Biomechanics

Hydrodynamic function of the shark's tail

The tail of most sharks has an elongated upper lobe that differs from the externally symmetrical tail structure common among bony fishes, but the hydrodynamic purpose of this asymmetric tail shape is unclear[1–3]. Here we quantify water flow patterns in the wakes of freely swimming dogfish sharks and find that they have a ring-within-a-ring vortex structure, in contrast to the single rings shed by symmetrical fish tails. The branched-ring vortex is generated by the inclined angle of the tail's trailing edge and by its motion at an angle to the horizontal body axis; the vortex directs water backwards and downwards, which may increase the shark's vertical manoeuvrability.

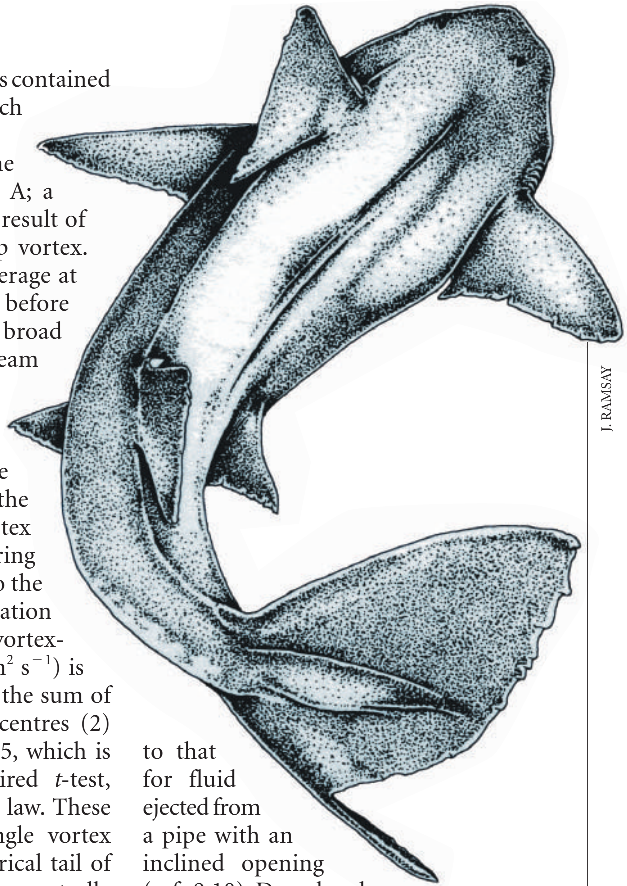
We used digital particle-image velocimetry[4,5] to analyse the hydrodynamic function of the tail in four spiny dogfish (*Squalus acanthias*; mean body length, 69 cm) swimming in a flow tank equipped with a vertical laser-light sheet. By using high-speed video (250 frames per second) to obtain particle images, we were able to analyse the time-dependent features of wake flow from the tail: six pairs of images were recorded throughout a tailbeat for five tailbeats from each of four individuals.

Three centres of vorticity were detected (Fig. 1a). The smaller dorsal vortex ring includes centres (1) and (2) and is contained within a larger vortex ring, which includes centres (1) and (3). Counter-rotating centres in the dorsal vortex ring produce jet A; a second jet B develops later as a result of flow induced by the ventral tip vortex. Jets A and B are directed on average at −35° to the freestream flow, before combining to produce a single broad jet C. Initially, little downstream flow is seen between same-sign vorticity centres (2) and (3) (Fig. 1a).

Velocity transects though the centres of vorticity confirm the presence of a small dorsal vortex ring linked to a larger vortex ring that has a diameter equivalent to the tail height (Fig. 1b,c). Circulation calculations show that mean vortex-centre (1) circulation (0.0160 $m^2 s^{-1}$) is not significantly different from the sum of negative circulation in vortex centres (2) and (3) (−0.0019 and −0.0165, which is −0.0184 $m^2 s^{-1}$ in total; paired *t*-test, $P=0.3$), as required by Kelvin's law. These findings contrast with the single vortex rings generated by the symmetrical tail of the bony fishes[6,7]. A strong posteroventrally directed jet flow is visible as a result of shark-tail motion (Fig. 1a,c), corroborating one classical model of shark-tail function[2,8].

We propose that the mechanism for generating the ring-within-a-ring vortex structure in swimming dogfish is similar to that for fluid ejected from a pipe with an inclined opening (refs 9,10). Dorsal and ventral tip vortices (1) and (3) are shed as the tail beats from side to side. The dorsal lobe leads the ventral, so the tail presents an inclined edge to oncoming flow[8]. In a pipe with an inclined opening, a ring-within-a-ring vortex structure is generated owing to the temporal asymmetry in vortex roll-up between the longer and shorter edges[9,10].

Previous work on the symmetrical tail of the bony fishes[6,7,11] has shown that the vortex wake consists of single-ring vortices with dimensions similar to tail height and tailbeat width. The difference in wake structure between sharks and bony fishes seems to be due to their different tail shape and motion. The effects of these wake morphology differences on manoeuvring performance and locomotor energetics remain to be determined.



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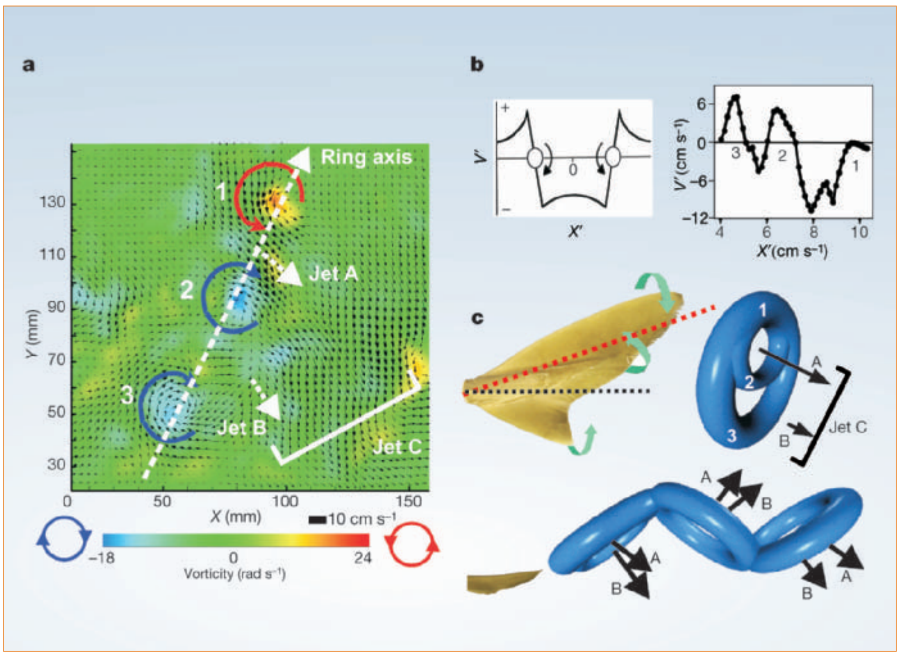

Figure 1 Digital particle-image velocimetry analysis, velocity profiles and vortex structures of rings shed from the tail of steadily swimming dogfish. **a,** Vorticity plot of a vertical slice through tail vortex rings; curved arrows indicate the three centres of vorticity. **b,** Theoretically predicted velocity distributions across a planar section of a vortex ring (left) and a similar plot based on empirical data from the sequence shown in **a** along the ring axis (right). *X*′, horizontal velocity; *V*′, vertical velocity (both relative to the ring axis). **c,** Side and top views of a shark vortex wake. The axis of tail rotation (red dotted line) is inclined to the horizontal axis of locomotion (black dotted line), generating a ring-within-a-ring vortex structure by a mechanism similar to a piston with an inclined exit orifice[10]. Successive tailbeats generate linked rings (bottom). Green arrows indicate dorsal and ventral tip vortices and roll-up of the vortex sheet along the trailing edge.