University of Groningen

Differences between upstroke and downstroke in swimming dolphins

Videler, J; Kamermans, P

Published in:
Journal of Experimental Biology

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1985

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):
Videler, J., & Kamermans, P. (1985). Differences between upstroke and downstroke in swimming dolphins. *Journal of Experimental Biology*, 119, 265-274.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

DIFFERENCES BETWEEN UPSTROKE AND DOWNSTROKE IN SWIMMING DOLPHINS

By JOHN VIDELER AND PAULINE KAMERMANS

*Department of Zoology, Groningen University, P.O. Box 14,
9750 AA Haren, The Netherlands*

Accepted 6 June 1985

SUMMARY

Steady swimming movements of dolphins were recorded in a search for direct evidence of asymmetry between upstrokes and downstrokes. Kinematic swimming and gliding data from frame-by-frame analysis of ciné pictures taken at constant frame rates with a camera in a 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: the net hydrodynamic force in the animal is always positive during the downstroke and negative 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 body lengths 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 that paradox (i.e. Parry, 1948; 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 protudes 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 ten frames whereas the first part of the upstroke, from maximum depression to the horizontal position, takes only five. 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 contradicts Slijper's (1961) findings. Smith, Browne & 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) found 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 of asymmetry between up- and downstroke, using measurements of kinematic parameters from ciné recordings of a swimming bottle-nosed dolphin, *Tursiops truncatus*, and an estuary dolphin, *Sotalia guianensis*.

METHODS

Cinematography

We filmed the swimming movements of the bottle-nosed dolphin and the estuary dolphin in 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 (1975), assuming isometry. The animals usually cruise up and down a 27-m long, 7-m wide and 3-m deep tank.

Table 1. *Parameters of the experimental animals*

Species	Name	Sex	Body			Tail blade		
			Length (m)	Mass (kg)	Surface area (m ²)	Span (m)	Mean chord length (m)	Area (one side) (m ²)
<i>Tursiops truncatus</i>	Dolly	♀	2.50	232	2.16	0.59	0.17	0.10
<i>Sotalia guianensis</i>	Eddie	♂	1.90	85	1.24	0.45	0.13	0.06

Fig. 1. Digitized outlines of a bottle-nosed dolphin during a downstroke: body length, 2.5 m; swimming speed, 2.63 m s^{-1} ; time between frames, 0.02 s.

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^{-1} 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 appeared in the view finder and stopped after the tip of the tail had left the field of view.

Kinematic analysis

Films were projected frame-by-frame on a Vanguard motion analyser. 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). Fig. 1 shows digitized outlines of the bottle-nosed dolphin as an example. We looked for an easily recognizable 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 five points differentiation equation of Lagrange (see Videler, 1981). The same method provides tail-tip 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 θ between the tail blade and the x-axis. Only three instead of five positions of the tail tip were used for calculation of the angle between the direction of movement of the tail tip and the x-axis (angle β). A straight line through the present, previous and next position gives a slightly more accurate estimate of β , 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 tail blade is equal to the difference between β and θ :

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

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

Each of the selected film sequences was digitized and processed five times. This procedure provides estimates of the accuracy of the kinematic data. For the velocities U , dx/dt and dz/dt the accuracy is better than $\pm 5\%$. The standard deviation of the rates of acceleration is less than 2% and of deceleration less than 5% of the average values. The angles are accurate to within $\pm 3^\circ$. Statistical analysis indicates that the correlation coefficients of the linear regressions are highly significant ($P < 0.001$) and that the slopes deviate significantly from zero ($P < 0.001$). 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:

$$Ma = \frac{1}{2}\rho A_b U^2 C_d, \quad (2)$$

where M is the mass of the animal (the added mass of water is not taken into consideration), ρ is the density of the water and A_b is the surface area of the body. See Videler (1981) for details.

Propulsive force calculations

We roughly 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 aim of the force calculations is to compare the combined kinematic parameters during upstroke and downstroke and not to establish precise propulsive force values for dolphins. The hydrodynamic forces in our quasi-steady-state model depend only on the instantaneous motion of the tail blade relative to the water. A quasi-steady approach is not unreasonable if the reduced frequency parameter, σ , of the oscillating tail blade ranges between 0 and 0.5.

$$\sigma = \frac{2\pi fc}{U}, \quad (3)$$

where f is the frequency, c is the mean chord length of the tail blade and U is the forward velocity of the animal (Lighthill, 1975). The values of the reduced frequencies in Table 2 cluster awkwardly close around the border value of 0.5, indicating that the calculated propulsive forces should be treated with suspicion. The approach followed was that of Weihs (1972), which has been 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

$$L_i = \frac{1}{2}\rho V_i^2 A_w C_{l_\alpha} \alpha_i. \quad (4)$$

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

Fig. 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.

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

Cl_{α_i} 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:

$$Cl_{\alpha} \approx \frac{2\pi^2}{180(1 + 2/AR)}, \quad (5)$$

where AR is the aspect ratio (span²/surface 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. The component of force along the x-axis equals

$$L_i \sin(\alpha + \theta), \quad (6)$$

and is calculated for every tail position, i , of a sequence (see Fig. 2 for example).

The inaccuracies of the kinematic data are of course reflected in the propulsive force values but will not violate a comparison between the order of magnitude of the forces during the up- and downstroke. Over each half-cycle of acceleration or deceleration, we will use average values of α , θ , dz/dt , dx/dt and L_i to compare upstrokes with downstrokes during slow 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 needed steady swimming with periodic tail movements along a straight horizontal track at uniform velocities and uninterrupted gliding bouts at one depth.

The animals usually cruise up and down the tank sluggishly when left alone without human disturbance and we filmed this behaviour. The slow movements appear to be rhythmic and the speed uniform. Animals swimming close to the surface or the bottom were not put on record. Unfortunately dolphins use a limited range of speeds under these circumstances.

We analysed six swimming sequences (five of *Tursiops* and one of *Sotalia*) and six straight horizontal gliding bouts (four of *Tursiops* and two of *Sotalia*).

RESULTS

Comparison of upstroke and downstroke

We start the presentation of the results by looking at Fig. 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 m s^{-2} and the subsequent deceleration is near 1.9 m s^{-2} . The same

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

Total sequence					Upstroke					Downstroke				
Sequence	Velocity	Freq.	Red. freq.	$\frac{1}{T}$	Acc.	θ	$\frac{dx}{dt}$	Force	$\frac{1}{T}$	Acc.	α	θ	$\frac{dz}{dt}$	Force
(No.)	(m s^{-1})	(L t^{-1})	(Hz)	(s)	(m s^{-2})	($^{\circ}$)	(m s^{-1})	(N)	(s)	(m s^{-2})	($^{\circ}$)	($^{\circ}$)	(m s^{-1})	(N)
<i>Turnings</i>														
1	1.77	0.71	0.7	1	0.60				0.54	1.4	6	28	1.31	1.80
					0.46	-0.8	4	30	0.50	—	6	24	1.12	1.76
2	1.83	0.73	0.9	0.83	0.48	-0.3	—	—	0.56	0.9	3	27	1.08	1.86
					0.58	-0.8	0	28	0.68	—	3	23	0.89	1.80
3	2.34	0.94	1.1	1.2	0.55				0.38	1.5	—	—	—	—
					0.38	-1.5	7	25	0.44	1.4	1	27	1.30	2.30
4	2.63	1.05	0.9	1.1	0.44	—	1	25	0.44	2.7	8	20	1.52	2.78
					0.44	-1.9	2	26	0.36	2.4	6	12	0.85	2.59
5	3.17	1.27	0.9	1.3	0.44				0.40	—	—	—	—	—
					0.36	-2.5	3	30	0.40	—	-1	25	1.43	3.10
Averages	2.35	0.94	0.9	1.1	0.50	-1.3	2.8	27	0.47	1.7	4	23	1.19	2.25
<i>Sotalia</i>														
1	2.40	1.30	0.9	1.4	0.48	-1.2	6	32	0.38	1.1	13	6	0.92	2.50
					0.30	-1.1	6	29	0.40	1.3	10	7	0.73	2.38

Acc., acceleration; Freq., frequency; Red. freq., reduced frequency.

division of velocity decrease and increase is found for all the up- and downstrokes measured (see Table 2). The net hydrodynamic force on the animal is always positive during the downstroke and negative during the upstroke. 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 tail blade is the basis of our thrust calculations. The forward velocity, dx/dt , of the tail tip 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 θ reaches large values soon after the start of upstroke or downstroke and decreases gradually during the rest of the half-cycle. *Tursiops*' average θ is slightly larger during the upstroke and the angle of attack is smaller. *Sotalia* uses a different swimming style: the sign of θ 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 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 relationship: a small force and deceleration for the upstroke and a larger force with acceleration for the downstroke. But this trend is not consistent. In sequences 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. Multiplication of the average acceleration values during the downstrokes by body mass gives estimates of the order of magnitude of the forces needed to accelerate the inert body. These inertial forces turn out to be up to five times the propulsive forces calculated with our quasi-steady model. Obviously the steady-state assumption and the comparison of the fluke with a flat plate causes this substantial underestimate.

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

Table 3. Average values of gliding parameters

Species	Sequence no.	Velocity (m s^{-1})	Deceleration (m s^{-2})	Cd
<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

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, 1985). In this respect dolphins are the most efficient swimmers measured so far.

Gliding drag

The gliding drag coefficients (Table 3) of *Sotalia* are of the same order of magnitude as the values given for dolphins in the literature and summarised by Webb (1975). Bilo & Nachtigall's (1980) value for the drag coefficient, based on the 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 of the order of magnitude of values found for gliding cod (Videler, 1981). The deceleration rates during the upstrokes are on average seven times higher than during gliding.

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 U.S.A. and the U.S.S.R., 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 analyses. Romanenko (1980) has analysed 'deformation of the body' during swimming of a 2.23 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 calculations based on one swimming sequence at 4.3 m s^{-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 contradict 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, during 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.

We would like to thank the staff of the Dolphinarium of Antwerp Zoo for access to facilities and cooperation. A. de Jong, A. Bult, W. H. Dudok van Heel, J. Nieweg, D. Weihs and F. Hess contributed in different ways and are gratefully acknowledged. Valuable comments of G. Thomas improved the text.

REFERENCES

- BILO, D. & NACHTIGALL, W. (1980). A simple method to determine drag coefficients in aquatic animals. *J. exp. Biol.* **87**, 357–359.
- GRAY, J. (1936). Studies in animal locomotion. VI. The propulsive powers of the dolphin. *J. exp. Biol.* **13**, 192–199.
- HOERNER, S. F. (1965). *Fluid Dynamic Drag*, 2nd edition. Brick Town, NJ, U.S.A.: Published by the author.
- JOHANESSEN, C. L. & HARDER, J. A. (1960). Sustained swimming speeds of dolphins. *Science, N.Y.* **132**, 1550–1551.
- LANG, T. G. (1966). Hydrodynamic analysis of Cetacean performance. In *Whales, Dolphins And Porpoises*, (ed. K. S. Norris), pp. 410–432. Berkely, U.S.A.: University of California Press.
- LANG, T. G. & NORRIS, K. S. (1966). Swimming speed of a pacific bottlenose porpoise. *Science, N.Y.* **151**, 588–590.
- LIGHTHILL, J. (1975). Aerodynamic aspects of animal flight. In *Swimming and Flying in Nature*, Vol. 2, (eds T. Y.-T. Wu, C. J. Brokaw & C. Brennen), pp. 423–491. New York: Plenum Press.
- PARRY, P. E. (1949). The swimming of whales and a discussion of Gray's paradox. *J. exp. Biol.* **26**, 24–34.
- PRANDTL, L. & TIETJENS, O. G. (1934). *Applied Hydro- and Aeromechanics*. New York: Dover.
- PURVES, P. E. (1963). Locomotion in whales. *Nature, Lond.* **197**, 334–337.
- PURVES, P. E., DUDOK VAN HEEL, W. H., & JONK, A. (1975). Locomotion in dolphins. I. Hydrodynamic experiments on a model of the bottle nosed dolphin, *Tursiops truncatus*. *J. aquat. Mammal.* **3**, 5–31.
- ROMANENKO, E. V. (1980). Experimental study of dolphin kinematics. Translated from *Doklady Akademii Nauk SSSR*, **253**, 741–743.
- SILBERBERG, G. G. (1966). Sea animal-locomotion and fish-propulsion studies. In *Whales, Dolphins and Porpoises*, (ed. K. S. Norris), pp. 477–481. Berkely, U.S.A.: University of California Press.
- SLIJPER, E. J. (1958). *Walvissen*. Amsterdam: De Boer Jr. N. V.
- SLIJPER, E. J. (1961). Locomotion and locomotory organs in whales and dolphins (Cetacea). *Symp. Zool. Soc., Lond.* **5**, 77–94.
- SMITH, G. J. D., BROWNE, K. W. & GASKIN, D. E. (1976). Functional myology of the harbour porpoise, *Phocoena phocoena* (L.). *Can. J. Zool.* **54**, 716–729.
- STRICKLER, T. L. (1980). The axial musculature of *Pontoporia blainvillei*, with comments on the organisation of this system and its effect on fluke-stroke dynamics in Cetacea. *Am. J. Anat.* **157**, 49–59.
- VIDELER, J. J. (1981). Swimming movements, body structure and propulsion in Cod (*Gadus morhua*). In *Vertebrate Locomotion*, (ed. M. H. Day). *Symp. Zool. Soc., Lond.* **48**, 1–27.
- VIDELER, J. J. (1985). Fish swimming movements: a study of one element of behaviour. *Neth. J. Zool.* **35**, 170–185.
- VIDELER, J. J. & HESS, F. (1984). Fast continuous swimming of two pelagic predators, saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*): a kinematic analysis. *J. exp. Biol.* **109**, 209–228.
- WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.
- WEBB, P. W. & KEYES, R. S. (1982). Swimming kinematics of sharks. *Fishery Bull., Fish. Wildl. Serv. U.S.* **80**, 803–812.
- WEIHS, D. (1972). A hydrodynamical analysis of fish turning manoeuvres. *Proc. R. Soc. B.* **182**, 59–72.