

## Dolphin swimming performance: differences between upstroke and downstroke

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### Summary

Steady swimming movements of dolphins were recorded to search for direct evidence of asymmetry between up- and downstrokes. Kinematic swimming and gliding data from frame by frame analysis of cine pictures taken at constant frame rates with a camera in fixed position are presented. We estimated the propulsive forces generated by the tail blade with a simple hydrodynamic model.

Dolphins accelerate during the downstroke and decelerate during the upstroke. Both parts of the stroke cycle are equally long. The propulsive forces of downstrokes are on average larger than the forces of the upstrokes. Occasionally the average forces within an upstroke are greater than within a downstroke of the same sequence. Our data suggest that the drag on the body during the upstroke exceeds the drag in the course of the downstroke. The specific swimming speed or stride length of dolphins swimming at low speeds is about 0.9 bodylengths per tail beat.

### Introduction

Swimming of Cetaceans has received a lot of attention since Gray (1936) implied that a large discrepancy existed between the power available from swimming muscles and the power needed to overcome drag on the body at high speeds. This implication became known as 'Gray's paradox'. Research directed to measurements of (top) speeds, power estimates and studies of drag and flow, refuted the existence of the paradox (i.e. Parry 1949; Johanessen & Harder 1960; Lang 1966; Lang & Norris 1966). It is surprising to find that little attention was paid to the actual swimming movements. Our knowledge of swimming kinematics of Cetaceans is based on one series of 30 photographs showing one cycle of swimming movement of a female bottle-nosed dolphin (*Tursiops truncatus*). This animal is giving birth to a young which protrudes tail-first from the vagina. The camera,

running at an unknown frame-rate, followed the animal aiming at the birth in progress (Parry 1949). Both Parry (1949) and Slijper (1958) used these frames to estimate velocity vectors and angles of attack on the fluke, resulting in diagrams showing estimated force vectors on the tail blade. This use of the film, however, is of dubious value because the movements of the camera make it impossible to measure real displacements let alone velocities. Purves (1963) uses the same frames to reach the conclusion that the power and velocity of the upstroke are 'apparently' greater than those of the downstroke. His conclusion is based on the observation that the downstroke from maximum elevation to the horizontal position takes 10 frames whereas the first part of the upstroke, from maximum depression to the horizontal position, only 5. Purves also estimates angles of attack on the tail blade and describes these as rapidly changing during the upstroke and not clearly defined during the downstroke, and uses this to justify his ideas about the different functions of up- and downstroke.

There is no unanimous opinion in the literature regarding the division of epaxial and hypaxial masses of locomotor muscles. Purves (1963) claims that the epaxial mass is approximately double that of the hypaxial mass, which is in contradiction with Slijper's (1961) findings. Smith, Brown & Gaskin (1976) studied the myology of the harbour porpoise (*Phocoena phocoena*) and found that the hypaxial muscles were smaller than the combined epaxial muscles, but they consider them powerful enough to flex the tail during an active downstroke. Strickler (1980) finds that the anatomy of the axial musculature of *Pontoporia blainvillei* does not support the idea that the upstroke is the main propulsive stroke. He suggests similar roles of tail elevators and depressors in propulsion. In any case, distribution of muscle mass can only provide circumstantial evidence. Purves' view that the upstroke is essentially the power stroke still remains to be proved. The aim of this paper is to search for direct evidence

**Table 1.** Parameters of the experimental animals

Species	Name	Sex	Length m	Mass kg	Body surface area m <sup>2</sup>	Tailblade	
						Span m	Area (one side) m <sup>2</sup>
<i>Tursiops truncatus</i>	Dolly	♀	2.50	232	2.16	0.59	0.10
<i>Sotalia guianensis</i>	Eddie	♂	1.90	85	1.24	0.45	0.06

of asymmetry between up- and downstroke, using measurements of kinematic parameters from cine recordings of a swimming bottle-nosed dolphin and an estuary dolphin (*Sotalia guianensis*).

### Methods

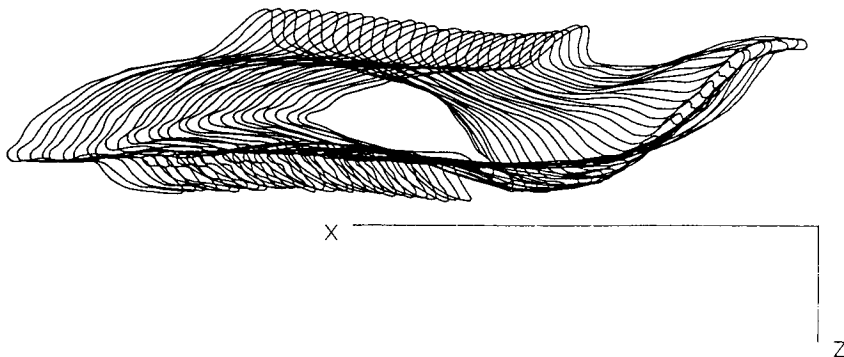
#### Cinematography

We filmed the swimming movements of the bottle-nosed dolphin and the estuary dolphin in the Antwerp Zoo. Information about length and mass of the animals was provided by the staff of the Zoo, the other dimensions given in Table 1 were calculated using the scale model of Purves, Dudok van Heel & Jonk (1976), assuming isometry. The animals usually cruise up and down a 27 m long, 7 m wide and 3 m deep tank. A locam (Red Lake) camera with intermittent film transport was mounted horizontally in a fixed position in front of a window in the middle of one of the long sides of the tank. The camera is fitted with a timing LED which marks one edge of the film every 0.01 s. This device allows accurate determinations of the frame rate. The camera was set at 50 frames/s and we used 400 ASA Eastman Ektachrome 7251 film exposed as 800 or 1600 ASA, because natural light conditions were rather poor.

Only dolphins passing down the centre of the tank were filmed. The camera was started just before the nose of the animal would appear in the viewfinder and stopped after the tailtip left the field of view.

#### Kinematic analysis

Films were projected frame by frame on a Vanguard motion analyzer. Each frame contained an earth bound reference grid. The horizontal axis was defined to be the X-axis (positive in the swimming direction) and the vertical axis the Z-axis (positive downward). We selected film sequences which showed regular periodic swimming movements of uniform velocities and to a good approximation along a horizontal path. The circumference of the image of the dolphin on each frame and the reference grid were digitized (see for details Videler & Hess 1984). Figure 1 shows digitized outlines of the bottle-nosed dolphin as an example. We looked for an easily recognisable point on the outline of the body and close to the pivot point of vertical movements. The point where the outline of the dorsal fin turns into the outline of the caudal part of the body was chosen. Displacements of this point were used to calculate the forward velocity  $U$ , using the 5 points differentiation equation of Lagrange (see



**Figure 1.** Digitized outlines of a bottle-nosed dolphin during a downstroke: Body length 2.5 m, swimming speed  $2.63 \text{ ms}^{-1}$ , time between frames 0.02 s.

Videler 1981). The same method provides tailtip velocities in the X-direction ( $dx/dt$ ) and Z-direction ( $dz/dt$ ) from displacements in time of the tip of the tail. Two digitized points on the tail of each frame of the sequence are then used to calculate the angle  $\theta$  between the tailblade and the X-axis. Only three instead of five positions of the tailtip were used for calculation of the angle between the direction of movement of the tailtip and the X-axis (angle  $\beta$ ). A straight line through the present, previous and next position gives a slightly more accurate estimate of  $\beta$ , especially near the extreme dorsal and ventral tail positions, than calculating it as the arctan of  $(dz/dt)/(dx/dt)$ . The angle of attack on the tailblade is equal to the difference between  $\beta$  and  $\theta$ :

$$\alpha = \beta - \theta \quad (1)$$

Average acceleration and deceleration values were calculated for up- and downstrokes separately from the slopes of linear regressions of the velocity ( $U$ ) against time curves. The bottom graph of Figure 2 gives an example of the results obtained for a sequence of swimming of the bottle-nosed dolphin.

Sequences of dolphins gliding (along an approximately straight horizontal path) were used to estimate average deceleration rates ( $a$ ) and gliding drag coefficients ( $C_d$ ) using the equation of motion during gliding

$$M \cdot a = \frac{1}{2} \rho A_b U^2 C_d \quad (2)$$

where  $M$  is the mass of the animal,  $\rho$  the density of the water and  $A_b$  the surface area of the body. See Videler (1981) for details.

#### Propulsive force calculations

We estimated the propulsive force generated by the tail blade with a simple steady state aerodynamic model, based on airfoil theory and assuming elliptical lift distribution on the tail (Prandtl & Tietjens 1934). The approach followed was that of Weihs (1972), used to study the forces on fish tail fins. For angles of attack up to the stalling angle the lift or side force on the fin, perpendicular to the direction of fin motion, equals

$$L_i = \frac{1}{2} \rho V_i^2 A_w C_{l\alpha} \alpha_i \quad (3)$$

$A_w$  is the area of the fin,  $V_i$  the velocity of the fin's centre of pressure in the direction of fin motion  $\{V_i^2 = (dx/dt)^2 + (dz/dt)^2\}$ ,  $\rho$  the density of the water,  $C_{l\alpha}$  the rate of change of lift coefficient with angle of attack and  $\alpha$  the angle of attack (see Figure 3).

$C_{l\alpha}$  depends on the shape of the fin. We assume the fluke of a dolphin to react as a flat plate and use Hoerner's (1965) equation on p. 7.3 to find:

$$C_{l\alpha} \approx \frac{2\pi^2}{180(1+2/AR)} \quad (4)$$

Where  $AR$  is the Aspect Ratio ( $\text{Span}^2/\text{Surface}$ )

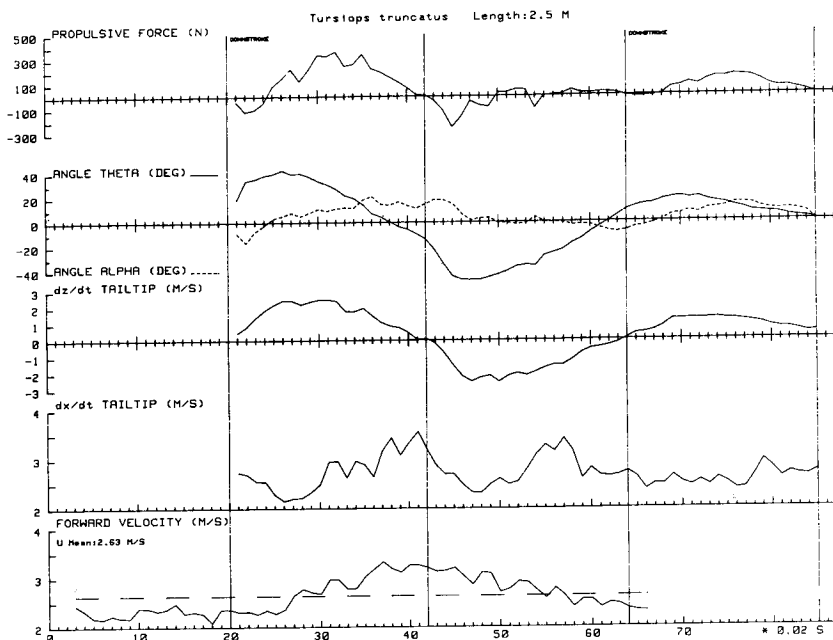


Figure 2. Kinematic data and propulsive force calculations of a bottle-nosed dolphin.

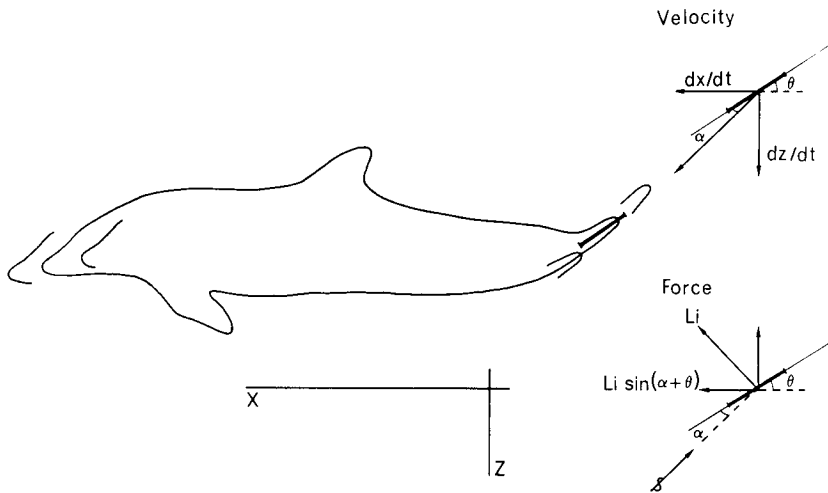


Figure 3. The speed and direction of movement of the tail blade used to estimate instantaneous propulsive forces generated by the fluke of a swimming dolphin.

Area) of the fin. (The angle of attack has to be expressed in degrees.)

The tail AR of our dolphins is about 3.5 which gives a rate of change of lift coefficient of about 0.07 per degree. For angles of attack higher than  $15^\circ$  we assume the lift coefficient to be constant and equal to 1. The component of force along the X-axis equals

$$L_i \sin(\alpha + \theta)$$

and is calculated for every tail position  $i$  of a sequence. See Fig. 2 for example.

Average values over each half cycle of acceleration or deceleration,  $\alpha$ ,  $\theta$ ,  $dz/dt$ ,  $dx/dt$  and  $L_i$  are used to compare upstrokes with downstrokes during steady swimming.

#### Selection of swimming and gliding sequences

Dolphins are highly mobile animals frequently banking, pitching, rolling, wheeling, turning, swimming up and down and changing speed. But sometimes the movements are less erratic and we selected steady swimming with periodic tail movements along a straight horizontal track at uniform velocities and uninterrupted gliding bouts at one depth.

We analysed 6 swimming sequences (5 of *Tursiops* and 1 of *Sotalia*) and 6 straight horizontal gliding bouts (4 of *Tursiops* and 2 of *Sotalia*).

### Results

#### Comparison of upstroke and downstroke

We start the presentation of the results by looking at Figure 2 where swimming sequence number 4 of *Tursiops* serves as an example of the rate of change of kinematic parameters and forces. The bottom

graph shows how the forward velocity  $U$  increases during the downstroke and decreases during the upstroke. The average acceleration is  $2.7 \text{ ms}^{-2}$  and the subsequent deceleration is near  $1.9 \text{ ms}^{-2}$ . The same division of velocity decrease and increase is found for all the up- and downstrokes measured (see Table 2). It is probably the most striking result of our analyses and leads to alternative explanations:

1. The downstroke generates more thrust than the upstroke.
2. Thrust generation is constant during the whole swimming cycle, but the drag on the animal is larger during the upstroke than during the downstroke.
3. A combination of differences in thrust and drag between half cycles.

Precise knowledge of the action of the tailblade is the basis of our thrust calculations. The forward velocity  $dx/dt$  of the tailtip usually decreases immediately after the beginning of each half cycle of a swimming stroke and increases strongly in the second half. The average velocities  $dx/dt$  and  $dz/dt$  differ slightly between up- and downstrokes but these differences are not consistent for *Tursiops* and *Sotalia*. The angle  $\theta$  reaches large values soon after the start of upstroke or downstroke and decreases gradually during the rest of the half cycle. *Tursiops'* average  $\theta$  is slightly larger during the upstroke and the angle of attack is smaller. *Sotalia* uses a different swimming style: The sign of  $\theta$  switches to negative in the second half of the downstroke and reaches high negative values near the end of it. There is no such change of sign during the upstroke. The average downstroke angle of attack is twice as large as the upstroke one.

The force calculations for *Sotalia* predict negative

Table 2. Average values of kinematic parameters and force calculations of swimming dolphins

Sequence Nr	Total sequence		Upstroke				Downstroke											
	Velocity $\text{ms}^{-1}$	$\text{LT}^{-1}$	Freq. Hz	$\frac{1}{2}T$ s	acc. $\text{ms}^{-2}$	$\alpha$ $^{\circ}$	$\theta$ $^{\circ}$	$\frac{dz}{dt}$ $\text{ms}^{-1}$	$\frac{dx}{dt}$ $\text{ms}^{-1}$	Force N	$\frac{1}{2}T$ s	acc. $\text{ms}^{-2}$	$\alpha$ $^{\circ}$	$\theta$ $^{\circ}$	$\frac{dz}{dt}$ $\text{ms}^{-1}$	$\frac{dx}{dt}$ $\text{ms}^{-1}$	Force N	
<i>Tursiops</i>																		
1	1.77	0.71	0.7	1	0.46	-0.8	4	30	-1.39	1.87	0.54	1.4	6	28	1.31	1.80	86	
2	1.83	0.73	0.9	0.83	0.60	-0.4	—	—	—	—	0.50	—	6	24	1.12	1.76	107	
3	2.34	0.94	1.1	1.2	0.58	-0.8	0	28	-1.11	1.94	0.56	1.0	3	27	1.08	1.86	32	
4	2.63	1.05	0.9	1.1	0.38	-1.5	7	25	-1.55	2.39	0.68	—	3	23	0.89	1.80	39	
5	3.17	1.27	0.9	1.3	0.44	—	1	25	-1.08	2.37	0.38	1.4	—	—	—	—	—	
					0.44	—	1	25	-1.08	2.37	0.44	1.4	1	27	1.30	2.30	56	
					0.44	-1.9	2	26	-1.33	2.78	0.44	2.7	8	20	1.52	2.78	141	
					0.36	-2.5	3	30	-1.75	3.38	0.36	2.4	—	6	0.85	2.59	70	
					0.47	-1.3	2.8	27	-1.37	2.45	0.40	—	-1	25	1.43	3.10	35	
<b>AVERAGES</b>	2.35	0.94	0.9	1.1	0.47	-1.3	2.8	27	-1.37	2.45	0.47	1.7	4	23	1.19	2.25	71	
<i>Sotalia</i>																		
1	2.40	1.30	0.9	1.4	0.38	-1.2	6	32	-1.10	2.19	0.38	1.1	13	6	0.92	2.50	48	
					0.30	-1.1	6	29	-1.02	2.40	0.40	1.3	10	7	0.73	2.38	28	

or braking forces on average over the upstroke period when the animal decelerates and large positive forces during the downstroke, coinciding with acceleration. The average *Tursiops* data show a similar straightforward relation: a small force and deceleration for the upstroke and a larger force with acceleration for the downstroke. But this trend is not consistent. In Sequence 1 and 3 the dolphin decelerates during the upstroke despite a larger average thrust force than during the downstroke where an acceleration was measured. These results indicate that drag is not the same during the two parts of the swimming cycle. Thrust obviously can be generated during the upstroke as well as during the downstroke. Our animals were swimming slowly and used the downstroke to generate enough propulsive force for acceleration. The total drag seems to be higher when the tail moves upward and our data suggest that this drag varies considerably. Compare for example force and deceleration of the first upstroke of Sequence 3 with those of the second upstroke of Sequence 2. There is no obvious difference in duration between upstroke and downstroke.

#### Swimming speed and tail beat frequency

The measured velocities probably represent slow cruising speeds for the animals involved. The average tail beat frequency of *Tursiops* is 1.1 Hz and 1.4 Hz for the *Sotalia* case. A dimensionless expression for speed in terms of body lengths per tail beat period ( $L/T$ ) makes interspecific comparison of swimming performance possible. Both *Tursiops* and *Sotalia* advance about 0.9 body lengths per tail beat. This value is high compared with the performance of fish. Figures for Saithe and Mackerel are near 0.8 (Videler & Hess 1984). Fish such as Cod, Trout, Dace and Goldfish score slightly over 0.6  $L/T$ , and the Eel reaches only 0.55  $L/T$ . Values for Sharks vary between 0.51 for the Nurse shark and 0.74 for the Bull shark (Webb & Keyes 1982). Experienced human swimmers fitted with mask and fins show a constant stride length of 0.5  $L/T$  while swimming at various speeds under water (Videler 1984). In this

respect are dolphins the most efficient swimmers measured so far.

#### Gliding and swimming drag

The gliding drag coefficients (Table 3) of *Sotalia* are in the same order of magnitude as the values given for dolphins in the literature and summarized by Webb (1975). Bilo & Nachtigall's (1980) value for the drag coefficient based on wetted surface area of a gliding penguin of 0.0044 is also in good accordance with the *Sotalia* values. Our *Tursiops* drag coefficients, however, are 2–4 times as high and in the order of magnitude of values found for gliding Cod (Videler 1981). The deceleration rates during the upstrokes are on average 7 times higher than during gliding. If we use the equation of motion for steady swimming (Videler 1981 eq.nr. 1.11) to calculate the swimming drag coefficient, we find on average 0.007 for *Tursiops* and 0.003 for *Sotalia*. These values are about as high as the lowest gliding drag coefficient figures. (The drag in a steady swimming fish is about 3 times greater than the drag on a fish gliding at the same speed (Videler 1981; Videler & Weish 1982).) During the upstroke the drag is obviously much larger than during the downstroke. This suggests that the drag on a dolphin's body during the downstroke must be extremely low.

#### Discussion

The lack of kinematic data on dolphin locomotion in the literature is most unexpected, especially because technically advanced facilities for this type of study have been developed in both the USA and the USSR, where the larger part of dolphin research is carried out. Silberberg (1966) has developed high speed filming facilities combined with flow visualization techniques, but so far no one seems to have used them for kinematic analysis. Romanenko (1980) has analysed 'deformation of the body' during swimming of a 2.24 m long alafin dolphin with the use of motion pictures and three accelerometers attached to the head, dorsal fin and tail blade. However, he only presents the final result of

Table 3. Average values of gliding parameters

Species	Sequence nr.	Velocity $\text{ms}^{-1}$	Deceleration $\text{ms}^{-2}$	$C_d$
<i>Tursiops</i>	1	1.85	-0.125	0.008
	2	2.00	-0.342	0.018
	3	1.70	-0.151	0.011
	4	2.00	-0.180	0.009
<i>Sotalia</i>	1	2.40	-0.196	0.005
	2	2.50	-0.156	0.003

calculations based on one swimming sequence at  $4.3 \text{ ms}^{-1}$ , without details of the analysis. The frequency of body oscillation in his Table 1 is the only figure we could have used for comparison with our data. But the cyclic frequency of body oscillation of 14 Hz is so unbelievably high that it must be a mistake. Our results are converse to the existing ideas about the asymmetry of kinematics and thrust generation between up- and downstroke: there is a velocity increase and larger thrust values during the downstroke and deceleration, and usually lower thrust values of the upstroke. It is important to keep in mind that we only investigated slow swimming movements. At high speeds we expect that the upstroke will increase its share of the thrust and will be at least high enough to balance the drag.

With regard to the expected drag differences between up- and downstrokes, it is interesting to note that the dermal ridges are orientated in dorso-caudal direction on the caudal peduncle (Purves 1963). This direction is parallel to the resultant flow over the peduncle during the downstroke (see Figure 1) but across the flow during the upstroke, which could contribute to the drag differences between the up- and downstroke.

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