The effect of temperature on the swimming speed of fishes is well documented and is generally attributed to differences in molecular kinetics and the rates of the biochemical reactions that convert chemical energy into propulsive thrust (Beamish, 1978). Differences in temperature also engender variations in the physical properties of water which may affect a fish’s movement. This potential physical effect of temperature on swimming is suggested by the equation for drag during steady (constant speed) swimming (Webb, 1975).

\[ D = \rho U^2 S_w C_D, \]

where \( D \) is total drag, \( \rho \) is the density of the water, \( U \) is swimming speed, \( S_w \) is the wetted surface area and \( C_D \) is a non-dimensional drag coefficient. Although \( C_D \) is often treated as a constant when the equation is applied to fishes, its value varies with the nature of the flow around an object (Vogel, 1981). The Reynolds number based on length (\( Re_L \)) is a convenient index of the hydrodynamic conditions governing that flow.

\[ Re_L = \frac{\rho U L}{\mu}, \]

where \( L \) is a characteristic length (usually the total length of a fish) and \( \mu \) is the dynamic viscosity of the water. On the basis of empirical data for a sphere or a cylinder oriented perpendicular to a flow, \( C_D \) is constant (\( C_D \approx Re_L^{-0.1} \)) when \( Re_L \) is greater than approximately 10^3 (the inertial hydrodynamic regime). When \( Re_L \) is less than approximately 10^1 (viscous hydrodynamic regime), \( C_D \) is approximately inversely proportional to \( Re_L \) (\( C_D \approx Re_L^{-1} \)) (Vogel, 1981). Substituting these relationships and assuming geometric similarity of body form (i.e. \( S_w \approx L^2 \)):

\[ D \propto \rho U^2 S_w \propto \rho U^2 L^2, \]

in the inertial regime, and

\[ D \propto \rho U^2 S_w (\rho U L \mu^{-1})^{-1} \propto U L \mu. \]

Therefore, total drag during steady swimming is dependent upon the density or the viscosity of the water, or a combination of both in the intermediate hydrodynamic regime (approximately \( 10^1 < Re_L < \approx 10^3 \)).

The importance of such physical effects of density and viscosity to an overall temperature response depends upon the range of temperatures a fish might experience naturally and the degree to which density or viscosity varies with temperature.
Many fishes typically experience a wide range of temperatures as a result of their vertical and horizontal movements. Others that live in shallow waters can experience temperature fluctuations of 10–15°C in a single day due to insolation and poor mixing, cloud cover and other meteorological or hydrographic events (Bamforth, 1962; Smid and Priban, 1978). In addition, fish larvae may experience different thermal conditions depending on the part of the spawning season in which they hatch. Differences in temperature have a much greater effect on the dynamic viscosity of water than on its density. For example, a 10°C decrease in temperature, from 15 to 5°C, produces a 33 % increase in dynamic viscosity, but less than a 0.1 % increase in density. This demonstrates that the physical effect of temperature on drag should be due almost entirely to the change in dynamic viscosity of the water. This effect will be strongest while a fish swims in the viscous hydrodynamic regime and will be small or negligible for a fish swimming in the inertial regime.

Routine swimming speeds of most adult fishes, spanning a large range of sizes, place them in the inertial hydrodynamic regime, with $Re_L > 10^4$ (Wu, 1977). Fish larvae experience much lower Reynolds numbers, typically as low as 20–60, because of their small size and correspondingly slow speeds (Webb and Weihs, 1986; Fuiman and Webb, 1988). The rough calculations given above provide circumstantial evidence that fish larvae should experience significant physical (viscosity) effects of temperature, in addition to the well-known physiological effects, and that larger fishes should not. However, the limits of the hydrodynamic regimes defined by the relationships between $C_D$ and $Re_L$ may not be directly applicable to swimming organisms because those limits are based on flows around inanimate, geometric solids and because of uncertainty about the validity of total length as the appropriate characteristic length.

This paper demonstrates that ecologically relevant variations in water viscosity can have measurable consequences for fish swimming. The results help to define the actual limits of the viscous and inertial hydrodynamic regimes for fishes that use large-amplitude, undulatory (anguilliform) mechanics. The data also show the importance of accounting for physical effects when estimating the physiological consequences of temperature differences for locomotor responses.

**Materials and methods**

Two experiments were conducted to measure the effects of temperature differences on the swimming performance and kinematics of fish larvae. The response to temperature (physiological and physical effects combined) was established by conducting trials in sea water over a realistic range of temperatures. The physiological and physical components of this response were partitioned by conducting additional trials in dilute solutions of methyl cellulose that were designed to achieve viscosities equivalent to colder fluids without altering the temperature. Experiments were conducted on two sizes of larvae to obtain a broad range of swimming speeds and hydrodynamic conditions.

**Larvae**

All experiments were conducted on Atlantic herring (Clupea harengus L.) larvae because they swim nearly constantly and in an anguilliform style. Large larvae were reared from eggs of the Clyde stock of herring fertilized in April 1991. They were 37 days old (post-hatching) and 18.2±1.8 mm (mean ± s.d.) in total length when used. At this stage of development, herring larvae are very elongate [fineness ratio (i.e. total length/maximum depth) of approximately 18], the caudal fin is nearly complete, the dorsal and anal fin margins are complete and their rays are beginning to ossify, the pectoral fins are poorly developed, the pelvic fins are lacking, and the median fin fold persists anterior to the dorsal fin and along most of the ventral margin of the body. Small larvae were reared from eggs of the Buchan (North Sea) stock fertilized in August 1991. They were much more uniform in size and developmental state than the large larvae, at the end of the yolk-sac stage at the time of the experiments (8 days old, 9.6±0.39 mm long). The small larvae had approximately the same fineness ratio as the larger larvae but lacked differentiation of any portion of the continuous median fin fold. Outlines of body form and swimming movements of herring larvae are given by Batty (1984).

Larvae were reared to these sizes in 100 l tanks supplied with flowing sea water at a salinity of approximately 32%. They were fed newly hatched Artemia sp. nauplii and natural zooplankton sieved to an appropriate size. Temperatures in the rearing tanks for large larvae increased gradually from 8°C at fertilization to 9°C at the stage when experiments were performed. Small larvae were reared at a constant 10°C.

**Experimental protocol**

Routine (voluntary, spontaneous) swimming behavior of both sizes of larvae was observed in sea water at three temperatures that spanned a range that herring larvae could experience naturally. Experiments were conducted in three temperature-controlled rooms maintained at the following nominal experimental temperatures: 6, 9 and 13°C for large larvae and 7, 10 and 14°C for small larvae. The full range of temperatures was less than 0.4°C within each level.

Routine swimming was examined under nine combinations of temperature and methyl cellulose concentration for each size of larva (Table 1). Dilute solutions of methyl cellulose (Sigma M0262, relative molecular mass 41 000) were made from a stock solution (1.4 g l⁻¹ in filtered sea water) to approximate the kinematic viscosities of colder sea water. Kinematic viscosities used in the experiments (1.2×10⁻⁶ to 2.0×10⁻⁶ m² s⁻¹) extended slightly beyond the maximum that herring larvae would experience in nature (approximately 1.6×10⁻⁶ m² s⁻¹) in order to model the influence of viscosity more completely. Kinematic viscosity ($ν$) is the ratio of $μ$ to $ρ$ and is easier to measure than $μ$. Since the density of the most concentrated test solution of methyl cellulose was only 0.02 % less than that of sea water, the measured differences in kinematic viscosity reflected differences in dynamic viscosity. The most concentrated solution of methyl cellulose used was...
Routine swimming behavior of the larvae was acclimated to the test solution. They were allowed to swim around, and then they were pipetted into a beaker containing a solution of methyl cellulose slightly more concentrated than the test solution to which they were assigned. They were allowed to swim around, and then they were pipetted into the appropriate acrylic dish. Larvae assigned to seawater trials were pipetted into beakers containing sea water. The dishes were left undisturbed at each test temperature for at least 2h to allow the larvae to recover from handling and acclimate to the test solution.

A high-speed video recording system (NAC, HSV400) was used to record swimming at 400 frames s\(^{-1}\). Silhouette images were obtained by placing each dish on a stand beneath the camera and immediately above a Fresnel condenser lens. Illumination from a stroboscopic lamp synchronized with the video system shone through a fiber-optic cable to provide a point source below the condenser lens (Batty and Blaxter, 1992). Routine swimming behavior of the larvae was recorded for 3 min in each test solution. The temperature and viscosity of each solution were recorded immediately after each trial.

**Analysis**

Routine swimming of herring larvae consists of continuous, relatively large-amplitude lateral undulations along most of the body. Swimming speed (\(U\)) can be decomposed into a small set of simple kinematic variables, given the following relationships:

\[
U = df, \quad (5)
\]

where \(d\) is the stride length (distance traveled per tail beat) and \(f\) is tail-beat frequency (the number of complete cycles of the tail per second). Over the course of a tail beat, the transverse motion of the tail tip sweeps twice the tail amplitude (\(a\)) at an average transverse speed of \(W\). Therefore:

\[
f = \frac{a}{2} W^{-1}. \quad (6)
\]

Substituting:

\[
U = \frac{a}{2} d W^{-1}. \quad (7)
\]

Performance (\(U\)) and kinematic (\(f, d, W, a\)) variables were calculated for 10 larvae in each trial by recording the locations of the tips of the snout and the tail in every fourth video frame (sampling interval 0.01 s). Larvae were included in the analysis only if they swam in a straight path at an apparently constant speed (judged by eye), with at least two full tail beats in view, and they did not touch the surface of the solution. The total length of each larva was measured along each fish’s midline from the video recordings. The start of each half tail beat was identified by mathematically rotating the Cartesian coordinates for the snout and tail tip so that their mean path (described by geometric mean regression) was on the x axis (Batty and Blaxter, 1992). The \(y\) values were then smoothed with a weighted, five-point moving average (weights 1, 2, 3, 2, 1) so that local minima and maxima of the smoothed \(y\) values indicated the start of each half tail beat.

For each fish, \(a, f\) and \(d\) were calculated for each of four consecutive half tail beats and then averaged. Tail amplitude was calculated as the difference between unsmoothed \(y\) values (in mm) at the start of consecutive half tail beats. Stride length was twice the difference (in mm) between the locations of the snout tip at the start of consecutive half tail beats. Tail-beat frequency was the inverse of the product of the sampling interval (0.01 s) and the number of video frames between the start of consecutive half tail beats. Swimming speed and transverse tail speed were calculated using equations 5 and 6.

**Results**

Results for large larvae are presented first because those fish were expected to be influenced to a lesser degree by differences in viscosity, making their responses to temperature more similar to those known for larger juvenile and adult fishes.
Results from larvae swimming in sea water at different temperatures establish the values for swimming performance and kinematics that are likely to occur in nature and provide a basis for comparing swimming behavior when viscosity has been manipulated independently.

Large larvae

Temperature effects in sea water

Mean swimming speeds of large larvae were 62% lower at 6°C than at 13°C, decreasing from 1.9 body lengths per second ($L_s^{-1}$; $Re_L=490$) at 13°C to 0.7 $L_s^{-1}$ ($Re_L=158$) at 6°C (Fig. 1). A linear relationship with temperature ($T$) provided a good fit to the observations ($U=4.97+2.93T$; $r^2=0.46$, $P<0.001$). Swimming speeds were highly correlated with transverse tail speed, tail-beat frequency and stride length, but not with tail amplitude (Table 2). The 62% decline in swimming speed with decreasing temperature was due to a decrease in both tail-beat frequency and transverse tail speed. Tail-beat frequency decreased by 42% ($f=1.21+0.39T$; $r^2=0.37$, $P<0.001$), and transverse tail speed...
decreased by 48% \((W=10.62+5.46 T; r^2=0.47, P<0.001)\). Mean tail amplitude decreased by 8.1% over the full temperature range, most of which occurred between 9 and 6°C. These apparent differences in mean amplitude among temperatures were not significant (ANOVA, \(F_{2,27}=1.20, P=0.32\)).

Mean stride length declined by 29% between 13 and 6°C, from 0.31 to 0.22 \(L\). Stride length at 13.0°C was significantly greater than that at the two colder temperatures \((P<0.04)\), but there was no difference between values at 9 and 6°C \((P=0.98)\). Stride length was most highly correlated with transverse tail speed \((r=0.52)\) and tail amplitude \((r=0.50)\) and weakly related to tail-beat frequency \((r=0.38)\), and all of these were statistically significant.
<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Large larvae</th>
<th>Small larvae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stride length</td>
<td>0.77</td>
<td>0.78</td>
</tr>
<tr>
<td>Tail-beat frequency</td>
<td>0.85</td>
<td>0.80</td>
</tr>
<tr>
<td>Transverse tail speed</td>
<td>0.90</td>
<td>0.86</td>
</tr>
<tr>
<td>Amplitude</td>
<td>0.18 ± 0.04</td>
<td>0.06 ± 0.24</td>
</tr>
</tbody>
</table>

*Not a statistically significant correlation (P=0.05).*

**Viscosity effects**

Increases in kinematic viscosity with no change in temperature resulted in reduced swimming speeds in larger larvae, but only when kinematic viscosity was between approximately $1.4 \times 10^{-6}$ and $1.6 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ (Fig. 2). For example, mean swimming speed at 13°C in sea water was the same as that in the methyl cellulose solution of $\nu=1.43 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ at the same temperature ($P>0.99$), but speed decreased significantly ($P=0.04$) by 32% in the more concentrated methyl cellulose solution ($1.62 \times 10^{-6} \text{m}^2 \text{s}^{-1}$). Similarly, mean speed decreased by 43% at 9.4°C as viscosity increased from $1.37 \times 10^{-6}$ (sea water) to $1.62 \times 10^{-6} \text{m}^2 \text{s}^{-1}$, yet mean speed remained unchanged at the higher kinematic viscosity. Swimming speeds at 6°C did not change significantly with increasing viscosity.

The relationships between swimming speed and the kinematic variables over all fluids and temperatures were essentially the same as described for sea water (Table 2). This suggests that large larvae swimming in dilute solutions of methyl cellulose use kinematics similar to those used in sea water and, therefore, that this use of methyl cellulose is a suitable method for studying the effects of viscosity on swimming. Although tail amplitude was not significantly correlated with swimming speed, temperature or kinematic viscosity, mean tail amplitude was lower at kinematic viscosities between $1.4 \times 10^{-6}$ and $1.6 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ (Fig. 2).

Within this range, tail amplitude averaged 6.1 ± 0.15 mm (mean ± s.e.m.). Outside this range of kinematic viscosities, mean amplitude was 6.5±0.10 mm.

Across all experimental conditions, most large larvae swam at $Re_L$ between 116 and 339 (interquartile range), with a median value of 160. Under the conditions that produced the two highest mean swimming speeds, where increased viscosity had no measurable effect on swimming speed, mean $Re_L$ were greater than 450 and the majority of individual $Re_L$ values were in excess of 400. The decline in swimming speeds between $1.4 \times 10^{-6}$ and $1.6 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ lowered mean $Re_L$ to 257 and 135 (upper and middle temperatures, respectively, at $1.62 \times 10^{-6} \text{m}^2 \text{s}^{-1}$). In fluids with kinematic viscosities greater than $1.7 \times 10^{-6} \text{m}^2 \text{s}^{-1}$, mean $Re_L$ varied little and was between 102 and 162 (interquartile range 90–140).

**Temperature effects in sea water**

Swimming speeds of small larvae in sea water did not differ significantly among temperatures (ANOVA, $F_{2,27}=1.77$, $P=0.18$; Fig. 1). The overall mean swimming speed was $15.5±0.8 \text{mm s}^{-1}$ (1.6 $L_s^{-1}$) (mean ± s.e.m.). Despite the relative constancy of swimming speeds, there were significant differences in the Reynolds numbers attained by the small larvae at the three temperatures (ANOVA, $F_{2,27}=3.79$, $P=0.04$). Larvae swimming at 7°C achieved significantly lower Reynolds numbers (mean $Re_L=91$) than at either of the
warmer temperatures (mean $Re_L=127$ and 121 at 10 and 14 °C, respectively; Fig. 2).

Variations in speeds of small larvae were most closely associated with variations in stride length (Table 2). Transverse tail speed and tail-beat frequency were also significantly correlated with swimming speed, but tail amplitude was not. Although variations in the speed of small larvae were correlated with the same kinematic variables as in larger larvae, there were important differences. The relative importance of transverse tail speed and tail-beat frequency was greatly diminished in small larvae. Further, the generally lower correlation coefficients for small larvae reflected greater variability in their locomotor kinematics compared with large larvae.

Although swimming speed did not change consistently with temperature, some kinematic variables did (Fig. 1).

Mean tail-beat frequency decreased by 33 % over the entire temperature range, showing strong temperature-dependence ($f=3.03+0.41T$; $r^2=0.76$, $P<0.001$). The slope of this relationship was not significantly different from that for large larvae (ANCOVA, $F_{1,55}=0.02$, $P=0.89$), but the small larvae had significantly greater tail-beat frequencies (ANCOVA, $F_{1,57}=40.5$, $P<0.001$). Adjusted mean tail-beat frequencies were 7.1±0.22 Hz for small larvae and 5.1±0.22 Hz for large larvae (mean ± s.e.m.) at the overall mean temperature of 10.0 °C. Changes in tail-beat frequency with temperature coincided with changes in transverse tail speed or amplitude, but not both simultaneously. Between 14 and 10 °C, mean tail amplitude increased significantly ($P=0.002$), but there was no significant change in transverse tail speed ($P=0.81$, mean tail speed 25.2±0.74 mm s$^{-1}$). Between 10 and 7 °C, mean tail amplitude remained unchanged ($P=0.99$) at 3.5±0.10 mm, but
transverse tail speed decreased significantly (P<0.004; Fig. 1).

Stride length varied with temperature in the same way as tail amplitude (Fig. 1), increasing significantly from 14 to 10°C (P=0.016), but not changing between the two colder temperatures (P>0.99). However, stride length in sea water was not significantly correlated with tail amplitude (r=0.30), tail-beat frequency (r=−0.22) or transverse tail speed (r=0.08).

Viscosity effects

The influence of kinematic viscosity, independent of temperature, on the swimming speeds of small larvae was striking (Fig. 2). Swimming speeds declined uniformly with increasing kinematic viscosity over the range of 1.3×10⁻⁶ to 2.0×10⁻⁶ m²s⁻¹ at a rate of approximately 1.8 mm s⁻¹ for each 0.1×10⁻⁶ m²s⁻¹ change. There was no detectable effect of temperature on this relationship. The only deviation was at the lowest viscosity (sea water at 14°C, 1.23×10⁻⁶ m²s⁻¹), where mean swimming speed was substantially below the trend defined by the remaining data and marginally lower than in the slightly more viscous solutions.

Swimming speeds over all fluids and temperatures were highly correlated with stride length, tail-beat frequency and transverse tail speed. Swimming speed was also significantly (negatively) correlated with tail amplitude (Table 2). All of these correlations were stronger than in sea water alone, especially tail-beat frequency, which became a better predictor of swimming speed than transverse tail speed. Stride length varied more closely with swimming speed among small larvae than it did among large larvae. Transverse tail speed varied less with swimming speed in small larvae than in large larvae. Tail amplitude was not strongly related to swimming speed and there was no apparent pattern to its variation with swimming speed.

There was a strong relationship between \( \text{Re}_L \) and kinematic viscosity for small larvae \( (\text{Re}_L=301.57–42.31v; r^2=0.61, P<0.001) \). Over all conditions, most small larvae swam at \( \text{Re}_L \) between 48 and 116, with a median of 74 and extremes of 14 and 192. Larvae in the coldest, most viscous treatment experienced a mean \( \text{Re}_L \) of 25 (extremes 14–36).

Partitioning physical and physiological effects on swimming performance

Calculations of the physical and physiological effects on swimming speed for the specific conditions studied would not be useful because the physiological effect was obviously very small compared with the variability due to viscosity. Taking all treatments into consideration, the multiple regression of swimming speed on kinematic viscosity and temperature accounted for 44% of the total variance \( (r^2=0.44) \), approximately the same as for large larvae. However, temperature was not a significant factor \( (P=0.55) \), and values for the standardized regression coefficients \( (0.70, 0.06) \) indicated that viscosity effects were more than 10 times more powerful than the temperature effects not caused by viscosity. A simple linear regression on all the data showed that kinematic viscosity alone could account for 43% of the variation in speed \( (P<0.001) \). Within the natural viscosity range \( (<1.65×10^{-6} \text{ m}^2\text{s}^{-1}) \), kinematic viscosity and temperature together accounted for 16% of the variation in speed. Temperature was not a significant factor \( (P=0.69) \) in the multiple regression, and the standardized regression coefficients \( (-0.41, -0.05) \) indicated that physical effects were eight times stronger than physiological effects. Thus, physiological effects were a negligible component of the locomotor response of small larvae to the temperature and viscosity treatments we imposed. Viewed another way, the distance-weighted least-squares smoothing of the data for \( \text{Re}_L \) had isopleths that were nearly perpendicular to the viscosity axis, highlighting the strong gradient produced by kinematic viscosity and the minimal physiological effect of temperature for this size of herring (Fig. 3).

Large and small larvae combined

In order to combine the data for small and large larvae in a single analysis, it is necessary to be able to account for the large differences in body size and small differences in experimental conditions (temperature, kinematic viscosity) in the two experiments. Equations 3 and 4 provide a suitable framework for predicting relative changes in drag for various conditions of speed, size and dynamic viscosity. Stride length, the distance traveled in one propulsive thrust cycle, is determined by total drag. Equation 4, then, predicts that stride length will be directly proportional to the viscous drag product, \( UL\mu \), for a fish swimming in the viscous regime. As \( \text{Re}_L \) increases beyond this region, stride length will depart from this proportionality until it becomes directly proportional to \( pUL^2S_w \) in the inertial regime (equation 3).

The principal assumption of equation 4 is that \( S_w=L^2 \) (isometric growth) over the range of sizes examined. Projected body area in herring larvae, excluding fin folds and fins, has been shown to be allometric, increasing as \( L^{2.76} \) or \( L^{2.62} \) (Fuiman, 1989; Langsdale, 1993). However, friction on the surfaces of fin folds and fins does contribute to drag, so these must be included in the total body surface area. We analyzed ten technical illustrations of young herring (6.3–41 mm in total length) collected from other sources by Jones et al. (1978), and found that total projected area, including fin folds and fins, increases as \( L^{2.05} \). The total projected area of an average large larva (18.6 mm) estimated from this relationship differs from the area predicted by isometric growth \( (L^{2.00}) \) by less than 5%. Therefore, the assumption of isometry is reasonable and the data from the two experiments can be combined.

A linear relationship between stride length and the viscous drag product \( (UL\mu) \) defined a viscous-regime trend which applied to all small larvae, regardless of speed, temperature or kinematic viscosity (Fig. 4). Data from large larvae were superimposed on the same relationship and extended it substantially. As values for the viscous drag product increased, strides of some larvae became shorter than predicted by the viscous-regime trend. We used a nonlinear regression technique (Systat, version 6.0) to fit two piecewise linear
segments to the data and to locate the break between those segments. The statistical results defined the break at a viscous drag product of 369, which corresponded to \( R_{EL} \) of approximately 130. Stride lengths for larvae beyond the break divided along the separate linear trends. Five large larvae at the extreme of the viscous-regime trend were characterized by \( 229 < R_{EL} < 463 \). Five larvae at the end of the other trend had \( 598 < R_{EL} < 775 \). A cluster of nine larvae just to the right of the break and distinctly below the viscous-regime trend (viscous drag product 659–782) experienced \( 297 < R_{EL} < 438 \). Therefore, herring larvae swimming at \( R_{EL} \) below approximately 300 follow the expectations of the viscous regime. Individuals swimming at Reynolds numbers between approximately 300 and approximately 450 may or may not be viscosity-dominated. Our data are not adequate to address the lower limit of the inertial regime for herring, but it is clear that larvae swimming at \( R_{EL} \) greater than approximately 450 are not in the viscous hydrodynamic regime.

**Discussion**

Ecologically relevant variations in water viscosity had a measurable influence on routine swimming performance and kinematics in herring larvae. It appears that, in small larvae, increases in kinematic viscosity at several constant temperatures impeded swimming performance through reductions in stride length and tail-beat frequency. The effects of temperature differences at equal viscosities were small by comparison. Large larvae showed similar, but weaker, trends with viscosity at constant temperatures but differences between temperatures were substantial.

The locomotor mechanics of large herring larvae in sea water were similar to those of juvenile and adult fishes of other species but differed from those of the small (viscosity-dominated) herring larvae. Bainbridge (1958) and Hunter and Zweifel (1971) showed that, in juvenile and adult fishes, speed during steady swimming is determined by tail-beat frequency (and fish length) and that tail amplitude is essentially constant when \( f \) is greater than 5 Hz. Large herring larvae were consistent with these observations. They modulated swimming speed by adjusting transverse tail speed without making significant changes to tail amplitude. Thus, the changes in transverse tail speed coincided with proportionate changes in tail-beat frequency. Small larvae, however, varied tail amplitude as well as transverse tail speed, despite the fact that their tail-beat frequencies were greater than 5 Hz (Fig. 1). Hunter (1972) observed in young (<3 days post-hatching) northern anchovy (\textit{Engraulis mordax}) that tail amplitude varied with average swimming speed during continuous swimming. The continuous swimming he described was not at a constant speed, and he attributed the variations in amplitude to acceleration during the swimming bouts. An alternative explanation is that the variations in tail amplitude were part of the response of anchovy larvae to a viscous hydrodynamic regime.

In a study similar to ours, Linley (1986) found that mosquito larvae (\textit{Culicoides variipennis}) were strongly affected by temperature and viscosity. These larvae were 5.6 mm long, used anguilliform locomotion, and swam at a mean \( R_{EL} \) of less than 100. Tail-beat frequency and swimming speed were strongly dependent upon temperature between 6 and 36°C. Swimming speed decreased dramatically when viscosity was increased fivefold using methyl cellulose at a constant 26°C (unnatural and much higher viscosities than we used), resulting in a mean \( R_{EL} \) of 8. The decline in speed diminished as viscosity increased further. The swimming mechanics of mosquito larvae in water at various temperatures were similar to those of small (viscosity-dominated) herring larvae. Mean swimming speed was positively correlated with mean transverse tail speed and mean tail-beat frequency. Mean tail amplitude decreased as swimming speed increased.

From the results for herring, anchovy and mosquito larvae, we suggest that the cadence of tail beats in steady swimming is determined by water temperature and the size of the animal. The effect of temperature on tail-beat frequency was the same for both small and large herring larvae, and the scatter around these relationships \( (r^2) \) was small (Fig. 1). The underlying mechanism for this probably involves temperature- and size-dependent contraction rates of aerobic trunk muscle (Rome, 1990). Tail amplitude remains constant as long as the animal can produce sufficient power to achieve the transverse tail...
speed necessary to match the prescribed frequency. Small larvae moving slowly (low Reynolds numbers) encounter the additional resistance to tail movement caused by water viscosity but lack the muscle power to achieve sufficient transverse tail speed. In order to maintain the temperature-specific tail-beat frequency, they must reduce tail amplitude. Significant variations in tail amplitude for anguilliform swimmers at low to moderate $Re_L$ may be a convenient indication of significant viscosity effects. The additional drag within the viscous regime also reduces stride length (Fig. 4; another sign of viscosity effects), resulting in an uncoupling of the relationship between tail-beat frequency and swimming speed (Table 2) and, ultimately, the relationship between swimming speed and temperature (Fig. 1).

The results from our manipulations of viscosity and temperature help to define the actual limits of the viscous and inertial hydrodynamic regimes for larval fishes. To date, these limits have been suggested by combining hydrodynamic theory with empirical results from geometric solids and fragmentary data on larval fish swimming (Vlymen, 1974; Weih, 1980; Webb and Weih, 1986). Our analyses of stride length, swimming speed and tail amplitude indicate that the viscous hydrodynamic regime extends to an $Re_L$ of approximately 300 for herring larvae and that total drag has a substantial viscous component up to an $Re_L$ of approximately 450. We had too few observations of swimming at $Re_L$>450 for a comparison of stride length with an inertial drag product (equation 4), so we cannot comment on the lower limit for inertial swimming.

Weih (1980) and Webb and Weih (1986) used hydrodynamic theory to suggest that fish larvae leave the viscous regime when $Re_L$>20 and enter the inertial regime when $Re_L$>200. Our empirical data indicate that the limits are somewhat higher. These differences mean that viscous forces and natural variations in viscosity are important to young fishes over a wider range of activities and for a longer period of life than previously thought. Investigations of larval fishes have acknowledged that temperature-induced changes in water viscosity can have an energetic cost, but that it is probably inconsequential (Kaufmann and Wieser, 1992). Energy budgets may need to be reassessed in the light of the expanded range of $Re_L$ over which viscosity affects swimming in herring. Combining our methods with new respirometry techniques designed especially for fish larvae (Kaufmann, 1990) would provide insight into the following questions. What are the costs of natural variations in viscosity? Do fish larvae select swimming speeds on the basis of a constant level of energy expenditure? Under what circumstances are the energetic requirements for swimming fast enough to escape the viscous regime less than the cost of combating viscosity? Can larvae accrue long-term energy savings by accelerating growth in length to escape the viscous regime? Some of these themes have been addressed by desktop studies (Ware, 1975; Webb and Weih, 1986; Müller and Videler, 1996), but better insight will follow direct experimentation.

The presence of a viscosity component in the response of a locomotor measurement to temperature means that indices of temperature effects, such as $Q_{10}$, overestimate the true physiological response (Podolsky and Emlet, 1993). Of the variables we measured, tail-beat frequency was most directly influenced by temperature: it showed the strongest and most consistent response to temperature. Tail-beat frequency will, therefore, serve as a convenient example to demonstrate the importance of quantifying the separate physical and physiological effects of temperature. The magnitude of the overall effect of temperature on tail-beat frequency was similar for both sizes of larvae, 0.40 Hz °C$^{-1}$. This represents an apparent $Q_{10}$ of 2.6 for large larvae and 1.9 for small larvae. After subtracting the viscosity effect, the physiological response of large larvae is 28% lower than the uncorrected value (0.29 Hz °C$^{-1}$, $Q_{10}$=2.2). For small larvae, the corrected physiological response is 58% lower (0.17 Hz °C$^{-1}$, $Q_{10}$=1.4). These corrected values are closer to the $Q_{10}$ of 1.6 obtained for maximum shortening velocity of red muscle measured in larger carp (Cyprinus carpio) (between 10 and 20 °C) by Rome (1990). Clearly, it is important that the consequences of temperature-induced changes in the physical properties of water be accounted for when interpreting physiological effects on locomotor responses of small fishes, especially when $Re_L$ is below 300 and perhaps when $Re_L$ is as high as 400–500.

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