At high speeds dolphins save energy by leaping

D. Au & D. Weihs*

NOAA National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038
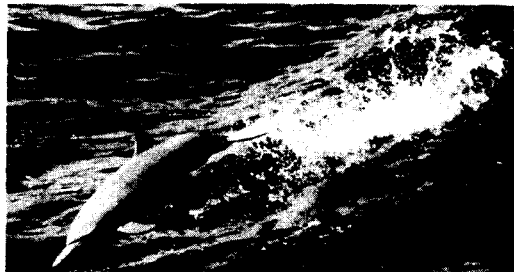

Fig. 1 A 'running' eastern spinner dolphin (*Stenella longirostris*) leaping approximately two body lengths in the rapid swimming mode. Photograph by R. Pitman.

An observer may wonder whether a school of 'running' dolphins, consisting of numerous, wildly splashing individuals, is using the most efficient mode of locomotion, because splashing wastes energy. Dolphins exhibit at least three modes of swimming. In leisurely, unhurried motion, they break the surface briefly and gently, often showing little more than the blowhole. At a faster, 'cruising' speed, frequently at 3–3.5 ms^{-1} (6–7 knots), the animals are seen swimming primarily just beneath the surface, and there is still little splashing. (Behaviour and speeds of dolphin schools were observed from a helicopter and will be described elsewhere by D. A. and W. Perryman.) Swimming speeds in this mode have been measured up to 4.6 ms^{-1} (9.3 knots). But in the fastest 'running' mode, the animals clear the water in sequential, parabolic leaps, accompanied by considerable splashing on exit and re-entry (Fig. 1). Leaps are interspersed with relatively brief, subsurface swimming. This swimming is common when dolphins are alarmed by vessels approaching within 500 m. We have examined dolphin swimming in terms of energy required per unit distance travelled and report here that beyond a certain 'crossover' speed, leaping must be more efficient than swimming.

The energy cost of leaping must be compared with that of continuous swimming very close to the surface. This is because during rapid swimming, as in escape behaviour, the rate of respiration increases, and the animals are therefore constrained to the surface layer. The extra energy required for jumping is approximately (neglecting air resistance)

$$J = WH\,(1+m) \qquad (1)$$

where W is the weight of the dolphin, H is the maximum height of the centre of gravity above the undisturbed sea level, and m is a correction term accounting for the spray carried along with the dolphin as it emerges. The dolphin is approximately neutrally buoyant[1] and so very little energy is required to raise the centre of gravity to surface level. The energy in equation (1) will be compared with that expended by a dolphin swimming continuously with its blowhole just out of the water. This swimming would be roughly equivalent to that of leisurely or cruising swimming, where no more than one-third of the body is out of the water at any instant.

The energy required for swimming at one equivalent body radius beneath the undisturbed surface (that is just submerged) is

$$E = DL \qquad (2)$$

where D is the hydrodynamic drag and L is the distance travelled. The drag can be written as[2]

$$D = \tfrac{1}{2}\rho_\omega\,V^{2/3}\,C_D\gamma U^2 \qquad (3)$$

where ρ_ω is the density of water, V is the dolphin volume, C_D the drag coefficient in deep water, γ the correction due to proximity to the surface[3,4], and U the swimming speed. Dolphins usually leap only for short periods so that other energy saving aspects of swimming, as when using beat-and-glide or diving[5], are not applicable.

We now write the ratio of energy J/E to find the range of speeds at which this ratio is <1, that is leaping is energy sparing.

* Permanent address: Department of Aeronautical Engineering, Technion, Haifa, Israel.

The energies must be compared over the same distance and therefore the length of the jump as a function of swimming speed has to be known. We neglect air resistance. The leaping dolphin has an approximate ballistic trajectory, for which the distance crossed while the centre of gravity of the animal is out of the water is

$$L = \frac{U^2}{g}\sin 2\alpha \qquad (4)$$

where g is the gravitational constant and α the emergence angle, measured from the horizon. The maximum height reached by the centre of mass is

$$H = \frac{U^2\sin^2\alpha}{2g} \qquad (5)$$

The longest leap for given speed U is obtained when $\alpha = 45°$. In this case, designated by subscript 'max',

$$L_{max} = \frac{U^2}{g};\ H_{max} = \frac{U^2}{4g} \qquad (6)$$

Using these results, we obtain the ratio J/E:

$$R = \frac{J}{E} = \frac{\rho_d g\,V\dfrac{U^2}{4g}(1+m)}{\tfrac{1}{2}\rho_\omega V^{2/3}C_D\gamma U^2\dfrac{U^2}{g}} = \frac{\rho_d g(1+m)V^{1/3}}{2\rho_\omega C_D\gamma U^2} \qquad (7)$$

where ρ_d is the density of the dolphin. Equation (7) shows that for a given dolphin swimming as described, the ratio R decreases monotonically as forward speed U increases. Thus, for every species, there will be a range of speeds for which leaping will be more efficient than shallow swimming. The lowest (crossover) speed at which this occurs is obtained by setting $R = 1$ in equation (7). This speed U_c is dependent on the size of the dolphin (through the volume V), its density, its shape (which will define C_D and m), and how far beneath the surface it swims (which defines γ).

To obtain specific values of the crossover speed, we substitute typical values of the different parameters in equation (7). The dolphin's density is affected by the degree of lung inflation and the extent of fat reserves. We take it to be approximately equal to the density of sea water[1], that is, $\dfrac{\rho_d}{\rho_\omega} = 1$. The spray mass coefficient is obtained from the longitudinal added mass, defined as the mass of water carried along when a body moves through a fluid. Thus when the dolphin leaves the water, this mass is carried along. The added mass coefficient for fusiform, elongated shapes such as the dolphin's is [6]$m \approx 0.2$. Hoerner[2] gives the relationship between the drag coefficient C_D based on volume and skin frictional drag C_f as

$$C_D/C_f = 4(l/d)^{1/3} + 6(d/l)^{1.2} + 24(d/l)^{2.7}$$

which gives a ratio of 8 for a dolphin with an l/d ratio of about 5, where d = diameter and l = length. Hoerner's Fig. 22 shows C_f to be between 0.002 and 0.003 for semi-turbulent flow in the appropriate range of Reynolds number, so that C_D was approximated here as 0.02. The surface effect correction γ is taken as 4.5 when the body is fully submerged, just below the surface. (If the dolphin were an exact body of revolution $\gamma = 5$)[3,4]. Both C_D and γ should be considered approximations, C_D because it may be a conservative estimate for a flexing body and γ because it is sensitive to submerged depth and decreases rapidly to 1 at a depth three times the body diameter. Substituting all the above values in equation (7) and setting $R = 1$, we obtain

$$U_c = 65.3 V^{1/3}$$

where U_c is in m s^{-1} and V in m^3. This general equation, while only an approximation for any specific dolphin, should give a good estimate of the expected speeds above which leaping will occur. Table 1 gives the values of the crossover speed, U_c, as a function of body volume.

Table 1 Predicted values of crossover speed U_c over which leaping becomes energy sparing as a function of body volume

V (m^3)	U_c (m s^{-1})	L_C (m)	H_C (m)	E (J)
0.005	3.34	1.14	0.28	17
0.05	4.90	2.45	0.61	368
0.1	5.50	3.09	0.77	928
0.15	5.89	3.54	0.88	1,590
0.2	6.18	3.90	0.97	2,340
0.25	6.41	4.19	1.05	3,160
1	8.08	6.66	1.67	20,100
5	10.57	11.40	2.85	172,000

Predicted leap length and height are shown, as well as the energy required for each leap ($g = 9.8$ m s^{-2}). For any given volume, underwater motion at less than U_c is less energy-consuming than leaping the same distance. A volume of 1 m^3 corresponds to a weight of 1,025 kg.

Table 1 indicates that for the usual size range (0.05-0.10 m^3) of most dolphin species[7,8], the crossover speed is about 5 m s^{-1} (10 knots), well within their available range of speeds[9]. During January and February 1977 and 1979, the RV David Starr Jordan approached various dolphin species (Stenella spp., Delphinus delphis) at speeds of 4.5-5 m s^{-1} (9-10 knots) in the eastern tropical Pacific. At that speed, the vessel could approach close to all schools as long as they could be tracked. However, it often took an hour for the ship to close onto schools initially seen at about 2 miles (3.6 km) distance. Evidently those dolphins were mostly moving at cruising speeds of 3.5-4 m s^{-1} (7-8 knots), similar to previous measurements. We observed that the leaping (running) mode occurred primarily after the ship had closed to within 500 m and the animals had become increasingly alarmed and had noticeably increased speed. No measurements of actual speed were possible as the leaping dolphins usually escaped abeam and when followed, continued along curved paths. The speeds attained appeared somewhat greater than that of the ship and were probably in excess of the crossover speed. The actual crossover speed is probably within 10% of the predicted value. Thus, because of their shallow swimming ($\gamma \approx 4.5$), the crossover speed must be approximately 5 m s^{-1} (10 knots), and dolphins must leap to obtain higher speeds efficiently.

Swimming speed can be estimated indirectly by measuring the distance between the emergence spot and the re-entry splash on photographs similar to Fig. 1, and comparing it to animal length. These distances were within the range of 2-4 m, as expected from Table 1. The height of the leaps (to the centre of gravity) is between 0.6 and 1.0 m, also in agreement with Table 1. Spotted and spinner dolphins (S. attenuata and S. longirostris) have been observed leaping distances of about three body lengths (5.4 m) when chased closely by speedboats, corresponding to a swimming speed of ~7.3 m s^{-1} (14.6 knots)[10]. After escaping purse seine nets, they continued leaping for 1,500 m, performing leaps of ~2.3 body lengths, which corresponds to a speed of 6.4 m s^{-1}, also greater than the crossover speed.

Larger cetaceans ($V > 1$ m^3, weight > 1 ton) probably cannot leap during fast swimming, as the energy required for leaping increases rapidly with body size (Table 1). Fishes, on the other hand, do not have to break surface to breathe and can stay sufficiently deep for surface proximity effects to be negligible ($\gamma = 1$). Crossover speed would then be increased by a factor of more than 2, and, except for large fish such as istiophorids and some large scombrids, is not likely to be an important factor in swimming.

Although the cetacean running mode has been described in the context of escape behaviour, it could occur in any situation where rapid speeds for short periods were required. Furthermore, leaping behaviour is not restricted to the running mode. At any speed, individual dolphins will often 'splash leap', that is leap out of the water with various contortions so as to re-enter with a large splash. The various attitudes of such leaps indicate, however, that they are not primarily related to horizontal velocity. Their function is most probably that of display–communication, the exact meaning depending on the situation, including the physiological state of the animal.

We thank Lorraine Prescott and Paul Webb for their help.

1. Lang, T. G. in Whales, Dolphins and Porpoise (ed. Norris, K. S.) 410-432 (University of California Press, Berkeley, 1966).
2. Hoerner, S. F. Fluid Dynamic Drag, 400 (Hoerner, S. F., Midland Park, New Jersey, 1965).
3. Hertel, H. Structure, Form and Movement, 251 (Reinhold, New York, 1966).
4. Webb, P. W. Bull. Fish. Res. Bd Can. 190, 158 (1975).
5. Weihs, D. J. mar. Res. 31, 195-209 (1973); J. theor. Biol. 48, 215-229 (1974).
6. Gero, D. R. Am. Mus. Novit. 1601, 1-32 (1952).
7. Leatherwood, S., Evans, W. E. & Rice, D. W. The Whales, Dolphins and Porpoises of the Eastern North Pacific, 175 (Naval Undersea Center TP 282, 1971).
8. Leatherwood, S., Caldwell, D. K. & Caldwell, M. C., Whales, Dolphins and Porpoises of the Western North Atlantic 176 (NOAA Tech. Rep., NMFS Circ. 396, 1976).
9. Lang, T. G. & Pryor, K. Science 152, 531-533 (1966).
10. Norris, K. S., Stuntz, W. E. & Rogers, W. The Behavior of Porpoise and Tuna in the Eastern Tropical Pacific Yellowfin Tuna Fishery—Preliminary Studies, 86 (Nat. Tech. Inform. Serv. P8283970, 1978).

2