

## THE SWIMMING OF WHALES AND A DISCUSSION OF GRAY'S PARADOX

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(Received 24 September 1948)

(With Plates 2 and 3 and Three Text-figures)

### INTRODUCTION

The swimming of whales, whose well-authenticated maximum speed is 15 knots or more, is of interest not only to the biologist but also to those who would emulate this performance by artificial means. Fundamental to such a study is a knowledge of the swimming movement, which is not easily observed and has long been disputed. In this paper we give an account of this movement based on two separate lines of evidence: a morphological study (published in detail elsewhere) of the swimming muscles and associated structures of two species of whale; and an examination of a film of living porpoises for which we are greatly indebted to the Marine Studios, Florida, and extracts from which we publish here by their kind permission. Based on this account of the swimming movement it is possible to give a theoretical treatment of the dynamics of swimming, which may guide future experiment. Such a treatment involves a consideration of the drag of moving whales and this in turn leads to a discussion of Gray's Paradox: the big discrepancy which Gray (1936) showed to exist between the power apparently needed to overcome this drag at high speed, and the maximum power to be expected from the swimming muscles.

### THE SWIMMING MOVEMENT

#### *Photographic evidence*

Pls. 2 and 3 show serial photographs of *Tursiops truncatus* from the film referred to above. It is a little unfortunate that the film was taken to show the birth of a young animal (seen projecting from the vagina) and so the photographs leave some doubt as to whether the movement is normal. The film itself, however, showed several other animals swimming about in the background, and although none of these provided a sequence suitable for reproduction, there was no doubt that they were swimming in the same way as the female on which the camera was concentrating.

The photographs show the tail and flukes moving as follows:

The *tail* moves up and down in a vertical plane about a centre of rotation just posterior to the dorsal fin, through an angle of approximately  $70^\circ$ .

The *flukes* move up and down in a vertical plane about a centre of rotation at the level of their insertion into the tail. Their movement is related to that of the tail as follows; when the tail is at the top of its stroke (and therefore momentarily at rest) the flukes are horizontal and so present the smallest possible resistance to motion

in that plane. As the tail moves downward the flukes bend upward until at the middle of the stroke they are bent at their maximum angle to the horizontal. As the tail reaches the end of the downstroke the angle of the flukes is reduced, and they finally become horizontal again when the tail is momentarily at rest at the bottom of its stroke. During the second half cycle the movement is reversed: the tail moves upward, and the flukes move down, making an angle to the horizontal which increases to a maximum at the middle of the stroke and then decreases to zero. These details can all be followed by reference to Pls. 2 and 3.

The photographs show no sign of any lateral movement of the tail, and the absence of any such movement was fully confirmed by the original film, which contained shots of animals swimming directly away from the camera.

#### *Anatomical evidence*

In a study of the swimming muscles and axial skeleton of *Phocaena phocaena* and *Balaenoptera physalus* (Parry, 1949a), we show that these structures are developed to produce movements of the tail and flukes in the vertical plane, and that both the supra-spinal and infra-spinal muscle complexes are differentiated so that independent flexion of tail and flukes is possible. Thus the swimming movement seen in the Florida photographs is provided with an anatomical basis. And as it would be easier to fit the morphology to the film than the film to the morphology, it is relevant to state that the morphological study was completed, and the nature of the swimming movement was deduced, before the film became available to confirm our conclusions.

#### *Discussion*

In the next section we shall consider the hydrodynamic implications of the swimming movement just described; here we shall discuss the various accounts which have been given of the movement itself. Petersen's (1925) brief account, based on *a priori* considerations, agrees with the one given here. Other writers have limited themselves to the tail alone, without considering the movement of the flukes relating to the tail which we shall show to be of great importance. They mostly fall into two parties: those who believe that the tail moves simply up and down; and those who attribute to it a sculling motion. We suspect that this sculling theory arose from a remark of Scoresby's (1820) who, after saying of the Greenland Whale that 'the greatest velocity is produced by powerful strokes against the water, impressed alternately upward and downward'; adds that 'a slower motion, it is believed, is elegantly produced, by cutting the water laterally and obliquely downward, in a similar manner as a boat is forced along, with a single oar, by the operation of sculling' (p. 466). This is repeated by Beale (1839) and is to be found in a number of text-books and monographs, but the sculling theory derives little support from subsequent original observations in which either the vertical motion is asserted (Lillie, 1915; Slijper, 1936, referring to the film 'Abenteuer auf dem Meersboden'), or the lateral motion is not observed (Galloway, 1925; Petersen 1925; True, 1909; and photographs by McBride, 1940; and *The Illustrated London News*, 1910, p. 1001). Only Murie (1865) and Townsend (1914) give some support

to sculling, the latter in very qualified terms after saying that the ordinary swimming motion is up and down. Reference should finally be made to the recent note by Woodcock (1948) where a vertical motion is implied and conditions in the clear waters of the Gulf of Panama were sufficiently good for the frequency of tail oscillation to be timed.

In a different category to the observations just referred to are the elaborate experiments of Shoulejkin and Stas, who believe that the swimming movement of dolphins consists of a circularly polarized wave passing down the body. Shoulejkin (1935) writes in Russian with an English summary in which the evidence for this theory is not given. In his text is a photograph from *The Illustrated London News* (1910, p. 382) of a school of dolphins taken from the fore-castle of a ship, their bodies distorted into corkscrew shapes by the surface ripples; and another of a large metal container on land, through a hole in the side of which there protrudes the hind-end of a dolphin. If the evidence for the circularly polarized wave goes no further than what is implied by these photographs, it is not very convincing. Stas (1939*a, b*), on the other hand, claims to provide experimental evidence for Shoulejkin's theory by means of a recorder strapped to the back of a dolphin which was then allowed to swim to the end of a 100 m. line. The recorder consisted of a drum lying mid-dorsally just posterior to the dorsal fin with its long axis fore-and-aft bearing a pulley wheel over which passed a string. This, guided by another pulley wheel on either side, ran posteriorly along the lateral lines, and was fastened to the lateral points of a bracelet encircling the peduncle. Lateral movements of the tail thus rotated the drum, on which a record was scratched by a needle mounted on a carriage which was itself moved slowly backwards parallel to the axis of the drum by a small propeller. The record was calibrated in one dimension by displacing the tail known amounts to one side by hand; and in the other dimension by towing it through the sea at the same speed as the Dolphin had swum (70 cm./sec.). A single record is reproduced, showing an oscillation 6 cm. in amplitude and a frequency of 1.7 per sec., which Stas interprets as the horizontal component of Shoulejkin's circularly polarized wave; superimposed on which are much slower oscillations which he takes to be steering movements.

In a second experiment (1939*b*) the needle was not moved steadily across the drum on a carriage, but was controlled by a string which ran along the mid-dorsal line to the mid-dorsal point of the bracelet. The needle thus moved to and fro for vertical movements of the tail; and the drum turned from side to side for lateral movements of the tail. The record so obtained, which is not published, is said to have been an ellipse with half-axes in the ratio 1:1.5, the shorter corresponding to the lateral component of motion.

From the photograph in Stas's first paper showing the dolphin fitted with the recorder it appears that the swimming movement was not seriously impeded and the recorder was thus potentially capable of providing valuable information. It is therefore particularly unfortunate that the experiments were not described in more detail. In the first experiment we would like to know the position of the rubber band which, the author says, was used to tension the lateral string. For supposing,

as we maintain, the swimming movement was in a vertical plane then, because the recorder was forward of the centre of rotation, each time the tail bent up or down the lateral string would become slack. And if the rubber band was at all asymmetrical in relation to this string then the slack would be taken up more on one side than the other, and so would rotate the drum and produce a record identical with that actually obtained in Stas's first experiment and interpreted by him as indicating *lateral* movement. This uncertainty would have been abolished if calibration records had been published showing the effect of displacing the tail (*a*) horizontally, and (*b*) vertically, whereas in fact we are not told that the latter calibration was done at all. The account of the second experiment is even more brief than the first, and there is no indication of how the dorsal string was tensioned. Neither are we told how clearly the record showed the predominant locus of the recording needle despite the numerous irregular marks which must have been made during turning and while the animal was being released and recaptured.

In view of these objections to Stas's experiments, we cannot accept Shoulejkin's theory in the face of the evidence of the Florida film, our studies of the anatomy, and the original observations of swimming whales discussed at the beginning of this subsection.

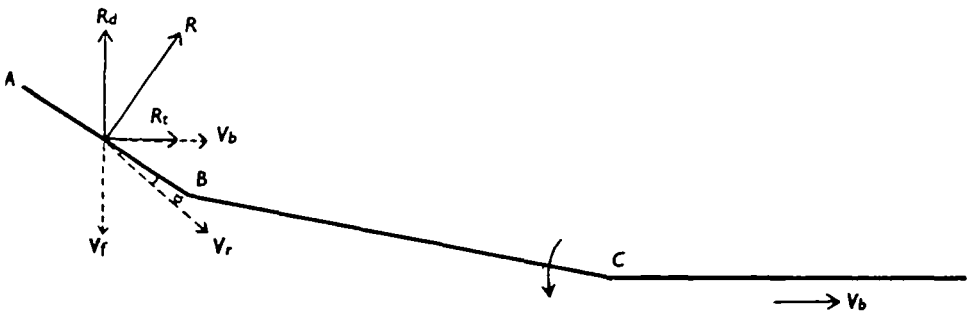


Fig. 1.

### THE DYNAMICS OF SWIMMING

It is easy to show qualitatively that the swimming movement already described will produce a forward thrust. *AB* (Fig. 1) represents the fluke and *BC* the tail, which is being considered during the downward stroke. The whole system is moving forward with a velocity  $V_b$ . Thus at any moment the true velocity of the fluke through the water is represented by  $V_r$ , which is the resultant of the forward velocity  $V_b$  and the downward velocity of the fluke  $V_f$ . This resultant velocity will produce a resultant  $R$  of the water on the fluke, which can be resolved into a forward thrust  $R_t$ , which propels the system; and a drag  $R_d$ , which opposes the movement of the tail and against which the swimming muscles do work. It will also be seen that if the thrust is to remain positive throughout the downstroke, the water must be incident on the *underside* of the fluke—i.e.  $V_r$  must lie clockwise from *AB*. This means that the angle of the fluke must be adjusted in relation to its speed: as  $V_f$  decreases, *AB*

must become more horizontal, until at the bottom of the stroke, when  $V_f$  is momentarily zero,  $AB$  will be exactly horizontal. Similarly, in the middle of the stroke, when  $V_f$  may be presumed to be maximum,  $AB$  will be inclined at its maximum angle.

A similar argument applies during the upstroke, when the water must be incident on the *upper* surface of the fluke.

Reference to the momentary condition illustrated in Fig. 1 will show that the flukes constitute an aerofoil moving through a fluid with a speed and direction represented by  $V_r$ , and with an angle of attack  $\alpha$ . Now the forces acting on such a system are well understood when  $\alpha$  is unchanging—this is the condition of an aeroplane wing in normal flight, and the forces are a known function of the angle, the shape of the wing, and its speed and area. A quantitative treatment of this method of propulsion is therefore possible if we can assume that the relationship between the angle of attack and the forces acting on the fluke is the same when the angle is changing as when it is constant. The little information that is available concerning aerofoils with oscillating angles of attack suggests that the above assumption is justified under certain conditions (see Farren, 1935; and Kuessner, quoted by v. Holst & Kuchemann, 1942). In the Appendix such a quantitative treatment is attempted, where we follow v. Holst & Kuchemann (1942) in integrating expressions for the instantaneous forward thrust and drag and so obtaining their mean values. Fig. 2 shows the mean thrust calculated in this way for a 180 cm. animal and plotted against speed for various arbitrary values for the frequency of the tail beat ( $n$ ). But at any given speed the forward thrust must equal the 'parasite drag' of the body, and this provides an independent relationship between forward speed and thrust which therefore determines  $n$  for any speed and so provides an opportunity of checking the whole theory against empirical data. Now the parasite drag depends upon the amount of turbulence in the flow round the whale's body, which is at present unknown but is thought (see next section) to be small. Curves for fully turbulent and completely non-turbulent flow are drawn in Fig. 2, and their intersection with the family of curves relating speed, thrust, and oscillation frequency gives the following information:

*For a 180 cm. animal*

Frequency of tail beat	...	$\frac{1}{4}$	$\frac{1}{2}$	1	per sec.
Speed (assuming non-turbulence)	...	320	650	—	cm./sec.
Speed (assuming complete turbulence)	...	200	400	800	cm./sec.

It will be noted that over the range considered the speed is proportional to the frequency of tail beat.

The only observation at present available of the rate of tail beat during swimming is that recently published (since these calculations were made) by Woodcock (1948), who found that dolphins (size unstated) swimming beside a ship travelling at 10 knots had an oscillation frequency of 2/sec. In view of the necessarily approximate nature of our calculations, this observation is considered to provide evidence in favour of the theory of swimming here put forward.

GRAY'S PARADOX

The problem

Gray's Paradox is this (see Gray, 1936). During vigorous exercise a man is known to develop about 17 Watts of mechanical power per kg. of muscle. If this factor is assumed to apply to whales, then the power available in their muscles can be found as soon as the weight is known. But the power needed to drive a rigid streamlined body through the water, at a speed  $V$ , is given by the expression  $\frac{1}{2}\rho AV^3 C_f$ , where  $C_f$  is the drag coefficient,  $\rho$  is the density of water, and  $A$  the surface area. Gray considered a porpoise and a dolphin swimming at about 15 knots, and found that

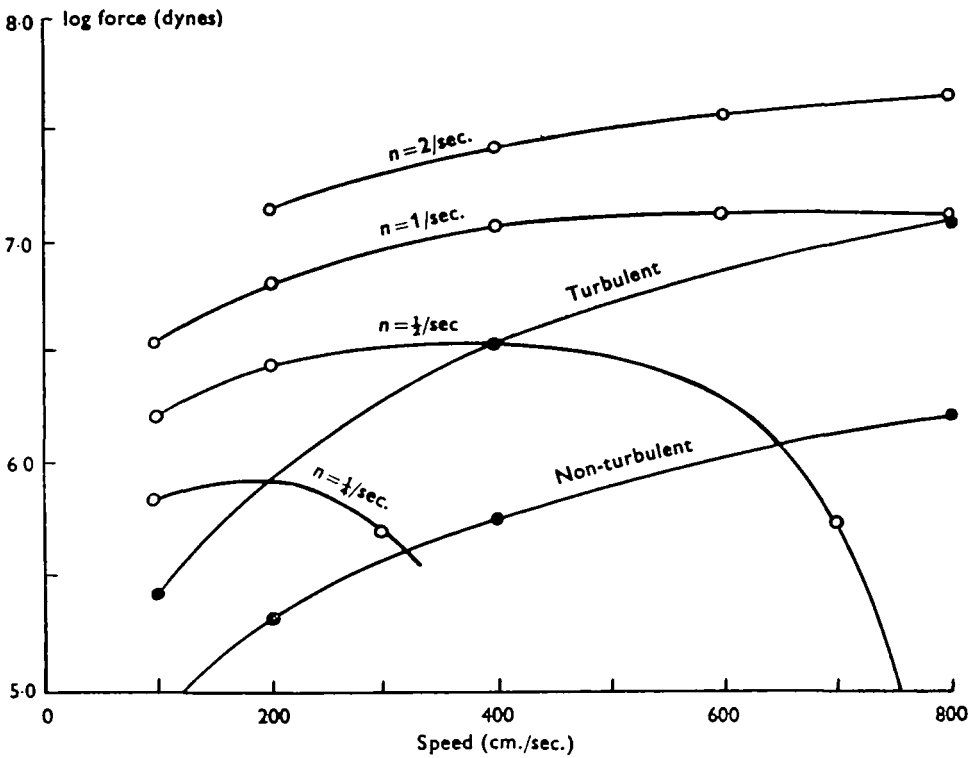


Fig. 2.

the power met the demand only when the drag coefficient of laminar flow was used, whereas according to current theory the flow should be almost completely turbulent. When the coefficient of turbulent flow was used the demand exceeded the supply by a factor of seven.

It will be seen from the above remarks that the supply is a function of the linear dimensions, whereas the demand is a function of the square. As the top speed of both large and small whales is about the same, it is the small ones that have the big power problem to solve. In fact, Gray's Paradox does not apply to whales over about 5 m. long.

*Parasitic drag*

Gray was inclined to resolve the paradox by suggesting that although the flow round a rigid body of the size and speed of a small whale was turbulent, that round and actively swimming whale might be almost completely laminar owing to the acceleration of the water due to the propulsive action of the flukes. Recent developments in fluid dynamics have modified earlier ideas concerning the transition between laminar and turbulent flow in a way favourable to Gray's hypothesis. It is now considered that the flow round a rigid body of the size of a small whale is unlikely to become turbulent until beyond the point of maximum cross-section (two-fifths of the length from the anterior end in the case of a whale-shaped body) and it is particularly in this posterior region, where turbulence would be expected in a rigid body, that the actively swimming whale differs from its rigid counterpart. As Gray suggested, the water here will be accelerating owing to the propulsive action of the flukes. Also the swimming movement will rhythmically lift and depress the tail out of the stream of water which has passed down the whale's body and is liable to become turbulent, and into undisturbed water which has not been in contact with the body at all.

Thus there is good reason to believe that the parasitic drag of an actively swimming whale is less than that of its rigid counterpart, and experimental evidence is now badly needed to establish whether or not this is so. But Gray's Paradox would only be resolved in the improbable event of all turbulence being suppressed; and even then the efficiency of the propulsive system, which for simplicity Gray assumed to be 100%, has still to be reckoned with. It is therefore necessary to examine the other side of the paradox and consider whether it is likely that whales can develop more than 17 W./kg. of mechanical power.

*Muscle power*

The figure of 17 W./kg. was derived from Henderson & Haggard's (1925) study of a rowing crew, and is approximately the greatest mechanical power which a man can develop without going into oxygen debt, when operating an efficient machine. Now it is well known that greater outputs are possible for short periods if an oxygen debt is allowed to accumulate. For example, we calculate from Dickinson's (1928) data on the bicycle ergometer (assuming a crank length of 18 cm. and a muscle mass of 10 kg.—see Vierordt, 1888) that a mechanical output of 40 W./kg. is possible under conditions of optimum efficiency. And so 17 W./kg. is not a limit set by the muscle itself, but by the supply of oxygen to the muscle (which determines the *total* power), and the efficiency of the system in which the muscle is operating (which determines how much of this total appears as *mechanical* power). If the rate of supply of oxygen to a whale's muscle, or the efficiency of the muscle during swimming, is greater than in Henderson and Haggard's rowing crew then a maintained mechanical power output of more than 17 W./kg. may be expected.

The efficiency of a whale's muscle during swimming is unlikely to exceed that of a man's muscle when the latter is operating such an efficient machine as a racing boat. But it is interesting to note that whereas the efficiency of a man's muscle

during ordinary running is probably far from optimum owing to the high rate of contraction and the light load, that of a whale during fast swimming may be near or at the optimum owing to the much greater load and the slower speed of contraction.

Information about the rate of oxygen intake is given by Scholander (1940) and Irving, Scholander & Grinnell (1941), who find that the tidal air of *Tursiops* and *Phocaena* is about the same as the maximum found in man (on a weight to weight basis), and that the oxygen utilization is 2-2½ times as great. But this advantage is counteracted by the fact that whereas man can breathe at a maximum rate of about forty breaths a minute a whale is unlikely to achieve half this rate even when swimming close to the surface.

We have briefly suggested elsewhere (Parry, 1948) that the rapidity with which whales recover their oxygen debt between dives might provide indirect evidence in favour of an unusually high rate of oxygen intake. This suggestion cannot be substantiated without data on the rate of underwater swimming. A porpoise has been observed blowing about three times between 4-5 min. dives. If it swam fast during these dives then under the most favourable hydrodynamic assumptions it would need to take up oxygen at a much greater rate than man in order to recover in three blows. But if it swam slowly then, owing to the dependence of power on the cube of speed, no special ability to absorb oxygen need be assumed even with fully turbulent flow.

Thus the possibility remains that whales can maintain a power output of over 17 W./kg. of muscle, but the best information we have about their respiration makes this unlikely.

#### SUMMARY

1. Whales swim by oscillating the tail and the flukes in a vertical plane. Tail and flukes move out of phase, the flukes leading on the tail by quarter of a wave-length. Photographic evidence is given and anatomical evidence referred to. Previous accounts of the movement are reviewed.
2. A theoretical treatment of the dynamics of swimming gives results in fair agreement with the only known observation of the frequency of tail-beat.
3. Support is given to Gray's suggestion that the drag of an actively swimming whale is less than that of a rigid model.
4. The possibility that whales develop more power (weight for weight) than man without going into oxygen debt is discussed. It is concluded to be unlikely.

I am most grateful to Prof. Gray for valuable discussion in connexion with the dynamics of swimming; to Mr J. H. Preston for information about recent work on the profile drag of aerofoils; to Dr R. H. J. Brown for drawing my attention to v. Holst & Kuchemann's theory of quasi-stable flow; and to Dr J. P. Harding for references to the Russian work on the swimming of whales. My indebtedness to the generosity of the Marine Studios, Florida, has already been noticed.

The work was done while I enjoyed a Senior Research Grant from the Department of Scientific and Industrial Research.



## APPENDIX

*Quantitative treatment of the dynamics of a swimming whale*

V. Holst & Kuchemann (1942), in their studies of bird flight, have considered the dynamic characteristics of a wing of semi-span  $s$ , moving forward with a velocity  $v$  and at the same time oscillating sinusoidally at right angles to its course with

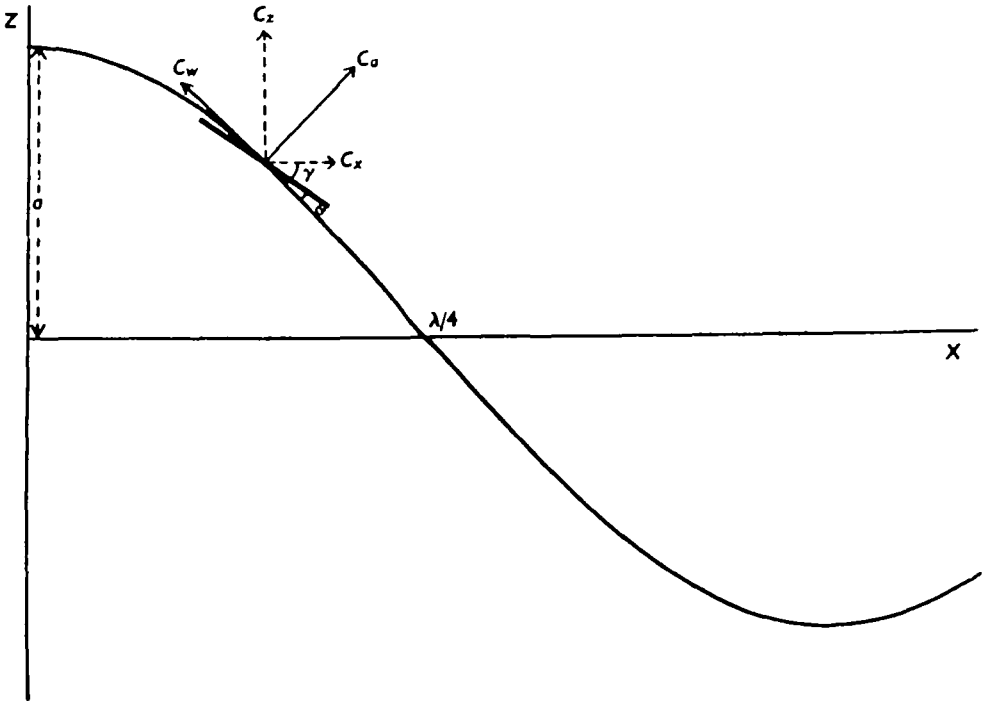


Fig. 3.

a frequency  $n$  and amplitude  $a$  (expressed in terms of  $s$ ). The angle of attack of the wing varies  $\phi$  out of phase with the wing beat about a mean value  $\alpha_0$  and with an amplitude  $\alpha_1$ . Their method is to obtain expressions for the momentary forces  $C_x$  and  $C_s$  in the mean direction of movement and at right angles to it; and then to find the mean forces  $\bar{C}_x$  and  $\bar{C}_s$  by integration over one wing beat. To obtain  $C_x$  and  $C_s$ , they use the expressions

$$C_a = C_a' \alpha = \frac{2\pi\alpha}{1 + (z/\Lambda)} \quad \text{and} \quad C_w = \frac{C_a^2}{\pi\Lambda} + \text{Profile Drag} \quad - \text{where } \Lambda \text{ is the Aspect Ratio.}$$

These expressions are derived from the study of wings at fixed angles of attack. The basic assumption is therefore made that the flow round the wing of varying angle of attack, at any instant when the angle is  $\alpha_1$ , is the same as it would be if the wing had remained indefinitely at  $\alpha_1$ . The authors quote Kuessner as showing that this assumption is justified so long as the reduced frequency ( $\nu = n \times s/V$ ) is not greater than 0.1 or 0.2.

The oscillating system considered by v. Holst & Kuchemann is similar to that of a whale's fluke and so their method can be applied if we make the basic assumption of stable flow.

Examination of Pls. 2 and 3 shows that the angle of attack is approximately  $90^\circ$  out of phase with the tail oscillation ( $\phi = \pi/2$ ); and the mean angle of attack is  $0$  ( $\alpha_0 = 0$ ). Thus the oscillation is symmetrical about the  $X$ -axis, and we have

$$\bar{C}_x = \frac{4}{\lambda} \int_0^{\lambda/4} (C_a \sin \gamma - C_w \cos \gamma) dx.$$

It can be shown that  $\gamma$  is fairly small, and so approximately  $\sin \gamma = \gamma$  and  $\cos \gamma = 1$ . Therefore

$$\bar{C}_x = C'_a \alpha_1 \pi a v - \frac{1}{2} C'_a \alpha_1^2 \frac{1}{\pi \Lambda} - C_{wp},$$

where  $C_{wp}$  is the profile drag coefficient, and the mean force  $\bar{C}_x$  is expressed in terms of  $\frac{1}{2} A_f V^2 \rho$ ,  $A_f$  being the area of the fluke,  $\rho$  the density of the fluid, and  $V$  the forward velocity.

Also 
$$\bar{C}_x = \frac{4}{\lambda} \int_0^a C'_a \alpha dx = \frac{C'_a \alpha_1 \pi}{4}.$$

*Forward thrust.* This is given by

$$\frac{1}{2} \rho A_f V^2 \bar{C}_x.$$

From measurements of a porpoise we find that

$$A_f = 3.4 \times 10^{-3} L^2, \quad \Lambda = 2, \quad a = 1.7, \quad s = 0.13L.$$

We have no means of knowing the maximum angle of attack ( $\alpha_1$ ) and so we will assume a likely value below the stall, i.e.  $10^\circ$  ( $= 0.174^\circ$ ). The density of sea water at  $10^\circ$  round the British coasts is about 1.027; and the profile drag for a wing of aspect ratio 2 is 0.023 (Bairstow, 1939, 2nd ed. p. 449).

The forward thrust can now be expressed in terms of the body length ( $L$ ), the oscillation frequency ( $n$ ), and the forward speed ( $V$ ).

$$\text{Thrust} = 1.75 \times 10^{-3} L^2 V^2 \left( \frac{0.38 L n}{V} - 0.047 \right).$$

Taking a whale of length  $L = 180$  cm. we can plot the thrust against the forward speed for different values of  $n$  (see Fig. 2).

*Parasite drag.* At any speed  $V$ , the drag of the body (parasite drag) must just equal the forward thrust. Now the parasite drag is given by

$$\frac{1}{2} \rho A_b V^2 C_f,$$

where  $A_b =$  body area  $= 0.39 L^2$  (see Parry 1949*b*) and  $C_f$  is the drag coefficient. The drag coefficient depends on the Reynold's Number  $\left( R = \frac{V \times L \times \rho}{\text{Viscosity}} \right)$  and the state of the boundary layer. In Fig. 2 we have plotted the drag for a laminar boundary layer ( $C_f = 1.328 R^{-1}$ ); and for a fully turbulent one ( $C_f = 0.455 (\log_{10} R)^{-2.58}$ , see Goldstein, 1938). Reasons are given in the text for thinking that the true drag lies nearer to the extreme of laminar flow.

Points at which the parasite drag curves cut the forward thrust curves indicate conditions of equilibrium, from which the results given on p. 28 are obtained.

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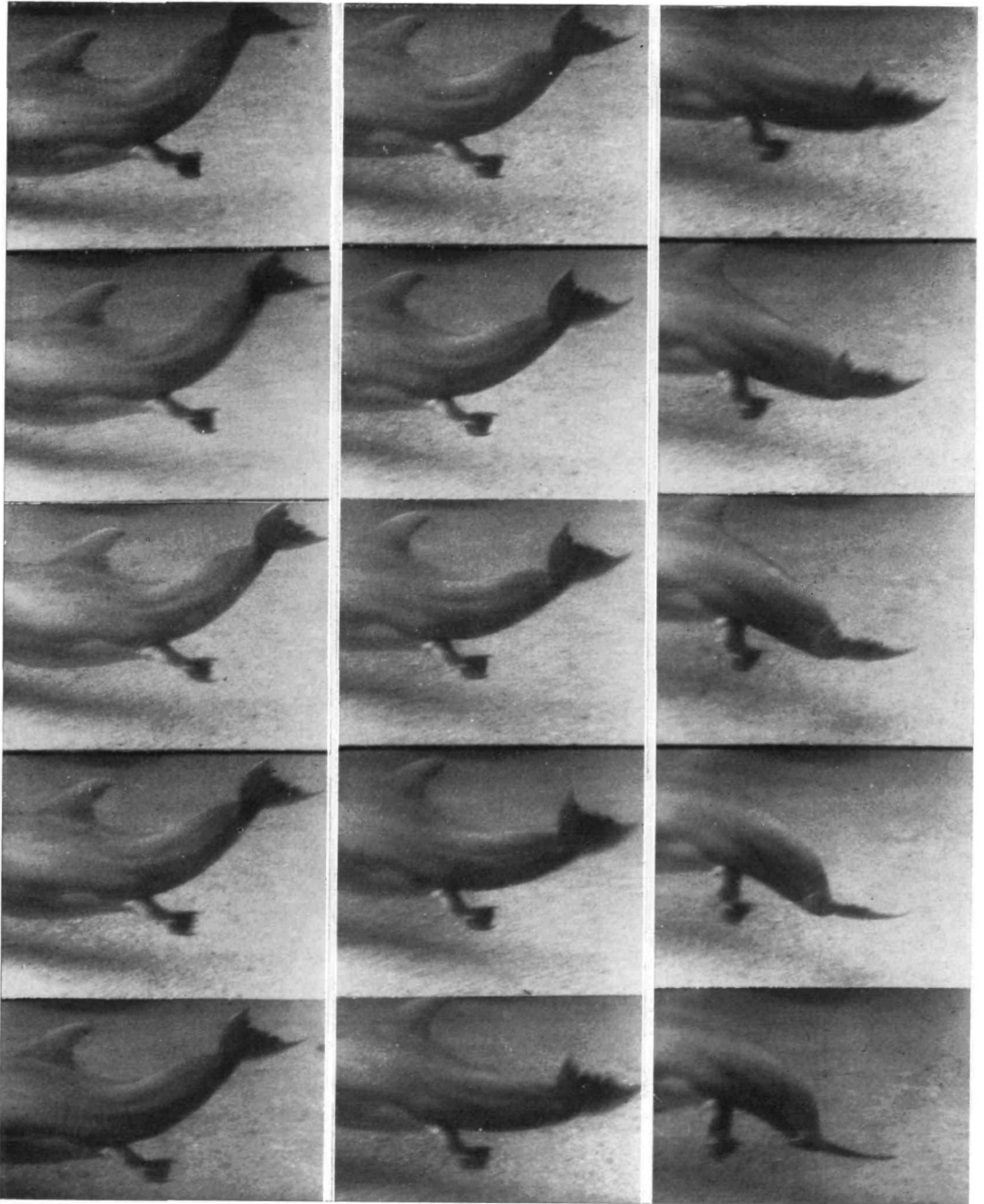
## EXPLANATION OF PLATES 2 AND 3

*Tursiops truncatus*. Serial photographs showing one cycle of the swimming movement. Parturition is in progress and the young can be seen protruding from the parent's vagina. See text. (*From a film taken by Marine Studios, Florida, and reproduced by permission.*)

Figs. 1-5

Figs. 6-10

Figs. 11-15

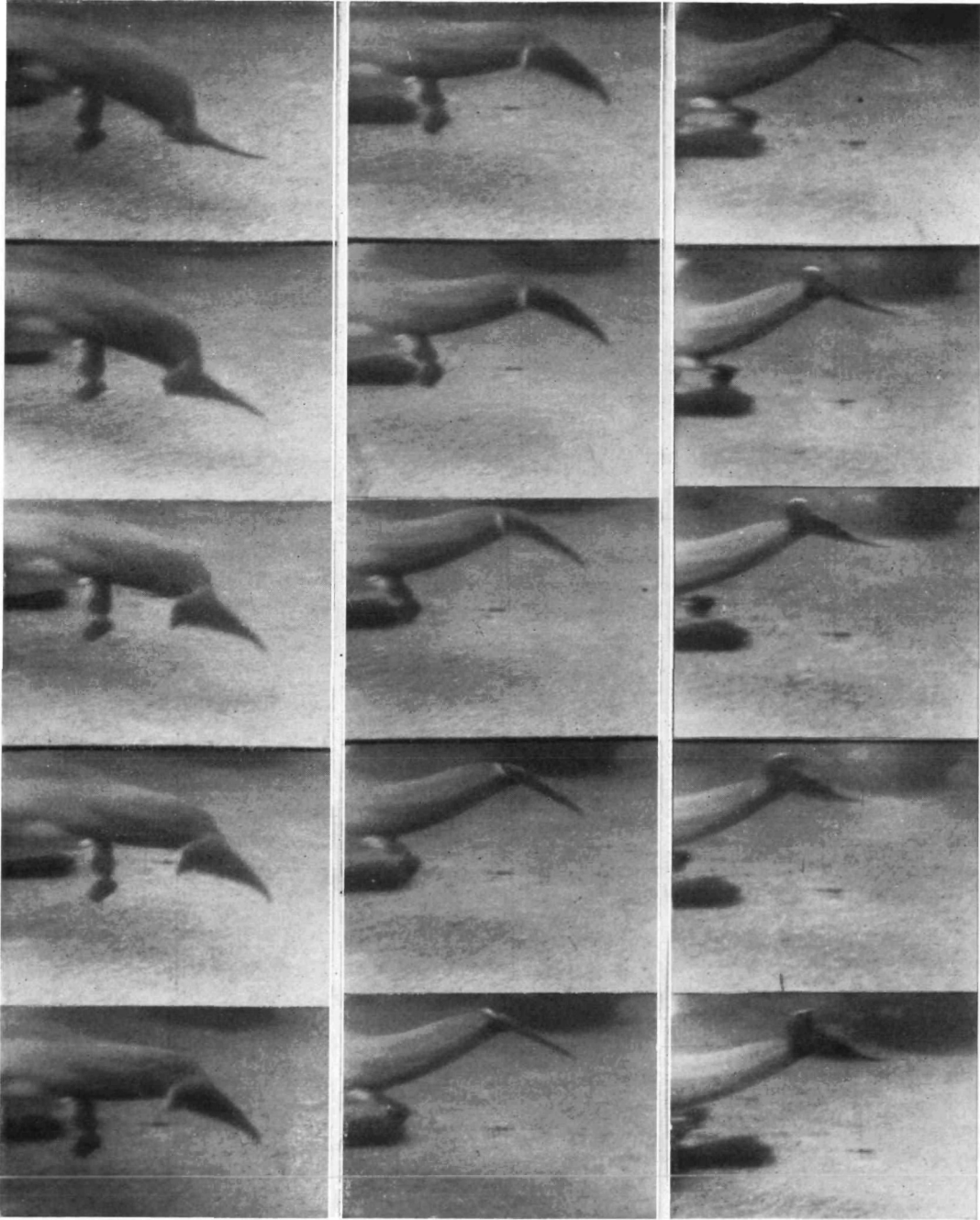


PARRY—THE SWIMMING OF WHALES, AND A DISCUSSION OF GRAY'S PARADOX

Figs. 16-20

Figs. 21-25

Figs. 26-30



PARRY—THE SWIMMING OF WHALES, AND A DISCUSSION OF GRAY'S PARADOX