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Estimates of pressure differences across the head of a swimming clupeid fish

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SUMMARY

This paper is concerned to estimate, for a regularly swimming clupeid fish, the effective pressure difference that drives those motions in the subcerebral canal which can stimulate the lateral-line neuromasts (see the preceding paper by Denton & Gray 1993). Hydrodynamic analysis indicates that pure sideslip of the head (at observed sideslip velocities) would generate a pressure difference so great that the neuromasts would be saturated; however, simultaneous yawing can enormously reduce the effective pressure difference.

For this purpose the angle of yaw would need to be kept in phase with sideslip velocity, with a magnitude only a little less than the ratio of sideslip velocity to swimming speed, making the 'crossflow' of water across the yawed head small. These moreover are conditions which tend to avoid any serious distortions of the boundary layer on the fish's surface by 'crossflow', such as are known from other evidence to increase significantly the resistance to the fish's motion.

It is noted that the lateral-line sensors would provide an appropriate feedback signal into a possible system for controlling yaw by oscillatory neck deflections so as to minimise the effective pressure difference and any associated crossflow effects. It is suggested that swimming clupeid fishes may use such an 'active' mechanism for reduction of hydrodynamic resistance.

The same ratio (around 0.87) of yaw angle times swimming speed to sideslip velocity is estimated: (i) to annul the signal sensed by lateral-line neuromasts; and (ii) to remove crossflow in the boundary layer over the head. The succeeding paper (Rowe *et al.* 1993) gives evidence, both that yaw is kept in phase with sideslip velocity, and that the above ratio (see their figure 4) remains close to 0.87, in a swimming herring.

1. INTRODUCTION

Denton & Gray (1993) have demonstrated in the preceding paper the importance for a clupeid fish of fluid motions in the subcerebral canal. These are driven by the effective pressure difference

$$(\Delta p)_{\text{eff}}, \quad (1)$$

between the two lateral recesses, here taken as situated a distance $2b$ apart on the two sides of the fish's head. This effective pressure difference

$$(\Delta p)_{\text{eff}} = \Delta p + 2b\rho A, \quad (2)$$

is defined as the actual pressure difference Δp corrected for the inertial effect of the head's lateral acceleration A acting on fluid of density ρ .

This paper is directed towards estimating the values of $(\Delta p)_{\text{eff}}$ associated with regular swimming movements of the fish. First, it considers (§ 2) the effect on Δp of any lateral accelerations A of the head (such as are an inevitable consequence of the periodic sideforces exerted by the water on the oscillating caudal fin) in the case when the head is not simultaneously subjected to yawing movements. This analysis gives

$$\Delta p = 2bk\rho A, \quad (\Delta p)_{\text{eff}} = 2b(1+k)\rho A, \quad (3)$$

where k is a numerical constant dependent on the shape of the head but estimated to take values around 1.6 for clupeid fishes.

Next, the estimation of Δp is carried out (§ 3) for the case when the head undergoes at one and the same time a lateral acceleration A and a yawing rotation with angular velocity Ω . The value of $(\Delta p)_{\text{eff}}$ in this case is found to take the form

$$(\Delta p)_{\text{eff}} = 2b(1+k)\rho A - 2bK\rho U\Omega \quad (4)$$

where U is the forward velocity of swimming while K is another numerical constant, estimated to take values around 3 for clupeid fishes.

How important is the correction due to angular velocity? If we were to assume that the front part of the fish (including the head and several proximal vertebrae) were kept essentially rigid, responding to sideforces on the caudal fin like a rigid body (immersed in water), then the expected values of angular velocity Ω would make only minor alterations to expression (4) for $(\Delta p)_{\text{eff}}$.

In such cases, however, Denton and Gray have been able to infer that the effective pressure difference $(\Delta p)_{\text{eff}}$ would stimulate fluid motions in the subcerebral canal and thence in the lateral-line system which

would saturate the associated sensors (neuromasts) even at quite moderate swimming speeds. Yet a clupeid fish is swimming continually under normal circumstances, and it is hard to believe that it does so with an important sensory system like the lateral-line neuromasts rendered ineffective by saturation.

In particular, the same authors in an earlier paper (Denton & Gray 1983) had shown how the lateral-line system – if unsaturated – could be effective for sensing movements of nearby fishes. Thus, although such movements may be shown (§ 4) to have no effect on $(\Delta p)_{\text{eff}}$ itself, nevertheless they can generate pressure gradients in the forward direction, capable of being equally sensed by neuromasts in lateral lines on both sides of the head. For a clupeid fish, which characteristically swims in a school, this capability may be highly advantageous.

All these considerations in combination have suggested that it could be valuable to ask (§ 4) whether a swimming clupeid fish may be able to control the angular velocity Ω of its head, by means of oscillatory neck deflections, in such a way that $(\Delta p)_{\text{eff}}$ is kept as small as possible. The lateral-line system, responding as we have seen to the signal $(\Delta p)_{\text{eff}}$, is well adapted to offer the feedback needed for a control system of this kind.

Such a control would bring hydrodynamic benefits of reduced resistance that are particularly advantageous for a continually swimming fish. Indeed the conditions under which $(\Delta p)_{\text{eff}}$ is kept as small as possible may be shown (§ 4) to be such as will minimize those crossflows within the boundary layer over the fish's head which are capable of seriously distorting that boundary layer and thereby enhancing hydrodynamic resistance. Essentially, the fluid in the boundary layer responds to exactly the same signal $(\Delta p)_{\text{eff}}$ as does the fluid in the subcerebral canal, and its crossflow response becomes small in precisely that case of small $(\Delta p)_{\text{eff}}$ when motions in the lateral-line system are greatly diminished.

These arguments lead to the tentative conclusion that the signal $(\Delta p)_{\text{eff}}$ could provide valuable feedback into a system for controlling neck deflections (the lateral-line system) able to achieve minimal resistance by keeping boundary-layer crossflows over the head as small as possible. When moreover such a system were operating effectively, lateral-line neuromasts would avoid saturation. In that case neuromasts on both sides of the head would be able to respond to those longitudinal and dorso-ventral pressure gradients that are generated (without altering $(\Delta p)_{\text{eff}}$ at all) by the movements of nearby fishes. For further discussion of these possibilities, see the preceding paper by Denton and Gray.

Finally, a simplified interpretation of the paper's conclusions is given at the end of § 4, where it is noted that the conditions for the effective pressure difference (4) to be minimized are close to those conditions under which, at each instant, the yawed head of the fish has at most a very small velocity component perpendicular to itself. These latter conditions require that the angle of yaw, in radians, should remain close to the ratio of sideslip velocity to swimming speed.

The plausible intuition that crossflows might in general be minimized in these conditions is confirmed by the paper's detailed analysis.

2. PRESSURE DIFFERENCE DUE TO LATERAL ACCELERATION

When the fish is swimming, the distribution of pressure over its head is governed by three principles: (i) the flow remains irrotational (devoid of vorticity) outside a very thin boundary layer attached to the surface of its head; (ii) at each point on the surface, the pressure takes almost exactly the same value as it takes just outside the boundary layer; and (iii) the distribution of pressure outside the boundary layer is given by the Bernoulli equation for unsteady irrotational flow.

This equation uses the velocity potential ϕ , defined so that it tends to zero at large distances from the fish and so that its gradient $\text{grad}\phi$ specifies the fluid velocity in magnitude and direction. Then the formula (see, for example, p. 83 of Lighthill (1986))

$$p = -\rho \frac{\partial \phi}{\partial t} - \frac{1}{2} \rho |\text{grad}\phi|^2, \quad (5)$$

specifies a quantity p which may be regarded as the pressure distribution in every dynamical context (more strictly, p represents the difference between the actual distribution of fluid pressure and a purely hydrostatic distribution).

An irrotational motion of fluid is uniquely determined at any instant (see, for example, p. 87 of Lighthill (1986)) by the instantaneous movement of the solid boundary. In this section we consider the case when the instantaneous movement of the fish's unyawed head has a forward component U in the direction of swimming (which we take as the x -direction) and a sideslip component V in a perpendicular direction (the y -direction) but is without any rotary component. In using equation (5) to determine the pressure distribution, however, we need a knowledge of $\partial\phi/\partial t$, which depends on changes from one instant to the next in the position and velocity of the body.

The position of the fish's head may be specified (see figure 1) in terms of the coordinates (x_0, y_0) of some central point, such as the point midway between the two lateral recesses. Then the rates of change of these coordinates are the velocity components

$$dx_0/dt = U, \quad dy_0/dt = V. \quad (6)$$

The velocity potential can be written as

$$\phi = U\phi_f(x - x_0, y - y_0, z) + V\phi_l(x - x_0, y - y_0, z), \quad (7)$$

in terms of two well defined functions ϕ_f and ϕ_l each representing, in terms of position relative to the central point, the velocity potential associated with the head's movement at unit velocity in the x - or y -direction respectively (figure 1).

When equation (7) is used to derive $\partial\phi/\partial t$, the rates of change (6) of x_0 and y_0 need to be taken into account as well as any rates of change of U and V themselves. The result is

$$\frac{\partial \phi}{\partial t} = \frac{dU}{dt} \phi_r - U \left(U \frac{\partial \phi_r}{\partial x} + V \frac{\partial \phi_r}{\partial y} \right) + \frac{dV}{dt} \phi_l - V \left(U \frac{\partial \phi_l}{\partial x} + V \frac{\partial \phi_l}{\partial y} \right), \quad (8)$$

which at first sight may seem quite a complicated expression (of six terms) for just the first part of equation (5) for the pressure.

It is, however, a consequence of the lateral symmetry of the fish's head that, essentially, only one of these six terms contributes to the pressure difference Δp between the two lateral recesses. If the distance between these is $2b$, then we are concerned with the difference of pressure between points with $y - y_0$ equal to $+b$ or $-b$ (and $x - x_0 = 0$). This quantity takes a simple form because of the symmetry properties (figure 1) of the potential functions ϕ_r and ϕ_l .

Thus, because ϕ_r represents a potential due to the head's movement in its plane of symmetry, ϕ_r is necessarily an even function of $y - y_0$; in other words, a function which is unchanged if simply the sign (but not the magnitude) of $y - y_0$ is altered. Its value, in short, is the same for $y - y_0$ equal to $+b$ or $-b$.

By contrast, ϕ_l represents a potential due to the head's movement at right angles to its plane of symmetry. Such a potential may readily be shown, by considering a reversal in that movement's direction, to be an odd function (one which changes its sign, but not its magnitude, when $y - y_0$ does the same). It follows moreover from these two properties of ϕ_r and ϕ_l that $\partial \phi_r / \partial x$ and $\partial \phi_l / \partial y$ are even functions while $\partial \phi_r / \partial y$ and $\partial \phi_l / \partial x$ are odd functions.

Accordingly, if as in (1) we use Δ to signify a value at $y - y_0 = +b$ minus a value at $y - y_0 = -b$ with $x - x_0 = 0$ in both cases (in other words, a difference across the subcerebral canal), then equation (8) gives

$$\Delta \frac{\partial \phi}{\partial t} = \frac{dV}{dt} \Delta \phi_l - UV \Delta \left(\frac{\partial \phi_r}{\partial y} + \frac{\partial \phi_l}{\partial x} \right). \quad (9)$$

This result may be used in (5) together with a corresponding result for

$$\begin{aligned} |\text{grad} \phi|^2 &= |U \text{grad} \phi_r + V \text{grad} \phi_l|^2 \\ &= U^2 |\text{grad} \phi_r|^2 + 2UV (\text{grad} \phi_r) \cdot (\text{grad} \phi_l) \\ &\quad + V^2 |\text{grad} \phi_l|^2; \end{aligned} \quad (10)$$

where the first and third terms on the right-hand side are even functions (remaining positive and of unchanged magnitude when the sign of $y - y_0$ is altered) but the middle one is an odd function. Thus

$$\Delta \left(\frac{1}{2} |\text{grad} \phi|^2 \right) = UV \Delta \left(\frac{\partial \phi_r}{\partial x} \frac{\partial \phi_l}{\partial x} + \frac{\partial \phi_r}{\partial y} \frac{\partial \phi_l}{\partial y} + \frac{\partial \phi_r}{\partial z} \frac{\partial \phi_l}{\partial z} \right). \quad (11)$$

Now equation (5) for p together with the results (9) and (11) gives Δp in the form

$$\begin{aligned} \Delta p &= -\rho \frac{dV}{dt} \Delta \phi_l + \rho UV \Delta \left[\left(1 - \frac{\partial \phi_l}{\partial y} \right) \frac{\partial \phi_r}{\partial y} \right. \\ &\quad \left. + \left(1 - \frac{\partial \phi_r}{\partial x} \right) \frac{\partial \phi_l}{\partial x} - \frac{\partial \phi_r}{\partial z} \frac{\partial \phi_l}{\partial z} \right]; \end{aligned} \quad (12)$$

where, however, the second term can be expected to be negligibly small. This is because, at each lateral recess, the conditions

$$\partial \phi_l / \partial y = 1, \quad \partial \phi_l / \partial x = 0, \quad \partial \phi_l / \partial z = 0, \quad (13)$$

are expected to be closely satisfied. Indeed, the definition of ϕ_l makes it the velocity potential associated with the head's movement at unit velocity in the y -direction. Accordingly, the three components of the velocity $\text{grad} \phi_l$ of fluid motion are constrained by the movement of the boundary to take values very close to those in (13).

Actually, equations (13) would be exact if the lateral recess were situated just at the stagnation point for steady flow in the y -direction past the stationary head. Inspection of diagrams in the preceding paper giving the position of the lateral recess indicates that this condition must be quite closely satisfied.

The value of Δp is seen, then, to be well approximated by the first term in equation (12), where the negative quantity $\Delta \phi_l$ has the dimensions of length (since ϕ_l is a potential associated with movement at unit velocity). Accordingly, we write

$$\Delta \phi_l = -2bk, \quad (14)$$

where k is a numerical constant which we now proceed to estimate, and infer that

$$\Delta p = 2bk\rho (dV/dt). \quad (15)$$

Here, the value of k depends on the shape of the fish's head. In the Appendix, details of this shape are indicated, and it is estimated that k lies in the interval between 1.45 and 1.8.

Briefly, 1.8 is the value given by 'elongated-body

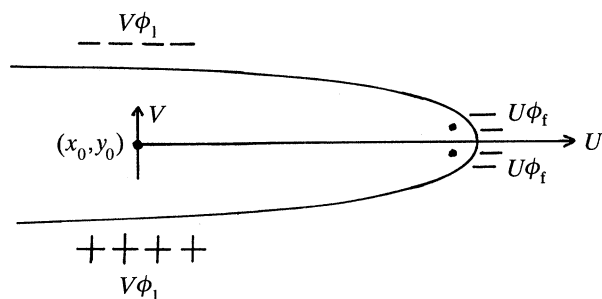


Figure 1. Movement of a fish's head without rotation generates fluid motions described by a combination of two potentials, as follows. Potential $U\phi_r$: associated with the forward component, at velocity U , of the head's movement is a symmetric potential $U\phi_r$ which takes negative values around the snout (giving rise, there, to positive pressures $-\rho(dU/dt)\phi_r$ when the velocity U increases).

Potential $V\phi_l$: associated with any lateral component, at velocity V , of the head's movement is an antisymmetric potential $V\phi_l$ which takes negative values on the side towards which the head is moving and positive values on the opposite side. When V is increasing these lead to an opposing pressure difference $-\rho(dV/dt)\Delta\phi_l$ across the head. This difference is unaffected by the presence of the symmetric potential $U\phi_r$.

theory' in terms of the local cross-section of the head through the lateral recesses. That cross-section is shaped like an ellipse of axis-ratio 1.8, and this quantity 1.8 is itself the value of k for a long elliptic cylinder with such a cross-section. On the other hand, the part of the head anterior to the lateral recesses tapers towards the mouth and is closer in shape to half of an ellipsoid with axes in the ratio 4.5:1.8:1. For the complete ellipsoid the value of k would be reduced to 1.45. The actual value of k is expected to lie between these limits because the shape anterior to the lateral recesses is very near that of the ellipsoid while the posterior shape is closer to that of the elliptic cylinder. For the research described in the preceding paper it is unnecessary to determine k more accurately, although where numerical results are given they are based on the value

$$k \doteq 1.6. \quad (16)$$

3. PRESSURE DIFFERENCE DUE TO COMBINED LATERAL ACCELERATION AND ROTATION

In this section the calculation of § 2 is extended to the case when the plane of symmetry of the fish's head makes a small angle α (which is a varying function of time) with the direction of swimming. As before, the point midway between the lateral recesses is taken to have coordinates (x_0, y_0) , where the x -axis is in the direction of swimming. However, the forward velocity U and the sideslip V are no longer equated to dx_0/dt and dy_0/dt as in (6); rather, they represent velocity components of the head in its plane of symmetry and at right angles (see figure 2). In the present case, moreover, the head is also subject to a rotation about this central point at an angular velocity

$$d\alpha/dt = \Omega, \quad (17)$$

given by the rate of change of the yaw angle α .

Once again, the Bernoulli equation (5) is used to estimate the pressure distribution in terms of the velocity potential ϕ . On the other hand, the expression (7) for ϕ as the sum of two terms, proportional to the velocity components U and V , must here

be replaced by an expression involving three terms, where the third term represents the velocity potential associated with rotation of the head at an angular velocity Ω about the central point (x_0, y_0) .

Studies in § 2 showed how important for the determination of Δp is the lateral symmetry of the head. On the other hand, the fish's head exhibits this symmetry not with respect to the x -direction but with respect to a different axis (see figure 2), inclined at a small angle α to the x -direction; namely, an axis in the fish's plane of symmetry.

It is convenient therefore to employ new coordinates X, Y with this last axis in the X -direction. We take the central point, midway between the lateral recesses, as the origin of this coordinate system so that the lateral recesses are defined as points with

$$X = 0 \quad \text{and} \quad Y = \pm b, \quad (18)$$

as well as with $z=0$ (the vertical z coordinate is the same in both systems).

At each instant, the velocity potential ϕ is uniquely determined as in § 2 by the instantaneous motion of the head, which now involves a rotation at angular velocity (17) as well as translation at the longitudinal and lateral velocities U and V . In the (X, Y, z) coordinates, therefore,

$$\phi = U\phi_r(X, Y, z) + V\phi_l(X, Y, z) + \Omega\phi_r(X, Y, z), \quad (19)$$

where the potential ϕ_r represents fluid motions generated in a rotary movement of the head with unit angular velocity. Evidently, the earlier equation (7) represents the special case of (19) when $\Omega=0$ and when the head is unyawed so that X and Y are simply $x-x_0$ and $y-y_0$.

However, in the case of yaw by a small angle α , this relationship between the coordinate systems is slightly altered (see figure 2) to become

$$X = x - x_0 + (y - y_0)\alpha, \quad Y = y - y_0 - (x - x_0)\alpha,$$

while, in addition,

$$U = \dot{x}_0 + \alpha\dot{y}_0, \quad V = \dot{y}_0 - \alpha\dot{x}_0. \quad (20)$$

As a consequence, the expression for $\partial\phi/\partial t$ (a differentiation of expression (19) with respect to time for

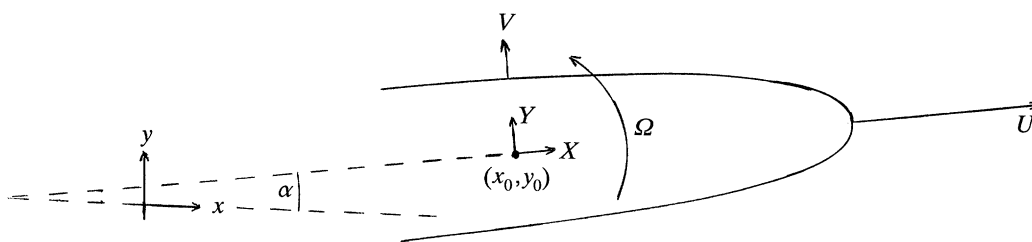


Figure 2. Illustrating horizontal movements of the fish's head as described in two alternative systems of axes: (i) the fixed axes (x, y) , in which the central point has coordinates (x_0, y_0) and velocity components (\dot{x}_0, \dot{y}_0) ; and (ii) the moving axes (X, Y) with their origin at that central point, and with the X -axis in the head's plane of symmetry, inclined at a variable angle α to the x -axis.

Velocity components in the (X, Y) coordinate system are $U = \dot{x}_0 + \alpha\dot{y}_0$, $V = \dot{y}_0 - \alpha\dot{x}_0$, while the angular velocity of rotation of the head is $\Omega = d\alpha/dt$.

Note: the swimming speed $U_0 = \dot{x}_0$ differs very little from U ; on the other hand, the sideslip velocity $V_0 = \dot{y}_0$ differs from V by the large correction $U\alpha$.

constant x , y and z) comprises not just six terms as in (8) but a still larger number:

$$\begin{aligned} \frac{\partial \phi}{\partial t} = & \frac{dU}{dt} \phi_r + \frac{dV}{dt} \phi_l + \frac{d\Omega}{dt} \phi_r \\ & - \left(U \frac{\partial \phi_r}{\partial X} + V \frac{\partial \phi_l}{\partial X} + \Omega \frac{\partial \phi_r}{\partial X} \right) [U - (y - y_0) \Omega] \\ & - \left(U \frac{\partial \phi_r}{\partial Y} + V \frac{\partial \phi_l}{\partial Y} + \Omega \frac{\partial \phi_r}{\partial Y} \right) [V + (x - x_0) \Omega]. \end{aligned} \quad (21)$$

Here, the time-differentiations of X and of Y (with x and y kept constant) are represented respectively as minus the two terms in square brackets.

As in § 2, on the other hand, the difference Δ of $\partial\phi/\partial t$ between the two lateral recesses (18), where $x = x_0$ and $y = y_0 \pm b$, is simplified because of the symmetry properties of the potential functions in (19). Of these, ϕ_r (resulting from symmetrical movement of the head) is an even function of Y , while ϕ_l and ϕ_r (resulting from antisymmetrical movements) are odd functions. It follows that

$$\begin{aligned} \Delta \left(\frac{\partial \phi}{\partial t} \right) = & \frac{dV}{dt} \Delta \phi_l + \frac{d\Omega}{dt} \Delta \phi_r - U \Delta \left(V \frac{\partial \phi_l}{\partial X} + \Omega \frac{\partial \phi_r}{\partial X} \right) \\ & + 2bU\Omega \frac{\partial \phi_r}{\partial X} - UV \Delta \left(\frac{\partial \phi_r}{\partial Y} \right); \end{aligned} \quad (22)$$

which can be further simplified to

$$\begin{aligned} \Delta \left(\frac{\partial \phi}{\partial t} \right) = & \frac{dV}{dt} \Delta \phi_l + \frac{d\Omega}{dt} \Delta \phi_r - U\Omega \Delta \left(\frac{\partial \phi_r}{\partial X} \right) + 2bU\Omega \frac{\partial \phi_r}{\partial X}, \end{aligned} \quad (23)$$

because the boundary condition on ϕ_r makes $\partial\phi_r/\partial Y$ practically zero at the lateral recesses, and where, in addition, as in § 2, $\partial\phi_l/\partial X$ may be neglected.

The right-hand side of equation (23) includes four terms of which the first involves the coefficient

$$\Delta \phi_l = -2bk, \quad (24)$$

as in § 2. Of the three new terms, the one involving $\Delta\phi_r$ is investigated in the Appendix where it is shown to be zero *both* on elongated-body theory and according to exact calculations for an ellipsoid. Accordingly, even though there is no necessity for $\Delta\phi_r$ to be precisely zero, it will be neglected in what follows.

By contrast the quantity $\Delta(\partial\phi_r/\partial X)$ is expected to be yet another negative quantity with the dimensions of length,

$$\Delta(\partial\phi_r/\partial X) = -2bk_1, \quad (25)$$

with the constant k_1 depending on the shape of the head. Its value is determined in the Appendix; (i) on elongated-body theory, which gives $k_1 = k$ so that k_1 may be estimated as 1.8 for the head shape there analysed; and (ii) for an ellipsoid with axes in the ratio 4.5:1.8:1, which gives a value $k_1 = 1.11$, a value considerably less than the value of $k = 1.45$.

It is reasonable as in § 2 to assume that k_1 lies between

these two extreme values 1.8 and 1.11; its exact value is by no means essential to the argument of this paper, although wherever numerical results are quoted k_1 has been taken equal to 1.4. (For the fourth term in (23), see below.)

The corresponding extension to equation (11), on the other hand, produces as in § 2 no significant contribution to Δp . It takes the form

$$\Delta \left(\frac{1}{2} |\text{grad}\phi|^2 \right) = \Delta [(U \text{grad}\phi_r) \cdot (V \text{grad}\phi_l + \Omega \text{grad}\phi_r)], \quad (26)$$

which, with $\partial\phi_r/\partial Y$ neglected as above, becomes

$$\begin{aligned} \Delta \left[UV \left(\frac{\partial \phi_r}{\partial X} \frac{\partial \phi_l}{\partial X} + \frac{\partial \phi_r}{\partial z} \frac{\partial \phi_l}{\partial z} \right) \right. \\ \left. + U\Omega \left(\frac{\partial \phi_r}{\partial X} \frac{\partial \phi_r}{\partial X} + \frac{\partial \phi_r}{\partial z} \frac{\partial \phi_r}{\partial z} \right) \right]. \end{aligned} \quad (27)$$

Here the terms in $\partial\phi_l/\partial X$ and $\partial\phi_l/\partial z$ are expected by (13) to be very small, and the term in $\partial\phi_r/\partial z$ may like ϕ_r itself be estimated as zero on both theories given in the Appendix. The leading term in (27) is therefore

$$U\Omega \frac{\partial \phi_r}{\partial X} \Delta \left(\frac{\partial \phi_r}{\partial X} \right) = U\Omega \frac{\partial \phi_r}{\partial X} (-2bk_1), \quad (28)$$

where the last factor was seen in equation (25) to be substantial. The immediately preceding factor $\partial\phi_r/\partial X$, however, makes the product (28) small compared with the important third term in (23). This is because the potential ϕ_r describes fluid motions generated by the head when it moves forward at unit velocity along its plane of symmetry. For a thin streamlined head, the value of $\partial\phi_r/\partial X$ must therefore be small compared with 1 at points like the lateral recesses, simply because the symmetrical movement of the head disturbs the fluid relatively little.

In further justification of the neglect of (28), we note that in combination with the last term in (23) it makes an overall contribution to Δp of $2b(k_1 - 1) \rho U \Omega \partial\phi_r/\partial X$. For both model problems treated in the Appendix this can be neglected because (i) in elongated-body theory it is zero since $\partial\phi_r/\partial X = 0$, while (ii) for the ellipsoid $\partial\phi_r/\partial X$ takes the small value 0.10 while also $k_1 - 1$ is only 0.11 so that their product is only about 1% of the value of k_1 itself.

Finally, then, the combination of the term (26) in Δp and the last term in (23) can be neglected, and Δp is given by equations (5), (23), (24) and (25) as

$$\Delta p = -\rho \Delta(\partial\phi_l/\partial t) = 2bk\rho(dV/dt) - 2bk_1\rho U\Omega. \quad (29)$$

However, in this expression the term dV/dt must not be directly equated to the head's lateral acceleration A , because at each instant U and V are taken as the components of velocity along the X -axis and the Y -axis. Figure 2 shows, in fact, that, because the X - and Y -axes are rotating,

$$A = dV/dt + U\Omega; \quad (30)$$

indeed, in a small time interval δt , the angular velocity Ω turns the X -axis through an angle $\Omega\delta t$ so that the velocity U in the X -direction acquires a

lateral component $U(\Omega\delta t)$ in addition to the change δV in the Y -component of velocity.

Equations (29) and (30) taken together give as this section's final conclusion

$$\Delta p = 2bk\rho A - 2bK\rho U\Omega, \quad (31)$$

where the constant K takes a value

$$K = k + k_1 \quad (32)$$

which, according to the previous discussion, is in the general neighbourhood of 3. Equation (31) for Δp is, of course, the source of the equation (4) for $(\Delta p)_{\text{eff}}$ already quoted in § 1. Some of the implications of this result are studied in the next section.

4. DO CLUPEID FISHES VARY Ω SO AS TO KEEP $(\Delta p)_{\text{eff}}$ SMALL?

Clupeid fishes are an exceptional group in that the lateral line is confined to the head. Lateral-line neuromasts, moreover, respond sensitively to flows induced by motions in the subcerebral canal. These, in turn, are forced by the effective pressure difference $(\Delta p)_{\text{eff}}$ across the head; which, in swimming, varies with the head's lateral acceleration A and angular velocity Ω in accordance with equation (4).

By contrast, Denton & Gray (1983) showed how pressure fields of neighbouring fishes can be expected to have essentially no influence on $(\Delta p)_{\text{eff}}$. This is because the density of the head is close to the density of water, ρ , while the flexibility of the neck allows the head to respond to any externally induced pressure difference Δp rather like a small volume of water, with an acceleration

$$A = -\frac{1}{\rho} \frac{\partial p}{\partial y} = -\frac{1}{\rho} \frac{\Delta p}{2b}, \quad (33)$$

which makes $(\Delta p)_{\text{eff}}$ zero.

No such requirement applies, on the other hand, to the effects of the fish's own regular swimming by oscillations of the caudal fin. These cause the water to act on the caudal fin with sideforces to which the fish's entire body must necessarily respond with 'recoil' movements including both sideslip and yawing movements. The head, in particular, is caused by sideslip to push against the water so that the resulting Δp , far from assuming the opposite sign to that of A as in (33), is a positive multiple of A – which makes $(\Delta p)_{\text{eff}}$ a still larger multiple as in (3).

If on the other hand the fish by muscular action could control the value of Ω by means of periodic neck deflections, then in principle it could cancel out this effect (3) of A on $(\Delta p)_{\text{eff}}$ by an equal and opposite contribution from Ω to expression (4). In this context uncertainty about the coefficients in (4) – whether on the part of the analyst or of the fish! – is of course quite irrelevant, because the lateral-line neuromasts provide the perfect 'closed-loop' control system, with feedback directly proportional to the quantity $(\Delta p)_{\text{eff}}$ which is to be kept small.

The question of what advantages this might bring to a clupeid fish is readily answered once attention is

redirected from the external irrotational motions (§§ 2 and 3) to the flow inside the thin boundary layer on the fish's head. This is the layer of fluid which the fish's swimming motion causes to be dragged forward through the action of viscous stresses within the water. Because water has such a low viscosity μ , the layer's thickness remains small, a typical estimate on a head of length a being

$$(\mu a / \rho U)^{1/2}, \quad (34)$$

which is considerably less than 1 mm for normal swimming velocities U of around 1 m s^{-1} .

Apart from the forces dragging forward the fluid in this boundary layer, there are also components of force within the plane of a cross-section acting on that fluid. These include, naturally, forces due to gradients of fluid pressure; but, when the fish's head (to which the boundary layer is attached) has lateral acceleration A , they include also an inertial effect, equivalent to a force $(-\rho A)$ per unit volume. In short, boundary-layer fluid is subjected to exactly the same influences as the fluid in the subcerebral canal.

We may show, furthermore, that when the effective pressure difference $(\Delta p)_{\text{eff}}$ forcing fluid in the subcerebral canal is zero then there is also no net force component acting on boundary-layer fluid within the plane of a cross-section. In order to demonstrate this, we use the coordinate Y (see § 3) which varies from $Y = -b$ to $Y = +b$ in the cross-section through the lateral recesses. Then the inertial effect on all the fluid moving with the cross-section is known to be equivalent to the effect of a pressure distribution ρAY , whose gradient would produce the same force per unit volume. If therefore we can show that the actual distribution of pressure p over a cross-section takes the value

$$(\Delta p)Y/2b, \quad (35)$$

then the total effective pressure distribution must take the value

$$(\Delta p)Y/2b + \rho AY = (\Delta p)_{\text{eff}} Y/2b, \quad (36)$$

which is negligibly small when and only when the same is true for $(\Delta p)_{\text{eff}}$.

The demonstration may now be concluded by noting that the pressure distribution over the cross-section is shown in the Appendix to take precisely the form (35) on both model problems treated there; that is, on elongated-body theory and also in exact calculations for an ellipsoid. (In both cases, moreover, this distribution is found in relation to each of the two potential terms $\Delta\phi_1$ and $\Delta(\partial\phi_r/\partial X)$ which contribute, as (23) shows, to Δp .) Probably, then, this form (35) is close enough for the flow over the real fish's head with its expected characteristics intermediate between these two models.

In the usual language of boundary-layer theory, the above analysis has indicated that crossflow in the boundary layer (motions in the plane of a cross-section) will be kept small over the head under

precisely the condition that $(\Delta p)_{\text{eff}}$ remains small. Almost certainly, this minimization of boundary-layer crossflow generates substantial reductions in hydrodynamic resistance that should be particularly advantageous to continually swimming fishes like clupeids.

Essentially, the boundary layer without any crossflow is similar to that appearing on a fish which is simply gliding forward. The streamlined shape of the fish is then being fully utilized to reduce resistance.

Intermittent swimming, as observed in many groups of fishes, often exhibits an alternation of 'beat' and 'glide' phases. In this swimming 'gait', dissipation of the fish's kinetic energy by hydrodynamic resistance is kept to a minimum during the 'glide' phase, even though restoration of that kinetic energy during the actively swimming 'beat' phase is accompanied by a much enhanced – perhaps, even quadrupled (Lighthill 1975, p. 115) – rate of dissipation, associated with an augmentation of resistance due to boundary-layer crossflows. Advantages in energy expenditure to achieve a given average swimming speed are easily seen in accrue under these circumstances.

For continually swimming fishes like the clupeids, however, it may be highly advantageous to win some of these benefits of reduced resistance even in the actively swimming condition. Admittedly, the suggested control system for minimizing $(\Delta p)_{\text{eff}}$ would only be effective for eliminating boundary-layer crossflow over the head; nevertheless, this effect by itself may be expected to eliminate a significant part of the extra resistance due to swimming. Furthermore, by starting the boundary layer off in a crossflow-free state over the head, it should delay any build-up of substantial boundary-layer crossflows on posterior parts of the fish's body.

The values of Ω which the fish would have to produce in order to win these benefits are indicated by equation (4). Essentially, Ω needs to be in phase with A and almost equal to A/U in magnitude; more accurately, Ω should be $0.87A/U$ where the factor 0.87 represents our estimate of $(1+k)/K$.

It is interesting that, according to equation (30), such a requirement keeps changes in V (the velocity component perpendicular to the yawed head of the fish) quite small. This moreover (see figure 1) requires that the yaw angle α is close to V_0/U , where $V_0 = \dot{y}_0$ is the velocity component perpendicular to the direction of fish swimming. (In other words, V_0 is the sideslip velocity; and, still more accurately, α should be kept close to $0.87V_0/U$.)

These conditions do not appear to demand any excessively large angles of neck deflection. On the other hand, it is important to note that both of them describe a condition that differs greatly from any likely passive response of the head to sideforces on the caudal fin. Such forces while producing directly an acceleration A are likely rather to generate a rate of change of angular velocity in an essentially passive response, in which case A and Ω would be not in phase but in quadrature. Again, the yaw angle α in a passive response might take a maximum value around $h/(\frac{1}{2}l)$ where h is the amplitude of the head's lateral displacement y_0 and l the fish's length; while the amplitude of

\dot{y}_0/U for radian frequency ω would be $\omega h/U$. The latter value would be five times greater than α in typical conditions of fish swimming with $\omega l/U \doteq 10$.

The control process proposed, then, is essentially an active one, directly dependent on feedback from the lateral-line neuromasts. For further details of this proposal, see the preceding paper by Denton & Gray (1993).

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APPENDIX. ESTIMATES OF THE VALUES OF THE CONSTANTS k AND k_1 FOR A CLUPEID FISH

A.1. INTRODUCTION

This paper's main conclusions (see equation (4), for example) are expressed in terms of two constants k and k_1 together with their combined form $K = k + k_1$. The constant k is defined by equation (14) in terms of the velocity potential ϕ_l of motions induced by a lateral movement of the fish's head at unit velocity. The constant k_1 is similarly defined by equation (25) in terms of a longitudinal gradient $\partial\phi_r/\partial X$ of the velocity potential ϕ_r of motions generated by rotation of the fish's head at unit angular velocity.

Evidently, the values of these constants depend on the shape of the head, which exhibits significant variation between different clupeid species and between individuals within a species. It is therefore fortunate that the general argument of this paper in no way depends on knowing k and k_1 precisely. On the other hand, it is desirable to estimate their values to a rough approximation.

The most obvious classical method by which such an estimate might be attempted is the elongated-body theory (see, for example, chapters 2, 4 and 5 of Lighthill (1975)). On this approximate theory, the values of the constants would depend only on the local shape of the cross-section of the head through the lateral recesses. In § A.2 some data on this cross-

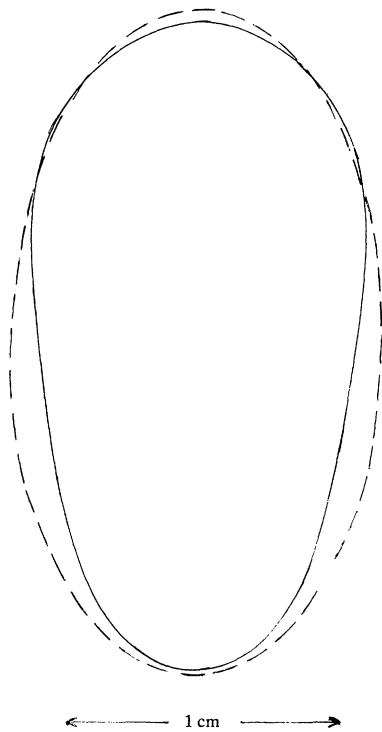


Figure 3. Plain line: cross-section through the lateral recesses of the head of a herring of length 10 cm. Broken line: ellipse of axis-ratio 1.8:1.

sectional shape obtained for a herring by Denton and Gray are shown to suggest that it does not deviate greatly from an ellipse with vertical and horizontal axes in the ratio 1.8:1.

For this elliptical shape, elongated-body theory is used in § A.2 to calculate both k and k_1 , and also to verify (see § 4) that the associated pressure distributions vary linearly with Y . It is shown, furthermore, how the basic expression (31) for the pressure difference is fully consistent with a standard formulation of elongated-body theory as presented on pp. 73–76 of Lighthill (1975).

On the other hand, those pages do themselves emphasize the only crudely approximate character of elongated-body theory. Indeed, this theory gives results which depend solely on the local cross-section of the fish's head, so that they neglect the variability of the shape of neighbouring cross-sections. It is desirable to obtain an estimate of to what extent this variability may affect k and k_1 .

The biggest variations in the cross-sectional shapes measured on a herring by Denton and Gray are of course found anterior to the lateral recesses, where the cross-section gradually tapers to a point at the mouth. This suggests the value of recalculating k and k_1 for a shape with this property that roughly approximates their measurements. Such a shape is the front half of an ellipsoid, with its axes in the ratio 4.5:1.8:1 (the greatest of these three axes being in the X -direction and the least in the Y -direction).

Actually, for the complete ellipsoid, ϕ_l and ϕ_r take forms that are classical (Lamb 1932, pp. 152–155) and

§ A.3 infers the numerical values of k and k_1 in this case, as well as verifying once more that the pressure distributions corresponding to ϕ_l and to $\partial\phi_r/\partial X$ are linear in Y . All of these results for an ellipsoid tend in the limit as its greatest axis becomes infinite to results for a cylinder of uniform elliptic cross-section which coincide with those of elongated-body theory.

The actual shape of a clupeid fish takes a form more like the ellipsoid anterior to, and more like the elliptic cylinder posterior to, the lateral recesses. This consideration suggests that, without entering into exhaustive computations, we may just use values of k and k_1 intermediate between the two cases (although slightly closer to the ellipsoid than in the elliptic cylinder because the fish's cross-section does taper – albeit far more gradually – towards the posterior end).

A.2. ESTIMATES FROM ELONGATED-BODY THEORY

E. J. Denton and J. A. B. Gray (unpublished results) took photographs of sections of the gelatine-embedded head of a herring, and the plain line in figure 3 reproduces a tracing of the cross-section through the lateral recesses. The broken line represents an ellipse with axis-ratio 1.8:1. In the context of an attempt to estimate k and k_1 to just a rough approximation the agreement may perhaps be regarded as good enough.

Elongated-body theory assumes that the local potential generated by the movement of any cross-section is simply the two-dimensional potential associated with that cross-section's shape. In other words, it is the potential associated with movement of a long cylinder with the same cross-section.

It is of course straightforward to derive the two-dimensional potential ϕ_l generated when an ellipse, of axes b and $c > b$ in the Y - and z -directions respectively, moves with unit velocity in the Y -direction. Classically, such a derivation utilises the conformal mapping (see, for example, p. 166 of Lighthill (1986)) of the exterior of the ellipse into the exterior of a circle.

In terms of a complex variable

$$Z = z + iY, \quad (\text{A1})$$

the required mapping takes a form

$$Z = \zeta + (R_0^2/\zeta), \quad (\text{A2})$$

where R_0 is a constant. Then the outside of the circle $|\zeta| = R_1$ (where $R_1 > R_0$ is another constant) is mapped into the outside of the above ellipse if

$$c = R_1 + (R_0^2/R_1), \quad b = R_1 - (R_0^2/R_1). \quad (\text{A3})$$

In particular, equation (A2) maps a point on the circle,

$$\zeta = R_1 e^{i\Theta}, \quad \text{into a point } z = c \cos\Theta, \quad Y = b \sin\Theta, \quad (\text{A4})$$

on the ellipse.

Now, in the ζ -plane, a motion for which the complex potential (that is, an analytic function of ζ of which the velocity potential ϕ is the real part) is

$$i(\zeta - (R_1^2/\zeta)) \quad (\text{A5})$$

represents a two-dimensional flow around the stationary circular boundary $|\zeta|=R_1$, and is mapped into a similar flow around the stationary ellipse that has unit velocity in the negative Y -direction at large distances (where it makes $\phi \sim -Y$). Addition of a uniform flow with unit velocity in the positive Y -direction, with complex potential

$$-iZ = -i(\zeta + (R_0^2/\zeta)), \quad (\text{A6})$$

now gives the required potential ϕ_1 (associated with the ellipse's movement at unit velocity through stationary fluid) as the real part of the sum

$$-i(R_1^2 + R_0^2)/\zeta, \quad (\text{A7})$$

of (A5) and (A6). On the ellipse itself, the results (A3) and (A4) show then that

$$\phi_1 = - (R_1^2 + R_0^2)/R_1 \sin \Theta = -c \sin \Theta = - (c/b)Y. \quad (\text{A8})$$

Equation (A8) demonstrates that proportionality of ϕ_1 to Y which was remarked upon in § 4, and also gives

$$\Delta\phi_1 = -2bk \quad \text{with} \quad k = c/b. \quad (\text{A9})$$

In short, the constant k as defined by equation (14) is simply equal to the axis-ratio of the ellipse, and assumes the value 1.8 for the shape illustrated in figure 3.

The other constant k_1 depends on the potential ϕ_r associated with a different instantaneous movement of the fish's head. This is a rotation about the central point $X=Y=0$ with unit angular velocity $\Omega=1$ (see figure 1), so that for each X the local cross-section moves in the Y -direction with velocity equal to X . Now, on elongated-body theory, the local potential is simply the two-dimensional potential associated with the shape and movement of the local cross-section; and, in the neighbourhood of $X=0$, it follows that

$$\phi_r = X\phi_1(Y, z) \quad (\text{A10})$$

where the ϕ_1 given above, as the real part of (A7), is simply the potential generated by the cross-section's movement at unit velocity.

In particular, the values of both ϕ_r itself and $\partial\phi_r/\partial z$ at the cross-section $X=0$ are zero as stated in § 3. By contrast, the X -gradient $\partial\phi_r/\partial X$ which dominates an important term in the pressure is actually equal to ϕ_1 ; and, like it, is proportional to Y as assumed in § 4. Furthermore, the constant k_1 is given by

$$\Delta(\partial\phi_r/\partial X) = \Delta\phi_1 = -2bk_1 \quad \text{with} \quad k_1 = k = c/b, \quad (\text{A11})$$

and it follows that $K = k + k_1 = 2k$ so that equation (31) takes the form

$$\Delta p = 2bk\rho(A - 2U\Omega), \quad (\text{A12})$$

on the approximations of elongated-body theory.

Although this theory can be simply used as above to estimate constants k and k_1 for insertion in the general analysis of § 3, nevertheless elongated-body theory is alternatively able to offer as follows a direct route to the determination of Δp . Such a determination may

be readily derived from the standard formulation of elongated-body theory, as given on pp. 73–76 of Lighthill (1975); even though this expresses results in terms not of Δp but of a closely related quantity: the sideforce,

$$Z \text{ per unit length}, \quad (\text{A13})$$

with which a cross-section of fish acts on the water.

The notation (different from that of the present paper) used in those pages takes x as the distance of a cross-section from the anterior end of a fish swimming with velocity U and $h(x, t)$ as the lateral displacement of that section at time t . Then, as water passes the fish's body at relative velocity U , it is pushed laterally with a velocity

$$w = \partial h/\partial t + U \partial h/\partial x. \quad (\text{A14})$$

The associated lateral momentum of water per unit length may be written

$$m(x) w(x, t), \quad (\text{A15})$$

in terms of an added-mass (or virtual-mass) coefficient. Finally, a slice of water (of unit thickness) travelling at speed U past the fish acquires momentum at a rate

$$Z = (\partial/\partial t + U \partial/\partial x) m(x) w(x, t), \quad (\text{A16})$$

equal to the sideforce Z per unit length.

Now, at any point where the sectional shape as reflected in the coefficient $m(x)$ is not varying significantly with x , the results (A14) and (A16) taken together give

$$\begin{aligned} Z &= m(x) \left(\frac{\partial}{\partial t} + U \frac{\partial}{\partial x} \right) \left(\frac{\partial h}{\partial t} + U \frac{\partial h}{\partial x} \right) \\ &= m(x) \left(\frac{\partial^2 h}{\partial t^2} + 2U \frac{\partial^2 h}{\partial x \partial t} + U^2 \frac{\partial^2 h}{\partial x^2} \right). \end{aligned} \quad (\text{A17})$$

In particular, for the head of a clupeid fish in rigid-body motion with α as the angle of yaw (and no centre-line curvature), the equations

$$\frac{\partial h}{\partial x} = -\alpha \left(\text{giving} \quad \frac{\partial^2 h}{\partial x \partial t} = -\Omega \right) \quad \text{and} \quad \frac{\partial^2 h}{\partial x^2} = 0, \quad (\text{A18})$$

may be used, so that expression (A17) for Z can be written

$$Z = m(A - 2U\Omega); \quad (\text{A19})$$

which accords with the form that was obtained in (A12) from application of the theory of § 3 with the constants K and k_1 given by (A11). This simple check (which need not be pursued further) has been included just to demonstrate that the present analysis is consistent with results obtained by other methods.

A.3. ESTIMATES FOR AN ELLIPSOIDAL SHAPE

The general idea of fitting the measured shape of a herring's head by the front half of an ellipsoid was

explained in § A.1. Here it is again emphasized that such a fit only needs to be made to quite a crude approximation, as given in figure 4 on the basis of photographs (E. J. Denton & J. A. B. Gray, unpublished results) of a herring's head and of cross-sections thereof.

Here an ellipsoid with axes in the ratios 4.5:1.8:1 has been used for such a crudely approximate fit. Figure 4a compares a tracing of the head's plane of symmetry with the corresponding curve (front half of an ellipse with axis-ratio 4.5:1) for the ellipsoid. In addition, figures 4b and 4c make comparisons of tracings of the cross-sections I and II with the corresponding cross-sections (ellipses of axis-ratio 1.8:1) for the ellipsoid. These are additional to the comparison at cross-section III made already in figure 3.

In attempting this rough fit, the criterion adopted was to represent the head by a half-ellipsoid as well as was practically possible without imposing any requirement that the cross-section III through the lateral recesses should be situated exactly at the ellipsoid's centre. Now the estimation of k and k_1 will be carried out in two stages. First of all, they are estimated on the oversimplified assumption that the lateral recesses lie on the central plane of the ellipsoid; afterwards, the effects of their position being somewhat displaced from the central plane are studied, and found to be insignificant.

In the first of these investigations, then, the central plane of the ellipsoid is taken as the plane defined by $X=0$ in the coordinate system of § 3. The semi-axis in the Y -direction is b (where $2b$ is the distance between the lateral recesses), while those in the X - and z -directions are a and c with

$$a:c:b = 4.5:1.8:1. \quad (\text{A20})$$

(These notations adhere to the convention that semi-axes, a , b , c , are in the directions X , Y , z respectively, though not to any convention that their magnitudes should be in descending order.) The equation of the ellipsoidal surface is then

$$\frac{X^2}{a^2} + \frac{Y^2}{b^2} + \frac{z^2}{c^2} = 1. \quad (\text{A21})$$

All of the required results are readily obtained by minor adaptations of the analysis on pp. 148–155 of Lamb (1932). (Readers should, however, be warned that the specification for the potential ϕ used in all modern work, including the present paper, with the fluid velocity equal to $+\text{grad}\phi$, has opposite sign to the potential which Lamb adopted, with velocity $-\text{grad}\phi$.)

The required potentials ϕ_1 and ϕ_r take simple forms in terms of ellipsoidal coordinates λ , μ , ν such that the given ellipsoid (A21) is the surface $\lambda=0$. The relationship between the cartesian coordinates X , Y , z and these ellipsoidal coordinates is such that

$$\frac{\partial X}{\partial \lambda} = \frac{\frac{1}{2}X}{a^2 + \lambda}, \quad \frac{\partial Y}{\partial \lambda} = \frac{\frac{1}{2}Y}{b^2 + \lambda}, \quad \frac{\partial z}{\partial \lambda} = \frac{\frac{1}{2}z}{c^2 + \lambda}, \quad (\text{A22})$$

(see Lamb 1932, p. 149).

The potential ϕ_1 may be shown to take a form

$$\phi_1 = -C_2 Y \int_{\lambda}^{\infty} \frac{d\lambda}{(a^2 + \lambda)^{1/2} (b^2 + \lambda)^{3/2} (c^2 + \lambda)^{1/2}}, \quad (\text{A23})$$

with C_2 constant. Here, the boundary condition on ϕ_1 , specifying unit velocity of the surface in the Y -direction, gives

$$\partial\phi_1/\partial\lambda = \partial Y/\partial\lambda \quad \text{for} \quad \lambda = 0. \quad (\text{A24})$$

By (A22), this may be written

$$\frac{C_2 Y}{ab^3c} - \frac{C_2 Y \beta_0}{2b^2 abc} = \frac{Y}{2b^2} \quad (\text{A25})$$

in terms of the non-dimensional constant

$$\beta_0 = abc \int_0^{\infty} \frac{d\lambda}{(a^2 + \lambda)^{1/2} (b^2 + \lambda)^{3/2} (c^2 + \lambda)^{1/2}}, \quad (\text{A26})$$

and this determines the value of C_2 as

$$C_2 = abc/(2 - \beta_0). \quad (\text{A27})$$

Equations (A23) and (A26) show that the value of ϕ_1 on the surface of the ellipsoid is

$$\phi_1 = -(C_2 Y \beta_0)/abc = -\beta_0 Y/(2 - \beta_0), \quad (\text{A28})$$

and this confirms its direct proportionality to Y as stated in § 4. Furthermore, equation (A28) gives

$$\Delta\phi_1 = -2bk \quad \text{with} \quad k = \beta_0/(2 - \beta_0). \quad (\text{A29})$$

A simple numerical integration in the case (A20) now gives

$$\beta_0 = 1.184, \quad k = 1.45. \quad (\text{A30})$$

It may be of some interest to quote also the value of ϕ_r which (as we find by interchanging the X and Y coordinates and the corresponding axes a and b) is

$$\phi_r = -C_1 X \int_{\lambda}^{\infty} \frac{d\lambda}{(a^2 + \lambda)^{3/2} (b^2 + \lambda)^{1/2} (c^2 + \lambda)^{1/2}}, \quad (\text{A31})$$

with

$$C_1 = \frac{abc}{2 - \alpha_0} \quad \text{where} \quad \alpha_0 = abc \int_0^{\infty} \frac{d\lambda}{(a^2 + \lambda)^{3/2} (b^2 + \lambda)^{1/2} (c^2 + \lambda)^{1/2}}. \quad (\text{A32})$$

Here, numerical integration gives $\alpha_0=0.185$. An estimate of $\partial\phi_r/\partial X$ for $X=0$, which was given in § 3, was obtained from (A31) as

$$\left(\frac{\partial\phi_r}{\partial X}\right)_{X=0} = -C_1 \frac{\alpha_0}{abc} = -\frac{\alpha_0}{2 - \alpha_0} = -0.102. \quad (\text{A33})$$

Next, ϕ_r is given in the form

$$\phi_r = -C_0 XY \int_{\lambda}^{\infty} \frac{d\lambda}{(a^2 + \lambda)^{3/2} (b^2 + \lambda)^{3/2} (c^2 + \lambda)^{1/2}} \quad (\text{A34})$$

and must satisfy the boundary condition

$$\frac{\partial\phi_r}{\partial\lambda} = X \frac{\partial Y}{\partial\lambda} - Y \frac{\partial X}{\partial\lambda} \quad \text{on} \quad \lambda = 0. \quad (\text{A35})$$

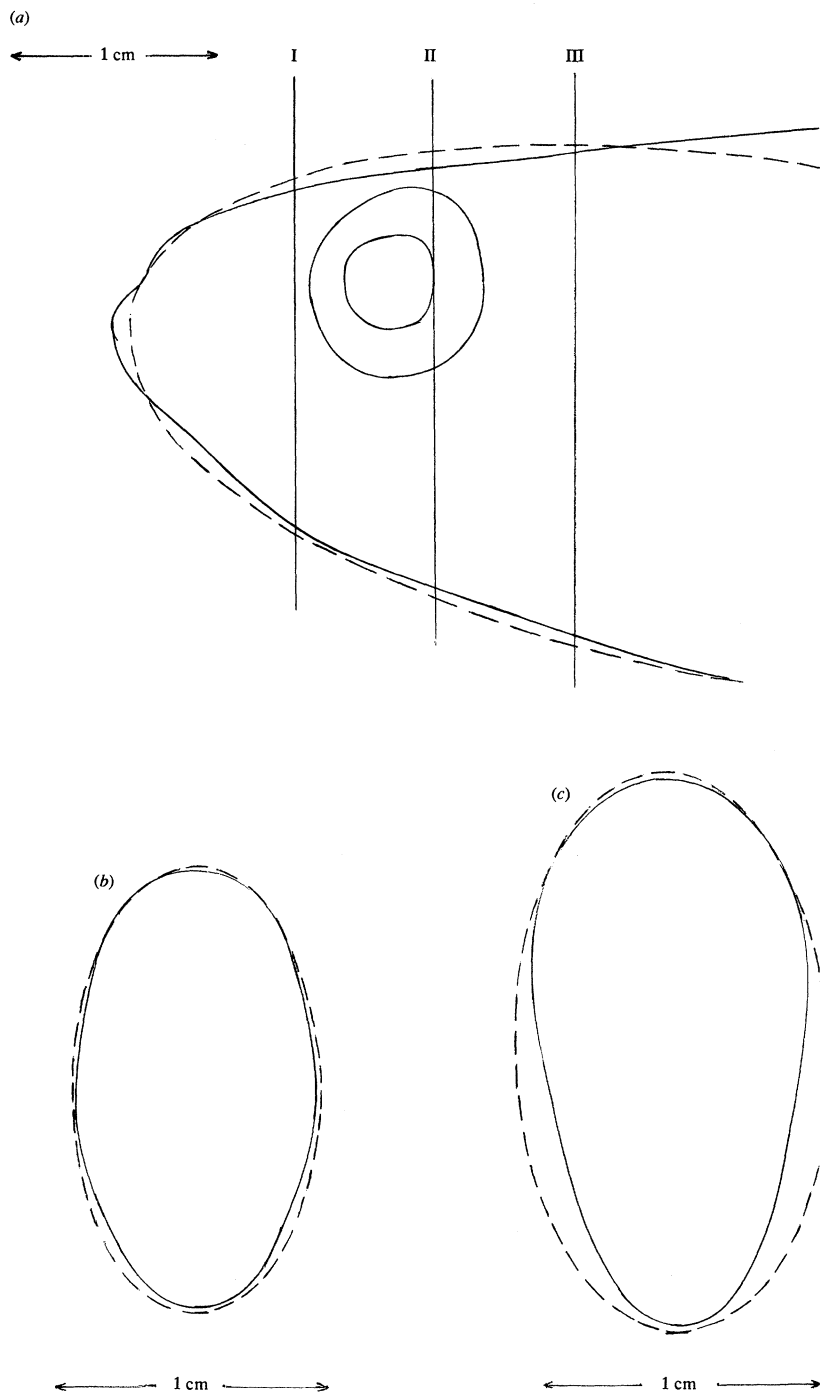


Figure 4. (a) Plain line: plane of symmetry of the head of a herring of length 10 cm. Broken line: ellipse of axis-ratio 4.5:1. For cross-sections at planes I, II and III see figures 4(b), 4(c) and 3 respectively. (b) Plain line: cross-section of herring head by plane marked I in (a). Broken line: ellipse of axis-ratio 1.8:1. (c) Plain line: cross-section of herring head by plane marked II in (a). Broken line: ellipse of axis-ratio 1.8:1.

But because, according to equations (A26) and (A32),

$$\beta_0 - \alpha_0 = abc(a^2 - b^2) \int_0^\infty \frac{d\lambda}{(a^2 + \lambda)^{3/2} (b^2 + \lambda)^{3/2} (c^2 + \lambda)^{1/2}}, \quad (\text{A36})$$

this boundary condition may be written

$$C_0 \left[\frac{XY}{a^3 b^3 c} - \frac{1}{2} XY \left(\frac{1}{a^2} + \frac{1}{b^2} \right) \frac{\beta_0 - \alpha_0}{abc(a^2 - b^2)} \right] =$$

$$\frac{1}{2} XY \left(\frac{1}{b^2} - \frac{1}{a^2} \right), \quad (\text{A37})$$

so that

$$C_0 = \frac{(a^2 - b^2) abc}{2 - \frac{a^2 + b^2}{a^2 - b^2} (\beta_0 - \alpha_0)}. \quad (\text{A38})$$

These results confirm once more that $\phi_r = 0$ on the plane $X=0$ as stated in § 3. Also, equations (A34) and

(A36) show that, on the cross-section $X=0$ of the ellipsoidal surface $\lambda=0$,

$$\frac{\partial\phi_r}{\partial X} = -C_0Y \frac{\beta_0 - \alpha_0}{abc(a^2 - b^2)} = -k_1Y, \quad (\text{A39})$$

with

$$k_1 = \frac{(a^2 - b^2)(\beta_0 - \alpha_0)}{2(a^2 - b^2) - (a^2 + b^2)(\beta_0 - \alpha_0)}. \quad (\text{A40})$$

Note that the X -differentiation (A39) is carried out keeping λ constant because the X -direction is tangential to the surface $\lambda=0$. Also, while once again confirming the proportionality to Y stated in § 4, equation (A39) specifies k_1 as the constant defined so that $\Delta(\partial\phi_r/\partial X) = -2bk_1$. Finally, the numerical values for α_0 and β_0 given above for the axis-ratios (A20) lead to the value $k_1 = 1.11$ quoted in § 3.

All of the above estimates for the ellipsoidal shape (A21) in relation to the case when the lateral recesses lie in the central plane $X=0$ are changed very little when they lie in a plane $X=X_0$ displaced, like the plane III of figure 4, by just a moderate fraction of the semi-axis a . In such a case, of course, the distance between the lateral recesses is altered to $2b_0$, with

$$b_0 = b \left(1 - \frac{X_0^2}{a^2}\right)^{1/2}, \quad (\text{A41})$$

and it is this value b_0 that must replace b in the definitions (14) and (25) of k and k_1 . On the other hand, since equations (A28) and (A29) give $\phi_1 = -kY$ on the surface, it follows that

$$\Delta\phi_1 = -2b_0k, \quad (\text{A42})$$

without any change whatsoever in k .

A little more care is needed to derive the corresponding result for k_1 . First of all, this depends on the potential $\phi_{r,0}$ for rotation at unit velocity about an axis $X=X_0$, $Y=0$. The relationship between $\phi_{r,0}$ and the potentials defined above (ϕ_r for rotation about $X=Y=0$ and ϕ_1 for translation in the y -direction) is readily seen to be

$$\phi_{r,0} = \phi_r - X_0\phi_1. \quad (\text{A43})$$

Secondly, in the determination of $\partial\phi_{r,0}/\partial X$, it is less obvious than in (A39) that λ can legitimately be kept

constant when the X -differentiation is carried out. If it could, then equation (A23) would give $\partial\phi_1/\partial X=0$ so that

$$\begin{aligned} \frac{\partial\phi_{r,0}}{\partial X} &= \\ \frac{\partial\phi_r}{\partial X} &= -k_1Y \quad \text{and} \quad \Delta\left(\frac{\partial\phi_{r,0}}{\partial X}\right) = -2b_0k_1, \end{aligned} \quad (\text{A44})$$

as in (A39) and (A40).

Although the results (A44) are not exact, nevertheless they are a close approximation where the surface is inclined at only a small angle Θ to the X -direction. Then, because $\phi_{r,0}$ is the potential for rotation at unit angular velocity about $X=X_0$, $Y=0$, the derivative $\partial\phi_{r,0}/\partial n$ along the outward normal to the ellipsoid is itself small (equal to $\pm b_0\sin\Theta$ at $Y=\pm b_0$) and the main difference between values of $\partial\phi_{r,0}/\partial X$ keeping Y constant or keeping λ constant is proportional to $\partial\phi_{r,0}/\partial n$. Specifically,

$$\frac{\partial\phi_{r,0}}{\partial X} = \left(\frac{\partial\phi_{r,0}}{\partial X}\right)_{\lambda\text{const}} \cos\Theta + \frac{\partial\phi_{r,0}}{\partial n} \sin\Theta, \quad (\text{A45})$$

so that

$$\Delta\left(\frac{\partial\phi_{r,0}}{\partial X}\right) = -2b_0(k_1 \cos\Theta + \sin^2\Theta), \quad (\text{A46})$$

where the bracketed quantity on the right-hand side represents a corrected value of k_1 . In a case like that shown in figure 4, however, with X_0/a about 0.3, the angle Θ is about 4° and then the correction to k_1 only changes it in the third decimal place, and is of no importance in the context of the present paper.

The final conclusion of this Appendix, then, is that the constants k and k_1 , which are both 1.8 on elongated-body theory (§ A.2), take the smaller values 1.45 and 1.11 respectively for the ellipsoidal shape. As explained at the end of § A.1, appropriate choices for the values of k and k_1 will be intermediate between the estimates given on the two theories, but slightly closer to those for the ellipsoidal shape; which leads to the proposed rough estimates

$$k = 1.6 \quad \text{and} \quad k_1 = 1.4. \quad (\text{A47})$$