

Comparison of different models to predict the in situ embryonic developmental rate of fish, with special reference to white sucker (*Catostomus commersoni*)

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Abstract: We performed laboratory incubations of white sucker (*Catostomus commersoni*) eggs to determine (i) the incubation time to organogenesis, eyed egg, hatching, and swim-up phases at eight different temperatures (8.5–21.2°C), and (ii) the best model to describe the relationship between these incubation times and temperature. Seven models (degree-day, power-law, Bělehrádek's equation, quadratic equation, first- and second-order exponentials, and a thermodynamic model) all gave comparable and highly significant fits to our data ($R^2 > 0.90$). We thus compared the in situ and predicted incubation times by (i) the degree-day model, because of its simplicity, and (ii) the thermodynamic model, because of its theoretical foundation. The degree-day model was at least as accurate as the thermodynamic model (overall mean difference between predicted and observed incubation times of 1.4 ± 1.0 and 1.2 ± 1.2 days for the thermodynamic and degree-day models, respectively). Given its high accuracy and simplicity of use, we conclude that the degree-day model should be used to predict the incubation times of white sucker. We also observed a synchronization of hatching in situ that suggested an influence of photoperiod in addition to that of water temperature.

Résumé : Nous avons procédé à des incubations d'oeufs de meunier noir, *Catostomus commersoni*, en laboratoire afin de déterminer (i) la durée d'incubation jusqu'aux phases d'organogénèse, d'oeuf oeuillé, d'éclosion et de larve pélagique (anglais : swim-up) sous huit températures différentes (8.5–21.2°C) et (ii) le meilleur modèle pour décrire la relation entre ces durées d'incubation et la température. Sept modèles (degrés-jours, une fonction de puissance, l'équation de Bělehrádek, une équation quadratique, des équations exponentielles de premier et second degré et un modèle thermodynamique) ont tous offert un ajustement aux données comparable et hautement significatif ($R^2 > 0,90$). Nous avons donc comparé les durées d'incubation in situ aux durées prédites par (i) le modèle degrés-jours, à cause de sa simplicité, et (ii) le modèle thermodynamique, à cause de ses fondements théoriques. Le modèle degrés-jours était au moins aussi précis que le modèle thermodynamique (différence moyenne globale de $1,4 \pm 1,0$ et de $1,2 \pm 1,2$ jours entre les durées d'incubation prédites et observées, avec les modèles thermodynamique et degrés-jours, respectivement). Étant donné sa grande précision et sa simplicité d'utilisation, nous concluons que le modèle degrés-jours devrait être utilisé pour prédire les durées d'incubation du meunier noir. Nous avons aussi observé un synchronisme de l'éclosion in situ qui suggère une influence de la photopériode en plus de celle de la température de l'eau.

Introduction

Temperature exerts a major influence on the developmental rate of poikilotherms, and it is often used to predict the incubation time of their eggs. Although there is a large body of literature concerning models relating the incubation time of eggs to temperature (or its inverse, the development rate: 1/time), no general consensus exists regarding a best model. It is recognized that the simple degree-day model, which assumes that developmental rate increases linearly with temperature, adequately describes the developmental rate over the central range of temperatures allowing development of a given species, but

not at lower or higher temperatures, where the relation becomes curvilinear (see reviews by Wagner et al. 1984 and Highley et al. 1986). Many models have been suggested to account for the nonlinearity of the developmental rate at low or high temperatures: a power law (Humpesch 1980, 1985; Crisp 1981; Butler and Burns 1989), Bělehrádek's equation (Alderdice and Velsen 1978; Herzig and Winkler 1986), a quadratic equation (Elliott et al. 1987; Tang et al. 1987; Wanzenböck and Wanzenböck 1993), exponential models (Berlin et al. 1977; Luczynski and Kirklewska 1984), and thermodynamic models (Sharpe and DeMichele 1977; Schoolfield et al. 1981). In situ validation of these models is of primary importance and has rarely been performed in past studies. Because the models are usually based on laboratory experiments done at constant water temperatures, they may lead to inaccurate estimations of in situ incubation times because of the influence of other factors, such as light intensity and photoperiod (Brännäs 1987; Kamler 1992), levels of dissolved oxygen (Hamor and Garside 1976; Luczynski and Kirklewska 1984), and fluctuating temperatures (Alderdice and Velsen 1978; Kamler 1992).

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Table 1. Mean incubation temperature (\pm SD) of white sucker eggs in the laboratory experiment (across time for all replicates pooled).

Treatment	Temperature ($^{\circ}$ C)	Range ($^{\circ}$ C)
1	8.5 \pm 0.9	7.0–11.0
2	10.8 \pm 1.6	8.5–15.0
3	11.7 \pm 1.9	8.0–15.0
4	13.5 \pm 1.7	10.5–18.0
5	15.2 \pm 1.4	13.5–19.0
6	16.6 \pm 1.7	14.0–19.5
7	17.7 \pm 2.3	11.0–21.0
8	21.2 \pm 2.4	14.0–24.5

Note: All temperatures were significantly different (ANOVA, $p < 0.0001$).

Raney and Webster (1942) reported the incubation time (fertilization to hatch) for white sucker (*Catostomus commersoni*) at five constant temperatures. Other studies, done in the laboratory or in the field, measured the incubation time at a mean temperature (Geen et al. 1966; Oseid and Smith 1971; Buynak and Mohr 1978; Corbett and Powles 1983) or the time necessary to reach different developmental stages at a single temperature (Long and Ballard 1976; McElman and Balon 1980; Walton 1980). Because these studies were done only for the entire embryonic period, or at only one temperature, they do not provide information on the relationship between incubation time and temperature for developmental stages other than hatching, nor do they cover a range of temperatures. The objectives of this study were then to (i) determine the incubation time to different developmental phases of white sucker at eight temperatures in the laboratory, (ii) determine the best model among those most frequently used in the literature to describe the relationship between incubation time and temperature for different developmental phases, and (iii) test the accuracy of the best model by following incubated eggs under natural conditions. Here, we defined the incubation time of a given developmental phase as the period between fertilization and the attainment of this phase.

Materials and methods

Egg development in the laboratory

In the spring of 1993, we incubated white sucker eggs in the laboratory at eight different temperatures ranging from 8.5 to 21.2 $^{\circ}$ C (Table 1). Eggs were obtained from ripe females captured on spawning beds on 29 May in the outlet of Lake Sauterelle in the Mastigouche Reserve, Quebec (46 $^{\circ}$ 36'N, 73 $^{\circ}$ 36'W). Eggs were fertilized artificially using the dry method (Piper et al. 1982), with cornstarch added to prevent the eggs from sticking together (Brown and Gratzek 1980). The eggs were allowed to water harden for 2 h at 12–14 $^{\circ}$ C before their transport to the laboratory. Three to five hundred eggs were placed in each of 48 incubators, which consisted of plastic boxes (30 \times 7 \times 4 cm depth) with substrates of artificial grass mats. The incubators were set in a stepped manner with six incubators for each of the eight tested temperatures (similar to Jungwirth and Winkler 1984). Cold water (8.5 $^{\circ}$ C) flowed from a reservoir into the first six incubators. When passing from one step to another, the water was heated by about 2 $^{\circ}$ C by mixing with 35 $^{\circ}$ C water from another reservoir. A water flow of 120–150 mL \cdot min $^{-1}$ was maintained in the incubators. City water dechlorinated with activated carbon, ultraviolet irradiance, and aeration was used. To prevent fungal contamination of the eggs, a malachite green oxalate treatment (5 ppm for 1 h) was

applied daily until hatching of the first larvae (Brown and Gratzek 1980). Water temperature was monitored twice daily (\pm 0.5 $^{\circ}$ C), and dissolved oxygen (which was always \geq 85% saturation) was monitored daily. A photoperiod of 15 h light : 9 h dark was used throughout the experiment with a light intensity of 32 lx.

At daily intervals for the five highest temperatures and every 2 or 3 days for the three lowest temperatures, 10 living embryos were sampled from each incubator and fixed in a 5% formalin solution. Determination of developmental stages followed the description of McElman and Balon (1980) for white sucker. We pooled the developmental stages into five major phases: (i) egg cleavage, starting at fertilization; (ii) organogenesis, starting with the elevation of the axial strand over the yolk, epiboly not completed; (iii) eyed egg, starting with the appearance of lenses in the eyes; (iv) hatching; and (v) swim-up larvae, starting with inflation of the swim bladder. We defined the incubation time of a given developmental phase as the period between fertilization and the attainment of this phase. We determined arbitrarily that the attainment of a given phase occurred when 90% or more of eggs attained this phase. This criterion was established to determine the time when the majority of the eggs were in the same phase. Attainment of the hatching phase at the five lowest temperatures and of the swim-up larval phase at all temperatures was determined by visual estimation because there were few living embryos remaining by the end of the experiment.

In situ egg development

To simulate the extent of the spawning period of white sucker, we incubated eggs on the bank of the spawning ground referred to above on 12, 14, 17, 19, and 21 May 1993. Eggs were obtained in the same way as for the laboratory experiments. Fifteen incubators were used, each consisting of PVC channels (6 cm depth \times 12 cm \times 2 m) with artificial grass mat substrates. To prevent excessive sedimentation over the eggs, the water brought by gravity from the spawning stream flowed into a receiving tank (a 6 cm \times 12 cm \times 2 m PVC channel filled with rocks) before being distributed to each incubator at a flow rate of 300–750 mL \cdot min $^{-1}$. The incubations were as follows: eggs from the first fertilization (12 May) were placed in three incubators; 2 days later, eggs from another fertilization were placed in three other incubators, and so on. About 1500 eggs were put in each incubator. Water temperature was monitored at 15-min intervals with an electronic thermograph (\pm 0.01 $^{\circ}$ C). Ten living embryos were removed daily from each incubator and fixed in a 5% formalin solution. Determinations of developmental phases and incubation times were the same as for laboratory experiments. However, unlike the laboratory experiments, the incubation times for hatching and swim-up larval phases were determined directly from sampling.

Data analysis

We first modeled the relationship between incubation time (y) and temperature (T) for laboratory incubations done at different temperatures. Seven models frequently used in the literature to predict incubation time were fitted to our data. These models are as follows:

Degree-day:

$$(1) \quad y = k/(T - t_0)$$

Power law:

$$(2) \quad y = aT^b$$

Bělehrádek's equation:

$$(3) \quad y = a/(T - t_0)^b$$

Quadratic equation:

$$(4) \quad y = a + bT + cT^2$$

Exponential:

$$(5) \quad y = ab^T$$

Table 2. Mean incubation time (days; \pm SD, $N = 6$) to organogenesis, eyed egg, hatching, and swim-up phases for white sucker eggs reared in the laboratory.

Temperature ($^{\circ}$ C)	Organogenesis	Eyed egg	Hatching	Swim-up
8.5	10.5 \pm 1.2	16.0 \pm 0.0	37.0 \pm 0.0	— ^a
10.8	7.3 \pm 0.5	10.5 \pm 1.2	22.0 \pm 0.0	— ^a
11.7	5.5 \pm 1.6	10.0 \pm 0.0	20.0 \pm 0.0	39.0 \pm 0.0
13.5	4.0 \pm 0.0	5.0 \pm 0.0	16.0 \pm 0.0	25.0 \pm 0.0
15.2	3.0 \pm 0.0	4.8 \pm 0.4	12.5 \pm 0.8	23.0 \pm 0.0
16.6	3.0 \pm 0.0	4.0 \pm 0.0	11.3 \pm 1.2	19.0 \pm 0.0
17.7	2.0 \pm 0.0	3.1 \pm 0.2	9.0 \pm 0.6	14.0 \pm 0.0
21.2	2.0 \pm 0.0	3.0 \pm 0.0	7.8 \pm 0.4	11.0 \pm 0.0

^aSwim-up time could not be determined at this temperature (see text).

Exponential (second order):

$$(6) \quad y = ab^Tc^{T^2}$$

Thermodynamic:

$$(7) \quad y = \frac{1 + \exp\left(\frac{\Delta H_L}{R} \left(\frac{1}{T_{1/2_L}} - \frac{1}{T}\right)\right)}{\rho(25^{\circ}\text{C}) \frac{T}{298} \exp\left(\frac{\Delta H_A}{R} \left(\frac{1}{298} - \frac{1}{T}\right)\right)}$$

where T is temperature (in degrees Celsius, except for eq. 7 where T is in degrees Kelvin), k is the sum of degree-days, t_0 is the temperature at developmental zero, and a , b , and c are constants. The last model (eq. 7) depicts developmental rate as if it were controlled by an enzyme that is reversibly denaturated at low temperatures (Schoolfield et al. 1981). The parameters of the model are thermodynamic constants associated with the rate-controlling enzyme reaction: ΔH_L is the change in enthalpy associated with low temperature inactivation of the enzyme ($\text{cal}\cdot\text{mol}^{-1}$), R is the universal gas constant ($1.987 \text{ cal}\cdot\text{deg}^{-1}\cdot\text{mol}^{-1}$), $T_{1/2_L}$ is the temperature (degrees Kelvin) at which the enzyme is half active and half low-temperature inactive; $\rho(25^{\circ}\text{C})$ is the developmental rate at 25°C , assuming no enzyme inactivation (time^{-1}), and ΔH_A is the enthalpy of activation of the reaction catalyzed by the rate-controlling enzyme ($\text{cal}\cdot\text{mol}^{-1}$). The value 25°C was chosen as a standard reference temperature at which most poikilotherms experience little if any low- or high-temperature enzyme inactivation (Schoolfield et al. 1981). Also, as suggested by Schoolfield et al. (1981) and Wagner et al. (1984), we used the four-parameter form of the thermodynamic model that accounts only for low-temperature inhibition of developmental rate rather than the six-parameter form accounting for low- and high-temperature inhibition because our tested temperatures were not sufficiently high to observe a decrease in developmental rate at the highest temperatures (this was verified with Arrhenius plots done for all developmental phases studied, as suggested by Schoolfield et al. 1981).

Models were fitted with a nonlinear least-squares regression procedure from SYSTAT software (NONLIN command with quasi-Newton estimation method) (SYSTAT Inc. 1992). The significance of the relationship was tested with an F test done on the linear transformation of the models, except for eqs. 3 and 7, which could not be linearized.

All the models gave a very good and comparable fit to our data (see Results and discussion section). We thus compared the in situ incubation times with times predicted by (i) the degree-day model because of its simplicity and (ii) the thermodynamic model because of its theoretical foundation in comparison with the other models. To predict the day of attainment of a given developmental phase, we considered each mean daily water temperature and calculated the corresponding incubation time (y) with the models. We then calculated the daily developmental rate as $1/y$, which is equivalent to the proportion of the total development occurring on each day. The predicted

day of attainment of a given phase corresponded to the day when the sum of these proportions was nearest to 1.

Results and discussion

Egg development in the laboratory

Incubation time

For all developmental phases studied, the incubation time decreased with increasing temperatures (Table 2). The swim-up times could not be determined for the two lowest temperatures: at the end of the experiment, 61 days after fertilization, no hatched embryo had reached this phase at 8.5°C , and only 40–50% of all embryos had reached it at 10.8°C .

The comparison of our results with previous studies on egg development of the white sucker in the laboratory suggests an important variability in the rate of egg development at a given temperature. Although we observed incubation times to organogenesis and eyeing similar to those reported in the literature, our times to hatching and swim up were considerably different from the results of other studies, particularly those of Raney and Webster (1942) and Oseid and Smith (1971) (Table 3). The discrepancies with the previous studies may simply reflect differences in the methodology used for egg incubation (e.g., number and density of eggs, flow rate of water), or differences in the way of determining the attainment of a developmental phase, i.e., while we determined the time when 90% of the eggs were in a given phase, the other studies did not always indicate if the development time measured corresponded to first, median, or complete occurrence of individuals in this phase. On the other hand, the discrepancies observed may also be due to interpopulation differences in the development rate of eggs, as demonstrated by Brännäs (1988) for chum (*Onchorynchus keta*) and Atlantic salmon (*Salmo salar*). However, this last hypothesis contradicts our in situ results, where the incubation times we observed were quite similar to the incubation times found in the literature (see below). Further research will be needed to determine the extent to which our predictive model is applicable to various populations of white sucker.

Comparison of the models

All of the models tested showed a very good fit to the data (Table 4). The adjusted values of the coefficients of determination (adjusted R^2) were always greater than 0.90, the residuals were always normally distributed, and a highly significant relationship was found between incubation time and temperature for the models that could be linearized (F test, $p < 0.0001$).

The second-order exponential, thermodynamic, and power-law models provided somewhat better fits to the data than the other models; their adjusted R^2 values were within approximately 1% of the highest value found for all developmental phases studied. These results support the observations of Humpesch and Elliott (1980), who pointed out that the power-law relationship was widely applicable to explain egg development of aquatic animals, and those of Jungwirth and Winkler (1984), who suggested the power law as a common function for egg development of fishes. The power law and Bělehrádek's equation, which is the power law with a correction constant for temperature, work well to describe egg development of cyprinids (Herzig and Winkler 1986), salmonids (Alderidge

Table 3. Results of previous studies done on incubation times of white sucker eggs reared at constant water temperatures in the laboratory.

Stage studied	Water temperature (°C)	Incubation time (days)	Reference
Organogenesis	10	4	Long and Ballard 1976
	15	2	McElman and Balon 1980
	15	2	McElman 1983
Eyed egg	10	10	Long and Ballard 1976
	15	4	McElman and Balon 1980
	15	3.75	McElman 1983
Hatch	10	19–22	Long and Ballard 1976
Hatch (95%)	12.3	14	Oseid and Smith 1971
Hatch (95%)	12.9	11–13	Oseid and Smith 1971
Hatch (95%)	15	9.75	McElman and Balon 1980
Hatch (100%)	15	10.5	McElman 1983
Hatch	15.6	7	Raney and Webster 1942
Hatch	18.3	5	Raney and Webster 1942
Hatch	21.1	4	Raney and Webster 1942
Swim-up	10	40	Long and Ballard 1976
	15	17.75	McElman and Balon 1980
	15	16	McElman 1983

Table 4. Adjusted R^2 values obtained with the models relating the incubation time to water temperature in the laboratory experiments.

Model	Organogenesis	Eyed egg	Hatching	Swim-up
Degree-day	0.911	0.938	0.992	0.975
Power law	0.927	0.960	0.989	0.973
Bělehrádek's equation	0.923	0.923	0.991	0.976
Quadratic	0.930	0.971	0.969	0.965
Exponential	0.921	0.959	0.961	0.959
Exponential (2nd order)	0.930	0.964	0.990	0.972
Thermodynamic	0.929	0.963	0.988	0.973

and Velsen 1978; Humpesch 1980, 1985; Crisp 1981; Jungwirth and Winkler 1984), and some other fish species (Laurence and Howell 1981; Humpesch 1985). However, unlike the above studies, where the power law was rarely compared with other functions, our results show that a second-order exponential or a model based on thermodynamics can be as accurate as the power law. From the results of the statistical analysis only, it is impossible to identify which of the second-order exponential, thermodynamic, or power-law models should be the best. No theoretical basis has been found for the second-order exponential or the power-law models (Humpesch and Elliott 1980; Butler and Burns 1989). In contrast, the thermodynamic model of Schoolfield et al. (1981) has a better biological foundation because it is based on recognized thermodynamic principles that apply to biochemical reactions; it depicts developmental rate as if it would be controlled by an enzyme in conformity with thermodynamic laws that apply to all enzyme-catalyzed reactions (for more details on the theoretical foundation of the model see Sharpe and DeMichele 1977; Wagner et al. 1984). However, the embryonic development is not determined by a single rate-controlling enzyme but more likely by numerous, sequential, and overlapping epigenetic processes. Despite its better theoretical foundation in comparison to the other equations, the

thermodynamic model could then be only a gross representation of the process.

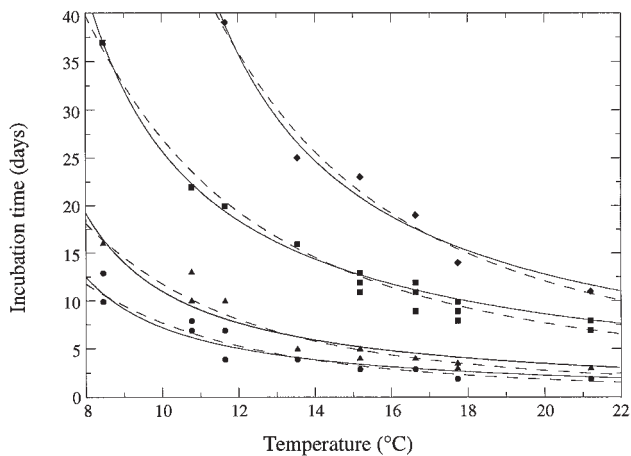
On the other hand, although it has often been criticized because of its lack of accuracy at extreme temperatures (see reviews by Bagenal and Braum 1971; Wagner et al. 1984; Highley et al. 1986), we cannot discard the degree-day model on the basis of our results. It is easy to compute and gave a very good fit to our data. In the same way, previous studies related to pest management obtained very good predictive power when using the degree-day model in the field (i.e., average deviation between observed and predicted mean hatching date of 3 days or less; Bernal and González 1993; Bergh and Judd 1993; Judd et al. 1993). Our laboratory experiments showed that the R^2 values for the degree-day model were only slightly lower than for the thermodynamic model (Table 4), leading to very little difference in the predicted incubation times with the two models (Fig. 1).

In situ egg development

Incubation time

Our in situ incubation times (Table 5) were consistent with those found in the literature for white sucker, suggesting that embryonic development is relatively similar in different locations. Organogenesis has been found to occur in 4 (the present study) or 5 days (Walton 1980) after fertilization; the eyed egg phase in about 8 days (Walton 1980, the present study); hatching in 16 (Walton 1980; Corbett and Powles 1983), 15–18 (Bond 1972), and 16–24 days (the present study); and the swim-up phase in 22–25 (Bond 1972) to 25–32 days (Geen et al. 1966; Corbett and Powles 1983; the present study). This variability in the timing of embryonic development among the different studies can be explained by the fact that this process is mainly temperature dependent. Nevertheless, it is possible to estimate the chronology of embryonic development as it proceeds naturally on the spawning grounds. As a general rule, we can state that organogenesis and the eyed egg stage occur 4 and 8 days after fertilization, respectively, and hatching in 16–20 days. After hatching, the benthic larvae stay in the

Fig. 1. Relationship between incubation time and temperature for organogenesis (circles), eyed egg (triangles), hatching (squares), and swim-up (diamonds) phases as predicted by the degree-day (solid lines) and thermodynamic (broken lines) models. Each point represents one to six samples. Models are based on raw data.



gravel for 10–12 days before downstream drift, which occurs approximately 1 month after fertilization.

Predicted versus observed incubation time

The parameter estimates for the degree-day and thermodynamic models are shown in Table 6. Both models closely predicted the incubation times observed in the field (Table 7). For the thermodynamic model, the highest mean difference between predicted and observed times was 2.1 days, occurring at the organogenesis phase (Table 7). The overall mean difference of the thermodynamic model (i.e., when all of the developmental phases were combined) was 1.4 ± 1.0 days (mean \pm SD; Table 7). In contrast to our laboratory experiments, where the thermodynamic model gave a better fit to the data, the in situ experiment showed that the degree-day model was at least as accurate in predicting incubation times. With the degree-day model, the highest mean difference between predicted and observed times was only 1.7 days, occurring at the organogenesis phase, and the overall mean difference was 1.2 ± 1.2 days.

The high overall accuracy of the thermodynamic and degree-day models, with only the mean daily water temperature as predictor, contrasts with the lower precision that one would expect from the literature. First, under fluctuating temperatures, such as we observed in our study (mean amplitude of daily fluctuations 3.4°C , range $1.2\text{--}7^\circ\text{C}$), it has been shown for insect eggs that the use of the mean water temperature generates inaccurate predicted incubation times (Hagstrum and Milliken 1991). This inaccuracy is also expected to apply to fish eggs. Because the relationship between developmental rate and temperature is curvilinear, an increase in temperature will accelerate the developmental rate more than a decrease in temperature of the same magnitude will decelerate it (Braum 1978). The use of the mean water temperature is then likely to underestimate the developmental rate (except at high temperatures where development is slowed). Alderdice and Velsen (1978) effectively showed that temperature fluctuations accelerate the developmental rate of chinook salmon (*Oncorhynchus tshawytscha*) eggs at low temperatures. Furthermore, the

lengthening photoperiod, which is known to accelerate the development of fish eggs (Brännäs 1987), would also have lowered the accuracy of our models. When considering the overall accuracy of our predictive models, neither fluctuating temperatures nor other factors such as photoperiod seemed to have had a significant influence on the in situ embryonic developmental rate of white sucker. Similar results were obtained by Colby and Brooke (1973) and Berlin et al. (1977), who worked on eggs of lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*). They reported that the predicted incubation times of the eggs differed by an average of only 6.6 and 5.5%, respectively, from the observed times when using the mean water temperature as predictor. These results show that for some fish species, incubation times can be accurately predicted from the mean daily water temperature alone. Also, the accuracy we observed probably resulted, at least in part, from the wide temperature range used to build our predictive models in the laboratory (relative to the temperatures experienced in nature by the developing embryos), which improved the reliability of the regression equations.

Our results showed that the simple degree-day approach, often criticized for its lack of accuracy, was at least as accurate as the more complex thermodynamic model under natural conditions. It seems that the numerous warnings found in the literature concerning the inaccuracy of the degree-day approach in the field were not applicable in our experiment. Perhaps this is because the temperature regime that prevailed in situ during the incubation period corresponded to the central range of temperatures where the degree-day model is known to fit the developmental data well. Indeed, Highley et al. (1986) stated that although curvilinear models (e.g., the thermodynamic model) are clearly better predictors when temperature extremes are encountered, in many and possibly most cases, the degree-day approach offers the same level of accuracy. The minimum and maximum temperatures found during the natural incubation period of the white sucker are reported to be approximately $6\text{--}16.8^\circ\text{C}$ in southeastern Ontario (Corbett and Powles 1983), $7.5\text{--}17^\circ\text{C}$ in Alberta (Bond 1972), and $10\text{--}19^\circ\text{C}$ in central British Columbia (Geen et al. 1966). These temperatures are quite similar to the temperature regime observed during our in situ experiments (range $8.2\text{--}21.8^\circ\text{C}$). Consequently, we expect that a simple degree-day model would give accurate predictions in most areas where white sucker occur.

Hatching synchrony

The number of days from fertilization to hatching decreased from the first to the last fertilization date, resulting in the synchronization of hatching in the 15 incubators. Although we fertilized eggs over a 10-day period (from 12 May through 21 May), the hatching period (i.e., the time elapsed from the first to the last hatching date in the 15 incubators) lasted only 5 days (from 4 to 8 June). Such a synchrony of hatching was also observed in white sucker by Walton (1980), who found that all hatching took place over a 2-day period even though eggs were fertilized over 17 consecutive days. Various hypotheses can be suggested to explain this synchrony. The first is that eggs fertilized earlier were subjected to lower water temperatures than those fertilized later, so that the observed differences in the developmental rates simply reflected differences in mean incubation temperatures. This is unlikely in our study because the mean incubation temperature prior to hatch

Table 5. Mean in situ incubation time (days) to organogenesis, eyed egg, hatching, and swim-up phases for white sucker eggs.

Fertilization date	Organogenesis		Eyed egg		Hatching		Swim-up	
	Mean incubation time	Mean temperature (°C)	Mean incubation time	Mean temperature (°C)	Mean incubation time	Mean temperature (°C)	Mean incubation time	Mean temperature (°C)
12 May	4.33	10.85	8.67	10.44	23.67	11.48	32.00	12.45
14 May	4.00	10.39	9.00	10.83	21.67	11.50	30.00	12.53
17 May	4.00	10.65	8.33	11.33	18.67	11.67	na	na
19 May	4.33	11.53	8.33	12.00	17.67	11.91	25.00	12.97
21 May	3.67	11.85	7.00	12.23	16.33	12.09	na	na
Mean	4.07	11.06	8.27	11.41	19.60	11.73	30.17	12.56

Note: The mean temperature is the mean water temperature from egg fertilization to attainment of each phase. na, data not available because less than 90% of the larvae were in the swim-up phase in the incubators at the end of the experiment.

Table 6. Parameter estimates, with asymptotic standard errors (ASE) given in parentheses, for the degree-day and thermodynamic models (see Data analysis section for definition of the parameters).

Developmental phase	Degree-day		Thermodynamic			
	<i>k</i>	<i>t</i> ₀	ΔH_L	<i>T</i> _{1/2_L}	ρ (25°C)	ΔH_A
Organogenesis	34.247 (2.053)	5.272 (0.244)	-34 694 (17 277)	284.833 (8.746)	0.847 (0.320)	10 261 (8788)
Eyed egg	51.394 (2.554)	5.329 (0.198)	-34 694 (nc)	285.182 (nc)	0.582 (nc)	10 261 (nc)
Hatching	130.323 (2.151)	4.935 (0.075)	-34 694 (4 531)	283.220 (1.237)	0.200 (0.018)	10 261 (1550)
Swim-up larvae	159.589 (5.333)	7.540 (0.174)	-34 694 (24 915)	285.594 (6.144)	0.137 (0.055)	10 261 (4221)

Note: nc, not computable.

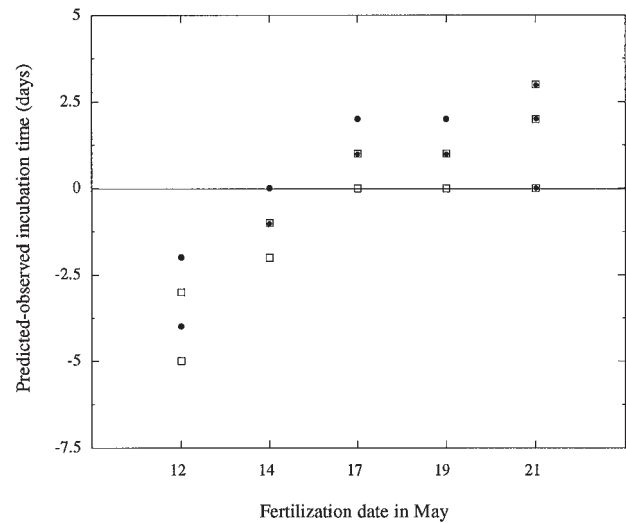
Table 7. Mean absolute difference between predicted and in situ incubation times (days; \pm SD) for the degree-day and thermodynamic models.

Developmental stage	Predicted time	Observed time	Mean absolute difference	Range	<i>N</i>
Degree-day model					
Organogenesis	5.8 \pm 0.8	4.1 \pm 0.4	1.7 \pm 0.9	0-3	15
Eyed egg	8.4 \pm 0.8	8.3 \pm 0.9	0.4 \pm 0.5	0-1	15
Hatching	19.0 \pm 0.9	19.6 \pm 2.9	1.5 \pm 1.5	0-5	15
Swim-up larvae	30.8 \pm 1.9	30.2 \pm 2.7	0.7 \pm 0.8	0-2	6
Overall difference			1.2 \pm 1.2		
Thermodynamic model					
Organogenesis	6.2 \pm 0.8	4.1 \pm 0.4	2.1 \pm 0.7	1-3	15
Eyed egg	9.0 \pm 0.9	8.3 \pm 0.9	0.9 \pm 0.6	0-2	15
Hatching	19.8 \pm 1.2	19.6 \pm 2.9	1.5 \pm 1.1	0-4	15
Swim-up larvae	30.8 \pm 1.9	30.2 \pm 2.7	0.7 \pm 0.8	0-2	6
Overall difference			1.4 \pm 1.0		

Note: The mean absolute difference was computed as the mean of the absolute values of the difference between the predicted and observed times.

varied only by 0.5°C among the five fertilization dates (range 11.48–12.06°C). Furthermore, if this were the case, the observed incubation times to hatch should have been nearly the same as the predicted incubation times (or systematically higher or lower than predicted); in contrast, the models over-estimated the developmental rates for the first fertilization dates and underestimated those of the last fertilizations (Fig. 2), suggesting that other factors were involved. It is also unlikely that fluctuating temperatures caused the observed acceleration in development rate because the amplitude of temperature fluctuations remained constant through time (*H*₀: the slope of the regression line = 0; *F* test, *p* = 0.2045). Another

Fig. 2. Difference between predicted and observed times to hatch in relation to the date of fertilization (*N* = 15 incubators). The predicted times were calculated from the degree-day (open squares) and thermodynamic (solid circles) models.



hypothesis is that the size variation of the eggs influenced the developmental rate. In this study, the mean egg diameter at the cleavage phase increased significantly with time, ranging from 3.00 mm at the first fertilization to 3.29 mm for the last eggs fertilized (Kruskal-Wallis test, *p* < 0.0001). The few workers who performed intraspecific comparisons of fish eggs found no effect of size on the incubation time (Kamler 1992). Consequently, it seems unlikely that an increase in egg size during our experiment would have shortened the incubation time.

Our results suggest that the length of the photoperiod may

have been responsible for the reduced incubation time to hatch in the later fertilizations. The day length increased regularly during the in situ experiments, changing from 893 min on 12 May (date of first fertilization) to 914 min on 21 May (date of last fertilization) and finally to 946 min on 13 June, the end of the experiment. MacCrimmon and Kwain (1969) compared the incubation times of rainbow trout (*Oncorhynchus mykiss*) eggs under different light intensities and observed earlier hatching at higher light intensity. Their work also demonstrated that light may affect the developmental rate of eggs through its influence on metabolic rate. In addition, Brännäs (1987) showed that the day length affected the time to 50% hatch in Baltic salmon (*Salmo salar*); eggs held under a 16 h light : 8 h dark photoperiod hatched 4 days before eggs held in constant darkness. These studies support the hypothesis that acceleration of the developmental rate of white sucker eggs was caused by the increased day length.

Finally, we cannot determine if the synchronization also occurred at the swim-up phase because only six incubators contained 90% or more swim-up larvae when the experiment was stopped on 13 June, which was the day of attainment of this phase in all six of these incubators. The nine other incubators contained proportions of swim-up larvae ranging from 24 to 84%.

Conclusions

The goal of the present study was to predict the incubation time for white sucker embryos to attain various developmental phases. We showed from laboratory experiments that temperature-based models frequently used to describe egg development of poikilotherms gave very good fits to the incubation times of the white sucker. The in situ validation of the thermodynamic and degree-day models revealed that the simple degree-day model was at least as accurate for predicting incubation times under natural conditions. Furthermore, the high overall accuracy obtained with the degree-day model in the field was achieved with the use of the mean daily water temperature only. This high accuracy contrasted with the expected imprecision thought to be intrinsic to the degree-day approach. Our results agree with the observations of Highley et al. (1986): for the majority of management purposes, the simple degree-day approach predicts incubation time with sufficient accuracy. This is probably true for egg development of aquatic poikilotherms because the extreme temperatures at which the degree-day model is known to be inaccurate rarely occur in the water, in contrast to the situation with terrestrial habitats. Given the high accuracy obtained with the degree-day model in the field and its simplicity of use, we conclude that managers should use this model to predict the incubation times of white sucker. In addition to mass removal, a way to lower the impact of introduced white sucker on exploited species would be to decrease their recruitment by controlling benthic or drifting swim-up larvae on their spawning grounds (with rotenone or electrofishing, for example; Magnan et al. 1997).

The synchrony of hatching suggests an influence of photoperiod in addition to that of water temperature. However, this influence seems small compared with that of water temperature, as we were able to predict the hatching date of white sucker with a mean accuracy of 1.5 days using only the mean water temperature as an independent variable. This synchronization

in the hatching process is interesting in terms of its management implications. Given the synchronization of hatching, a control directed at the hatched larvae would greatly reduce the costs of such operations because fewer treatments would be required than for a control directed at earlier developmental phases.

Finally, although the spawning run of white sucker is known to start when the water temperature first reaches 10°C (Geen et al. 1966; Bond 1972; Corbett and Powles 1983), little is known about the factors determining the spawning date. Further research will be needed on the precise timing of spawning to know when to start the summation of degree-days. The accuracy of our degree-day model must also be validated for different populations of white sucker to see if interpopulation variability exists in the embryonic developmental rate, as suggested by our review of incubation times.

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