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LEAP-SWIM BEHAVIOR OF "PORPOISING" DOLPHINS

ABSTRACT

Dolphins leap or "porpoise" when swimming fast. Hypothetically, there is a "crossover" speed, above which leaping is energy saving. Field measurements indicate this speed is near 3.5 m/s. Observations also show that when moving at high speed, dolphins can continue to swim long distances under water, a behavior that current models of leaping-swimming behavior had not predicted.

A school of leaping dolphins that is literally churning the sea to froth obviously utilizes (and wastes) considerable energy, though we now know that these mammals possess no special mechanisms of power utilization (Hui 1987). It is also obvious that at high swimming speeds, dolphins find leaping advantageous, whatever the energy costs. Au and Weihs (1980) explained this by introducing the concept of "crossover" speed, above which dolphins should actually save energy by leaping. Their model and equation for this speed was based on an idea, first proposed by Hertel (1966), that leaping can be a way for fast-swimming animals to escape the increased drag encountered in the near-surface layer due to the animals' generation of surface waves. Recently, Blake (1983) discussed crossover speeds for a variety of aquatic animals after deriving a relationship that simplified to:

$$U_c = 18.47 \sqrt{L}$$

(where U_c = the crossover speed in cm/s, and L = animal length in cm). This equation appeared in some respects to be more realistic than that of Au and Weihs because it took into account the effects of propulsive body oscillations in addition to the previously considered, simple energetics of leaping vs. swimming. A typical 200-cm dolphin would accordingly have a U_c of 2.61 m/s or 5.1 knots (1 m/s = 1.94 knots).

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Nevertheless, certain field observations of swimming and porpoising dolphins indicate that the crossover speed of a typical dolphin may be higher, though perhaps not as high as the 5 m/s (9.7 knots) predicted by Au and Weihs. Table 1 summarizes swimming speeds of dolphins (*Stenella spp.*) measured by Au and Perryman (1982) that, for the most part, appeared to be swimming at below crossover speeds. These dolphins, it was noted, broke the surface with little commotion and swam relatively long distances between leaps, even at speeds of 3.6-4.6 m/s (although "splash-leaping" was observed once at 3.4 m/s and at 5.2 m/s). Their mean speed was 3.5 m/s.

Table 1. Speeds of swimming dolphins (*Stenella spp.*) in meters per second.

School	No. of Speed Measurements	Mean Speed (m/s)	Speed Range (m/s)
1	7	3.1	2.1 - 4.3
2	11	3.0	2.2 - 4.3
3	11	3.7	2.5 - 6.7
4	6	2.6	1.5 - 3.4
5	5	4.5	1.3 - 4.8
6	7	4.4	3.6 - 5.2
7	6	3.7	1.3 - 5.9

These speeds were calculated from the relative distances and motions of schools with respect to the observation ship. The field notes describe these dolphins as mostly "swimming smoothly" (Au & Perryman 1982).

The long swimming distances between leaps is significant because Au and Weihs implied, in their derivation of crossover speed, that dolphins moving faster than this speed should swim short distances underwater between leaps, both to minimize their time in the impeding water medium and to accommodate a higher respiration rate. This seemed to be supported by shipboard observations, but that impression may need reconsideration. Figure 1 is a schematic of how they viewed dolphin locomotion at different speeds.

Described here will be some recent observations of dolphin swimming behavior that bear on these ideas.
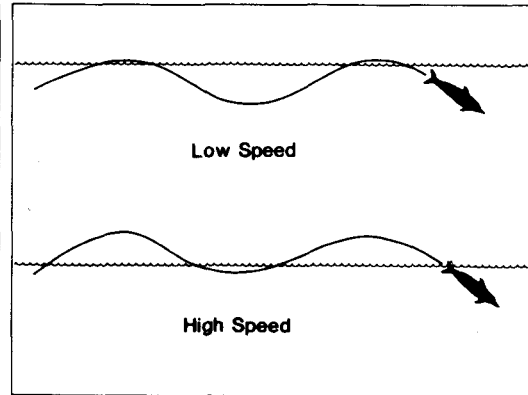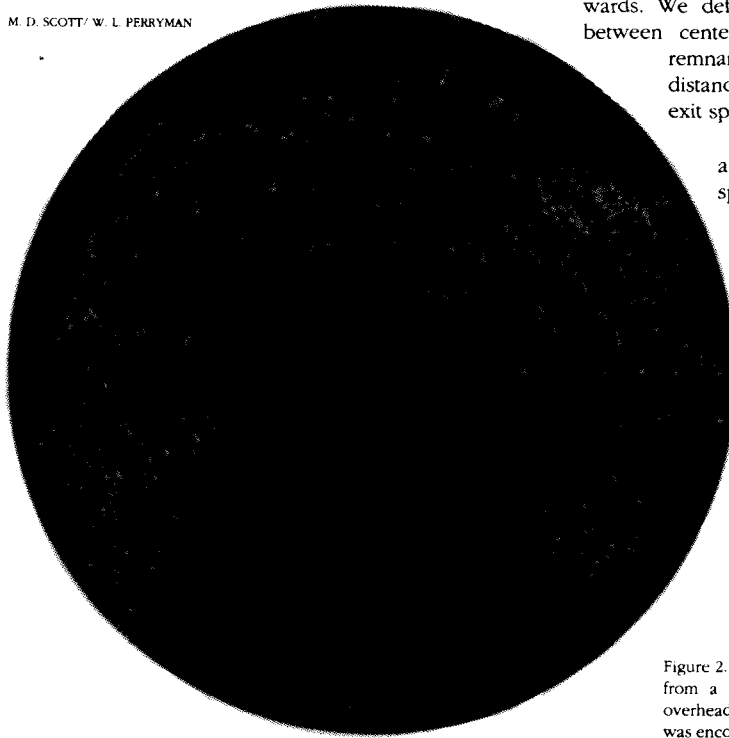
Figure 1. Schematic model of porpoising behavior.

The data to be presented come from examination of an aerial photograph of spotted dolphins (*Stenella attenuata*) leaping at high speed.

DATA AND RESULTS

Scott et al. (1985) and Scott and Perryman (in press) took vertical aerial photographs of dolphin schools off southwestern Mexico using a 127 mm (5 in.) film size reconnaissance camera. We found one photograph (Figure 2) to be particularly useful because it showed several sequences of leaping-swimming behavior, each indicated by a series of splash remnants trailing behind a dolphin. The photograph was taken from an altitude of 247 m (810 ft). The dolphins then had been moving rapidly ("running") probably for less than two minutes. With close inspection, the animals can be seen along the perimeter of the splashes or splash remnants.

Each completed leap within a leap-swim sequence leaves a characteristic splash remnant, which consists of white water on the sea surface in the shape of a lengthwise cut mushroom. The actual exit splash creates the mushroom "stem" of the splash remnant from water carried out and then shed by the leaping animal. The actual re-entry splash creates the mushroom "cap" of the remnant, apparently from water whose modified trajectories originate from both antero-lateral sectors of the actual splash, which is cone-shaped and inclined backwards. We define the leap length as the distance between centers of the exit and re-entry splash remnants. Similarly, swimming length is the distance between centers of the re-entry and exit splash remnants.

Actual lengths of animals (in meters) and of distances between sequential splash remnants (in body lengths and in body lengths converted to meters) were calculated from the photograph using the basic photogrammetric formula (Thompson 1966):

$$L = (H/f)\, i$$

(where L = actual length, H = altitude of the photographing aircraft, f = focal length of the camera, and i = image length of the animal or of the splash (or remnant) interval on the photograph). We carefully measured the image lengths

Figure 2. Aerial photograph of spotted dolphins scattering from a disturbance (presumably the airplane directly overhead). This school, estimated to contain 300 dolphins, was encountered in the eastern tropical Pacific off Mexico.

on the film to the nearest 0.025 millimeter using a calibrated stage micrometer on a 3X-power dissecting microscope. The precision of and bias in such calculated lengths and distances involves several considerations and is discussed by Hammond et al. (MS), and Scott and Perryman (in press). In their work, they found that the coefficient of variation of multiple measurements on individual dolphin images varied from 0.5-1.6 percent.

These lengths and distances in turn enabled the calculation of swimming speeds from the simple ballistic equation:

$$U = \sqrt{Rg/\sin 2\Theta}$$

(where U = swimming speed at leap exit in m/s, R = leap length in m, g = 9.8 m/s², and Θ = launch angle).

The average leap length was an impressive 6.8 m (Table 2). From it we calculated the mean horizontal speed of the dolphins to be 8.2 m/s, using the above equation and assuming a ballistic trajectory with 45° launch angle. (Reducing the average leap length by two standard errors would give 7.7 m/s; angles other than 45° would give higher speeds.) Between leaps, the dolphins were often clearly visible; frequently, they appeared to be swimming less than 2 m under the surface with little change of depth.

Interestingly, the splash remnant patterns show that swim lengths were greater (on average, 1.9 times greater) than leap lengths (Table 2). (This ratio should be little affected by errors.) This finding is contrary to the model for high speed swimming shown in Figure 1-B. Thus, these dolphins swam long distances even when traveling above crossover speed.

DISCUSSION

It is possible to show that the crossover speed of a 200-cm dolphin can be 3.4 m/s, or even 6.3 m/s, if it is assumed that the dolphin swims below the high-drag surface layer between leaps and that the leap actually begins and ends beneath the sea surface, or if certain other assumptions are made regarding the mass of water carried out by the leaping animal. These variants of the crossover speed equation would accommodate some of the ideas of Gordon (1980). But all such calculations merely show that moderate adjustments in multi-parameter equations lead to a range of results. We are not confident that these equations are realistic.

We have not been able to determine crossover speed empirically and can only suggest its approximate value. Part of the reason is that it is unclear how to recognize this speed when it occurs. Are dolphins that are porpoising gently, with their bodies barely clearing the water,

actually leaping or even in the leaping mode? The dolphins described in Table 1 appeared to be porpoising gently at 3.5 m/s on average (6.8 knots); long, splashing leaps were seldom seen. In contrast, the dolphins in Figure 2 were clearly above crossover speed; their long leaps and large exit and re-entry splashes exemplified that spectacular locomotory behavior that so strongly imparts the impression of power in these animals. Their average speed was calculated at 8.2 m/s (15.9 knots). Such speeds are not sustainable, for elsewhere when we have pursued dolphins of the genus *Stenella* with a ship traveling at 5.2 m/s, those dolphins (which would often break into the leaping mode) still could not escape except by scattering. These observations suggest that the crossover speed lies below 8.2 m/s and is near 3.5 m/s.

Table 2. Means of size, leap length, and swim length of individuals from a school of "running" spotted dolphins (*Stenella attenuata*).

	n	x̄	st. dev.
Animal length	19	1.71 m	0.21 m
Leap length			
in body lengths	26	3.96	1.11
in meters	26	6.77 m	1.90 m
Swim length			
in body lengths	9	7.45	1.01
in meters	9	12.74 m	1.73 m

Animal length measurements tend to be underestimates because of the difficulty in discerning the exact limits of body size from the photograph (see Figure 2) due in part to slight flexing of the body. Twenty animals were tracked and measured. One calf was eliminated from the calculation of mean length. From 0-2 swim lengths and 1-3 leap lengths could be measured for each animal.

It was surprising that the fast-moving dolphins of Figure 2 swam underwater an average distance almost double the leap length, for we thought that the high-speed, leap-swim sequence should at least be symmetrical with respect to the sea surface, if not like that of Figure 1-B. Why should these dolphins swim so long underwater when leaping was already clearly advantageous? Their speed should have induced frequent leaping, even if swimming were well below the high-drag surface layer. It is possible that they accelerated to leap, that between leaps they were swimming more slowly than when they were leaping. But, if so, it is unclear why that would be advantageous in-flight behavior. Perhaps the dolphins were using a variant of the energy-saving, two-phase power and glide swimming (Weihs 1974), where the glide phase begins at the top of the leap. Hui (1986) photographed penguins of the genus *Spheniscus*

leaping and swimming at a mean speed of 3.7 m/s, which was above the empirically determined speed of 3.0 m/s at which they regularly began leaping. The birds' swim lengths averaged 3.6 times their leap lengths, an even larger factor than measured for the dolphins in Figure 2. He also noted the discrepancy with previous models of leaping and suggested that breathing rate and time required for inhalation, rather than swimming speed alone, might control porpoising behavior. That would be consistent with the observations since neither the dolphins nor the penguins were likely very tired or breathing rapidly when photographed. At faster breathing rates, swim lengths may very well decrease, while leap lengths may change little.

The long swim lengths, apparently at speeds that should induce leaping, remain an enigma of our present understanding, which is admittedly rudimentary. But however complex leap-swim behavior may actually be, the principle of energy efficiency and conservation is probably maintained. Even the great splashes that accompany leaping probably represent a compromise between the energetic needs of streamlined, underwater propulsion and the requirements for smooth exit and re-entry through the water surface.

Certainly there is more to be learned. Why, for example, is it advantageous for some species of dolphins to bunch tightly when porpoising while, for some others, porpoising in lines abreast appears characteristic? And why do leaping dolphins re-enter the water with their pectoral fins extended?

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