SWIMMING OF DOLPHINS: EXPERIMENTS AND MODELLING

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Summary

A critical analysis of the numerous works on dolphin swimming shows that several uncertainties led to incorrect conclusions concerning the estimates of dolphin drag coefficients. Original results on dolphin kinematics and hydrodynamics indicate the existence of a drag-reduction mechanism, caused by the formation of a negative pressure gradient along the body during active swimming. The mathematical model for this mechanism is presented.

Introduction

For many years, researchers have focused attention on dolphin hydrodynamics. They are primarily interested to know whether these animals have special mechanisms for decreasing their resistance during swimming when the critical Reynolds number is exceeded. In 1936, Gray suggested that they do have such a mechanism owing to the favourable (negative) dynamic pressure gradient developing on the body during active swimming. Some other hypotheses for drag reduction were offered later, such as the damping properties of the integument (Kramer, 1960; Babenko et al. 1972), reducing resistance by eye and skin secretions (Uskova et al. 1975), etc.

The world scientific community has divided on the problem of Gray’s paradox. One group of scientists (chiefly from Western Europe and America) believes that Gray’s hypothesis is unfounded and that dolphins have no special mechanisms to reduce drag, with the possible exception of their body shape. The other group of scholars (mainly those from Russia and the countries of the former Soviet Union) claims that dolphins do have certain mechanisms to decrease their drag coefficient.

The conclusion that dolphins lack special mechanisms for decreasing their drag coefficient or increasing their critical Reynolds number (Webb, 1975; Yates, 1983; Fish and Hui, 1991; Fish, 1993) is based on indirect estimates and not on direct measurements (Fig. 1). There are flaws in the estimates, however, and the errors may be classified as follows.

1) In the feathering parameter $\alpha U/(\omega h)$, introduced by Lighthill (1969), the angle $\alpha$ is used by some authors (Webb, 1975; Fish, 1993) as the angle between the wing plane (the plane of the dolphin’s caudal lobe) and the tangent to the trajectory of its rotation axis: i.e. what is traditionally called the angle of attack of a wing. The angle $\alpha$ should instead be the inclination of the wing plane to the horizontal axis.

Key words: boundary layer, dolphin, drag, hydrodynamics, kinematics, shearing stress.
Fig. 1. Comparison of cetacean drag coefficients $C_D$ estimated from hydromechanical models based on kinematics. Drag coefficients are plotted against Reynolds number $Re$. Open circles represent depth-corrected drag coefficients $C_{Dd}$ for *Tursiops truncatus* from Fish (1993). Other symbols represent *Delphinus bairdi* (○), *Lagenorhyncus obliquidens* (□), *Phocoenoides dalli* (△). Data are from Lang and Daybell (1963), Webb (1975), Chopra and Kambe (1977) and Yates (1983). The solid line represents the minimum drag coefficient assuming a turbulent boundary layer; the broken line is for the minimum drag coefficient assuming laminar conditions (from Fish, 1993).

(2) Even when the angle $\alpha$ is chosen correctly, its absolute value has been used (Yates, 1983) instead of its tangent, contrary to the warning by Chopra (1976). Furthermore, the one experimental paper (Lang and Daybell, 1963) cited by the above authors does not give an accurate value for the angle, and Yates relied on the suggested value of 0.66 rad.

(3) To estimate the thrust power, Webb (1975) uses the following equation from Parry (1949):

$$E = 0.0175L^2U^3[(0.38L\beta/U) - 0.047], \quad (1)$$

where $L$, $U$ and $f$ are the length of the body, the swimming velocity and the frequency of body oscillations, respectively. However, the numerical coefficients are wrongly specified in this equation, and the error is almost tenfold.

(4) The errors introduced by a number of theoretical assumptions were neglected, although they were specially emphasized by Chopra and Kambe (1977). Other differences between theory and experiments might also have contributed errors: e.g. the elasticity of the caudal lobe, the swimming depth of the dolphin, etc.

In addition to these errors, there are certain practical difficulties which decrease the reliability of the above estimates: it is very difficult to define exactly the spatial position of the rotation axis of the dolphin’s lobe, and to differentiate the shape of the lobe from
Fig. 2. The corrected values of the frictional drag coefficient. Symbols representing species as in Fig. 1, plus *Sotalia guianensis* (×). Minimum drag coefficients are shown for turbulent (solid line) and laminar (broken line) boundary layers. Data from Webb (1975), Kayan (1979), Yates (1983), Videler and Kamermans (1985), Romanenko (1986) and Fish (1993).

that of theoretical wings. There are also some divergences in the theoretical approach to the problem and, hence, in the conclusions (Ahmadi and Widnall, 1985; Lan, 1979; Chopra and Kambe, 1977). All of this questions the reliability of the estimates and the conclusions drawn from them.

Fig. 2 shows corrected values of frictional drag coefficients, with the data from Fish (1993) presented for selected speeds of 2 and 6 m s⁻¹. It is clear that the dolphin frictional drag coefficients are in good agreement with theoretical values for a turbulent boundary layer on the plate. However, the results cannot be used to conclude whether the dolphin has any special drag-reducing mechanisms. To investigate such mechanisms, it is necessary to measure directly the flow pattern and the fine structure of the boundary layer.

It seems premature to close the problem on dolphin hydrodynamics and to reject Gray’s paradox. Moreover, the experiments carried out by scientists from Russia and from the countries of the former Soviet Union testify that dolphins do indeed have special
Flow velocities and pressure gradients

We have been working on Gray’s hypothesis for many years, trying to develop it further and to verify it in two ways: experimentally and by mathematical modelling. In our experiments, we measured the flow velocities at three points on the lateral surface of the swimming dolphin. The points were situated 1.2, 1.5 and 1.7 m from the nose tip, the dolphin’s body being 2.24 m long. The velocities were measured by microvanes, and the data were recorded by radiotelemetry to the shore; a small radio transmitter was fixed on the dorsal fin. The results are presented in Fig. 3. The vertical axis shows the ratios between the flow velocities measured at the third and first points along the body and at the second and first points. Horizontally, we display the acceleration of the dolphin. It is easy to see that when the dolphin moves at constant velocity, or with positive acceleration, the streamline flow is accelerated to faster velocities downstream on the body. The results were obtained at an average swimming velocity of $4\pm0.5\,\text{m}\,\text{s}^{-1}$. Knowing the flow velocities and using Bernoulli’s equation, it is not difficult to calculate pressures and

![Fig. 3. Relative velocities of flow along the dolphin’s body. ■, the ratio of velocities $U/U_1$ for the third and first points on the body; □, the same ratio for the second and first points. Ratios are plotted against the swimming acceleration $dU/dt$.](image-url)
pressure gradients. Fig. 4 presents normalised pressure gradients for swimming at constant velocity and at accelerations of 0.14 m s$^{-2}$ and 0.4 m s$^{-2}$.

Table 1 shows values of the form parameter of the velocity profile, which is more directly linked with the critical Reynolds number than is the pressure gradient. The expression for the form parameter $\Lambda$ is:

$$\Lambda = -\left(\frac{\delta^2}{\nu}\right)(dp/dx),$$

where $\delta$ is the thickness of the boundary layer, $\nu$ is the kinematic viscosity of water, $\rho$ is

<table>
<thead>
<tr>
<th>$x/l$</th>
<th>$dU/dt$ (m s$^{-1}$)</th>
<th>$2(dp/dx)/(\rho U^2)$</th>
<th>$\Lambda$</th>
</tr>
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<tbody>
<tr>
<td>0.6</td>
<td>0</td>
<td>-0.093</td>
<td>1.6</td>
</tr>
<tr>
<td>0.65</td>
<td>0</td>
<td>-0.168</td>
<td>3.0</td>
</tr>
<tr>
<td>0.65</td>
<td>0.14</td>
<td>-0.24</td>
<td>4.35</td>
</tr>
<tr>
<td>0.65</td>
<td>0.4</td>
<td>-0.36</td>
<td>6.5</td>
</tr>
<tr>
<td>0.71</td>
<td>0</td>
<td>-0.28</td>
<td>5.6</td>
</tr>
</tbody>
</table>

Values for the normalized pressure gradient are taken from Fig. 4.
the water density, $U$ is the velocity of the advancing flow and $p$ is dynamic pressure (Romanenko, 1976). The values of the form parameter are quite sufficient to stabilize the laminar flow or, which is the same, to increase the critical Reynolds number considerably. Indeed, our direct measurements of Reynolds number in the transition from the laminar to the turbulent boundary layer on a freely swimming dolphin, using special devices to register pressure pulsations, revealed the critical Reynolds number to be much higher than on a flat plate and on a rigid model of the dolphin. We also found that the critical Reynolds number depends on the acceleration during swimming.

The favourable (negative) gradient of dynamic pressure along the body is known not only to stabilize the laminar flow but also to damp out turbulent flow, by decreasing the degree of turbulence down to a complete reverse transition. The decreased turbulence in the boundary layer on the dolphin’s body, caused by a negative pressure gradient, was determined experimentally by Romanenko (1976, 1986).

The level of pressure pulsations is unambiguously related to the shearing stresses on the body, and these stresses govern the resistance to movement. The decreased level of pressure pulsations during the dolphin’s active swimming (either with acceleration or at constant velocity), compared with that during the animal’s inert movement, demonstrates that the coefficient of frictional drag should be lower when the dolphin is active than when it is inert. And this is exactly what explains Gray’s paradox.

**Shearing stresses**

This conclusion is so important that we cannot accept it without reservations, even if it seems obvious from the results presented above. For confirmation, it is vital to measure directly the shearing stresses within the boundary layer of a freely swimming dolphin. This was accomplished using a specially designed device to measure shearing stresses, together with a data logger fixed on the dorsal fin. The shearing stress sensor was sequentially placed at different points on the right side of the dolphin: the distances from the nose tip were 0.4, 0.5, 0.67 and 0.78 of the body length $l$. The sensor was also installed on the caudal lobe of the dolphin. The sensor was situated at 3 mm from the body surface, which equalled about 0.2–0.25 of the boundary layer thickness. According to Schlichting (1974), at this distance from the surface the shearing stresses practically coincide with those at the surface itself.

Fig. 5 displays typical results for points under measurement coinciding with 0.5 of the body length $l$. The horizontal axis shows time in seconds from the onset of the dolphin’s movement; the vertical axis shows the swimming velocity (filled squares) and the local coefficient of resistance (crosses) in relative units. There are sections illustrating swimming with positive acceleration, with constant velocity and with deceleration. During the time interval from 6.4 s and 7.4 s, the dolphin surfaced for inspiration–expiration. The swimming velocity decreased slightly before it surfaced, probably because of the termination of thrust. The local coefficient of frictional resistance is lowest during accelerated swimming, and it is highest during decelerations. The difference between the lowest and highest values is very large. It should be noted that the local coefficient of frictional drag reached its highest value twice during the sequence:
immediately before the dolphin surfaced for inspiration–expiration, and when it decelerated at the end of the run. Other cases of surfacing for inspiration–expiration did not always reveal a deceleration and the accompanying increase in the local coefficient of frictional drag, but these were always observed at the end of swimming.

The results at 0.78/l show that the local coefficient of frictional drag is 4.7 times lower compared with that at 0.4/l for a dolphin swimming at constant velocity. When the sensor was placed on the caudal lobe, however, the local coefficient proved to be extremely unstable. This result can be attributed to the unstable pressure gradient on the caudal lobe at different stages of the swimming cycle.

**Mathematical modelling**

Let us investigate the mechanism underlying the pressure gradient caused by the body oscillations. We shall consider the body as a long cylinder of elliptic or circular profile which makes bending oscillations within one plane. To calculate the dynamic pressure on
the body surface, we may use the expression for a circular cylinder in transverse motion (Logvinovich, 1969):

$$ p - p_\infty = \frac{\rho v^2}{2} (1 - 4\sin^2 \theta) + (\rho \cos \theta/R) \frac{d(R^2 v_n)}{dt} , $$

where $R$ and $\theta$ are cylindrical coordinates, $t$ is time, and $v_n$ is the transverse velocity of the body given by:

$$ v_n = \left( \frac{\partial h}{\partial t} \right) + U \left( \frac{\partial h}{\partial x} \right) , $$

where $h$ is the transverse displacement and $U$ is the swimming velocity along the $x$ axis (Fig. 6).

Transverse oscillations of the dolphin’s body during active swimming can be well described by the following expression (Romanenko, 1986; Yanov, 1990):

$$ h(x,t) = h_0 \frac{h}{h} + a(X) + c(X)^2 + d(X)^3 \sin \left( \frac{\omega t}{l} + \frac{k_0}{b} \ln [1 + lb(X)] \right) . $$

where $X=x/l$, $h_0$ and $h_\infty$ are the oscillation amplitudes at the head and tail, $k_0$ is the number of wavelengths in the head, $b$ is a parameter for the increase in the phase velocity of the locomotor wave, $\omega=2\pi f$ ($f$ is the frequency of oscillations) and $a$, $c$ and $d$ are constants. This equation incorporates the main features of the locomotor wave spread along the dolphin’s body: i.e. the variation in wave amplitude and phase from head to tail. We shall calculate the dynamic pressure distribution on a dolphin’s body (*Tursiops truncatus*) for two regimes of swimming, their parameters being presented in Table 2.

Fig. 7 presents the minimum and maximum values of the dynamic pressure gradient for the lateral side of the dolphin’s body ($\theta=\pi/2$). These values were reached twice during each oscillation. The magnitude of the positive gradient is obviously small, while that of the negative gradient is considerably higher and depends on the swimming regime. In the front part of the body, the gradient permanently remains negative and of large magnitude, being determined by the shape of the body. Fig. 7 also includes the experimental data of Fig. 4 for comparison. The experimental data are in good agreement with the calculated results for the second swimming regime of Table 2.

Some important conclusions can be drawn from the shape of the calculated curves in Fig. 7. The negative pressure gradient is considerable in the head and tail parts of the

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*Fig. 6. Definition of the coordinate system for mathematical modelling. See text for details.*
Table 2. The parameters of dolphin swimming under two different regimes

<table>
<thead>
<tr>
<th>Parameters</th>
<th>First regime</th>
<th>Second regime</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U$ (m s$^{-1}$)</td>
<td>1.5</td>
<td>4.3</td>
</tr>
<tr>
<td>$h/l$</td>
<td>0.18</td>
<td>0.123</td>
</tr>
<tr>
<td>$f$ (Hz)</td>
<td>1.46</td>
<td>2.22</td>
</tr>
<tr>
<td>$b$ (m$^{-1}$)</td>
<td>0.55</td>
<td>0.23</td>
</tr>
<tr>
<td>$dU/dt$ (m s$^{-2}$)</td>
<td>2.6</td>
<td>0</td>
</tr>
<tr>
<td>$h_0/h_1$</td>
<td>0.27</td>
<td>0.21</td>
</tr>
<tr>
<td>$C_0/U$</td>
<td>1.24</td>
<td>0.97</td>
</tr>
<tr>
<td>$a$</td>
<td>-0.58</td>
<td>-0.66</td>
</tr>
<tr>
<td>$c$</td>
<td>1.0</td>
<td>1.1</td>
</tr>
<tr>
<td>$d$</td>
<td>0.31</td>
<td>0.35</td>
</tr>
</tbody>
</table>

$C_0$ is the phase velocity of the locomotor wave in the region of animal’s head and other variables are defined in the text.

Fig. 7. Comparison of the calculated and experimental pressure gradients along the dolphin’s body. Line 1, maximum values of the pressure gradient; lines 2 and 3, minimum values of the pressure gradient for the second and first regimes, respectively, of dolphin swimming in Table 2; line 4, pressure gradient resulting from the body shape peculiarities on the anterior part of the dolphin’s body; symbols represent experimental data (see Fig. 4).

Dolphin swimming

body, and its favourable effect on the boundary layer should be concentrated in those regions. Turbulence in the boundary layer might begin not in the posterior part of the body, which is the case with flow over rigid streamlined bodies, but in the middle part where the pressure gradient is small and perhaps positive. Thus, there might be turbulent
flow over the middle of the body with a laminar, or considerably laminated, flow over the head and tail.

Experimental support

Wood (1979) describes observations of a group of Pacific white-side dolphins swimming in phosphorescent water. Fig. 8 shows their sketches. The light areas on the dolphins' bodies indicate a turbulent boundary layer, which is clearly seen to embrace the middle part of the body; the front part and the tail column reveal dark places corresponding to laminar flow. The upper and lower parts of the body are phosphorescent, identifying narrow sections of turbulence on the back and underside of the animals. This observation also agrees with calculations for the dorsal side of the body ($\theta=0$).

The dynamic pressure gradient on the body of the actively swimming dolphin seems to play the leading role in defining the flow pattern. This conclusion follows from an analysis of the body shape of this animal. There are three main parameters of the body, illustrated in Fig. 9, that affect the flow pattern: (i) relative elongation ($l/d_{max}$), which is the ratio of the body length to the circle diameter equalling in its area the maximum cross section; (ii) the relative position ($l/l$) of the maximum cross section; and (iii) the descent angle ($\alpha$) of the body of rotation that best approximates the animal's body. In some species of dolphins and large whales, the body shape cannot be approximated very well by a body of rotation. Nevertheless, it is useful to construct a table of comparative data on the body shape of different species of dolphins and whales.

Table 3 presents values for the morphometric parameters derived from the catalogue and pictures in Leatherwood et al. (1972). It is important to note that, because there are no accurate data on the maximum cross-sectional area of whales, we used the maximum

Fig. 8. Illustration from Wood (1979). See text for details.
Table 3. Morphometric parameters for whale and dolphin

<table>
<thead>
<tr>
<th>Species</th>
<th>$l/d_{\text{max}}$</th>
<th>$l_1/l$</th>
<th>$\alpha$ (degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tursiops truncatus</td>
<td>5.4</td>
<td>0.35</td>
<td>10</td>
</tr>
<tr>
<td>Phocoena phocoena</td>
<td>4.7</td>
<td>0.40</td>
<td>15</td>
</tr>
<tr>
<td>Lagenorhynchus obliquidens</td>
<td>6.9</td>
<td>0.36</td>
<td>8</td>
</tr>
<tr>
<td>Stenella graffmani</td>
<td>7.1</td>
<td>0.35</td>
<td>7</td>
</tr>
<tr>
<td>Stenella longirostris</td>
<td>7.6</td>
<td>0.34</td>
<td>7</td>
</tr>
<tr>
<td>Delphinus delphis</td>
<td>6.1</td>
<td>0.36</td>
<td>-</td>
</tr>
<tr>
<td>Phocoenoides dalli</td>
<td>4.6</td>
<td>0.33</td>
<td>13</td>
</tr>
<tr>
<td>Lissodelphis borealis</td>
<td>7.5</td>
<td>0.36</td>
<td>7</td>
</tr>
<tr>
<td>Eschrichtius robustus</td>
<td>4.5</td>
<td>0.40</td>
<td>10</td>
</tr>
<tr>
<td>Berardius bairdi</td>
<td>6.0</td>
<td>0.39</td>
<td>-</td>
</tr>
<tr>
<td>Pseudorca crassioleus</td>
<td>6.9</td>
<td>0.38</td>
<td>-</td>
</tr>
<tr>
<td>Physeter catodon</td>
<td>5.1</td>
<td>0.45</td>
<td>-</td>
</tr>
<tr>
<td>Kogia breviceps</td>
<td>4.0</td>
<td>0.42</td>
<td>-</td>
</tr>
</tbody>
</table>

width of the body as the maximum diameter. For all whales in the table, the relative elongation ranges from 4 to 7.6, the relative position of the cross-section is between 0.33 and 0.45, and the descent angle varies between 7° and 15°.

To assess these data, we turn to the paper of Alekseyeva et al. (1968), where the authors calculate parameters of the laminar boundary layer for a series of bodies of rotation which vary in shape. We shall not dwell on their calculation methods but instead cite their main results: (i) when the boundary layer is laminar, flow separation is avoided for $\alpha \leq 6.5$; (ii) the minimum resistance in laminar flow with Reynolds numbers of the order of $10^8$ is found when the elongation is 9 and the relative position of the maximum cross section equals 0.21; (iii) the minimum resistance in turbulent flow is obtained with an elongation of 5.5–7 and the relative position of the maximum diameter around 0.4.

When the results of Alekseyeva et al. (1968) are compared with those in Table 3, the following conclusions can be made.

1. The descent angle in whales exceeds the maximum angle at which the laminar boundary layer remains attached. Thus, either the laminar boundary layer of dolphins
must separate, or they must somehow be able to prevent this separation. As we saw above, a negative pressure gradient develops on their body when dolphins are swimming actively, and this gradient may prevent separation of the laminar boundary layer.

2. The body of whales is not optimal to minimize resistance in laminar flow, meaning that there is a danger of the boundary layer separation discussed above. However, as we could see for whales, and for dolphins in particular, such a danger does not exist.

3. The body shape in whales approaches the optimum for minimal resistance in turbulent flow.

Thus, given the negative pressure gradient on the dolphin’s body (and, most likely, on the body of other whales), their body shape may be considered as optimal both for laminar and for turbulent flow. This is a most important adaptive device created by nature in whales.

References


