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A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes

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SUMMARY. Information on temperature (T°C) and time from fertilization to 50% hatch (D days) for five species of salmonid fishes has been used to assess several mathematical models relating D and T. No single equation gave the best fit to all five data sets. The power law with temperature correction (α), $\log_{10}D=\log_{10}a+b\ \log_{10}\ (T-\alpha)$ and the quadratic, $\log_{10}D=\log_{10}a+bT+b_1T^2$ (where a, b, b_1 and α are constants), each accounted for over 97% of the variance of D and were good fits to the observed data points for all five species. There was little difference between the predictions obtained from these two equations within the range of observed temperatures. Therefore, the simpler power-law model is preferred. However, there were substantial within-species differences between values of D predicted from extrapolations of the two models from 2 or 3°C down to 0°C. When more data for low temperatures become available it will be possible to make a more objective choice of model.

Introduction

Knowledge of the relationship between water temperature and hatching time for the eggs of salmonid fishes would be of considerable value in hatchery management, in the management of field research projects concerned with this part of the life history, and in giving insight into differences in the time of oviposition in different salmonid populations. The literature contains relatively few data on these relationships for salmonids. Most of the published information is on North American species.

Humpesch & Elliott (1980) briefly review models used to describe the relationship between hatching and temperature (T) for poikilotherms and conclude that the general equation for a hyperbola and power law, $D=a(T-\alpha)^b$ where a, b and α are constants, if frequently an adequate empirical model. Several basic models were described by Hayes (1949) with special reference to salmonid fishes and a number of variants of these and other basic forms are possible. However, apart from a comprehensive analysis of data for the chinook salmon [*Oncorhynchus tshawytscha* (Walbaum)] by Alderdice & Velsen (1978), there has been little attempt to evaluate the models by comparing them with the available data.

In the present paper published data for five salmonid species are considered in terms of three basic models and several variants thereof.

Materials

A summary of the sources and nature of the data is given in Table 1. Embody (1934) gave results

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TABLE 1. A summary of the sources and nature of the five data sets used in the analysis. All refer to approximately constant temperatures. n is the number of data pairs

Species	Sources	Temperature range (°C)	n
Brown trout (*Salmo trutta* L.)	Embody (1934)	1.89–11.24	29
Brook trout (*Salvelinus fontinalis* Mitchill)	Embody (1934)	1.64–14.80	39
Rainbow trout (*Salmo gairdneri* Richardson)	Embody (1934)	3.23–15.50	23
Chinook salmon [*Oncorhynchus tshawytscha* (Walbaum)]	Alderdice & Velsen (1978)	1.60–18.10	57
Atlantic salmon (*Salmo salar* L.)	Peterson *et al.* (1977), Gunnes (1979), Carrick (1979)	2.40–12.00	10

for four salmonid species but his information on lake trout [*Salvelinus namaycush* (Walbaum)] consisted of only seven data pairs and was excluded from the present analysis. The bulk of Embody's results were obtained by that author using specially designed flowing-water tanks to give constant temperatures. A few of his results were obtained from outside sources. He fitted exponential curves (see Model 2 below) to his results and found that for some species two or more intersecting curves had to be fitted to cover the observed temperature range

Alderdice & Velsen (1978) based their analysis on a large collection of data from a variety of published and unpublished sources. They examined information on several *Oncorhynchus* species but concluded that adequate data for analysis were available only for the chinook salmon. They examined a variety of models and assumed a single unbroken relationship between temperature and incubation time over the whole range of observed temperatures. The present analysis concentrates mainly on their data for constant temperatures.

Published information on the relationships between hatching and temperature for the Atlantic salmon appears to be sparse and scattered. Carrick (1979) stated that British salmon eggs kept at 4°C gave 50% hatch in 115 days, whilst Gunnes (1979) gave 50% hatch times for Norwegian material at 8, 10 and 12°C. Peterson, Spinney & Sreedharan (1977) examined temperature relationships of Canadian Atlantic salmon eggs. From their published figures and tables it is possible to obtain six data pairs for constant temperatures. The Atlantic salmon has been included in the analysis on the basis of these few results, chiefly for the sake of completeness.

Model equations

Throughout the following account, the independent variable (temperature as °C) is T, the dependent variable is D (= days from fertilization to 50% hatch) or $1/D$ (= rate of development), α is a temperature correction in °C and a, b and b_1 are constants. Throughout the text and tables the equations for Models 1 and 2 and their variants are given in their linear form unless the contrary is clearly indicated; log refers to common logarithms with base 10, 'ln' refers to natural logarithms (base e).

Model 1

A power-law relationship in two forms (1a and 1b). The basic linear form is

$$\log D = b \log T + \log a \tag{1a}$$

A plot of D against T is a parabola, i.e., $D = aT^b$ A better fit can often be obtained if a temperature correction factor (α) is incorporated (e.g., McLaren, 1963) in the basic equation to give

$$\log D = b \log (T - \alpha) + \log a \tag{1b}$$

In the more specialized case where $b = -1.0$ in the basic equation, (1a), the curve is a hyperbola and a thermal sums approach, in which hatching requires a constant number of degree-days above a threshold temperature, is applicable (Elliott, 1978). The appropriate linear form is then:

$$1/D = bT + a \tag{1c}$$

The theoretical development threshold temperature is $-a/b$ and the required thermal sum above this temperature is $1/b$.

Model 2

An exponential relationship in linear form:

$$\ln D = bT + \ln a \qquad (2)$$

Model 3

Polynomial expressions which are extensions of Models 1 and 2. The simple quadratic (cf., Model 1a):

$$\log D = \log a + b \log T + b_1 (\log T)^2 \qquad (3a)$$

was used by Bottrell (1975) for the eggs of Cladocera and Copepoda. The semi-logarithmic version (cf., Model 2):

$$\log D = \log a + bT + b_1 T^2 \qquad (3b)$$

was used by Colby & Brooke (1973) for eggs of lake herring and by Sarvala (1979) for the eggs of Copepoda. Equation 3b has been examined in the present paper.

Methods

Equations 1a,b, 2 and 3b were fitted to the data points for each salmonid species and goodness-of-fit was assessed by inspection of plotted data points and calculated regression lines and by comparison of values of the coefficient of determination (r^2) and the sums of squares of differences between observed and predicted values of D. The latter was the most sensitive method of assessment.

Values of the temperature correction (α) for eqn 1b were estimated to the nearest 0.5°C by an iterative process. Changes of ±0.5°C in the value of α had negligible effect on the calculated regressions.

Where plots of data points (after appropriate transformation) for Models 1a and 2 suggested that a single straight line was an inadequate representation of the relationship, then two straight lines were fitted and their point of intersection was determined by an iterative process. The results of fitting two intersecting lines are not given in the tables but references to them are made in the text.

Results

All of the equations 1a,b, 2 and 3b are a reasonably good fit to the data, in that all of them account for 94% or more of the variance of D in its regression on T, for each species (Table 2). In eqn 1a all of the values of b were significantly different from −1.0, at the 95% confidence level, so eqn 1c is inappropriate for these data sets and has not been used.

The two best-fitting equations for all species are 1b and 3b which account for over 97% of the variance of D for each species. For all species except the brook trout the best fit is given by eqn 3b but the fit for this model is only marginally better than that given by eqns 2 and 1b for brown trout or eqn 1b for the other species (Table 3). If eqns 1a and 2 are fitted as two intersecting lines, then eqn 1a for brook trout and eqn 2 for rainbow trout give rather smaller values of the sum of squares of differences between observed and predicted values than does the quadratic expression (1131.3 and 70.5, respectively) but the improvement is small and, for this reason, the complication of using two calculated regressions has been avoided.

Mean values of D predicted from eqns 1b and 3b are shown in Table 4. For each species the predictions cover the range of observed temperatures, together with extrapolated values down to 0°C. For brown trout, the two sets of predictions differ by less than 0.5 days throughout the observed temperature range and they differ by only 2.1 days when extrapolated to 0°C. For the remaining species the two sets of predictions differ by 2.5 days or less over most of the observed temperature range, though discrepancies of up to 4 days occur at the upper end of the temperature range for brook trout and chinook salmon. However, for all species except the brown trout there are discrepancies of up to 29 days between the predicted values of D at 0°C.

For reasons which will be discussed more fully below, eqn 1b has been preferred and the raw data points and calculated regressions are shown in Fig. 1; to assist calculation, the subtotals from

TABLE 2. Calculated values for constants α, log a (or ln a for eqn 2), b and b_1 in eqns 1a, 1b, 2 and 3b; n is the number of data pairs. r^2 is the coefficient of determination

Equation	Species	n	r^2	log $a \pm$ 95% CL	$b \pm$ 95% CL	α or b_1	
1a	Brown trout	29	0.947	2.4909 ± 0.0538	−0.8385 ± 0.0778	—	
1a	Brook trout	39	0.948	2.4872 ± 0.0526	−0.8288 ± 0.0646	—	
1a	Rainbow trout	23	0.978	2.6638 ± 0.0733	−1.1623 ± 0.0765	—	
1a	Chinook salmon	57	0.975	2.6370 ± 0.0399	−0.9231 ± 0.0403	—	
1a	Atlantic salmon	10	0.976	2.5925 ± 0.0996	−0.9070 ± 0.1161	—	
1b	Brown trout	29	0.992	28.8392 ± 0.9206	−13.9306 ± 0.4769	−80.0	
1b	Brook trout	39	0.989	19.6765 ± 0.6224	−9.5948 ± 0.3318	−65.0	
1b	Rainbow trout	23	0.982	4.0313 ± 0.1496	−2.0961 ± 0.1268	−6.0	α
1b	Chinook salmon	57	0.992	3.9166 ± 0.0521	−1.8126 ± 0.0433	−6.0	
1b	Atlantic salmon	10	0.996	5.1908 ± 0.1561	−2.6562 ± 0.1235	−11.0	
2	Brown trout	29	0.992	5.3307 ± 0.0335	−0.1613 ± 0.0056	—	
2	Brook trout	39	0.987	5.2106 ± 0.0415	−0.1315 ± 0.0050	—	
2	Rainbow trout	23	0.960	4.9023 ± 0.1237	−0.1384 ± 0.0125	—	
2	Chinook salmon	57	0.956	5.2951 ± 0.0786	−0.1236 ± 0.0071	—	
2	Atlantic salmon	10	0.994	5.3526 ± 0.0768	−0.1477 ± 0.0093	—	
3b	Brown trout	29	0.992	2.3236	−0.0736	0.00028	
3b	Brook trout	39	0.991	2.3147	−0.0757	0.00116	
3b	Rainbow trout	23	0.976	2.3475	−0.1123	0.00278	b_1
3b	Chinook salmon	57	0.996	2.4769	−0.1002	0.00248	
3b	Atlantic salmon	10	0.998	2.3921	−0.0877	0.00166	

TABLE 3. Sums of squares of differences between observed and predicted values of D for the four main model equations considered in this paper

Model	1a	1b	2	3b
Species				
Brown trout	3953.0	939.8	849.1	842.6
Brook trout	11 084.7	1416.8	1469.9	1533.2
Rainbow trout	412.0	102.0	416.4	89.6
Chinook salmon	10 834.6	388.3	5670.3	162.7
Atlantic salmon	778.3	66.9	127.7	58.6

the regression are given in the Appendix. If daily values of $100/D$, based on daily mean temperatures taken from the day of fertilization, are summed, then the total will reach 100 on the predicted day of 50% hatch.

Additional sources of variation

The literature refers to a number of possible causes of variation in incubation time, additional to mean incubation temperature. In several instances the authors give some indication of the amount of variation arising. The following four major causes have been identified.

Variation in hatching time (D) between eggs from a single individual

Hatching within batches may cover 3–4 days in high temperatures and 15–20 days in low tem-

TABLE 4. Mean values of *D* calculated from eqns 1b and 3b. Values based on extrapolations below the observed temperature range are marked *

	Brown trout		Brook trout		Rainbow trout		Chinook salmon		Atlantic salmon	
T (°C)	1b	3	1b	3	1b	3	1b	3	1b	3
0	212.8 *	210.7	191.4 *	206.4	251.3 *	222.6	320.7 *	299.8	265.9 *	246.7
1	179.0 *	177.9	165.3 *	173.8	181.9 *	173.0	242.5 *	239.4	211.0 *	202.3
2	150.9	150.5	143.1	147.2	137.5 *	136.2	190.4	193.4	170.6	167.2
3	127.4	127.4	124.1	125.3	107.4	108.5	153.8	156.0	140.1	139.3
4	107.9	108.1	107.9	107.3	86.1	87.7	127.1	130.6	115.6	116.9
5	91.5	91.7	94.0	92.3	70.5	71.7	106.9	109.1	98.3	98.9
6	77.7	78.0	82.0	79.8	58.8	59.4	91.3	92.3	83.7	84.3
7	66.1	66.4	71.7	69.4	49.7	49.8	79.0	78.9	71.9	72.4
8	56.4	56.6	62.8	60.7	42.6	42.8	69.0	68.2	62.3	62.6
9	48.2	48.3	55.2	53.4	36.8	36.5	60.9	59.7	54.3	54.6
10	41.3	41.3	48.5	47.2	32.2	31.8	54.2	52.8	47.7	48.0
11	35.4	35.3	42.7	41.9	28.3	28.1	48.6	47.3	42.2	42.5
12	—	—	37.7	37.4	25.1	25.1	43.8	42.8	37.5	37.9
13	—	—	33.3	33.6	22.4	22.8	39.7	39.2	—	—
14	—	—	29.5	30.4	20.1	20.9	36.2	36.3	—	—
15	—	—	26.1	27.6	18.2	19.4	33.1	34.0	—	—
16	—	—	—	—	—	—	30.4	32.3	—	—
17	—	—	—	—	—	—	28.1	30.9	—	—
18	—	—	—	—	—	—	26.0	30.0	—	—

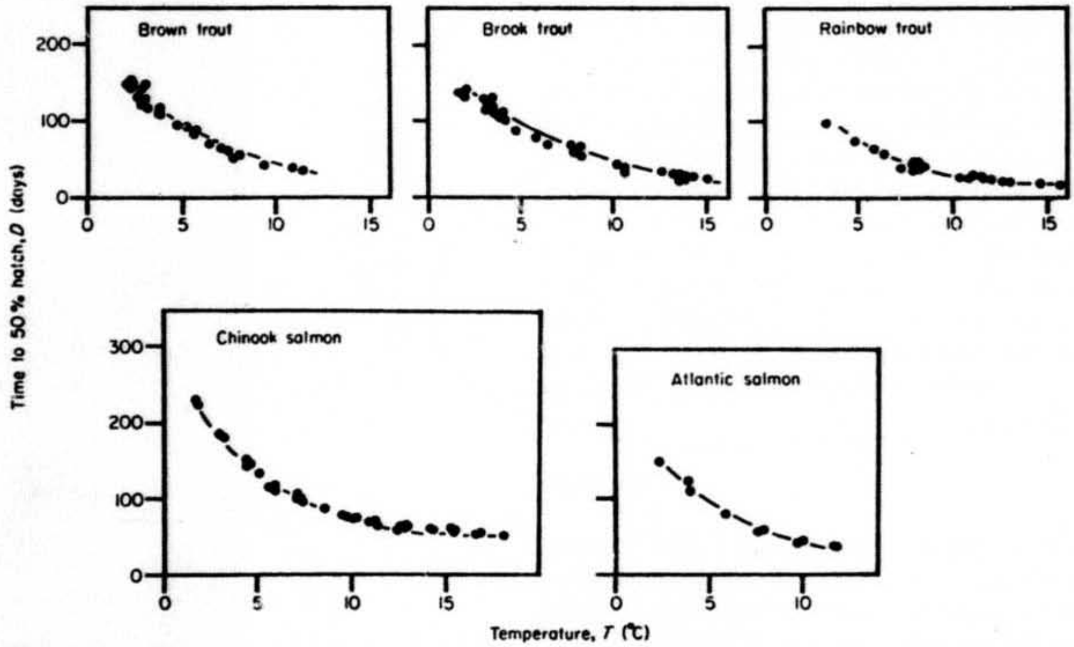

FIG. 1. Observed data points for five salmonid species and Model 1b regression lines plotted on arithmetic scales.

peratures. This represents ± 10% of the observed mean for rainbow trout over the 5.7–17.6°C range (Embody, 1934).

Variation in D between eggs from different females.

In females of the same strain, variation in hatching time can be ±2.3% of the mean and between eggs from different strains of the same species it can be ±4.3% of the mean (Embody, 1934).

Effects of temperature fluctuation

For chinook salmon eggs below 6–7°C, developmental velocity seems slower at constant than at ambient temperatures (Alderdice & Velsen, 1978).

Changes of temperature coefficient within the observed range of temperatures

Gray (1928) suggested that embryonic development and hatching is a complex of different processes, all of which may have different temperature relationships. The fitting of a single line or even two or more lines is, therefore, an oversimplification. In particular, Gray distinguished two major processes, namely embryonic development and hatching. He stated that the latter had a much higher temperature coefficient than the former and that the two processes are, to some extent, independent. This probably explains the observation by Embody (1934) that for lake trout eggs the incubation time was reduced (below the expected value) for one batch of eggs which was allowed to develop until well-eyed and then plunged into water 8°C warmer.

Thus, variation in incubation time of at least ± 10% of the mean can occur within a species and further variation may be caused by the finer detail of temperature fluctuation during incubation. Therefore, the calculated regressions in this paper cannot give more than an approximate estimate of incubation time.

Discussion

Gray's (1928) comments (see above) on the complexity of the development and hatching process imply that the fitting of two or more intersecting lines to any given data set may be biologically reasonable. In two instances, namely eqn 1a for brook trout and eqn 2 for rainbow trout, the use of two intersecting lines gives the best fit but the sums of squares of observed minus expected values are only marginally less than the values obtained by use of eqns 1b or 3b and this difference is too small to justify the more complex procedure.

The two best equations for general application to all of the five species considered are the power-law relationship (with temperature correction) (eqn 1b) and the quadratic expression relating log D and T (eqn 3b). The latter gives marginally the better fit for four of the species but it is more complex to calculate and its theoretical application to biological processes can be questioned (Humpesch & Elliott, 1980).

The predictions given by these two equations are similar or identical over most of the observed temperature range for each species (Table 4) so that eqn 1b might be preferred as the more simple one for practical use.

Extrapolation of 0°C gives more substantial differences (several weeks for some species) between the predictions given by the two equations. Alderdice & Velsen (1978) noted the scarcity of data points below about 3.6°C for the chinook salmon. A similar paucity of data at the lower end of the temperature range is apparent for the other four species (Table 1, Fig. 1). The acquisition of more data at these lower temperatures would permit a more meaningful choice of model equation. Despite this problem and the fact that extrapolation beyond the range of observed data points is statistically unsound, some extrapolation into the 0–3°C range may be necessary in order to obtain a 'best available estimate', because in many of the areas where salmonid fishes spawn, water temperatures may be below 3°C for a substantial proportion of the incubation period. In these circumstances most of the development will occur during the higher temperatures of autumn and spring. Relative to these, winter temperatures in the range 0–3°C will give low values of $100/D$ and errors in prediction of these will make only a small difference to predicted hatching dates. It is important to note that part of the extrapolation down to 0°C may be rendered redundant by the lower thermal death point, though the value of this is unknown with any precision for any of the species considered.

Alderdice & Velsen (1978) examined data for chinook salmon eggs at both constant and ambient temperatures and stated that below 6–7°C developmental velocity seems slower at constant than at ambient temperatures. Separate model 1b regressions for constant and ambient temperatures, calculated from Alderdice & Velsen's data, do predict more rapid development at ambient than at constant temperatures. For example, $D = 106.9$ (97.5–117.2) days at constant 5°C and $D = 98.3$ (91.0–106.2) days at ambient temperatures averaging 5°C. Similarly, for 3°C, $D = 153.8$ (140.1–168.9) days at constant and 146.1 (135.1–158.0) days at ambient temperatures.

The predicted values at ambient temperatures generally fall within the 95% confidence envelope of the predicted values at constant temperatures and an appreciable proportion of the difference between values predicted from the regressions for constant and ambient temperatures can be accounted for in terms of the properties of the constant-temperature regression alone.

For example, the constant-temperature regression (Table 2) can be used to show that chinook salmon eggs will have 50% hatch in 106.9 (97.5–117.2) days at constant 5°C or in 104.0 days when a mean temperature of 5°C is achieved by means of alternate days at 2.5 and 7.5°C. This difference of 2.9 days is equivalent to 33% of the difference between the means for predictions for 5°C from the two separate regressions.

More data on hatching times at low water temperatures are needed for salmonid fishes. If these could be obtained and used in conjunction with determinations of 'lower thermal death point' or some more biologically meaningful assessment of the relationship between temperature and mortality rate, then a more objective choice of model equation could be made. However, in the present state of knowledge, the power-law relationship, with temperature correction is a good fit to the observed points and is a relatively simple model. Humpesch & Elliott (1980) point out that the power law appears to be an adequate one for egg development in a wide range of aquatic animals. They also state that it can be used only as an empirical model and this is also true for the other models examined in the present paper.

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APPENDIX. Information required for calculation of confidence limits for values of D predicted from equation 1b

	Brown trout	Brook trout	Rainbow trout	Chinook salmon	Atlantic salmon
Σx	55.976074	72.432721	27.052770	68.222792	12.619000
Σx^2	108.052346	134.5515005	32.003942	82.470286	15.985075
Σy	56.555500	72.404400	36.016500	99.584400	18.390000
Σy^2	111.623291	136.829112	57.223465	176.682217	34.252103
Σxy	109.069248	134.224672	41.976626	117.7143548	23.043893
α	−80.0	−65.0	−6.0	−6.0	−11.0
n	29	39	23	57	10