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REPORT

Water-escape velocities in jumping blacktip sharks

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This paper describes the first determination of water-escape velocities in free-ranging sharks. Two approximations are used to estimate the final swimming speed at the moment of penetrating the water surface. Blacktip sharks were videotaped from below the surface and parameters were estimated by analysing the sequences frame by frame. Water-escape velocities averaged 6.3 m s^{-1} . These velocities for blacktip sharks seem accurate and are similar to estimates obtained for other shark species of similar size.

Keywords: *Carcharhinus limbatus*; swimming speed; elasmobranch

Swimming speed is important when considering the potential for active swimming behaviour to influence dispersal, energetics and metabolism. There are numerous methods for examining the swimming capabilities of fishes. Although difficult to obtain, undisturbed measurements of swimming speed have the advantage that speed is measured in the animal's natural environment.

Published estimates of the swimming speeds of sharks vary widely, in part due to differences in methodology (Carlson *et al.* 2004). In one experiment, free-ranging sharks were equipped with speedometers (Carey & Scharold 1990), while measurements were taken from animals swimming in a water tunnel in another (Graham *et al.* 1990). These methods cannot estimate maximum swimming speeds because the fishes cannot be induced to swim at a high speed (Webb & Keyes 1982) and the circumstances under which maximum swimming speeds occur are not known.

One opportunity for calculating a high swimming speed without manipulating the animal is by observing fishes jump from the water. This behaviour involves a 'standing jump', rather than porpoising, and probably requires a high level of burst swimming performance (Blake 1983). Many shark species jump and spin out of the water under certain circumstances (Compagno 1984, 2001). Members of at least two families (Lamnidae and Carcharhinidae) are known to jump with

some regularity (Compagno 1984; Last & Stevens 1994; Anderson *et al.* 1996; Klimley *et al.* 1996). Few studies have addressed the ecological context in which jumps are performed (Castro 1996; Ritter & Brunnenschweiler 2003). Detailed description of actual jumping behaviour is also lacking, mostly because of the difficulty of monitoring the behaviour of elasmobranchs in the open sea. Although other marine animals such as penguins and cetaceans are regularly seen performing jumping and porpoising behaviour (Jacobsen 1986; Hui 1987), sharks are observed jumping and spinning only by chance. This makes it impossible to collect meaningful amounts of data. Consequently, a detailed description of the swimming behaviour (swimming speed and body angle) of sharks under natural circumstances during vertical movements has not yet been produced.

Here, I introduce formulae for calculating water-escape velocity for a jumping shark. Two different approximations are used to estimate the final swimming speed at the moment of penetrating the water surface. The first approximation uses the conservation of energy equation

$$E_h = \frac{1}{2}mv^2 + mgh, \quad (1)$$

where E_h is the energy needed at a given height (h), m is the animal's mass and v equals speed at any point during a projectile-like motion. At the water surface

$$E_0 = \frac{1}{2}mv_0^2. \quad (2)$$

Water-escape velocity can be expressed as $v = v_0 \cos \alpha$, where v_0 is the speed while penetrating the water surface and α is the angle of the motion during the jump. E_h equals E_0 during any phase of the jump, which means that speed at the surface of the water can be expressed as

$$v_0 = \sqrt{\frac{2gh}{1 - \cos^2 \alpha}}. \quad (3)$$

The second approximation used to calculate speed (v_0) includes the duration (t) of the jump. With the shark projecting at an upward angle, the vertical component of the parabola is

$$y = v_y t - \frac{1}{2}gt^2. \quad (4)$$

Replacing v_y , it can be shown that

$$y = v_0 t \sin \alpha - \frac{1}{2}gt^2, \quad (5)$$

where y equals the height (h) of the jump and, hence,

$$v_0 = \frac{h + \frac{1}{2}gt^2}{t \sin \alpha}. \quad (6)$$

By analysing jump sequences of blacktip sharks (*Carcharhinus limbatus*) videotaped from below the surface, I estimated swimming speeds. Between April 2000 and November 2001, three blacktip sharks were filmed while performing jumps that were triggered by the presence of sharksuckers (Ritter & Brunnenschweiler 2003). Jumping out of the water was observed only three times in more than 10 h of behavioural observation, in each case involving adult females approximately 1.6 m in total body length. I used two of these jumps to estimate final swimming speeds at the

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Table 1. Parameter estimates used to calculate water-escape velocity for the two sharks (h , maximum height; α , angle of penetration; t , duration of jump.)

parameter	shark 1	shark 2
h	1 m	0.5 m
α	45°	30°
t	0.438 s	0.375 s

moment when the surface of the water was penetrated, but excluded the third because it was not possible to reliably estimate all parameters. The two jumping sharks were observed and filmed prior to accelerating towards the surface of the water for 45 and 68 s, respectively. They were swimming horizontally at a constant cruising speed and started the acceleration to the surface from a depth of 10 m.

Two parameters, α and t , were measured by analysing the jumping sequences frame by frame (24 frames per second; table 1). The maximum height of the jump was estimated from the video by the extent to which the shark's body cleared the water. The equations used to calculate the errors are

$$\Delta v_0 = f'(h)\Delta h + f'(\alpha)\Delta\alpha \\ = \frac{g}{\sin\alpha} \frac{1}{\sqrt{2gh}} \Delta h + \left| -\sqrt{2gh} \frac{\cos\alpha}{\sin^2\alpha} \right| \Delta\alpha, \quad (7)$$

for equation (3) and

$$\Delta v_0 = f'(h)\Delta h + f'(\alpha)\Delta\alpha + f'(t)\Delta t \\ = \frac{1}{t \sin\alpha} \Delta h + \left| \frac{h + \frac{1}{2}gt^2}{t} \left(-\frac{\cos\alpha}{\sin^2\alpha} \right) \right| \Delta\alpha \\ + \left| -\frac{h}{\sin\alpha} \frac{1}{t^2} + \frac{g}{2 \sin\alpha} \right| \Delta t, \quad (8)$$

for equation (6). Parameters used for error calculation are $\Delta\alpha = \pi/36$, $\Delta h = 0.2$ m and $\Delta t = 1/24$ s for both jumps.

Both equations produce the same estimates of water-escape velocities for the two sharks (table 2). Swimming speed at the moment when the surface of the water was penetrated was about 6.3 m s⁻¹. This is higher than the maximum speeds measured under laboratory conditions for mako sharks (Graham *et al.* 1990) and other species (Carlson *et al.* 1999). In general, laboratory studies produce lower estimated swimming speeds than field studies (Block *et al.* 1992), presumably because jumping requires a very high burst of speed and cannot easily be triggered under laboratory conditions.

The analysis used to estimate swimming speed is simple but requires simplifying assumptions. For example, the influence of drag was not considered. It is also assumed that the mass of the shark is concentrated at its centre of gravity. Therefore, the calculated speed is

Table 2. Estimated final swimming speeds (v_1 , v_2) at the moment of penetrating the water surface for jumping sharks 1 and 2

equation	shark 1 (m s ⁻¹)	shark 2 (m s ⁻¹)
(3)	$v_1 = (6.3 \pm 1.2)$	$v_2 = (6.3 \pm 2.2)$
(6)	$v_1 = (6.3 \pm 1.2)$	$v_2 = (6.4 \pm 3.8)$

valid only if that point reaches height h . In reality, the shark's buoyancy contributes to propelling it from the water and this buoyancy decreases as the shark's body clears the water surface. The escape velocity of an animal performing a lower jump at a low angle will be most strongly affected when incorporating buoyancy: the value of g in equations (3) and (6) will decline and v_0 will be too high. One way to include buoyancy is to modify the numerator in equation (3) to $2g(h-h_1/2)$, where $h_1 = L/2 \sin\alpha$ and L = body length of the shark. This results in $v_1 = 5.4$ m s⁻¹ (−15%) and $v_2 = 4.9$ m s⁻¹ (−23%; table 2).

Although both methods produce similar estimates of velocity for both sharks, there were considerable differences in the calculated error. For shark 2, the error was between 35 and 59% of the estimated speed (table 2). In comparison with shark 1, shark 2 jumped out of the water at a lower angle, reached a lower elevation and remained clear of the water for a shorter time. The error therefore increased when using the same parameters for error calculation as for shark 1.

Measuring swimming speeds in large free-ranging fishes is difficult. Various methods have been applied in different species (Block *et al.* 1992; Nelson *et al.* 1997; Carlson *et al.* 2004). Variation also arises from differences in venue. For obvious reasons, fishes swim faster in the open ocean than in confined aquaria. Therefore, the method itself might be highly accurate, but the venue could strongly affect speed just because animals behave differently in different settings (Sims 2000). This variability makes comparison among species difficult. Furthermore, the method itself, for example, external speed sensing transmitters, can be problematic because additional drag might be induced, which lowers the overall performance of the animal (Sundström & Gruber 2002). Tag attachments can adversely affect fishes, biasing field data on their movement and behaviour (Mellas & Haynes 1985). It is therefore important to develop methods to estimate swimming speeds that do not include handling the fishes. The method proposed here offers the possibility of estimating speed by observing a jumping sequence occurring under natural conditions.

This paper adds an estimated swimming speed value for a shark species that has not previously been included in swimming speed measurement studies, and enlarges the dataset on estimated swimming speed in sharks. The calculated water-escape velocities for the two blacktip sharks seem accurate and are similar to estimates obtained for other shark species of similar size, for example, the lemon shark (*Negaprion brevirostris*; Sundström *et al.* 2001).

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