
Dolphin swimming—a review

FRANK E. FISH and CLIFFORD A. HUI*

*Department of Biology, West Chester University, West Chester, PA 19383 and
*Chemistry and Biochemistry Branch, Code 521, Naval Ocean Systems Center, San Diego,
CA 92152, U.S.A.*

ABSTRACT

Research into dolphin swimming has historically been guided by false assumptions of 'effortless', 'high-speed' swimming. These assumptions have instigated the development of drag-reduction hypotheses but tests of these hypotheses have generally had little success. The autecological approach has dominated recent efforts and has been more successful. In this review we summarize results of decades of research efforts to study these creatures. (1) Drag is minimized primarily by the streamlined shape of the body and appendages, with no known contributions from compliant dampening, dermal ridges, secretions, boundary layer heating, or skin folds. All indications are that the boundary layer is turbulent. (2) Muscles for the upstroke and downstroke of swimming dolphins provide approximately equal power. (3) Output force is enhanced by insertions occurring on the long processes of the vertebrae and on the subdermal connective tissue sheath. (4) Measured swimming speeds are lower than previously believed, with maximum reported routine speeds being approximately 3 m/s. (5) Porpoising behaviour appears to be the most energetically conservative manner in which to breathe when swimming at high speed. (6) Riding surf and wind waves involves the balance between the wave slope and the weight of the animal whereas riding the bow wave involves the interaction of the pressure wave in front of a ship and the drag of the dolphin.

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*Current address: U.S. Fish and Wildlife Service, Pacific Research Group, Davis, Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, U.S.A.

INTRODUCTION

Swimming is the only mode of locomotion for dolphins and is a primary component of their time and energy budgets. While swimming, dolphins forage, socialize, copulate, and undergo parturition. Unlike some other marine mammals (pinnipeds, sea otter), dolphins never leave the water. As a result these animals represent important models for studying adaptations for aquatic activity. In addition, by understanding dolphin swimming we gain insight to a part of dolphin biology which affects its entire natural history.

Dolphins present an image of effortless high-speed swimming by an air-breather perfectly adapted to an aquatic environment. Impressed by this image, early investigators directed their efforts to discovering the adaptations they considered to be more perfect than man-made designs. Theories were advanced to explain various aspects of dolphin swimming perfection and subsequently tested with negative results. Recent research, however, indicates that 'high-speed', 'effortless' and 'perfect' are inappropriate descriptors of dolphin swimming. This new appreciation has developed only since the assumptions of the dolphin as a perfectly designed swimmer have been replaced by that of the dolphin as an organism fitting an ecological system.

Because information regarding the swimming capabilities and hydrodynamic adaptations of dolphins has been scattered throughout both the engineering and biological literature, a review on swimming dolphins, integrating this information, can help to direct new investigations. Swimming is an amalgam of many components, but the review can usefully be organized into the broad areas of drag minimization, propulsion, and swimming behaviours.

DRAG MINIMIZATION

Drag is the force resisting movement through water. Minimization of drag would be an expected corollary to the high-speed swimming observed in dolphins. Because dolphins had been viewed as 'perfectly' adapted, they have been examined (with varying degrees of precision) for demonstrations of every drag-reducing mechanism known or theorized. These mechanisms range from body shape to exotic characteristics of the skin.

These putative mechanisms affect drag by modifying the boundary layer (a layer of water defined as extending out from the body to the point at which it is moving at 99% of the free stream speed; Prandtl & Tietjens, 1934). Drag can be minimized by (1) maintaining the boundary layer in a laminar condition, thereby minimizing the frictional component of the drag force, or (2) inducing turbulent conditions in the boundary layer early in the flow, thus minimizing the pressure component of drag. The turbulent boundary layer has greater stability, causing boundary-layer separation to occur further downstream than in laminar flow. This reduces the size of the pressure wake substantially (Potter & Foss, 1975) and ultimately the total drag by several orders of magnitude (Webb, 1975). Hydrodynamic models based on kinematics or rigid bodies generally show dolphins to maintain turbulent-boundary-layer flow (Fig. 1). However, most of the efforts to observe drag minimization by dolphins have focused on maintenance of laminar flow. In general, the nature of the boundary layer of a swimming dolphin has yet to be directly measured.

Morphology

Body. The fusiform, streamlined body shape of dolphins (Fig. 2) is similar to engineering 'laminar' profiles (Hertel, 1966) which reduce the pressure component of

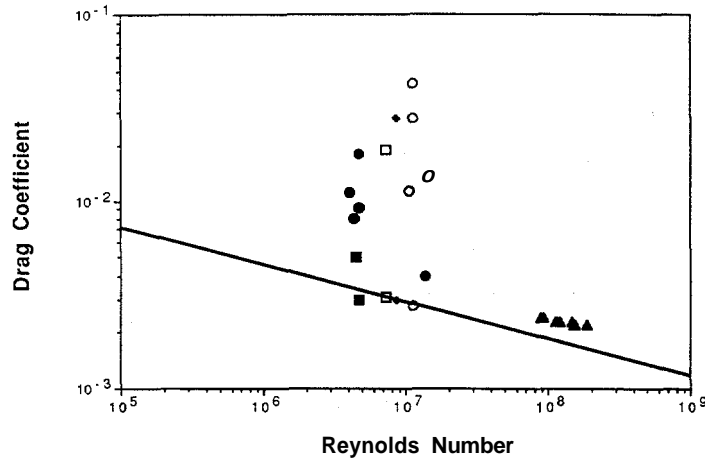


Fig. 1. Comparison of cetacean body drag estimated from hydrodynamic models based on kinematics and rigid bodies. The non-dimensional drag coefficient is directly related to the drag on the body. The non-dimensional Reynolds number is directly related to length and velocity of the dolphin. The solid line represents the limit above which the boundary-layer flow is considered turbulent. The dolphin genera are *Delphinus* (\square), *Lagenorhynchus* (\circ), *Phocoena* (\circ), *Phocoenoides* (\blacklozenge), *Sotalia* (\blacksquare), and *Tursiops* (\circ). In addition, the mysticete genus *Balaenoptera* (\blacktriangle) is shown. Data are from Aleyev (1977), Lang & Daybell (1963), Purves *et al.* (1975), Videler & Kamermans (1985), Webb (1975) and Yates (1983).

drag through maintenance of laminar flow (Walters, 1962; Webb, 1975). The position of the shoulder (maximum thickness) is important because this is where transition to turbulent flow and boundary-layer separation is likely to develop (Blake, 1983a). The shoulder position of dolphins is 0.34–0.45 of the body length from the beak (Hertel, 1966; Aleyev, 1977). Therefore, a maximum of 45% of the dolphin body may have laminar flow due to a favourable pressure gradient up to the shoulder. Separation of the boundary layer behind the dorsal fin (Purves, Dudock van Heel & Jonk, 1975), which is posterior to the shoulder, has been shown by tests with paint on a rigid model of *Tursiops truncatus*. However, the flow became non-uniform well before the dorsal fin when using dye patches on the head of a swimming dolphin (Rosen, 1963).

Another indicator of body streamlining is the fineness ratio (FR) ($FR = \text{body length} / \text{maximum diameter}$). The FR of the dolphin body (3.85–5.55; Hertel, 1966; Aleyev, 1977) approximates the optimum value of 4.5 (von Mises, 1945; Hertel, 1966; Blake, 1983a). This ratio presents the lowest drag, where volume is maximized and surface area minimized (Hertel, 1966).

Appendages. The flippers, dorsal fin and flukes, which are used for stability, manoeuvrability, and the production of thrust, are also streamlined (Felts, 1966). The cross-sections of the flukes and fin present a streamlined profile outline ($FR = 4.7\text{--}6.6$; shoulder/chord = 0.32–0.36) with a rounded leading edge and tapering trailing edge (Lang, 1966), similar to 'laminar' shapes providing high lift and low drag characteristics. The appendages have a greater effect on total body drag at low speeds than at high speeds when the flow is turbulent (Lang & Daybell, 1963; Purves, Dudok van Heel & Jonk, 1975; Yasui, 1980). The drag added by the appendages has been estimated as 28% of the body drag (Lang & Pryor, 1966).

The planar areas of flukes and fin can be used to compute aspect ratios ($AR = \text{span}^2 / \text{surface area}$). A high AR provides a reduction in the drag encumbered by a hydrofoil

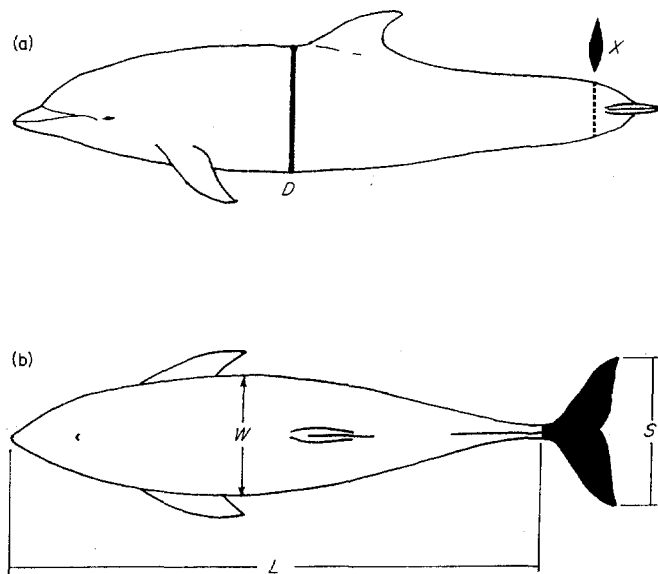


Fig. 2. Streamlined body forms of *Tursiops truncatus* (a) and *Phocoena phocoena* (b). The position of the maximum body diameter, (D), for *Tursiops* is indicated by the thick solid line, and the position of the peduncle cross-section (X) is indicated by the broken line. As illustrated for *Phocoena*, L is the body length without the flukes, W is the maximum body width, S is the span of the flukes, and the planar surface area of the flukes is shaded. These features are important in estimating hydrodynamic characteristics of the dolphin body form (see text). Redrawn from Aleyev (1977).

while simultaneously producing large lift forces for thrust (Webb, 1975). In aquatic vertebrates, a high AR tail is associated with high-speed cruising (Lighthill, 1969). Dolphin flukes have moderate to high AR ($AR = 3.4-5.5$; Lang & Daybell, 1963; Videler & Kamermans, 1985).

The caudal peduncle also helps minimize drag because it is streamlined in the plane of oscillation (Fig. 2a; Lighthill, 1969, 1970). The extreme tapering of the body at the caudal peduncle (Fig. 2b) effectively separates the body anterior to the peduncle from the virtual mass affects and recoil forces generated by the motion of the flukes (Aleyev, 1977; Blake, 1983a). The body acts as an inertial mass (Webb, 1975) reducing unstable movements and minimizing drag, which reduces energy consumption.

Skin

Compliant dampening. Kramer (1960a,b, 1965) proposed that dolphin skin is a compliant surface, which reduces drag by distributed viscous dampening. His argument is based on dermal morphology. Dolphin integument is composed of a smooth, hairless epidermal surface forming an elastic membrane (Aleyev, 1977) anchored to the dermis by longitudinal dermal crests with rows of papillae, which penetrate the lower epidermis (Kramer, 1960b, 1965; Sokolov, 1960; Aleyev, 1977; Yurchenko & Babenko, 1980). Therefore, it has been hypothesized that the surface of the epidermis may transmit boundary layer pressure pulsations to the lower epidermis and dermal papillae where the energy is absorbed through elastic deformation (Kramer, 1965; Aleyev, 1977). Total drag would therefore be reduced due to the dampening of beginning turbulence, thereby extending laminar flow. Also, dampening may be enhanced by actively adjusting the flexibility and movement of the skin (Sokolov, 1962; Lang, 1966). Although this scheme seems possible, turbulence reduction by dolphin skin has

never actually been demonstrated. Independent experiments to verify the large drag reductions reported by Kramer for compliant surfaces have failed (Gad-El-Hak, 1987; Carpenter, 1990).

Dermal ridges. The dermal crests and papillae form visible ridges on the epidermal surface (Purves, 1963, 1969; Purves *et al.*, 1975). If the dermal ridges indicate the water flow paths, then the water moves in an oblique, not length-wise, path about the dolphin body (Purves, 1963). Therefore, the flow path for water is significantly lower than that based on total body length (Gray, 1936; Kramer, 1960b), providing conditions favourable to the maintenance of laminar flow. The drag-reducing benefits of ridges have been demonstrated on engineering forms (Reidy, 1987). However, dolphin dermal ridges do not have sharp edges as do the engineering forms and their effects, if any, have not been demonstrated.

Secretions. Epidermal cell production in *Tursiops truncatus* occurs at a rate 250–290 times that of humans (Palmer & Weddel, 1964). These cells contain masses of tonofilaments and lipid droplets which, when concentrated, are similar to a mucopolysaccharide (Harrison & Thurley, 1972). Although long chain, high-molecular-weight polymers (like mucopolysaccharides) can reduce drag when added into the boundary layer (Hoyt, 1975), cells shed from the epidermis have negligible effect on hydrodynamic drag (Sokolov, Bulina & Rodionov, 1969). The sloughing of the skin may help to maintain low drag characteristics by preventing fouling by encrusting organisms on the dolphin surface (Gucinski & Baier, 1983), rather than being a secretion to modify the boundary layer flow. Secretions from the dolphin eye also were found to have no effect on drag characteristics (Sokolov *et al.*, 1969).

Boundary-layer heating. Increasing the temperature of water will change its viscosity, thereby making boundary-layer laminar flow more stable. The surface temperatures of *Stenella longirostris* and *Tursiops gilli* have been reported to be higher than water temperature by as much as 9°C (McGinnis *et al.*, 1972; Hampton & Whittow, 1976). In water at 27°C, a reduction in viscosity of only approximately 11% would be realized. This viscosity reduction would result in drag reduction only if the water were heated instantaneously; based on calculations for tuna, this is not likely (Walters, 1962; Webb, 1975). The effectiveness of such a drag reduction mechanism is considered limited (Lang & Daybell, 1963; Lang, 1966) or insignificant (Webb, 1975).

Skinfolds. Skin folds have been observed on accelerating dolphins (Essapian, 1955). They represent a parasitic feature which does not reduce drag (Backhouse, 1960; Aleyev, 1977). On naked women towed through water, similar skin folds developed passively from the interaction of dynamic water pressure and skin elasticity; these folds increased drag (Aleyev, 1977). Skin folds caused by flexion of the dolphin body during swimming are probably minimized by the crossed helically wound layer of collagen fibres underlying the blubber (Wainwright, Pabst & Brodie, 1985; Pabst, 1988).

Induced turbulent boundary layer. Dolphins swimming in a phosphorescent sea have been reported to have, as the only visible disturbances, two diverging lines in the wake (Stevens, 1950) or a single thin line (Hill, 1950). These observations indicate that the

boundary layer remains attached over the entire length of the body, with the narrow lines in the wake assumed to be tip vortices (Webb, 1978). The adherence of the boundary layer indicates that it is largely turbulent. This interpretation has been reinforced by experiments using a tripping wire to induce turbulence over the surface of a live dolphin. The drag was the same with or without the wire, indicating that the normal boundary layer is turbulent (Lang & Daybell, 1963; Lang & Pryor, 1966; Webb, 1975).

Swimming motions

The propulsive movements of dolphins are confined to the vertical plane in the posterior one-third of the body, with the greatest amplitude at the flukes and caudal peduncle (Petersen, 1925; Parry, 1949a; Slijper, 1961; Lang & Daybell, 1963; Videler & Kamermans, 1985). With maximum dorso-ventral deflections confined to the tapered posterior of the body, the anterior part of the body acts as an inertial mass minimizing energy loss from body oscillations (see reviews by Lighthill, 1971; Webb, Kostecki & Stevens, 1984).

The swimming motion of dolphins has been described as a carangiform mode with semilunate tail (Webb, 1975). This mode is shared with other fast-cruising aquatic vertebrates that possess a fusiform body, an extremely narrow caudal peduncle, and a high aspect ratio tail (Lindsey, 1978; Fish, Innes & Ronald, 1988). This mode enables efficient propulsion with high thrust production (Webb, 1975; Lindsey, 1978). Using models for lunate tail hydrodynamics (Lighthill, 1970; Chopra & Kambe, 1977) and data from *Lagenorhynchus obliquidens* (Lang & Daybell, 1963), the propeller efficiency has been calculated to be 0.77–0.92 (Webb, 1975; Yates, 1983).

It has been argued that the oscillations of the flukes generate unsteady velocity and pressure gradients by accelerating water over the body, thereby extending the range for laminar flow (Gray, 1936; Lang, 1963). Active swimming, then, may reduce turbulence in the boundary layer compared to that when coasting (Romanenko, 1976). However, the few studies which have examined boundary layer flow do not support this hypothesis (see *Body*, above).

PROPULSION

Dolphins propel themselves by vertical oscillation of their tail flukes. This oscillation produces hydrodynamic thrust. The motion is generated by the linked actions of tendons, muscles, and metabolic processes, each of which has unfortunately been studied independently of the others.

Kinematic models

Power output of dolphin swimming can be estimated from kinematic models (Parry, 1949a; Lighthill, 1970; Wu, 1971; Chopra & Kambe, 1977; Yates, 1983). Models for flexible and for rigid bodies have been developed. A general model for vertebrates using body undulations for propulsion (Lighthill, 1971) predicts a power output requirement about four times that of rigid body models. Using kinematic data from trained dolphins (Norris & Prescott, 1961; Lang & Daybell, 1963), power output estimates were 4 to 16 times greater than estimates assuming a high-drag turbulent boundary layer on a rigid model (Webb, 1975; Yates, 1983). The differences between the various estimates and from the expected values are attributed to increased drag when swimming near the surface (Webb, 1975) and the different models used. Further refinements of the models and improvements in data collection should provide consistent estimates. These models assume that the upstrokes and downstrokes are equivalent. Their refinement may be

influenced by cine analysis which indicate that the up- and downstrokes in fact differ (Videler & Kamermans, 1985).

Cine analyses

Differences between the sizes of the epaxial (dorsal to spine) and hypaxial (ventral to spine) muscle masses (Parry, 1949a,b; Slijper, 1961; Purves, 1963; Strickler, 1980; Bello *et al.*, 1985) led to the early contention that the up and down movements of the tail and flukes were not equivalent: the upstroke was considered to produce thrust while the downstroke was passive, functioning as a recovery stroke (Purves, 1963, 1969; Pilleri *et al.*, 1976). However, early cine analyses (Purves, 1963, 1969) had been based on a film of a dolphin swimming during parturition (Parry, 1949a), an obviously abnormal swimming condition. Recent cine analyses of swimming captive *Tursiops truncatus* and *Sotalia quianensis* also show that the animals alternately accelerate and decelerate throughout the stroke cycle. This pattern, in contrast to the interpretation of differential muscle mass, indicates that net hydrodynamic force is positive during the downstroke but negative during the upstroke (Bello *et al.*, 1985; Videler & Kamermans, 1985). The constraints of captivity may have influenced this pattern. However, measurable angles of attack of the flukes during each phase of the stroke indicate thrust production during both phases, although the magnitude of thrust differs between the up- and downstroke (Lang & Daybell, 1963; Videler & Kamermans, 1985).

Muscle anatomy

Despite the disparity between the hypaxial and epaxial muscle masses, and the cine data from captive animals, the two muscle masses could produce equivalent propulsive forces and dorsoventral bending moments, given the similar arrangement of the fasciculi, tendons, and insertions (Arkowitz & Rommel, 1985). Equivalent numbers of slow-twitch oxidative and fast-twitch glycolytic fibres in the epaxial and hypaxial musculature also indicate similar power distribution (Mankovskaya, 1975; Ponganis & Pierce, 1978; Bello *et al.*, 1983, 1985; Suzuki, *et al.*, 1983). In addition, abdominal muscles may add large bending moments which help depress the tail (Arkowitz & Rommel, 1985), although there have been some arguments against this concept (Purves & Pilleri, 1978).

Other aspects of the musculoskeletal design also affect the magnitude of the propulsive forces. There may be a significant mechanical advantage from tendons inserted on the long lever arms of the spinous and transverse processes and chevron bones of the tail vertebrae (Slijper, 1961; Smith, Browne & Gaskin, 1976; Pabst, 1990). These lever arms amplify the forces compared to those resulting from tendon insertions closer to the vertebral bodies. Pabst (1987) has suggested that insertion of the epaxial muscles on the connective tissue sheath under the blubber allows for a portion of the force to be developed at the caudal vertebrae.

It has been suggested that cetacean tendons function analogously to the elastic tendons of running mammals (Russell *et al.*, 1983; Bello *et al.*, 1985). Theoretically, collagen fibres under the blubber layer would store elastic energy generated during the stroke (Wainwright, Pabst & Brodie, 1985), and energy would subsequently be released to reaccelerate the flukes, requiring no additional input of metabolic energy (Bennett, Ker & Alexander, 1987). A model proposed by Bennett *et al.* (1987) examined the relationship between ratios of strain energy to kinetic energy and hydrodynamic force to inertial force for the tendons of two dolphin species. The model predicted optimum compliance for the tendons necessary to minimize muscular work and metabolic

energy during swimming. However, tendon measurements indicate that their elastic compliance is above the optimum and may actually increase the energy cost of swimming (Bennett *et al.*, 1987).

The propulsion forces of swimmers differ from those of runners in several critical aspects: terrestrial animals push off from a substrate and against the force of gravity to produce thrust. With muscles maintained in a tetanic condition, the leg tendons stretch, and store elastic energy as a spring, when the foot restrikes the substrate with the force of the animal's body weight. The elastic rebound helps with the push-off phase of the next step without requiring muscle shortening. Swimmers, on the other hand, create thrust by moving the propulsor through water; the movement creates its own resistance. With no movement, there is no thrust. Because there is no substrate to restrike and stretch tendons, maintaining muscles in a tetanic condition does not result in storage of energy. Consequently, energy storage by tendon elasticity in dolphins would be possible only under a novel mechanism as yet undescribed.

Metabolic power output

Oxygen consumption during swimming at known speeds has not been measured for dolphins. Because such direct measurements of metabolic rate are so difficult to obtain, there have been many estimates and extrapolations. Initial calculations were based on comparisons with other animals and on estimates of hydrodynamic drag. Gray (1936) calculated the power output for a dolphin swimming at 10 m/s at 14 W/kg of muscle if the animal had a low-drag laminar boundary layer and 122 W/kg if it had a high-drag turbulent boundary layer. Because previous studies on other mammals (i.e. dogs and humans) could not produce the higher power estimates, Gray assumed dolphins were similarly limited and therefore had a laminar boundary layer.

Sustained power output of muscles is not simply a function of muscle mass but of the entire body mass, because other body systems are necessary to support muscle power output (Kramer, 1960b). Under optimum conditions of oxygen supply and mechanical efficiency, an output of 40 W/kg may be possible (Parry, 1949a).

Power requirements may have been exaggerated due to overestimates of swimming speed. Recent measurements of sustainable maximum swimming speeds are less than half of previous estimates [4.5 m/s (Au & Perryman, 1982) vs. 10 m/s (Gray, 1936)]. The high swimming speed used by Gray (1936) in his calculations of dolphin energetics was based on a single shipboard observation of short duration (< 7 s). At lower routine speeds, dolphins are able to swim with a high-drag turbulent boundary layer requiring a metabolic rate only 13.4 times their calculated resting metabolic rate, a factorial scope comparable to other aerobic performers (Hui, 1987). Captive Harbor Porpoises *Phocoena phocoena* swimming at self-selected speeds (estimated to be 2 m/s) and restricted to breathe into a respiratory hood had metabolic rates (4.0 and 5.2 W/kg) which were 3.2–3.7 times the calculated basal metabolic rate for a terrestrial mammal of equivalent size (Worthy *et al.*, 1987). This rate corresponds well with a mean daily metabolic rate of three times resting rate for a terrestrial mammal (Karasoff, 1981; Kenagy, Sharbough & Nagy, 1989). Major participation of extraordinary mechanisms for decreasing drag or increasing power apparently are not required so previous deductions about the nature of the boundary layer and the power required to overcome its drag (Gray, 1936; Hill, 1950; Gero, 1952; Kramer, 1960b; Schmidt-Nielson, 1972) appear to be irrelevant.

Short-term burst power can, of course, be greater than sustained power output. With anaerobic contributions, *Tursiops truncatus* could generate an estimated 110 W/kg of

muscle at a tail-beat frequency of 4 Hz (Weis-Fogh & Alexander, 1977). The Weis-Fogh–Alexander model is a physiologically based computation and is consistently lower than hydrodynamics-based computations derived from swimming dolphins. In one experiment, a *Lagenorhynchus obliquidens* accelerating for 1 second with a tail-beat frequency of 2 Hz had an estimated total power output of 1567 W (Lang & Daybell, 1963). If 18% of the total body mass of this 91-kg animal was working muscle (36% of body mass represents the total swimming muscle, approximately as in other dolphins (Goforth, 1986)), it could produce a maximum of only 1802 W with a tail beat frequency of 4 Hz according to the 110-W/kg estimate of Weis-Fogh & Alexander (1977). The hydrodynamic assumptions used for these calculations may have been invalid because of the small experimental tank (97.5 m long, 3.5 m wide and 1.8 m deep) (Lang & Daybell, 1963; Rehman, 1961). In the less-confining conditions of an open lagoon, a trained *Stenella attenuata* apparently generated 4518 W during a 1.5-s acceleration according to calculations by Lang & Pryor (1966). With 18% of the 52.7-kg animal's mass (Lang & Pryor, 1966) as working muscle at any instant, the Weis-Fogh–Alexander rate of 110 W/kg would result in 1043 W of total available power, a notable difference. It will require careful new measurements to reconcile these computational differences.

SWIMMING BEHAVIOUR

It is reasonable to assume that the evolution of a suite of adaptations which minimize energy expenditure for swimming would include behavioural adaptations. Unlike most swimmers (both vertebrate and invertebrate), dolphins breathe air. Therefore, no energy is expended to force water through gill structures, but energy is expended to obtain air by breaching. This requirement ties them unremittingly to the surface where a portion of their total behaviour repertoire can be easily observed. This has facilitated the collection of a greater amount of swimming data than is possible for continuously submerged gill breathers. We review here the swimming behaviours of dolphins that are free ranging, unencumbered by fishing lines, attached sensors, aquarium walls, or pursuit.

Swimming speed

Accurate swimming speed measurements of free-ranging dolphins are rare, and few data are available concerning the duration of swimming effort. Table 1 lists the available information on swimming speed and duration for dolphins. We selected entries that appear to be actual measurements, not estimates, and are clearly not bow-riding behaviour. All the species listed are pelagic, except *Sotalia guianensis* which is estuarine. *Tursiops truncatus* is both an inshore and a pelagic inhabitant. Inshore species are generally slower than pelagic species (Lang & Pryor, 1966). The accuracy and precision of the measurements vary among reports. The data reported by Johannessen & Harder (1960) were based on surveys and were not documented well enough to ensure that the shipboard observations were accurate. Kooyman (1989) has questioned the validity of the high, sustained swimming speeds reported for dolphins in that observers of *Stenella attenuata* over-estimated the actual swimming speed by 25%.

In general, dolphins have remarkably low sustained and routine swimming speeds. The swimming speeds of *Tursiops gilli* reported by Lang & Norris (1966) clearly demonstrate that swimming speed is associated with duration. High-speed, high-drag swimming is not long endured by dolphins.

Table 1
Reported dolphin swimming speeds

Species	Speed (m/s)	Performance	Source
<i>Delphinus bairdi</i>	1.5	maximum sustained	Norris & Prescott (1961)
<i>Delphinus delphis</i> *	1.6	routine	Hui (1987)
<i>Delphinus delphis</i>	9.3	maximum	Kellogg (1940)
<i>Delphinus delphis</i>	10.3	7 s	Gray (1936)
<i>Globicephala</i> sp.	11.3	maximum sustained	Johannessen & Harder (1960)
<i>Lagenorhynchus obliquidens</i> *	7.7	2 s	Lang & Daybell (1963)
<i>Orcinus orca</i>	15.5	20 min	Johannessen & Harder (1960)
<i>Sotalia guianensis</i> *	2.4	routine	Videler & Kamermans (1985)
<i>Stenella</i> sp.	6.7	burst	Au & Perryman (1982)
<i>Stenella</i> sp.	4.6	maximum cruise	Au & Perryman (1982)
<i>Stenella</i> sp.	0.4–1.9	16h	Perrin, Evans & Holts (1979)
<i>Stenella attenuata</i> *	11.1	burst	Lang & Pryor (1966)
<i>Tursiops truncatus</i> *†	8.3	7.5 s	Lang & Norris (1966), Lang (1975)
<i>Tursiops truncatus</i> *†	7.01	10s	Lang & Norris (1966), Lang (1975)
<i>Tursiops truncatus</i> *†	6.09	50s	Lang & Norris (1966), Lang (1975)
<i>Tursiops truncatus</i> *†	3.08	indefinitely	Lang & Norris (1966), Lang (1975)
<i>Tursiops truncatus</i> *	1.77–3.19	routine	Videler & Kamermans (1985)
'Dolphins'	7.2–9.3	maximum	Johannessen & Harder (1960)

*Captive animals.

†*Tursiops truncatus* listed in source as *Tursiops gilli*.

Porpoising

Porpoising behaviour consists of rhythmic, serial leaps in which the animal leaves and re-enters the water nose-first during continuous rapid swimming. According to the models of Au & Weihs (1980a,b) and Blake (1983b), the energy to leap at low speeds is greater than the energy to swim. The energy needed for swimming a given distance increases with swimming speed at a faster rate than does the energy to leap that distance. Therefore, the energies needed to leap and to swim a given distance converge as swimming speed increases and should be equal at some critical swimming speed (U_c). At speeds greater than U_c , it should be energetically cheaper to leap than to swim, and porpoising behaviour will predominate. Using reasonable hydrodynamic assumptions, these models assumed that the animals would maximize leap distance by employing an emergence angle of 45°. Another consideration, however, is that fast-swimming animals should try to maintain their forward speed by using an emergence angle of 30°, the compromise between maximum distance and maximum forward speed of a leap (Gordon, 1980).

Recent data contradict the concept of U_c . Porpoising dolphins swim twice the distance they leap, whereas the assumptions of U_c predict that dolphins would spend more time leaping than swimming at speeds greater than U_c (Au, Scott & Perryman, 1988). Video data of free-ranging dolphins indicate a graded transition from minimal blowhole exposure at the surface at the low swimming speeds, to quasi-leaps in which the dolphin is never completely out of the water at any instant at the medium swimming speeds, and to complete porpoising leaps at the highest swimming speeds (Hui, 1989). These observations are consistent with maintaining a minimum blowhole exposure

time for respiratory inhalation as swimming speed increases. Measured emergence angles were neither 45° nor 30° but had a wide distribution between those limits which may indicate another mechanism to control blowhole exposure time (Hui, 1989). Consequently, porpoising behaviour may be energy conserving only in the sense that it is energetically the cheapest way to breathe, not the energetically cheapest way to swim.

Wave riding

Dolphins have been riding the bow waves of boats probably since shortly after the invention of the sail. The first careful description of the behaviour of bow-wave riding by dolphins (Woodcock, 1948) was used to develop models of the mechanics of the behaviour (Woodcock & McBride, 1951; Hayes, 1953, 1959; Scholander, 1959a,b). These models were all shown to be inadequate, however, due partly to their common requirement that the behaviour could occur only when the dolphin was in a specific location holding a specific pose. In reality, the behaviour is complex: for any given ship the animals do not ride in only a single stereotypic position but may ride at various depths, various distances in front and to the sides of the bow, and with various body orientations in any one of the positions. Dolphins also readily change positions (Fejer & Backus, 1960) and their flukes are not maintained in any specific orientation (Yuen, 1961). These observations were explained by a model based on the pressure wave in front of the bow (Fejer & Backus, 1960). The pattern of the pressure distribution relative to boat length and to dolphin drag coefficient prescribes an optimum distance for bow riding, depending on various hydrodynamic characteristics of the animal and sea state (Fig. 3).

Dolphins ride waves in the same manner as human surfers. The behaviour is stereotypic and can be explained by the interaction of the dolphin's weight and the slope of the wave front (Hayes, 1953; Fejer & Backus, 1960; Perry, Acosta & Kiceniuk, 1961). Steering is possible. Wind-wave riding and surf-wave riding (Caldwell & Fields, 1959) are similar to each other but different from bow wave riding (Fejer & Backus, 1960).

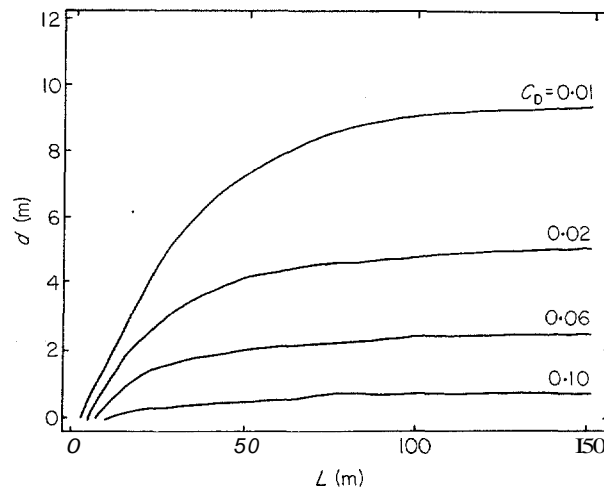


Fig. 3. Distance (d) between bow of vessel and tail of bow-riding dolphin relative to length of vessel (L) and drag coefficient (C_D) of dolphin. The dolphin's posture affects its C_D . The sea state, ship motion, distance from the surface, and bow shape influence the pressure field. Therefore, myriad combinations of postures and locations are possible for bow-riding dolphins. (Redrawn after Fejer & Backus (1960).)

CONCLUDING COMMENTS

Because dolphins are large and require a large body of water to display their total range of swimming behaviours, it is difficult to obtain precise measurements or observations. Many early efforts suffered from these difficulties. The history of research into dolphin swimming shows that a large amount of effort was expended to confirm the assumption that dolphins have special adaptations facilitating their 'high-speed', 'effortless' swimming — apparently they have neither.

The streamlined shape of the dolphin body surely eases its swimming efforts but the skin apparently provides no drag reduction through compliant damping, dermal ridges, secretions, or boundary-layer heating. The turbulent boundary layer may indicate that the smoothness of the skin is not to maintain laminar flow but has some other function. Swimming speeds are not as fast as had been thought.

With the rise of the autecological approach, precise measurements have led to a better understanding of dolphin swimming. However, current understanding is incomplete. Basic questions regarding energetic costs and mechanical efficiency have not been addressed and their answers await the results of further research.

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