Three Gray Classics on the Biomechanics of Animal Movement

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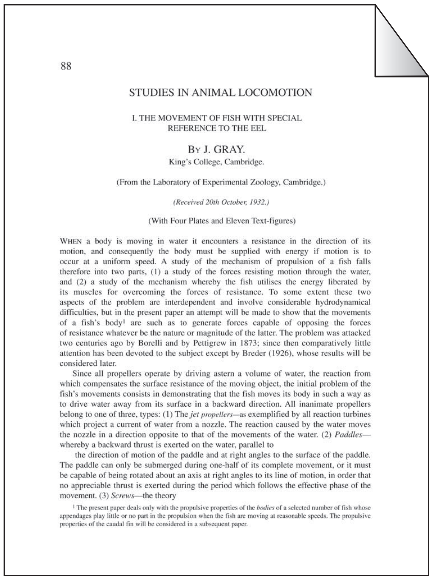
JEB Classics

THREE GRAY CLASSICS ON THE BIOMECHANICS OF ANIMAL MOVEMENT



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STUDIES IN ANIMAL LOCOMOTION

I. THE MOVEMENT OF FISH WITH SPECIAL
REFERENCE TO THE EEL

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(Received 20th October, 1932.)

(With Four Plates and Eleven Text-figures)

WHEN a body is moving in water it encounters a resistance in the direction of its motion, and consequently the body must be supplied with energy if motion is to occur at a uniform speed. A study of the mechanism of propulsion of a fish falls therefore into two parts, (1) a study of the forces resisting motion through the water, and (2) a study of the mechanism whereby the fish utilises the energy liberated by its muscles for overcoming the forces of resistance. To some extent these two aspects of the problem are interdependent and involve considerable hydrodynamical difficulties, but in the present paper an attempt will be made to show that the movements of a fish's body[1] are such as to generate forces capable of opposing the forces of resistance whatever be the nature or magnitude of the latter. The problem was attacked two centuries ago by Borelli and by Pettigrew in 1873; since then comparatively little attention has been devoted to the subject except by Breder (1926), whose results will be considered later.

Since all propellers operate by driving astern a volume of water, the reaction from which compensates the surface resistance of the moving object, the initial problem of the fish's movements consists in demonstrating that the fish moves its body in such a way as to drive water away from its surface in a backward direction. All inanimate propellers belong to one of three, types: (1) The *jet propellers*—as exemplified by all reaction turbines which project a current of water from a nozzle. The reaction caused by the water moves the nozzle in a direction opposite to that of the movements of the water. (2) *Paddles*—whereby a backward thrust is exerted on the water, parallel to

the direction of motion of the paddle and at right angles to the surface of the paddle. The paddle can only be submerged during one-half of its complete movement, or it must be capable of being rotated about an axis at right angles to its line of motion, in order that no appreciable thrust is exerted during the period which follows the effective phase of the movement. (3) *Screws*—the theory

[1] The present paper deals only with the propulsive properties of the *bodies* of a selected number of fish whose appendages play little or no part in the propulsion when the fish are moving at reasonable speeds. The propulsive properties of the caudal fin will be considered in a subsequent paper.

George Lauder and Eric Tytell write about James Gray's 1933 ground breaking publications on fish locomotion. Pdf files of Gray's papers can be accessed as supplemental data at jeb.biologists.org

It is a rare scientific paper that, 70 years later, is still being used as a source of both figures for review papers and experimental data for current research. And yet many still turn to the figures and plates published in 1933 by James Gray to understand how animals propel themselves through water. Gray's three papers on aquatic animal locomotion published in volume ten of the *Journal of Experimental Biology* in 1933 (Gray, 1933a–c) form the cornerstone of modern attempts to understand aquatic locomotion. These papers, made easily available again with this issue of the journal, ushered in the era of quantitative studies of animal movement that had its heritage in the work of Borelli, Muybridge, Pettigrew and Marey, and continues to the present day as the burgeoning field of animal locomotor mechanics (Alexander, 2003; Bels et al., 2003; Biewener, 2003).

Gray's remarkable physical insights into the complex physics of locomotion in the water combined with the detailed analysis of his experimental data are the touchstone for current research on locomotor kinematics, muscle dynamics, and computational fluid dynamic analyses of animals moving through water. Virtually every recent textbook in the field either reproduces one of Gray's figures directly or includes illustrations that derive their inspiration from his figures (e.g. Alexander, 2003; Biewener, 2003).

In his 1933a paper, Gray aimed to provide the first quantitative analysis of the body movements of a swimming fish, and link these motions to the forces that propel the fish forward. He used frames from motion picture films taken of fish swimming to visualize the deformation of the body, and relied on a clever timing circuit that he had developed earlier for his studies of ciliary motion (Gray, 1930) to ensure that he had precise knowledge of the time between each film frame. Knowledge of accurate inter-frame times was critical for calculating velocities of points on the fish body. Other than the reference to this earlier paper, Gray gave few details of the experimental arrangement, number of fishes, and methods of analysis used for his study.

From his analysis of sequences of film frames, Gray was able to track the crest of waves on the body of swimming fish, and he recognized that the body wave traveled backward faster than the forward swimming speed of the fish. In a further significant conceptual breakthrough, he divided the body of swimming eels into a series of interconnected segments which he treated as flat plates and considered the velocity of each segment. He realized that segments changed their angle to oncoming flow in a cyclical manner, and that the velocity of each segment was greatest as it passed near the midline. Because high velocity is correlated with high force, he inferred that each segment would produce maximal thrust as it crossed the midline. Additionally, the recognition that each segment has an angle of attack to the flow, like a small wing, immediately suggested the application of airfoil theory to eel segments, inspiring an entire class of theoretical models (e.g. Taylor, 1952). His illustration (figure 14 of Gray, 1933a) of the angles of the tail segment and the figure-eight pattern it makes is an oft-reproduced classic image. Gray's kinematic analysis also served as the foundation for James Lighthill's enormously important theoretical work on aquatic propulsion (e.g. Lighthill, 1960, 1969, 1970, 1971), and has inspired a generation of modeling efforts (Weihs, 1972; Wu et al., 1975, 1961).

The other two papers in this series explore results from the first paper in more detail. In his 1933b paper Gray uses patterns of body bending in the eel to infer how the muscles are acting to place body segments at an angle appropriate for thrust generation. The 1933c paper is noteworthy for its investigation of tail function by removing the tail of a whiting (a cod-like fish) to examine the effect of the tail on swimming performance. Gray concluded that whiting could still swim forward at a slow swimming speed even though they lacked a tail, but that the motion of the body changed significantly after tail removal. He analogized the fish tail to a propeller, and estimated that the tail generates 40% of total thrust in a non-anguilliform fish. Better estimates are still not available today.

It is the four plates from the 1933a paper (containing figures 2–11), however, that provide the most enduring practical legacy of Gray's work. These plates show how a variety of fishes bend their bodies as they swim. Gray used a movie camera to capture a series of images of fishes swimming over a background grid, then printed frames from these movies, and finally assembled a composite figure aligning the images through time side-by-side using the background grid and a known reference point. Each separate figure within the plates thus illustrates motion of the fish body in both space and time, clearly showing the wave-like pattern of body movement and forward progress of the fish. By marking the locations of maximal body curvature with dots on the pictures, the reader could easily see the wave of bending that passes down the body, propelling the fish forward like a screw propeller, to use Gray's analogy. Gray's plates not only illustrate forward locomotion, but also backward movement (an issue only recently addressed again: D'Août and Aerts, 1999) and the ontogeny of locomotion, by showing body movements of glass eels which have yet to complete their metamorphosis into the juvenile eel morphology.

These plates have influenced subsequent research in three other noteworthy ways. First, although the 1933a paper focused on locomotion of the eel, the locomotion of six other species is represented in the plates, forming the first broadly comparative analysis of aquatic locomotion in fishes. Gray demonstrated that the underlying physical principle he described in eels, in which a wave travels backward down the body faster than the eel moves forward, is a general one underlying aquatic undulatory propulsion.

Second, these plates have continued to be a source of kinematic data for biomechanical analysis. Because obtaining kinematic data on moving animals is difficult and time-consuming, it is perhaps not surprising that Gray's plates have themselves been digitized to obtain data on the pattern of eel body motion. One example of this is the elegant work of Carling et al. (1998), who used the kinematic data from Gray's (1933a) eel plates to define a computational fluid dynamic model. This model calculated the forces exerted on the water by the bending eel, and, in turn, the forces exerted back on the eel by the water. Carling et al. (1998) were able to calculate the movement of their virtual eel resulting from the interplay of these forces, show that the eel swims forward reaching a constant average speed, and predict the pattern of fluid flow around the swimming eel.

One downside to using the Gray (1933a) images for quantitative data is that Gray did not specify the precise conditions under which he obtained his data. Given the relatively brief time represented in each sequence of images, it is hard to tell if the fish are accelerating, turning slightly, or if they are moving up or down in the water column. Modern research uses flow tanks to minimize these confounding effects, often with two simultaneous camera views to select sequences with minimal unsteady or out-of-plane motion. In fact, recent kinematic data obtained under controlled conditions indicates that Gray's eels may have been accelerating as they moved across the field of view. One indication of this acceleration is the relatively large lateral head movement. Recent data show convincingly that head motion is minimal during constant speed swimming at speeds less than two body lengths per second (Gillis, 1996, 1998a,b). However, during linear acceleration or during searching behavior, lateral head movement increases dramatically. Nonetheless, the large sideways head excursion Gray observed during eel locomotion endures in the literature, and eel outlines derived from his figures are reproduced in countless reviews (e.g. Lindsey, 1978) with lateral head excursions substantially greater than observed during carefully controlled constant speed swimming. These new results suggest strongly that Gray's eels were accelerating and that kinematic data derived from his plates need to be treated with caution.

Even so, Gray's (1933a) plates can still illuminate interesting features of fish locomotion. For example, his Plate II of a mackerel swimming shows a complex pattern of movement in the tail itself, strongly indicative of intrinsic tail bending and three-dimensional deformation. The three-dimensional nature of fish tail function has only recently been explored in detail. In particular, image two in figure 5 of Plate II shows the mackerel tail as a forked surface, inclined significantly to the bottom plane of the tank, while image seven shows the tail as a thin plate at a small angle of inclination. There must be bending and tilting of the tail even during relatively steady forward propulsion, and Gray's images provide the first convincing evidence of the complexity of tail motion. It was, in part, study of these figures in the mid-1990s that led one of us to undertake a more comprehensive three-dimensional analysis of tail function in fishes (Lauder, 2000). All of us who study animal propulsion owe a tremendous debt to Sir James Gray, whose elegant papers continue to inspire new experiments.

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