

**TEMPERATURE AND THE EFFICIENCY OF DEVELOPMENT DURING
ENDOGENOUS FEEDING IN HERRING EMBRYOS AND YOLK SAC LARVAE.**

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Abstract

Oxygen uptake, dry weights and energy contents of herring (*Clupea harengus*) were measured periodically from the time of egg fertilization to the end of the yolk sac stage (without added food). Temperature of incubation (3.5°C to 17°C) had little effect on efficiency of conversion of egg reserves to body material.

Introduction

The effects on fishes of changes in water temperature, due to inter-annual variation and to climate change, are likely to be greatest on the younger life stages (Blaxter, 1992). Optimum temperatures for larval stages of fish have been estimated based on hatching rates (eg. Rana, 1990a) and on upper and lower lethal temperatures (Kamler, 1992). Enzyme parameters and metabolic rates have also been used to define optimum development temperatures; thus enzyme K_m s show a minimum at the optimum temperature (Klyachko & Ozernyuk, 1991; Klyachko & Ozernyuk, 1994; Ozernyuk *et al.* 1994). Time-integrated oxygen consumption has a minimum over the optimum temperatures range and this minimum value can increase by as much as 100% at extremes of temperature (Zotin & Ozernyuk, 1966; Alexeeva & Ozernyuk, 1987).

Because of the metabolic costs of development at different temperatures, which are reflected by oxygen consumption values, it would be expected that larvae dry weights and heat contents (heats of combustion) would show a maximum over the optimum temperature range. Yolk utilization efficiencies based on dry weights and energy contents have been used to demonstrate temperature optima in Dover sole (*Solea solea*), (Flüchter & Pandian, 1968), California grunion (*Leuresthes tenuis*), (Ehrlich and Muszynski, 1982), yellowtail flounder, (*Limanda ferruginea*), (Howell, 1980), American plaice, (*Hippoglossoides platessoides*), (Howell & Caldwell, 1984), *Oreochromis niloticus*, (Rana 1990b) and African catfish (*Clarias gariepinus*), (Kamler *et al.*, 1994).

In the work reported here, dry weights, energy contents and time-integrated oxygen consumptions were measured as a function of temperature to test the hypothesis that an optimal temperature for development to hatch and to first feeding in herring (*Clupea harengus*) larvae could be determined from these measures of yolk conversion efficiency, and thus be of use in predicting the responses of different populations of herring to climate change.

Materials and Methods

Herring were caught by trawl at their spawning grounds in the Firth of Clyde, and ripe gonads were removed and placed on ice on board ship. Gonads were returned to the laboratory on ice, and within a few hours the eggs were spread thinly onto glass plates and fertilized with sperm from 3 or 4 males (Blaxter, 1968). Embryos and larvae were incubated at the following temperatures: 3.5, 5, 8, 15, and 17°C

For the purpose of calculation of total oxygen consumed, elapsed times from fertilization to hatch and from fertilization to exhaustion of the yolk sac were required.

Individual embryos or larvae were filtered onto pre-weighed discs of Whatman glass fibre filter paper type GF/C (which had been heated to 450°C overnight to destroy any combustible material), and washed well with distilled water to remove seawater salts. After drying in vacuo the discs were weighed and energy contents (heats of combustion) determined by micro bomb calorimetry (Scott & Marlow, 1982).

Oxygen uptake rate was determined by measuring the decrease in oxygen tension in a closed respirometer chamber. The oxygen content was determined by aspirating the sample with oxygen-free nitrogen and measurement of the oxygen in the gas stream with a cadmium fuel cell (Peck & Uglow, 1990). The uptake rate was determined from the linear portion of the plot of oxygen concentration versus time. (In the case of larvae the linear portion extended from saturation to 50-60% of saturation.)

The total oxygen consumed from fertilization to hatch or from fertilization to exhaustion of the yolk sack was determined by integration of the measured uptake rates with respect to time. For this purpose the uptake rates were assumed to be a linear function of time starting at zero, since the data did not justify a more complex model (for example see Figure 1). From regressions through the origin of the uptake rates on time, the slopes and 95% confidence intervals were calculated. In the case of measurements of progeny of a single fish at six temperatures it was not practical to measure the oxygen uptake of embryos as well as larvae and so the data for Figure 9 were calculated from the measurements of oxygen consumption of larvae only, using either the number of days from fertilization to hatch or from fertilization to exhaustion of the yolk sack as the integration limits.

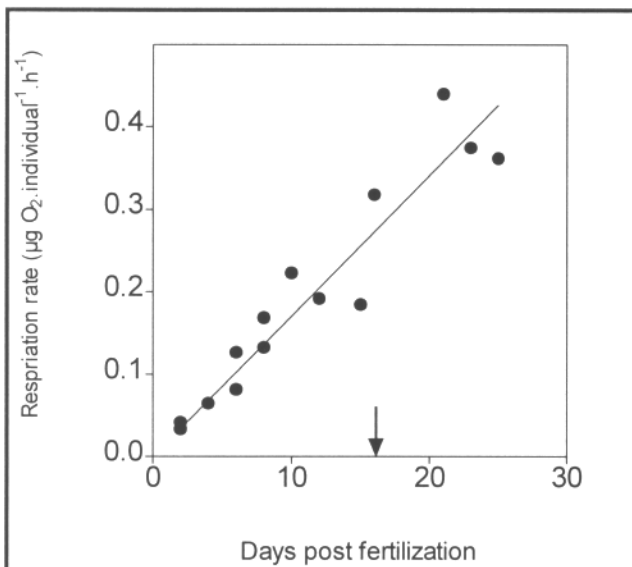


Fig. 1 Typical plot of respiration rate of developing embryos and yolk sac larvae versus number of days after fertilization; in this case Clyde herring at 8°C (with regression line through the origin). The arrow indicates hatch date.

Results

Dry weights and heats of combustion. The dry weights of newly hatched larvae and of larvae at the point of exhaustion of their yolk sacs showed a remarkable constancy over the temperature range studied, and this was reflected in the corresponding heats of combustion (albeit with greater errors), Figures 2 & 3. The two batches of eggs chosen had weights not differing greatly from each other but curiously, the heavier batch produced the lighter progeny with corresponding lower efficiencies of egg conversion (Table I).

Source and cohort	Efficiency by weight	Efficiency by energy content	Biological zero T_0
Clyde (3.5-17°C) no 1	51.3 (hatch)	44.9 (hatch)	0.8°C (hatch)
	40.2 (exhaust)	36.2 (exhaust)	0.0°C (exhaust)
Clyde (3.5-17°C) no 78	74.7 (hatch)	76.3 (hatch)	
	53.0 (exhaust)	48.7 (exhaust)	

Table I. Efficiencies of conversion of egg to larva, and temperature of biological zero, T_0 , calculated for times to hatch and to exhaustion of yolk sac.

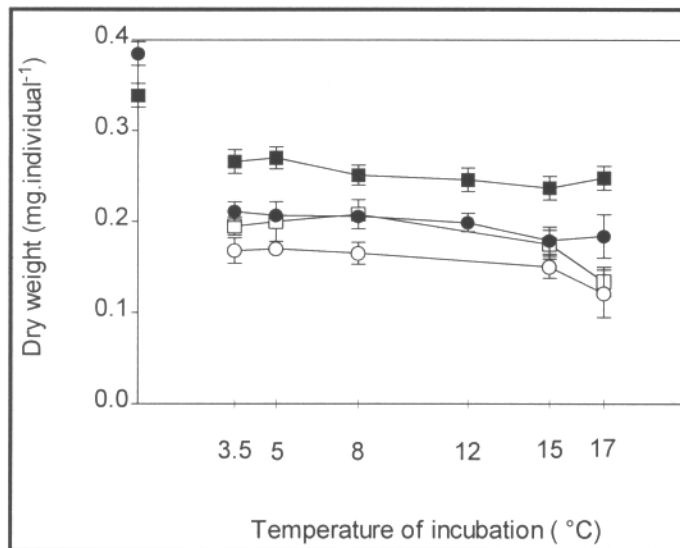


Fig. 2 Dry weights of unfertilized eggs (symbols on ordinate axis), of newly hatched larvae (solid symbols) and larvae at the point of exhaustion of their yolk-sacs (unfilled symbols). ● ○, Progeny of Clyde fish no. 1, and ■ □, progeny of fish no. 78. The centres of the symbols represent means of 10 individuals and the bars the SDs.

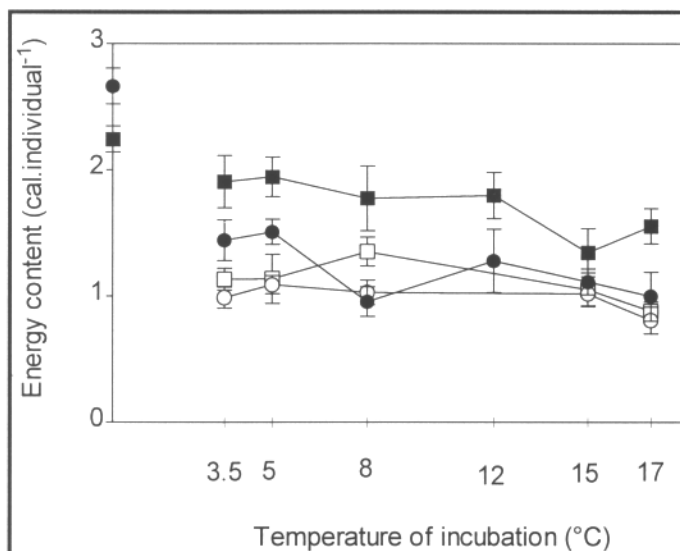


Fig. 3 Energy contents (heats of combustion) of unfertilized eggs (on ordinate axis) and of newly hatched larvae (solid symbols) and of larvae at the point of exhaustion of their yolk sacks (unfilled symbols). ● ○, Progeny of fish no 1, and ■ □, progeny of Clyde fish no. 78. The centres of the symbols represent means of 9 or 10 individuals and the bars the SDs. (1 calorie = 4.187 joules)

Oxygen consumption

Oxygen consumptions to hatch and to exhaustion of yolk sack stages showed little variation with temperature (Figure 4) and certainly not the U shaped response with high values at the extremes of temperature found by other investigators for a terrestrial fish (Alexeeva & Ozernyuk, 1987, Zotin & Ozernyuk, 1966). Indeed, the highest oxygen consumption found here was recorded for yolk-sack-exhausted larvae at 8°C - which is likely to be near the optimum temperature for the species.

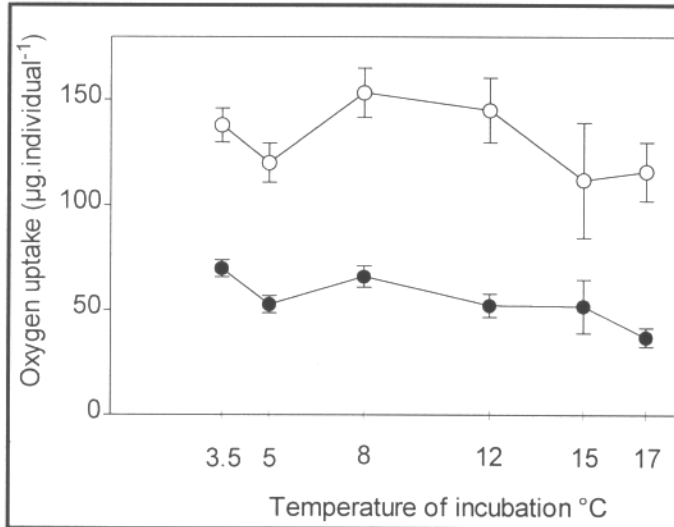


Fig. 4 Total oxygen consumed from fertilization to hatch, ●, and from fertilization to the point of exhaustion of yolk sack, ○, for batches of larvae from Clyde fish no 1. Error bars represent 95% confidence intervals of the slopes of each regression (such as Fig. 1).

Discussion and Conclusion

Herring larvae were raised from the fertilized egg to the stage of exhaustion of the yolk sack over as wide a range of temperature as has been found practical in this laboratory, such that the extremes of temperature used (3.5°C and 17°C) must be close to the limits for herring. For a fish with a biological zero of 0°C, this represents a 4.9 fold temperature range. On the basis of previous work in other laboratories it was expected that plots of dry weights or energy contents versus temperature would show domed curves and plots of oxygen consumptions versus temperature would show U shaped curves. There was no such effect; therefore the original hypothesis that a region of greatest efficiency could be found and used to determine the optimal temperature range for herring stocks appears untenable. Examination of Figures 7, 8 & 9 suggest that there may be a slight decrease in dry weights, energy contents and oxygen uptakes for newly hatched Clyde herring larvae as the temperature increases. However the effect is small and, if real, is contradictory since a decrease in dry weight or energy content would imply an increase in oxygen consumption rather than a decrease. An increased loss of metabolites to the medium with temperature would be required to account for this.

It must be concluded that either the "fitness" of yolk sac larvae and larvae at the point of exhaustion of the yolk sac is approximately equal from 3.5°C to 17°C, or that fitness is determined by some parameter which does not impinge on efficiency of conversion of egg tissue to larval tissue. This then raises the question of what are the biochemical compensatory mechanisms which enable herring to achieve this constancy of efficiency, what are the biochemical constraints which finally determine the limits of temperature and at what developmental stage do they operate? There are a few tantalizing clues in the literature regarding possible biochemical compensatory mechanisms. Different K_m s for the same enzyme isoform have been found for fish acclimated at different temperatures, which was attributed to differences

in tertiary structure (Klyachko & Ozernyuk, 1991; Klyachko & Ozernyuk, 1994; Ozernyuk *et al.* 1994). In addition different isoforms of the same myosin ATPase have been shown to be induced either by acclimation to different temperatures (Gerlach *et al.* 1990) or by rearing at different temperatures (Crockford & Johnston, 1993).

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