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# BENDING MOMENTS AND MUSCLE POWER IN SWIMMING FISH

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SUMMARY Many fish propel themselves through the water by sending waves of lateral curvature along their bodies from head to tail. A kinematic analysis of high-speed motion pictures of swimming saithe and eel, and a subsequent hydrodynamic analysis based on slender-body theory, shows that the bending moment generated by the muscles does not run like a wave along the body, but has a standing-wave character. This finding yields a completely novel insight into the way fish muscles work.

## 1 INTRODUCTION

Gray (1933), describing the movements of fish, noted that "waves of curvature pass along the body alternately on the two sides". Just how a fish manages to achieve this is the subject matter of this paper. I consider the dynamics of fish swimming with periodic lateral movements of body and tail. Obviously the fish must generate bending moments inside its body. This paper deals with the bending moment and the power associated with it, and is based on an analysis of the swimming motion of saithe (Pollachius virens) and eel (Anguilla anguilla) as recorded on high-speed films. The data for saithe (from 13 sequences) are reported in more detail elsewhere (Videler & Hess, 1983; Hess & Videler, 1983a), and the results for eel (from 9 sequences) are preliminary, the full analysis (Hess & Videler, 1983b) not being completed at the time of writing this paper. For a general survey of the hydrodynamics of animal locomotion the reader is referred to Lighthill (1969).

I use dimensionless quantities: the length unit is the fishlength L, the time unit is the period T of the lateral motion, and the mass unit is such that the density of water (which is also the mean density of the fish) $\rho$ equals 1.

## 2 LATERAL MOTION

The coordinate system x, y, z is such that the fish stays near the x-axis, its nose at x = 0, its tail at x = 1. The water flows in x-direction with velocity U. (U is the fish's swimming speed.) The z-axis points in lateral direction and the y-axis downward. The centre line (physically: the backbone) of the fish is described by:

$$z = h(x,t) \quad 0 \leq x \leq 1 \tag{1}$$

For any point x the lateral deflection can be represented by a Fourier series with odd frequencies:

$$h(x,t) = \sum_{j=1,3,5} \{a_j(x)\cos 2\pi jt + b_j(x)\sin 2\pi jt\} \tag{2}$$

As the higher frequencies are only significant in the tail region (Videler & Hess, 1983), and since they contribute negligibly to thrust and net power (Hess & Videler, 1983a), I consider in this paper only the first frequency and take

$$\begin{aligned} h(x,t) &= a(x)\cos 2\pi t + b(x)\sin 2\pi t \\ &= h^*(x)\cos 2\pi(t - \tau(x)) \end{aligned} \tag{3}$$

I choose the origin of the time coordinate at the instant of maximum first frequency tail deflection; hence $\tau(1) = 0$ by definition. The lateral body curvature $h''(x,t)$ is denoted by f:

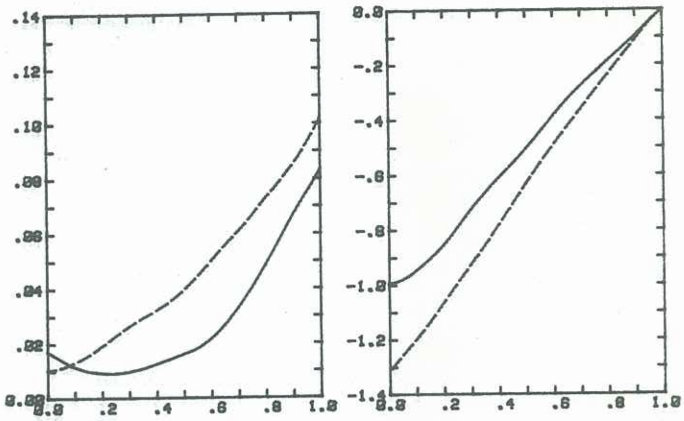

Fig. 1. Lateral deflection h(x, t) along body in saithe (drawn) and eel (dashed). (horizontal unit: L, nose at x = 0, tail at x = 1). Left: amplitude $h^*(x)$ (unit: L). Right: phase $\tau(x)$ (unit: T).

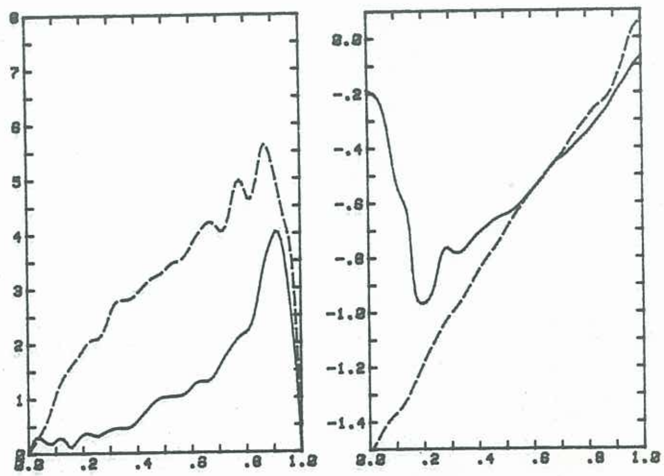

Fig. 2. Lateral curvature $-f(x,t)$ along body in saithe (drawn) and eel (dashed). Left: amplitude $f^*(x)$ (unit: $L^{-1}$). Right: phase $\sigma(x) + \frac{1}{2}$ (unit: T). The small-scale undulations in $f^*$ are due to noise in the original data, therefore the phase curve for saithe has no physical meaning for x < .2.

$$f(x, t) = a''(x)\cos 2\pi t + b''(x)\sin 2\pi t$$
$$= f^*(x)\cos 2\pi(t - \sigma(x)) \quad (4)$$

Although the actual swimming speeds in m/s varied over a large range, the swimming style as characterised by the dimensionless U, $h^*(x)$ and $\tau(x)$ appears to be fairly constant for a species (Videler & Hess, 1983). Therefore it makes sense to construct an "average" saithe and an "average" eel by taking the average values of the Fourier coefficients for each species. Some characteristic kinematic quantities for "average" saithe and eel are listed in Table 1. The Reynolds numbers varied between $2 \times 10^5$ and $8 \times 10^5$ for saithe, and between .7 $\times 10^4$ and $6 \times 10^4$ for eel.

Figure 1 shows the amplitude function $h^*(x)$ and the phase function $\tau(x)$ for "average" saithe and eel. Obviously a wave of lateral deflection runs along the body from head to tail. The amplitude is greatest at the tail. The wave speed V follows from $\tau'(x) = 1/V$; it is approximately constant in the posterior half of the body. Figure 2 gives graphs for the body curvature $-f(x, t)$. (I reversed the sign because f and h are mostly opposite in phase), it shows the curvature amplitude $f^*(x)$ and the phase function $\sigma(x) + \frac{1}{2}$. In both species a wave of lateral curvature runs from the anterior part to the tail. In eel the body curvature is much stronger, especially in the first three quarters of the body.

TABLE 1

SOME KINEMATIC QUANTITIES

| | | saithe: | eel: |
|---|---|---|---|
| Length (m) | L = | .37 | .14 |
| Period (s) | T = | .278 | .276 |
| Speed ($LT^{-1}$) | U = | .86 | .55 |
| Tail amplitude (L) | $h^*(1)$ = | .083 | .102 |
| Body wave speed ($LT^{-1}$) | V = | 1.04 | .79 |
| | U/V = | .82 | .69 |

## 3 DYNAMICS

The fish is treated as a thin flexible rod under the influence of hydrodynamic forces. This approach was outlined earlier by Wu (1971). Let M(x, t) be the lateral bending moment and $m_b(x)$ the body mass per unit length. The following equation between M and h can be derived:

$$\frac{\partial^2 M(x,t)}{\partial x^2} = m_b(x)\frac{\partial^2 h(x,t)}{\partial t^2} - L(x, t) \quad (5)$$

L(x, t) is the hydrodynamic lateral force acting on the fish per unit length. According to Lighthill's (1960) slender-body theory:

$$-L(x, t) = \left(\frac{\partial}{\partial t} + U\frac{\partial}{\partial x}\right)\{m_a(x)\left(\frac{\partial}{\partial t} + U\frac{\partial}{\partial x}\right) h(x, t)\} \quad (6)$$

where $m_a(x)$ is the sectional lateral added mass. At the nose and tail ends M and M' must vanish:

$$M(0, t) = M(1, t) = 0, \; M'(0, t) = M'(1, t) = 0 \quad (7)$$

For given U, $m_a(x)$, $m_b(x)$ and h(x, t) the equations (5) and (6) can be solved for M''(x, t). Integrating twice yields M(x, t). Two of the conditions (7) can be satisfied by adjusting the constants of integration. There remain two conditions, equivalent to Lighthill's (1960) recoil conditions, which generally will not be automatically satisfied for our h(x, t). A "recoil correction" can be made by adding a suitable (and hopefully very small) amount of stiff-body motion A(t) + x B(t). For details see Hess & Videler (1983a).

The power exerted by the bending moment per unit length is given by:

$$P_1(x, t) = M(x, t)\frac{\partial}{\partial t} h''(x, t) \quad (8)$$

For any x, both M and $\partial f/\partial t$ are periodic functions, oscillating around zero, hence $P_1$ becomes both positive and negative in the course of one period.
In the simplified periodic case M(x, t) is represented by:

$$M(x, t) = p(x)\cos 2\pi t + q(x)\sin 2\pi t$$
$$= M^*(x)\cos 2\pi(t - \mu(x)) \quad (9)$$

and $P_1(x, t)$ fluctuates around the mean value:

$$\bar{P}_1(x) = \pi\{p(x)b''(x) - q(x)a''(x)\}$$
$$= \pi\, f^*(x)M^*(x)\sin 2\pi(\sigma(x)-\mu(x)) \quad (10)$$

which is positive if $k < \sigma(x) - \mu(x) < k + \frac{1}{2}$ (k is any integer).

Using Lighthill's (1960) formulas for the mean total power $\bar{P}$ and the mean thrust $\bar{\Theta}$, yields:

$$\bar{P} = \tfrac{1}{2}U\, m_a(1)\{4\pi^2(a^2+b^2)+2\pi U(ba'-ab')\} \quad (11)$$

$$\bar{\Theta} = \tfrac{1}{4}\, m_a(1)\{4\pi^2(a^2+b^2) - U^2(a'^2+b'^2)\} \quad (12)$$

where the coefficients a, b, a', b' are taken at x = 1.
The hydrodynamic Froude efficiency $\eta$ is given by:

$$\eta = U\,\bar{\Theta}/\bar{P} \quad (13)$$

## 4 BODY SHAPE

The body mass distribution $m_b(x)$ and the lateral added mass distribution $m_a(x)$, as derived from body measurements, are shown in fig. 3. Obviously eel is far more slender than saithe. The marked variation of body height in the posterior part of saithe prevents slender-body theory from giving accurate results. Indeed the hydrodynamic forces acting on the tail of saithe are overestimated (Hess & Videler, 1983a) and a substantial stiff motion had to be added to satisfy the conditions (7). With eel this was no real problem.

Some geometric quantities of hydrodynamic interest are listed in Table 2.

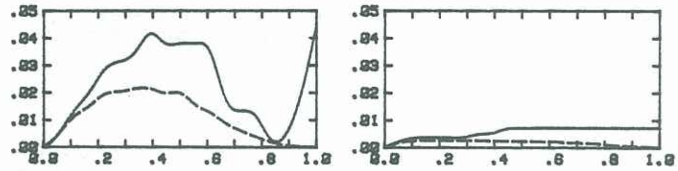

Fig. 3. Sectional body mass $m_b(x)$ (dashed) and sectional lateral added mass $m_a(x)$ (drawn). Left: saithe. Right: eel (unit: $\rho L^2$).

TABLE 2

SOME GEOMETRIC QUANTITIES

| | | saithe: | eel: |
|---|---|---|---|
| Tail height (L) | | .24 | .096 |
| Body volume ($L^3$) | $m_f$ = | .0113 | .0018 |
| Wetted surface area ($L^2$) | $A_w$ = | .401 | .196 |

## 5 RESULTS

The main results are presented in fig. 4 for saithe and in fig. 5 for eel. The bending moment has an amplitude $M^*(x)$ which is greatest in the central part of the fish. The phase function $\mu(x)$ is nearly constant in saithe. The bending moment reaches its maximum at $t \cong -.2$, that is just after the tail point has passed the plane of symmetry. In eel the bending moment reaches its maximum around $t \cong -.4$ and $\mu(x)$ is not as constant as in saithe.

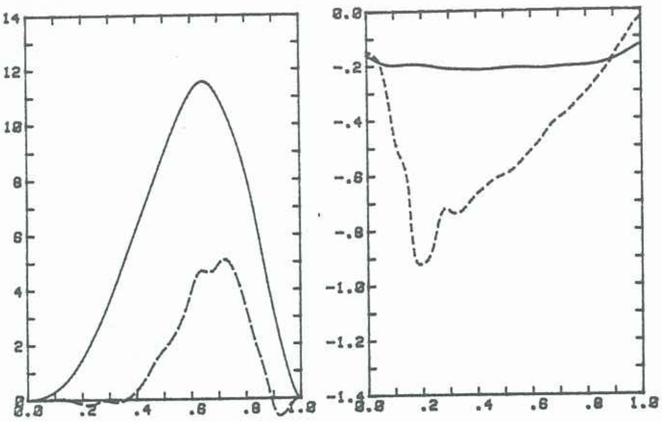


Fig. 4. (a) Drawn curves: bending moment $M(x, t)$ for saithe. Left: amplitude $M^*(x) \times 10^4$ (unit: $\rho L^5 T^{-2}$). Right: phase $\mu(x)$ (unit: T), compared with curvature phase (dashed). (b) Left: (dashed) mean differential bending power $\bar{P}_1(x) \times 10^3$. (unit: $\rho L^4 T^{-3}$).

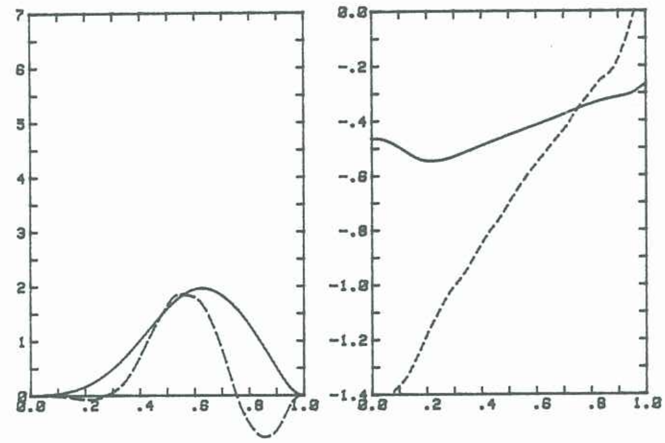


Fig. 5. (a) Drawn curves: bending moment $M(x, t) \times 10^4$ for eel. (b) Left: (dashed) mean differential bending power $\bar{P}_1(x) \times 10^3$. See caption of fig. 4.

The bending moment appears to run along the body at a speed very much higher than the body curvature wave speed, whereas in saithe the speed is virtually infinite.

Also shown is the mean differential bending power $\bar{P}_1(x)$. It vanishes in the anterior part of the fish, reaches a peak in the central part and is negative in the tail region.

Table 3 lists some hydrodynamic quantities for saithe and eel. $C_T$ is the thrust coefficient, defined by:

$$\bar{\Theta} = \tfrac{1}{2}\,\rho U^2 A_w\, C_T \qquad (14)$$

6 CONCLUSION

The most striking result of the above analysis is that the bending moment inside the fish does not run as a wave from head to tail, like the body curvature does, but oscillates with very small phase differences throughout the body.

Corresponding to the oscillating body curvature, the lateral muscles shorten and lengthen alternately on either side. If the shortening muscle fibers exert a contraction force then they do positive work; the bending moment is in phase with the rate of change of body curvature (see eq. (8)). This happens in the central part of the fish body. In other parts the muscles may be stretched while they exert a contracting force; there they do negative work. As the head is stiff, the bending moment does no work at all in the front part. The tail fin contains no muscles, and I would expect $\bar{P}_1$ to be zero there or slightly negative. The substantial negative peak of $\bar{P}_1$ in the posterior part of eel I cannot explain functionally.

TABLE 3

SOME HYDRODYNAMIC QUANTITIES

| | | saithe: | eel: |
|---|---|---|---|
| Mean total power ($\rho L^5 T^{-3}$) | $\bar{P}$ = | .0014 | .00038 |
| Mean thrust ($\rho L^4 T^{-2}$) | $\bar{\Theta}$ = | .0013 | .00049 |
| Thrust coefficient | $C_T$ = | .009 | .017 |
| Froude efficiency | $\eta$ = | .83 | .71 |

These results suggest that a fish's swimming strategy may involve an alternating contraction of all the lateral muscles on either side of the body. It is the interaction with the water flow that produces the familiar wave shape running along the body during swimming. During starting, however, a similar bending moment distribution would produce a quite different body curvature. This is borne out by Hertel's (1963) picture of a trout swimming and starting. And, as anglers may confirm, a fish floundering in air moves like a standing rather than a running wave.

7 ACKNOWLEDGEMENTS

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