

**PHYSICAL VERSUS PHYSIOLOGICAL EFFECTS OF TEMPERATURE ON BURST  
SWIMMING OF HERRING LARVAE.**

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**Abstract**

The burst swimming performance of herring larvae following c-start escape responses was analysed using high speed video recordings (400 frames per second). Varying viscosity independently of temperature (using methyl cellulose dissolved in seawater) showed that the physical effects of a change in temperature accounted for 30% of the variation in swimming performance.

**Introduction**

It is generally accepted that most mortality occurs during the early life history of marine fish and that predation upon larvae is one of the major causes. The speed with which larvae can react to and escape from predator attacks is an important factor determining vulnerability to predation (Bailey and Batty, 1983). A positive relationship between temperature and burst swimming speed of fish larvae was demonstrated by Batty and Blaxter (1992).

There is considerable variation in the temperature of inshore waters between years as well as in the time at which vertical thermal stratification develops. Due to these variations, the temperature to which larvae are exposed will be subject to considerable variation both between years and even during the same day. Laboratory experiments have shown, however, that herring larvae prefer the warmer waters above a thermocline (Batty, 1994).

Changing temperature affects aquatic organisms in two ways. Firstly, as temperature decreases the rates of biochemical reactions are reduced. This results in muscle contraction times being extended (Wardle, 1975) and contraction velocities being reduced. In studies on fish larvae, Batty and Blaxter (1992) and Batty et al. (1993) provided evidence that, for larvae of the same size, environmental temperature during development does not affect burst swimming

performance. They did show, however, that temperature directly affects tail beat frequency and maximum burst swimming speed. Other studies have shown that both muscle structure of larvae (Vieira and Johnston, 1992) and power output of adult fish (Johnson and Johnston, 1991) can be modified by acclimation temperature.

Secondly, the physical properties of water vary with temperature; viscosity increases as temperature decreases. For small organisms, this will lead to increased drag at lower temperatures and may contribute to the observed positive relationship between swimming speed and temperature. Two studies have already addressed the problem of separating the physiological and physical effects of temperature at low Reynolds numbers. Podolsky and Emllet (1993) found that the feeding rate of ciliated echinoderm larvae was affected by temperature-induced change in viscosity independent of physiological effects. Bacterial locomotion is also affected by viscosity as temperature declines (Mitchell *et al.*, 1991).

In this study we aim to separate the physical and physiological effects of varying temperature on the burst swimming of herring larvae.

## Methods

### *Fish*

Larvae were reared from artificial fertilisations of herring eggs from the Buchan (North Sea) spawning stock in August 1991. Fish were dissected on board ship and gonads transported to the laboratory in sealed jars at 0-2°C. Following artificial fertilisation, eggs and larvae were maintained at 10°C in 100 litre tanks of flowing seawater of approximately 32ppt salinity. Experiments were performed on Yolk-sac larvae at 8 days after hatching.

### *Test media*

Viscosity was adjusted by dissolving methyl cellulose (Sigma Chemical Company) in sea water. A stock solution (1% w/v methyl cellulose in sea water) was diluted with sea water to give a series of viscosities at each of three test temperatures (7, 10 and 14°C). Kinematic viscosity at the test temperatures was then measured using an Ostwald viscometer. The combinations of test temperature and viscosity used are given in Table 1.

% stock methyl cellulose solution	7°C	10°C	14°C
0	1.47	1.32	1.20
20	1.77	1.56	1.39
40	1.96	1.76	1.58
100	2.87	2.54	2.26

Table 1. Kinematic viscosities (cStokes) of the test solutions and temperatures.

### *Experiments*

All experiments were performed in temperature controlled rooms. For each temperature-viscosity combination, 20 larvae were captured from the rearing tank 6 hours before experiment and were transferred to an acrylic plastic dish 11.5 cm diameter with a water depth of 4 cm. These dishes and larvae were placed in temperature controlled rooms at the required temperature during the acclimation period before the experiments were conducted.

### Stimulation

A blunt glass rod (1 mm diameter) was used to administer tactile stimuli and elicit c-start escape responses.

### Filming

A high speed video recording system (NAC, HSV400) was used to record swimming at 400 frames per second. Subsequent frame by frame replay with the video recorder interfaced with a personal computer allowed the positions of the snout, the posterior edge of the yolk-sac, and the tip of the tail to be digitised in each frame. After transforming the x,y coordinates so that the x-axis ran along the mean path of motion (Batty and Blaxter, 1992) velocity, tail beat frequency, tail beat amplitude and stride length (the distance swum per tail beat) were measured over the second complete tail beat.

## Results

The results are plotted against kinematic viscosity in Figure 1. Although tail beat frequency is dependant on ambient temperature it is independent of kinematic viscosity. Other characteristics of burst swimming are dependent on viscosity; swimming speed, stride length and tail amplitude all decrease as viscosity increases. It is clear that viscosity affects swimming speed by reducing the stride length (the distance swum per tail beat) and that tail beat frequency cannot be adjusted to compensate. The reduction in tail amplitude indicates that there are also other changes in swimming movements related to viscosity. Reynolds number which increases both with swimming speed and decreasing viscosity can be used as an indicator of hydrodynamic similarity. The data for stride length are plotted against Reynolds number in Fig. 2 which shows the positive relationship between stride length and Reynolds number. There are significant differences between temperatures; stride length decreases with increasing temperature.

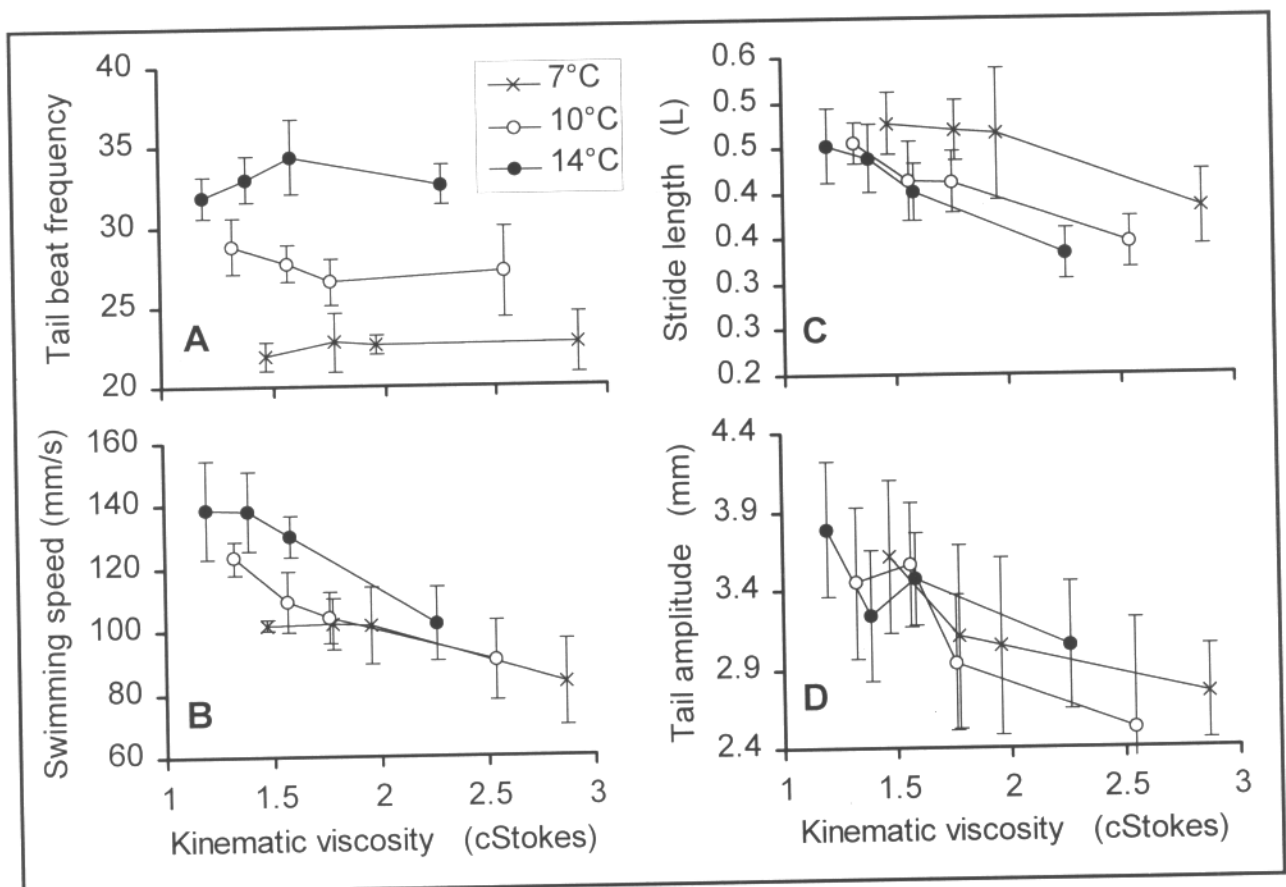


Figure 1. The effects of viscosity on burst swimming of herring larvae.

After fitting a linear model to the stride length,  $\log(\text{Reynolds's number})$  and temperature data predictions of the change in swimming speed due to variation in viscosity as temperature is decreased could be made. Over the range of temperatures used in our experiments, viscosity accounts for 30% of the variation in swimming speed due to temperature change.

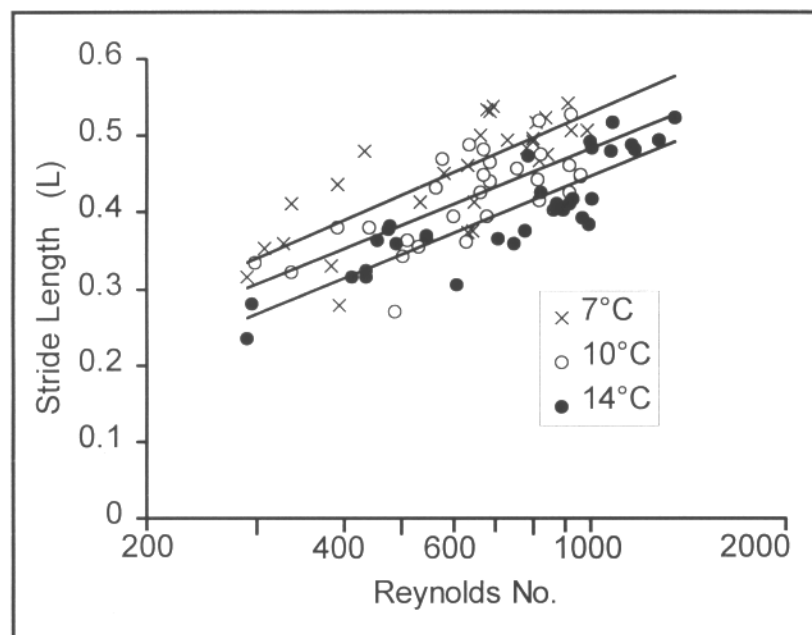


Figure 2. The relationship between larval herring stride length, temperature and Reynolds number.

## Discussion

Our results demonstrate the importance of viscosity in the burst speed swimming of fish larvae despite the fact that, according to the Reynolds number at which they are operating, inertial rather than resistive forces would be expected to be most important (Weihs, 1980). Batty and Blaxter (1992) established the link between stride length and Reynolds number for swimming up to  $10^4$ . In the present study, the increased stride length at lower temperature for a given Reynolds number indicates an in built mechanism in herring larvae in order to optimise their swimming performance over the wide range of temperatures that may be experienced in the sea as larvae move through the water column (Batty, 1994).

A related work on the effects of viscosity and temperature on routine swimming of herring larvae (Fuiman and Batty, in preparation) showed similar influences of viscosity on swimming movements, especially on stride length. There were however additional effects; tail beat frequency, for example, increasing in response to raised viscosity to compensate for the decreased stride length. This is of course not possible during maximum speed burst swimming.

It is unlikely that the change in viscosity due to variation in temperature will be of importance in the swimming of larger, juvenile and adult fish operating at much higher Reynolds numbers.

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