*, 72:25-33.
- Kramer, M. O. 1960. The dolphins' secret. *New Sci.*, 7:1118-1120.
- Kramer, M. O. 1965. Hydrodynamics of the dolphin. In V. T. Chow (ed.), *Advances in Hydroscience*, Vol. 2, pp. 111-130. Academic Press, New York.
- Aleyev, Yu. G. 1977. *Nekton*. Junk, The Hague.
- Riley, J. J., Gad-el-Hak, M. and Metcalfe, R. W. 1988. Compliant coatings. *Ann. Rev. Fluid Mech.*, 20:393-420.
- Landahl, M. T. 1962. On stability of a laminar incompressible boundary layer over a flexible surface. *J. Fluid Mech.*, 13:609-632.

48. Blick, E. F. and Walters, R. R. 1968. Turbulent boundary-layer characteristics of compliant surfaces. *J. Aircraft*, 5:11-16.
49. Gad-el-Hak, M. 1987. Compliant coatings research: A guide to the experimentalist. *J. Fluid. Struct.*, 1:55-70.
50. Toedt, M. E., Reuss, L. E., Dillaman, R. M., and Pabst D. A. 1997. Collagen and elastin arrangements in the blubber of common dolphin (*Delphinus delphis*). *Amer. Zool.*, 37:56A.
51. Essapian, F. S. 1955. Speed-induced skin folds in the bottlenosed porpoise, *Tursiops truncatus*. *Breviora Mus. Comp. Zool.*, 43:1-4.
52. Lang, T. G. and K. Pryor. 1966. Hydrodynamic performance of porpoises (*Stenella attenuata*). *Science*, 152:531-533.
53. Rosen, M. W. 1961. Experiments with swimming fish and dolphins. *Amer. Soc. Mech. Eng. Paper* 61-WA-203.
54. Latz, M. I., Rohr, J. and Hoyt, J. 1995. A novel flow visualization technique using bioluminescent marine plankton - Part I: Laboratory studies. *IEEE J. Ocean. Eng.*, 20:144-147.
55. Rohr, J., M. I. Latz, E. Hendricks, and J. C. Nauen. 1995. A novel flow visualization technique using bioluminescent marine plankton - Part II: Field studies. *IEEE J. Ocean. Eng.*, 20:147-149.
56. Williams, T. M. and Kooyman, G. L. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol. Zool.*, 58:576-589.
57. Fish, F. E., Innes, S., and Ronald, K. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.*, 137:157-173.
58. Romanenko, E. V. 1976. Acoustics and hydrodynamics of certain marine animals. *Sov. Phys. Acoust.*, 22:357-358.
59. Romanenko, E. V. 1981. Distribution of dynamic pressure over the body of an actively swimming dolphin. *Sov. Phys. Dokl.*, 26:1037-1038.
60. Videler, J. and Kamermans, P. 1985. Differences between upstroke and downstroke in swimming dolphins. *J. Exp. Biol.*, 119:265-274.
61. Fish, F. E. 1993. Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.*, 185:179-193.
62. Lighthill, J. 1975. *Mathematical biofluidynamics*. Soc. Ind. Appl. Math., Philadelphia.
63. Walters, V. 1963. The trachipterid integument and an hypothesis on its hydrodynamic function. *Copeia*, 1963:260-270.
64. Bone, Q. 1972. Buoyancy and hydrodynamic functions of integument in the castor oil fish, *Ruvettus pretiosus* (Pisces: Gempylidae). *Copeia*, 1972:78-87.
65. AbdulNour, B. S. and Mueller, M. K. 1993. Hybrid laminar flow over wings enhanced by continuous boundary-layer suction. *SAE Tech. Paper* 931386.
66. Walters, V. 1962. Body form and swimming performance in scombrid fishes. *Am. Zool.*, 2:143-149.
67. Lang, T. G. 1966. Hydrodynamic analysis of cetacean performance. In K. S. Norris (ed.), *Whales, Dolphins and Porpoises*, pp. 410-432. Univ. of California Press, Berkeley.
68. von Mises, R. 1945. *Theory of flight*. Dover, New York.
69. Hess, J. L. 1976. On the problem of shaping an axisymmetric body to obtain low drag at large Reynolds numbers. *J. Ship Res.*, 20:51-60.
70. Bannasch, R. 1995. Hydrodynamics of penguins - an experimental approach. In P. Dann, I. Norman, and P. Reilly (eds.), *The penguins: Ecology and management*, pp. 141-176. Surrey Beatty and Sons, Norton, NSW.
71. Fish, F. E. 1993. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Aust. J. Zool.*, 42:79-101.
72. Feldkamp, S. D. 1987. Swimming in the California sea lion: Morphometrics, drag and energetics. *J. Exp. Biol.*, 131:117-135.
73. Felts, W. J. L. 1966. Some functional and structural characteristics of cetaceans flippers and flukes. In K. S. Norris (ed.), *Whales, Dolphins and Porpoises*, pp. 255-276. University of California Press, Berkeley.
74. Lang, T. G. 1966. Hydrodynamic analysis of dolphin fin profiles. *Nature*, 209:1110-1111.
75. Sokolov, W. 1962. Adaptations of the mammalian skin to the aquatic mode of life. *Nature*, 195:464-466.
76. Mordvinov, Yu. E. and Kurbatov, B. V. 1972. Influence of hair cover in some species of Phocidae upon the value of general hydrodynamic resistance. *Zool. Zh.*, 51:242-247.
77. Ling, J. K. 1970. Pelage and molting in wild mammals with special reference to aquatic forms. *Quart. Rev. Biol.*, 45:16-54.
78. Romanenko, E. V., Sokolov, V. E., and Kalinichenko, N. M. 1973. Hydrodynamic patterns of hair cover in *Phoca sibirica*. *Zool. Zh.*, 52:1537-1542.
79. Kooyman, G. L. 1989. *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
80. Bandyopadhyay, P. R. 1989. Viscous drag reduction of a nose body. *AIAA Journal*, 27:274-282.
81. Bandyopadhyay, P. R. and Ahmed, A. 1993. Turbulent boundary layers subjected to multiple curvatures and pressure gradients. *J. Fluid Mech.*, 246:503-527.
82. Videler, J. J. 1995. Body surface adaptations to boundary-layer dynamics. In C. P. Ellington and T. J. Pedley (eds.), *Biological fluid dynamics*, pp. 1-20. Soc. Exp. Biol., Cambridge.
83. Maisey, J. G. 1979. Finspine morphogenesis in squalid and heterodontid sharks. *Zool. J. Linn. Soc.*, 66:161-183.
84. Videler, J. J. and Weihs, D. 1982. Energetic advantages of burst-and-coast swimming of fish at high speeds. *J. Exp. Biol.*, 97:169-178.
85. Weihs, D. and Webb, P. W. 1983. Optimization of locomotion. In P. W. Webb and D. Weihs (eds.), *Fish biomechanics*, pp. 339-371. Praeger, New York.
86. Weihs, D. 1974. Energetic advantages of burst swimming of fish. *J. Theor. Biol.*, 48:215-229.
87. Fish FE, Fegely, J, Xanthopoulos CJ. 1991. Burst-and-coast swimming in schooling fish (*Notemigonus crysoleucas*) with implications for energy economy. *Comp. Biochem. Physiol.*, 100A:633-637.
88. Rosen, M. W. 1959. Water flow about a swimming fish. *U.S. Nav. Ord. Test Sta Tech. Publ.* 2298:1-96.
89. Triantafyllou, G. S., Triantafyllou, M. S., and Gosenbaugh, M. A. 1993. Optimal thrust development in oscillating foils with application to fish propulsion. *J. Fluids Struct.*, 7:205-224.
90. Gopalkrishnan, R., Triantafyllou, M. S., Triantafyllou, G. S., and Barrett, D. 1994. Active vorticity control in a shear flow using a flapping foil. *J. Fluid Mech.*, 274:1-21.
91. Fish, F. E. and Battle, J. M. 1995. Hydrodynamic design of the humpback whale flipper. *J. Morph.*, 225:51-60.
92. Nakaya, K. 1995. Hydrodynamic function of the head in the hammerhead sharks (Elasmobranchii: Sphrynidae). *Copeia*, 1995:330-336.
93. Shevell, R. S. 1986. Aerodynamic anomalies: Can CFD prevent or correct them? *J. Aircraft*, 23:641-649.
94. Bragg, M. B. and Gregorek, G. M. 1987. Experimental study of airfoil performance with vortex generators. *J. Aircraft*, 24:305-309.
95. Chamberlain, J. A., Jr. and Westermann, G. E. G. 1976. Hydrodynamic properties of cephalopod shell ornament. *Paleobiology*, 2:316-331.
96. Videler, J. 1993. *Fish swimming*. Chapman and Hall, London.
97. Romberg, G. F., Chianese, F., Jr., and Lajoie, R. G. 1971. Aerodynamics of race cars in drafting and passing situations. *Soc. Auto. Eng. Paper* 710213.
98. Kyle, C. R. 1979. Reduction of wind resistance and power output of racing cyclists and runners traveling in groups. *Ergonomics*, 22:387-397.
99. Hagberg, J. M. and McCole, S. D. 1990. The effect of drafting and aerodynamic equipment on energy expenditure during cycling. *Cycling Sci.*, 2:19-22.
100. Zabot, M., Frascaroli, S., and Browand, F. K. 1994. Drag measurements on 2, 3 and 4 car platoons. *Soc. Auto. Eng. Paper* 940421.
101. Fish, F. E. 1994. Energy conservation by formation swimming: metabolic evidence from ducklings. In L. Maddock, Q. Bone, and J. M. V. Rayner (eds.), *Mechanics and physiology of animal swimming*, pp. 193-204. Cambridge University Press, Cambridge.
102. Weihs, D. 1973. Hydromechanics of fish schooling. *Nature*, 241:290-291.
103. Bill, R. G. and Herrnkind, W. F. 1976. Drag reduction by formation movement in spiny lobsters. *Science*, 193:1146-1148.

104. Fish, F. E. 1995. Kinematics of ducklings swimming in formation: Energetic consequences of position. *J. Exp. Zool.*, 272:1-11.
105. Saunders, H. E. 1957. *Hydrodynamics in ship design*. Soc. Nav. Arch. Mar. Eng., New York.
106. Wehausen, J. V. 1973. The wave resistance of ships. In C. S. Yih (ed.), *Advances in applied mechanics*, Vol. 13, pp. 93-245. Academic Press, New York.
107. Fish, F. E. 1993. Comparison of swimming kinematics between terrestrial and semiaquatic opossums. *J. Mamm.*, 74:275-284.
108. Hammitt, A. G. 1975. *Technical yacht design*. Van Nostrand Reinhold, New York.
109. Marchaj, C. A. 1964. *Sailing theory and practice*. Dodd, Mead and Co., New York.
110. Taylor, D. W. 1933. *The speed and power of ships*. Ransdell Inc., Washington, D. C.
111. Livezey, B. C. and Humphrey, P. S. 1983. Mechanics of steaming in steamer-ducks. *Auk*, 100:485-488.
112. Bloedel, P. 1955. Hunting methods of fish-eating bats, particularly *Noctilio leporinus*. *J. Mamm.*, 36:390-399.
113. Suthers, R. 1965. Acoustic orientation by fish-catching bats. *J. Exp. Biol.*, 158:319-348.
114. Fish, F. E., Blood, B. R., and Clark, B. D. 1991. Hydrodynamics of the feet of fish-catching bats: Influence of the water surface on drag and morphological design. *J. Exp. Zool.*, 258:164-173.
115. Withers, P. C. and Timko, P. L. 1977. The significance of ground effect to the aerodynamic cost of flight and energetics of the black skimmer (*Rhyncops nigra*). *J. Exp. Biol.*, 70:13-26.
116. Lighthill, J. 1977. Introduction to scaling of aerial locomotion. In T. J. Pedley (ed.), *Scale effects in animal locomotion*, pp. 365-404. Academic Press, London.
117. van Dam, C. P. 1987. Efficiency characteristics of crescent-shaped wings and caudal fins. *Nature*, 325:435-437.
118. Bose, N., Lien, J., and Ahia, J. 1990. Measurements of the bodies and flukes of several cetacean species. *Proc. Roy. Soc. Lond. B*, 242:163-173.
119. Daniel, T., Jordan, C., and Grunbaum, D. 1992. In R. McN. Alexander (ed.), *Advances in comparative & environmental physiology 11: Mechanics of animal locomotion*, pp. 17-49. Springer-Verlag, Berlin.
120. Rayner, J. M. V. 1985. Vorticity and propulsion mechanics in swimming and flying animals. In J. Riess and E. Frey (eds.), *Konstruktionsprinzipien lebender und ausgestorbener Reptilien*, pp. 89-118. University of Tübingen, Tübingen, F.R.G.
121. Webb, P. W., and Buffrénil, V. de. 1990. Locomotion in the biology of large aquatic vertebrates. *Trans. Amer. Fish. Soc.*, 119:629-641.
122. Küchermann, D. 1953. The distribution of lift over the surface of swept wings. *Aero. Quart.*, 4:261-278.
123. Ashenberg, J. and Weihs, D. 1984. Minimum induced drag of wings with curved planform. *J. Aircraft*, 21:89-91.
124. Au, D. and Weihs, D. 1980. At high speeds dolphins save energy by leaping. *Nature*, 284:548-550.
125. Hui, C. A. 1987. The porpoising of penguins: an energy-conserving behavior for respiratory ventilation? *Can. J. Zool.*, 65:209-211.
126. Williams, T. M. 1987. Approaches for the study of exercise physiology and hydrodynamics in marine mammals. In A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini (eds.), *Approaches to marine mammal energetics*, pp. 127-145. Spec. Publ. Soc. Mar. Mamm. No. 1.
127. Fish, F. E. 1990. Wing design and scaling of flying fish with regard to flight performance. *J. Zool., Lond.*, 221:391-403.
128. Azuma, A. 1992. *The biokinetics of flying and swimming*. Springer-Verlag, Tokyo.
129. Blake, R. W. 1983. Energetics of leaping in dolphins and other aquatic animals. *J. Mar. Biol. Assoc. UK.*, 63:61-71.
130. Hui, C. A. 1989. Surfacing behavior and ventilation in free-ranging dolphins. *J. Mamm.*, 70:833-835.
131. Liu, H., Wassersug, R. J., and Kawachi, K. 1996. A computational fluid dynamics study of tadpole swimming. *J. Exp. Biol.*, 199:1245-1260.
132. Moin, P. and Kim, J. 1997. Tackling turbulence with supercomputers. *Sci. Amer.*, 276:62-68.