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JEB CLASSICS

A PORPOISE FOR POWER



Frank Fish writes about James Gray's 1936 publication on the power output of a swimming dolphin.

Sometimes the most innocent of scientific endeavors can have the most far-reaching and profound ramifications. For James Gray, a simple calculation to determine the power output of a swimming dolphin (Gray, 1936) would launch a contentious argument known as 'Gray's Paradox'. Gray's classic study would provide the impetus for studies of bio-hydrodynamics and would affect the fields of material science, hydrodynamics, biorobotics, and diving physiology.

The Gray's Paradox controversy resulted from the first attempt to evaluate swimming energetics in animals (Webb, 1975). In his 1936 study, Gray used a rigid-body hydrodynamic model to calculate drag power and applied it to a dolphin and a porpoise swimming at high speeds ($>7.6 \text{ m s}^{-1}$). The results indicated that the estimated drag power could not be reconciled with the available power generated by the muscles. Gray (1936) stated: *'If the resistance of an actively swimming dolphin is equal to that of a rigid model towed at the same speed, the muscles must be capable of generating energy at a rate at least seven times greater than that of other types of mammalian muscle.'*

Gray's calculations assumed that turbulent flow conditions existed in the boundary layer between the dolphin's skin and the water, because of the speed and size of the animal. His resolution to the problem was that the drag on the dolphin would have

had to be lower than the turbulent conditions dictated, and that this could be achieved by maintenance of a fully laminar boundary layer against the dolphin's skin. In other words, the water against the dolphin skin flowed in orderly, parallel streams over the entire body, although this ran counter to accepted hydrodynamic theory. Gray proposed that the motion of the dolphin's flukes, which are the broad, lateral extensions of the tail used for propulsion, accelerated water flow over the posterior half of the body and that this action could provide a mechanism to laminarize the boundary layer. This mechanism was largely ignored in subsequent work, but the basic premise that dolphins could somehow maintain a laminar boundary remained and became the focus and justification of much of the work on dolphin hydrodynamics for the next 60 years (Fish and Hui, 1991; Fish and Rohr, 1999).

This basic premise of Gray's Paradox, however, was flawed, because of potential errors in estimation of dolphin swimming speed and inconsistencies between dolphin swimming performance and data on muscle power outputs. To measure drag power, Gray used a shipboard observation of a dolphin swimming along the side of the ship from stern to bow in 7 s. If the dolphin was swimming close enough to utilize the flow pattern around the ship, its speed may have been artificially enhanced and energetic effort reduced due to free-riding behaviors (Lang, 1966; Williams et al., 1992; Weihs, 2004). More important than the actual speed of the dolphin, the duration of this high performance swimming was for a sprint and Gray used measurements for muscle power output of sustained performance (3–5 min) by human oarsmen (Henderson and Haggard, 1925). Muscle fibers specialized for quick bursts of anaerobic activity can produce maximum metabolic power output 2–17 times greater than muscle fibers using a sustained aerobic metabolism (Hochachka, 1991; Askew and Marsh, 1997). The higher muscle power outputs produced by anaerobic mechanisms offset the power required to overcome the drag when the boundary layer is turbulent.

In effect, the dolphin has the capacity to swim at high speeds for short durations while maintaining a fully attached turbulent boundary layer between itself and the surrounding water. These turbulent boundary flow conditions would delay separation of the boundary layer from the dolphin's skin surface. When the boundary layer separates from the skin surface and interacts with outer flow, this results in a

broader wake and increased drag, so delaying separation is beneficial to the dolphin. Separation is more likely to occur with a laminar boundary flow, producing a greater drag penalty compared to turbulent boundary conditions. Thus, the turbulent boundary layer remains attached longer, because it has more energy than the laminar boundary layer. The increased drag of a turbulent boundary layer is small compared to the increase in drag due to separation, which is more prone to occur with a laminar boundary layer.

The idea that laminar flow could be maintained over the entire body of the dolphin was invigorated by Kramer (1960a,b). Kramer claimed that the dolphin's smooth, compliant skin could achieve a laminar boundary layer without separation. The skin was proposed to deform and eliminate drag by the process of viscous dampening. In viscous dampening, the compliance of the skin due to its viscoelastic properties would absorb energy from pressure oscillations and dampen turbulence-forming perturbations to maintain laminar flow. A torpedo with an artificial skin based on the skin of a dolphin was reported to produce a 59% reduction in drag when compared to a reference model with fully turbulent flow. These results exposed the 'dolphin's secret' and provided what Kramer (1960b) erroneously believed was the resolution to Gray's Paradox.

The promise of faster submarines, ships and torpedoes was equally enticing to the great navies of the world as the Cold War heightened (Fish and Rohr, 1999). In what has been characterized as 'enthusiastic optimism' (Vogel, 1994), research on compliant coatings and dolphin hydrodynamics was accelerated (Lang and Daybell, 1963; Wood, 1973; Aleyev, 1977; Riley et al., 1988). Attempts to later verify Kramer's results on passive compliance subsequently failed (Landahl, 1962; Riley et al., 1988). Possible mechanisms for drag reduction then focused on active skin compliance by dolphins. Fast swimming dolphins were observed to have large mobile skin folds that moved posteriorly along the body. To determine if mobile skin folds observed in dolphins were actively controlled, naked women were towed through water to emulate passive

skin deformations (Aleyev, 1977). Although amusing, the skin folds in the women were shown to increase drag. Recent analyses of swimming kinematics, bioluminescence, physiology and diving behaviors have demonstrated no special drag-reduction mechanisms for dolphins (Fish, 1998; Rohr et al., 1998; Fish and Rohr, 1999; Williams et al., 2000), while the low drag performance of tuned compliant panels and robotic fish continue to be bolstered by Gray's Paradox (Barrett et al., 1999; Carpenter et al., 2000).

We can look with hindsight at Gray's work on dolphin hydrodynamics and see some of the mistakes that created the paradox. In 1936, there were very limited data on muscle physiology, hydrodynamics, and swimming performance. However, the error seems to have had the fortunate effect of stimulating more research than probably would have occurred had all the answers been known. The real paradox was that, despite its inaccuracies, Gray's paper was the impetus for novel innovations that have furthered the areas of dolphin biology, hydrodynamics and biomimetics. There is still more to be discovered; perhaps the dolphin has not given up all its secrets. It may be as written by Scholander (1959): *'When playing around in the ocean, dolphins are pleasing to the eye no end, but let it only add to your thrill that these rascals are a graveyard to our wits. For is not finding out infinitely more exciting than knowing the answer?'*

A PDF file of the original paper can be accessed online: <http://jeb.biologists.org/cgi/content/full/208/6/977/DC1>
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