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MODÉLISATION DE LA CHRONOLOGIE DU DÉVELOPPEMENT EMBRYONNAIRE DU MEUNIER NOIR, *CATOSTOMUS COMMERSONI*.

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AVANT-PROPOS

Ce travail de recherche est présenté sous forme de deux articles scientifiques dont la présentation a été organisée de manière à respecter les recommandations aux auteurs du *Journal canadien des sciences halieutiques et aquatiques*. Une introduction et une conclusion générales accompagnent les articles pour faire le lien entre eux et illustrer leur complémentarité.

Les deux articles ont été rédigés en anglais, mais un résumé substantiel en français de chacun d'eux est présenté aux annexes A et B respectivement. De plus, un court résumé rédigé en français et en anglais précède chaque article.

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INTRODUCTION GÉNÉRALE

L'introduction d'une nouvelle espèce entraîne souvent des impacts néfastes pour les espèces indigènes. Ceci est particulièrement vrai en ce qui concerne l'introduction du meunier noir, *Catostomus commersoni*, dans de nombreux lacs du Québec où l'omble de fontaine, *Salvelinus fontinalis*, était originellement retrouvé en allopatrie. La présence du meunier noir dans ces lacs se traduit par un changement de la niche alimentaire de l'omble de fontaine du zoobenthos au zooplancton, un changement de la distribution spatiale des individus de la zone littorale à la zone pélagique, une diminution du succès des ensemencements, et surtout, par une diminution marquée du rendement annuel moyen (baisse de 50 à 80%), ce qui se répercute évidemment sur la qualité de la pêche sportive (Magnan 1988[1], 1989[2]).

Face à l'ampleur du problème, le ministère de l'Environnement et de la Faune et la Fondation de la Faune du Québec ont accordé en 1990 un contrat de cinq ans au Laboratoire de recherche sur les communautés aquatiques (LRCA) de l'Université du Québec à Trois-Rivières afin d'effectuer la recherche et le développement de modes de contrôle de cette espèce nuisible. Une des méthodes de contrôle proposées par le LRCA serait de diminuer le recrutement de nouveaux individus par un contrôle visant les oeufs ou les larves de meunier noir retrouvés sur les frayères, à l'aide par exemple d'un traitement à la Roténone, par l'utilisation de la pêche électrique, ou encore de barrières électriques lors de la dérive des larves. Cependant, pour qu'une méthode de contrôle visant les jeunes stades de

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[1]Magnan, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and nonsalmonid species: ecological shift, morphological shift, and their impact on zooplankton communities. Can. J. Fish. Aquat. Sci. 45: 999-1009.

[2]Magnan, P. 1989. The impact of cyprinid and catostomid introductions on brook charr, *Salvelinus fontinalis*, populations: a review. Physiol. Ecol. Japan, *Spec. Vol.* 1: 337-356.

développement s'avère efficace, les interventions devront viser les stades les plus sensibles au mode de contrôle utilisé. De plus, il sera essentiel de pouvoir prédire l'apparition des différents stades de développement embryonnaire de l'espèce dans le temps. L'évaluation de la sensibilité des jeunes stades de développement à la Roténone et à l'électricité fait actuellement l'objet de recherches dans le cadre d'autres projets.

L'objectif global de ce projet était de développer un modèle permettant de prédire l'atteinte des principales phases du développement embryonnaire du meunier noir sur les frayères (organogénèse, oeuf oeillé, éclosion et larve pélagique). Le premier volet de cette recherche (chapitre 1) visait à construire un modèle pour décrire la relation entre la durée d'incubation requise pour l'atteinte de chaque phase de développement et la température de l'eau, puis à vérifier la précision de ce modèle in situ avec des oeufs fertilisés artificiellement. Dans ce volet, nous avons comparé les modèles les plus fréquemment rencontrés dans la littérature pour prédire le développement embryonnaire. Dans un deuxième volet (chapitre 2) nous avons suivi l'évolution de la fraie du meunier noir sur six frayères dans le but d'identifier les facteurs déterminant la date de ponte, afin de connaître le temps t_0 du développement embryonnaire nécessaire à l'utilisation des modèles prédictifs. Nous avons également suivi le développement des oeufs pondus naturellement sur les frayères afin de valider la précision des modèles retenus dans le premier volet pour les différentes populations étudiées.

CHAPITRE 1

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*, to determine (1) the incubation time to organogenesis, eyed egg, hatching, and swim-up phases at eight different temperatures (ranging from 8.5°C to 21.2°C), and (2) the best model to describe the relationship between these incubation times and temperature. We fitted seven models to our data: degree-day, power-law, Bělehrádek's equation, quadratic equation, first- and second-order exponentials, and a thermodynamic model. All the models gave comparable and highly significant fits to our data ($R^2 > 0.90$). We thus compared the in-situ incubation times with times predicted by (1) the degree-day model, because of its simplicity, and (2) the thermodynamic model, because of its theoretical foundation in comparison to the other models. The degree-day model was at least as accurate as the thermodynamic model when predicting in-situ incubation times (overall mean difference between predicted and observed incubation times of 1.4 ± 1.0 and 1.2 ± 1.2 d for the thermodynamic and degree-day models, respectively). Given the high accuracy obtained with the degree-day model in the field and its simplicity of use, we conclude that this model should be used to predict the incubation times of white sucker. We also observed a synchronization of hatching in-situ (the hatching period lasted only 5 d although the fertilization of eggs was done over a 10-d period), suggesting 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 (1) la durée d'incubation jusqu'aux phases d'organogénèse, d'oeuf oeillé, d'éclosion, et de larve pélagique (angl.: "swim-up") sous huit différentes températures (allant de 8.5°C à 21.2°C), et (2) le meilleur modèle pour décrire la relation entre ces durées d'incubation et la température. Sept modèles ont été ajustés à nos données: un modèle 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. Tous les modèles ont 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 (1) le modèle degrés-jours, à cause de sa simplicité, et (2) le modèle thermodynamique, à cause de ses fondements théoriques comparativement aux autres modèles. Le modèle degrés-jours était au moins aussi précis que le modèle thermodynamique pour prévoir les durées d'incubation in situ (différence moyenne globale de 1.4 ± 1.0 et de 1.2 ± 1.2 d entre les durées d'incubation prédites et observées, avec les modèles thermodynamique et degrés-jours respectivement). Étant donné la grande précision obtenue sur le terrain avec le modèle degrés-jours, et sa simplicité d'utilisation, nous concluons que ce modèle devrait être utilisé pour prédire les durées d'incubation du meunier noir. Nous avons aussi observé un synchronisme de l'éclosion in situ (la période d'éclosion s'est étendue sur seulement 5 d bien que la fertilisation des oeufs ait été faite sur une période de 10 d), suggérant 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 in the prediction of the incubation time of poikilotherm 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 which model is best. 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 (reviews of 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 due to 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).

Raney and Webster (1942) reported the incubation time (fertilization to hatch) for white sucker, *Catostomus commersoni*, at five constant temperatures. Other studies, done in 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 (1) determine the incubation time to different developmental phases of white sucker at eight temperatures in the laboratory, (2) 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 (3) test the accuracy of the best model by following eggs incubated under natural conditions.

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°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, Québec (46°36'N, 73°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°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 x 7 x 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°C) flowed from a reservoir into the first six incubators. When passing from one step to another, the

Table 1. Mean incubation temperature (± SD) of white sucker eggs in the laboratory experiment (across time for all replicates pooled). All temperatures were significantly different (ANOVA, $p < 0.0001$).

Treatment	Temperature (mean ± SD) (°C)	Range (°C)
1	8.5 ± 0.9	7.0 - 11.0
2	10.8 ± 1.6	8.5 - 15.0
3	11.7 ± 1.9	8.0 - 15.0
4	13.5 ± 1.7	10.5 - 18.0
5	15.2 ± 1.4	13.5 - 19.0
6	16.6 ± 1.7	14.0 - 19.5
7	17.7 ± 2.3	11.0 - 21.0
8	21.2 ± 2.4	14.0 - 24.5

water was heated by about 2°C by mixing with 35°C water from another reservoir. A waterflow of 120 to 150 $mL \cdot min^{-1}$ was maintained in the incubators. City water dechlorinated with activated carbon, UV irradiance, and aeration was used. To prevent fungal contamination of the eggs, a malachite green oxalate treatment (5 ppm for one hour) was applied daily until hatching of the first larvae (Brown and Gratzek 1980). Water temperature was monitored twice daily (±0.5°C), and dissolved oxygen (which was always ≥85% saturation) 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 2-3 d 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 McElman and Balon (1980). We pooled the developmental stages into five major phases: (1) egg cleavage, starting at fertilization; (2) organogenesis, starting with the elevation of the axial strand over the yolk, epiboly not completed; (3) eyed egg, starting with the appearance of lenses in the eyes; (4) hatching; and (5) swim-up larvae, starting with inflation of the swim bladder. We defined the incubation time to 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. Determination of the attainment of hatching phase at the five lowest temperatures and of swim-up larvae phase at all temperatures was done by visual estimation because there were few living embryos remaining by the end of the experiment.

In-situ egg development

To simulate the extented 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 x 12 cm x 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 X 12 cm X 2 m PVC channel filled with rocks) before being distributed to each incubator at a flow rate of 300 to 750 $mL \cdot min^{-1}$. The incubations were as follows: eggs from the first fertilization (12 May) were placed in three incubators; two 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 (± 0.01°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 larvae 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. We fit seven models to our data that are used frequently to predict incubation time in poikilotherms. These models are,

1) Degree-day: $y = k / (T-t_0)$

2) Power-law: $y = aT^b$

3) Bělehrádek's equation: $y = a / (T-t_0)^b$

4) Quadratic equation: $y = a + bT + cT^2$

5) Exponential: $y = ab^T$

6) Exponential (2nd-order): $y = ab^{T}c^{T^2}$

7) Thermodynamic:

$$y = \frac{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2_L}} - \frac{1}{T}\right)\right]}{\rho(25°C)\frac{T}{298}\exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right]}$$

where T is temperature (°C, except for model 7 where T is in Kelvin), k the sum of degree-days above t_0, t_0 the temperature at which no development occurs (developmental zero), and a, b and c are constants. The last model (7), depicts developmental rate as if it would be controlled by an enzyme which is reversibly denaturated at low temperatures (Schoolfield et al. 1981). The parameters of model (7) 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 (cal•mol^{-1}); R is the universal gas constant (1.987 cal•deg^{-1}•mol^{-1}); $T_{1/2L}$ is the temperature (K) at which the enzyme is 1/2 active and 1/2 low temperature inactive; $\rho(25°C)$ 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 (cal•mol^{-1}). 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).

We fit the models with a nonlinear least squares regression procedure using the Quasi-Newton estimation method (SYSTAT, 1992). The significance of the relationship was tested with an F-test done on the linear transformations of the models, except for models 3 and 7 which could not be linearized.

All the models gave good and comparable fits to our data (see Results and Discussion section). We thus compared the in-situ incubation times with times predicted by (1) the degree-day model, because of its simplicity, and (2) the thermodynamic model, because of its theoretical foundation in comparison to 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

Table 2. Mean incubation time (days ± SD) to organogenesis, eyed egg, hatching, and swim-up phases for white sucker eggs reared in the laboratory. Data are mean (± SD) of six replicates.

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

[a] The swim-up times could not be determined at those temperatures (see text).

temperatures: at the end of the experiment, 61 d after fertilization, no hatched embryo had reached this phase at 8.5°C and only 40% to 50% of all embryos had reached it at 10.8°C.

The comparison of our results with previous studies done on egg development of the white sucker in the laboratory suggests variability in the rate of egg development at a given temperature. Altough the incubation times to organogenesis and eyeing that we observed were similar to those reported in the literature, our times to hatching and swim-up differed 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 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 do 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, *Salmo salar*, salmon. However, this last hypothesis contradicts with our in-situ results, where the incubation times we observed were similar to the incubation times in previous reports (see below). Further research is needed to determine whether our predictive model is applicable to other populations of white sucker.

Comparison of the models

All the models tested showed comparable and highly significant fits to the data (Table 4). The adjusted values of the coefficients of determination (adjusted R^2) always exceeded 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, $p < 0.0001$).

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

The second-order exponential, thermodynamic, and the 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) 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, described well the egg development of cyprinids (Herzig and Winkler 1986), salmonids (Alderdice 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 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 applicable to 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. We view the thermodynamic model as a gross representation of the developmental process, but one with greater theoretical foundation compared to the other equations.

On the other hand, although it has often been criticized because of its lack of accuracy at extreme temperatures (reviews of Bagenal and Braum 1971, Wagner et al. 1984, Highley et al. 1986), we cannot discard the degree-day model based on our results. The degree-day model is easy to compute and fit our data well. Similarly, previous studies related to pest management have used the degree-day model in the field with satisfactory results (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 white sucker from different locations. Organogenesis has been found to occur in either 4 (this study) to 5 d (Walton 1980) after fertilization; the eyed egg phase in about 8 d (Walton 1980, this study); hatching in 16 (Walton 1980, Corbett and Powles 1983), 15-18 (Bond 1972), and 20-24 d (this study); and the swim-up phase in 22-25 (Bond 1972) to 27-32 d (Geen et al. 1966, Corbett and Powles 1983, this 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 d after fertilization, respectively, and hatching in 16-20 d. After hatching, the benthic larvae stay in the gravel for 10-12 d before downstream drift, which occurs approximately 1 mo after fertilization.

Figure 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 (—) and thermodynamic (---) models. Each point represents 1 to 6 samples. Models are based on raw data.

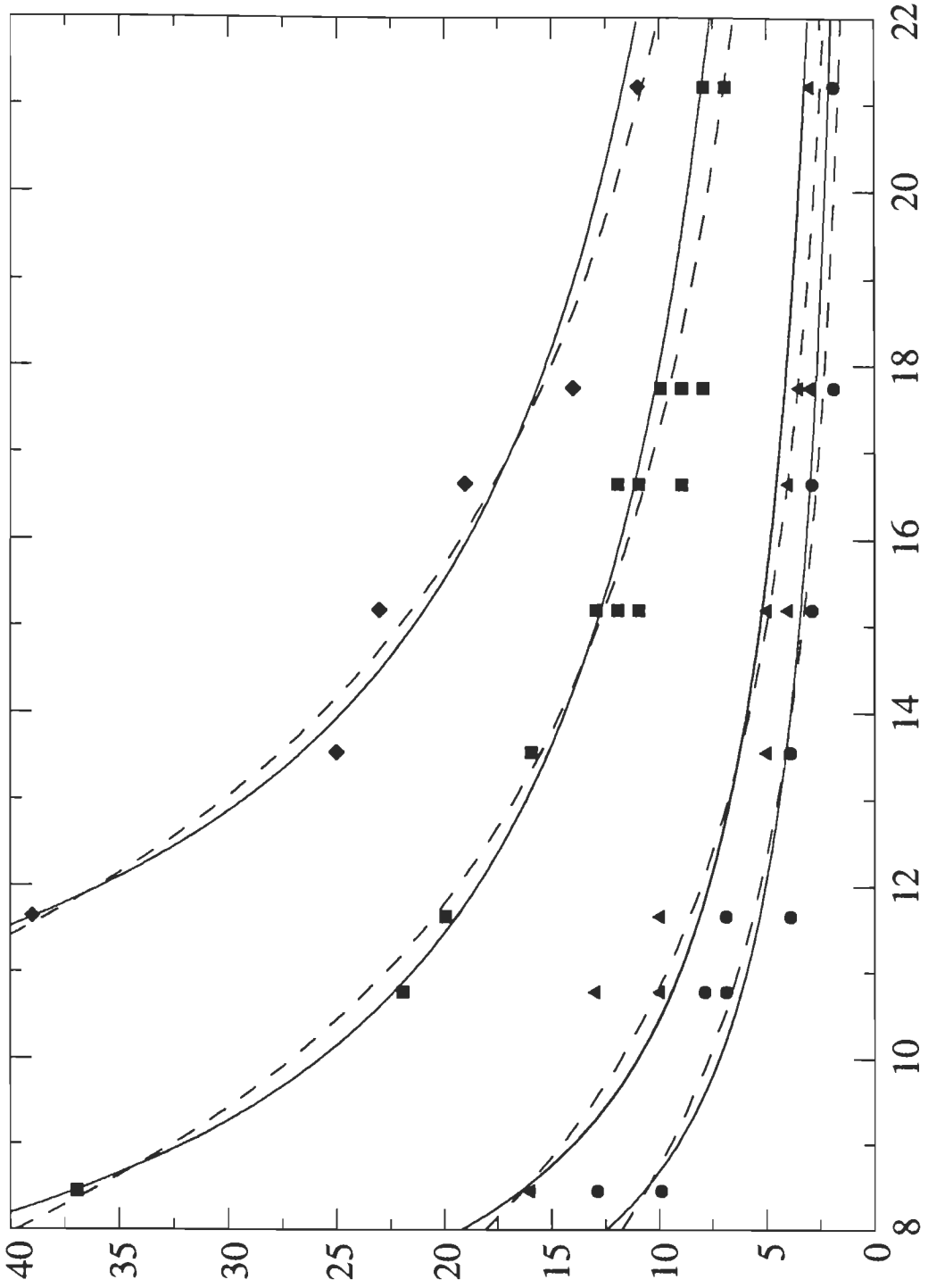

Incubation time (days)
0
5
10
15
20
25
30
35
40
8
10
12
14
16
18
20
22
Temperature (°C)

Table 5. Mean in-situ incubation time (days) to organogenesis, eyed egg, hatching, and swim-up phases for white sucker eggs. The mean temperature (°C) is the mean water temperature from egg fertilization to attainment of each phase.

	Organogenesis		*Eyed egg*		*Hatching*		*Swim-up*	
Fertilization date	Mean incub. time	Mean temp. (°C)	Mean incub. time	Mean temp. (°C)	Mean incub. time	Mean temp. (°C)	Mean incub. time	Mean temp. (°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	N.A.	N.A.
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	N.A.	N.A.
Mean	4.07	11.06	8.27	11.41	19.60	11.73	30.17	12.56

N.A.: 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.

Predicted vs. 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 d, occurring at the organogenesis phase (Table 7). The overall mean difference of the thermodynamic model (i.e. when all the developmental phases were combined) was 1.4 ± 1.0 d (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 d, occurring at the organogenesis phase, and the overall mean difference was 1.2 ± 1.2 d.

The high overall accuracy of the thermodynamic and degree-day models, with only the mean daily water temperature as predictor, contrast 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°-7°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 accelerated 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

Table 6. Parameter estimates and asymptotic standard errors (ASE) for the degree-day and thermodynamic models (see Data analysis section for definition of the parameters). NC: not computable.

	Degree-day		Thermodynamic			
Developmental phase	k (ASE)	t_0 (ASE)	ΔH_L (ASE)	$T_{1/2L}$ (ASE)	ρ (25°C) (ASE)	ΔH_A (ASE)
Organogenesis	34.247	5.272	-34694	284.833	0.847	10261
	(2.053)	(0.244)	(17277)	(8.746)	(0.320)	(8788)
Eyed egg	51.394	5.329	-34694	285.182	0.582	10261
	(2.554)	(0.198)	(NC)	(NC)	(NC)	(NC)
Hatching	130.323	4.935	-34694	283.220	0.200	10261
	(2.151)	(0.075)	(4531)	(1.237)	(0.018)	(1550)
Swim-up larvae	159.589	7.540	-34694	285.594	0.137	10261
	(5.333)	(0.174)	(24915)	(6.144)	(0.055)	(4221)

Table 7. Mean absolute difference between predicted and in-situ incubation times (days ± SD) for the degree-day and thermodynamic models. The mean absolute difference was computed as the mean of the absolute values of the difference between the predicted and observed times.

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

of our predictive models, it seems that fluctuating temperatures or other factors such as photoperiod had little, if any, 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 *Coregonus clupeaformis* and *C. artedii*. They reported that predicted incubation times of the eggs differed by an average of 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 adequately 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°-16.8°C in southeastern Ontario (Corbett and Powles 1983), 7.5°-17°C in Alberta (Bond 1972), and 10°-19°C in central British Columbia (Geen et al. 1966). These temperature are quite similar to the temperature regime observed during our in-situ experiments (range:

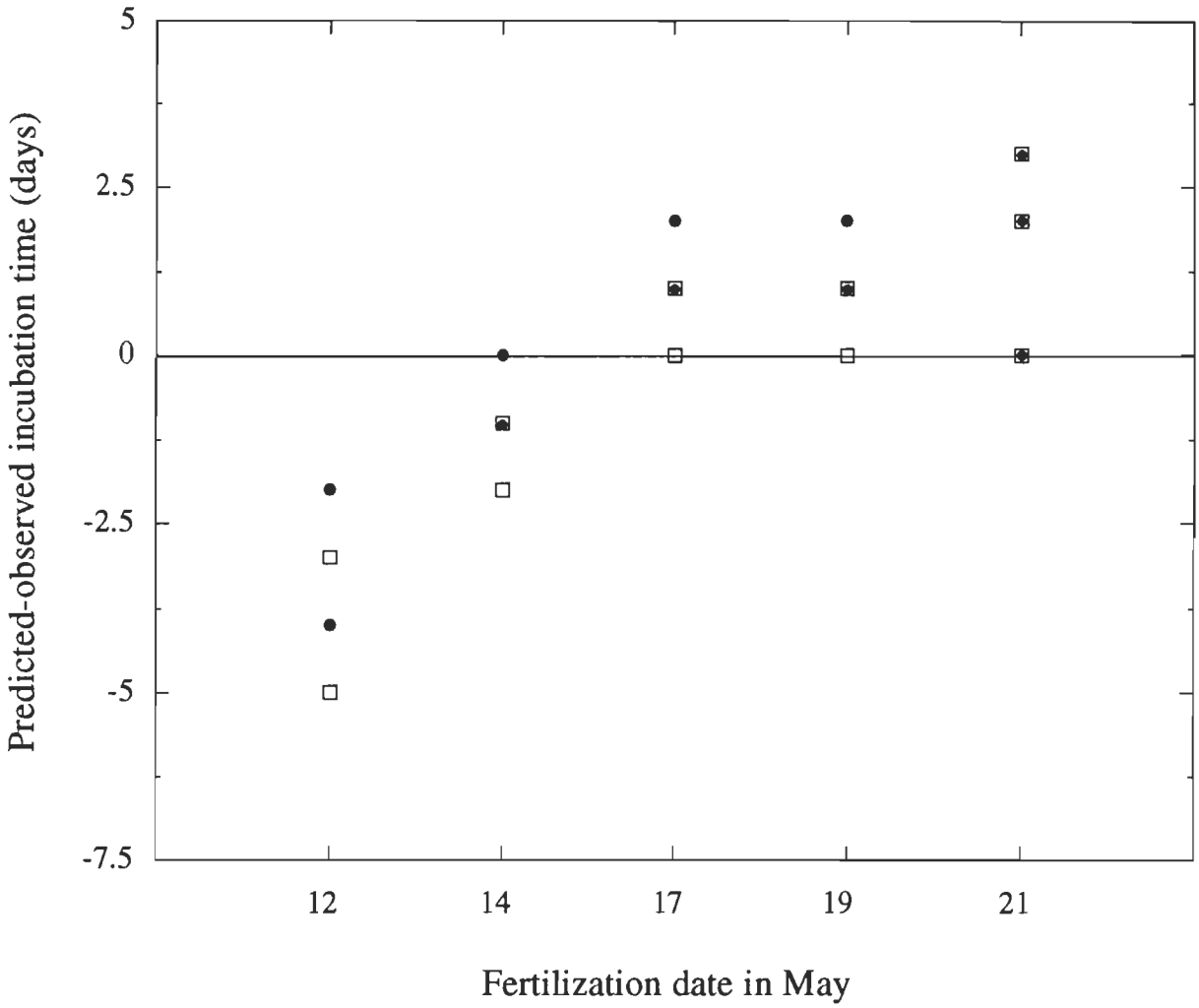
8.2°C-21.8°C). Consequently, we expect that a simple degree-day model would give accurate predictions in most areas where white sucker occur.

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-d 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 d (from 4 to 8 June). Such a synchrony of hatching was also observed in white sucker by Walton (1980), where all hatching took place over a 2-d 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 colder 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 varied only by 0.5°C among the five fertilization dates (range: 11.48°-12.06°C). Furthermore, if this was 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 overestimated the development 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: no difference in the amplitude of temperature fluctuation through time; F-test, $p=0.2045$). Another hypothesis is that the size variation of the eggs influenced the developmental rate. In this study, the mean egg diameter at 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

Figure 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 (filled circles) models.


5
2.5
0
-2.5
-5
-7.5
Predicted-observed incubation time (days)
12
14
17
19
21
Fertilization date in May

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 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 minutes on 12 May (date of first fertilization) to 914 minutes on 21 May (date of last fertilization) and finally to 946 minutes on 13 June, the end of the experiment. MacCrimmon and Kwain (1969) compared the incubation time of rainbow trout eggs, *Salmo gairdneri*, 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 16:8 photoperiod hatched four days before eggs held in constant darkness. These studies support the hypothesis that acceleration of 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 of swim-up larvae when the experiment was stopped on 13 June, which was the day of attainment for this phase in all of these six 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 fit incubation times of white sucker well. 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 as compared to 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.

The synchrony of hatching suggests an influence of photoperiod in addition to that of water temperature. However, this influence seems small compared to that of water temperature as we were able to predict the hatching date of white sucker with a mean accuracy of 1.5 d using only the mean water temperature as an independent variable. This synchronization in the hatching process is interesting in terms of management implications. As suggested by Magnan et al. (1996), a way to lower the impact of introduced white sucker on exploited species, in addition to mass removal, would be to decrease recruitment by controlling benthic or drifting swim-up larvae on their spawning grounds (with Rotenone or electrofishing for example). Given the synchronization of hatching, a control directed at the hatched larvae would reduce the costs of the operation because fewer treatments would be required comparatively to a control directed at the earlier developmental phases.

Finally, although the spawning migration of the 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 (i.e. laying and fertilization of eggs) of the white sucker. 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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CHAPITRE 2

Timing of spawning and validation of a degree-day model to predict the in-situ embryonic developmental rate of white sucker, *Catostomus commersoni*.

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Abstract

We sampled eggs and larvae of white sucker, *Catostomus commersoni*, on six spawning grounds to (1) determine the factors responsible for the timing of spawning (laying and fertilization of the eggs), and (2) validate four degree-day equations that predict the attainment of organogenesis, eyed egg, hatching, and swim-up phases in the field. We estimated a threshold temperature for spawning of 13°C at the four warmer sites, and 10°C at the two colder sites. A delay of 2-3 d was observed between the threshold and the onset of spawning. On average, the degree-day equations predicted the day of attainment of the developmental phases with an accuracy of 1.6 d, except at the two colder sites, where developmental rates were faster than predicted. The threshold temperature was considered to be a synchronizing cue activating the final oocyte maturation; the delay observed between the attainment of the threshold temperature and the beginning of spawning is consistent with the time required for the final maturation of oocyte in white sucker. The lower spawning temperatures and faster developmental rates observed at the colder sites were interpreted as adaptations to the reduced growing season. Finally, at one site the drift of swim-up larvae occurred during a 6-d period even though spawning lasted 24 d (it was not possible to determine the exact duration of the drift at the other sites). This synchronization of the drift could be an adaptation that lowers the risk of predation on individual larvae (by a dilution effect), as all the larvae enter the lake within a few days.

Résumé

Nous avons échantillonné des oeufs et des larves de meunier noir, *Catostomus commersoni*, sur six frayères afin de (1) identifier les facteurs déterminant la date de ponte (expulsion et fertilisation des oeufs), et (2) valider quatre équations degrés-jours prédisant la date d'atteinte des phases d'organogénèse, d'oeuf oeillé, d'éclosion, et de larve pélagique (angl.: "swim-up") sur le terrain. Nous avons estimé une température seuil pour la ponte de 13°C aux quatre sites les plus chauds, et de 10°C aux deux sites les plus froids. Un délai de 2-3 d a été observé entre ce seuil et le début de la ponte. En moyenne les équations degrés-jours ont prédit la date d'atteinte des phases de développement avec une précision de 1,6 d, excepté aux deux sites plus froids, où les taux de développement ont été plus rapides que prédit. La température seuil a été interprétée comme étant un signal activant la maturation finale des oocytes; le délai observé entre l'atteinte de la température seuil et le début de la ponte concorde avec le temps nécessaire à la maturation finale des oocytes chez le meunier noir. Les températures de ponte plus basses et les taux de développement plus rapides observés aux sites plus froids ont été interprétés comme des adaptations pour la saison de croissance réduite. Finalement, à un des sites la dérive des larves est survenue durant une période de 6 d, malgré que la ponte ait eu lieu durant 24 d (il n'était pas possible de déterminer la durée exacte de la dérive aux autres sites). Cette synchronisation de la dérive pourrait être une adaptation pour diminuer le risque de prédation des larves (par un effet de dilution), toutes les larves arrivant dans le lac dans un délai de quelques jours.

Introduction

The white sucker, *Catostomus commersoni*, is often considered a pest species by fisheries managers because of its impact on many exploited fish species (Johnson 1977, Barton 1980, Magnan et al. 1990, Hayes et al. 1992), notably in many lakes of eastern Canada, where it was introduced by bait fishers or colonized the watersheds following logging activities (Magnan et al. 1994). For example, the mean annual yield of brook trout, *Salvelinus fontinalis*, decreased by 50 to 80% when living in sympatry with white sucker in these lakes (Magnan 1988, 1989). Given their strong impact on brook trout populations and the concurrent socioeconomic losses, fisheries managers are interested in developing new management tools to control these introduced white sucker populations. One method to lower the impact of white sucker on brook trout populations would be to decrease their recruitment by controlling benthic larvae with Rotenone or drifting swim-up larvae with electrofishing on the spawning grounds (Magnan et al. 1996). Such interventions require knowledge of the timing of these developmental stages in nature.

Based on laboratory and in-situ incubations of white sucker eggs, Hamel et al. (1996) built four degree-day equations to predict the attainment of organogenesis, eyed egg, hatching, and swim-up larval phases. To use these equations properly, one must know the exact time of white sucker spawning and validate their reliability on natural populations. Most studies that were done during the reproductive period of white sucker have dealt mainly with the migration of the species to their spawning grounds. It is well documented that adults move into the spawning streams only when a threshold water temperature is reached, somewhere between 7.2°C (Raney and Webster 1942) and 10°C (Geen et al. 1966, Bond 1972, Walton 1980, Corbett and Powles 1983), and when adequate discharge of water is encountered (Barton 1980, Walton 1980). In contrast, little information exists on the timing of spawning itself (laying and fertilization of the eggs). Anectodal informations suggest that

spawning occurs between 9°C and 15°C (Stacey et al. 1984). Lalancette (1973) reported that spawning occurred between 13°C and 15°C and that no spawning occurred at higher temperatures.

The degree-day equations built by Hamel et al. (1996) have not been tested on natural populations of white sucker. Interpopulation variations in the embryonic response to temperature have been shown in insect (Campbell et al. 1974, Dingle and Mousseau 1994) and fish eggs (Smoker 1986, Brännäs 1988). In white sucker, there are considerable differences in the hatching and swim-up incubation times observed in different studies (Hamel et al. 1996), suggesting interpopulation differences in response to temperature.

The objectives of this study were (1) to determine the factors responsible for the timing of white sucker spawning in the field, and (2) to validate the degree-day equations built by Hamel et al. (1996) on natural populations of white sucker. To do so, we sampled eggs and larvae on six distant spawning grounds and followed the embryonic development in relation with water temperature.

Materials and methods

Study sites

The six spawning grounds were located in the province of Québec (Canada), along a 485 km east-west axis crossing the Saint Laurence River. The spawning grounds were two inlets of Lake Cinq Doigts, Rouge-Matawin Reserve (46°36'N; 74°32'W), referred to hereafter as the Fernand and Prunier spawning grounds (being the source lakes of these inlets), two inlets of Lake Sans-Nom, Mastigouche Reserve (46°35'N; 73°35'W), referred to hereafter as the Cigale and Sauterelle spawning grounds (source lakes), the inlet of Lake Basque, Saguenay region (48°37'N; 70°40'W), and the inlet of Lake Blanc, Rimouski Reserve (48°01'N; 68°16'W). As suggested by Duchesne and Magnan (1996), we used the numerical climate

classification of Litynski (1984, 1988) to identify regional differences in climate. The inlet of Lake Basque is located in a region subject to colder annual temperatures and to more precipitation than the five other study sites, which are considered to be in the same climatic region by Litynski's classification. On the other hand, when considering the climate normals (Environment Canada 1982), the inlet of Lake Blanc is located in the coldest region among these remaining five sites (mean daily air temperature in May and June of 8.8 and 15.1°C respectively in Rimouski; 10.0 and 15.5°C in St-Alexis-des-Monts, near Mastigouche Reserve; and 10.6 and 15.8°C in l'Annonciation, near Rouge-Matawin Reserve). We therefore considered that white sucker populations of lakes Basque and Blanc are subject to colder climates than those of lakes Cinq Doigts and Sans-Nom (which was supported by mean water temperatures measured on these spawning grounds, see Fig. 1 in the Results section).

Sampling on the spawning sites

To determine the date of spawning (laying and fertilization of the eggs) and the duration of embryonic development of white sucker, eggs and benthic larvae were sampled with Surber samplers or dip nets (sampling area of 900 cm^2) at all sites in spring 1993, and at Sauterelle in spring 1994. The sampling of eggs began before the spawners entered the streams or soon after the first spawners were seen on the spawning grounds. Samples were taken every 2-3 d on all spawning grounds, with the exceptions of Cigale and Sauterelle in 1993, where odd and even stations were sampled on alternate days. Fifteen stations were surveyed on the Fernand, Prunier, Cigale, and Sauterelle spawning grounds, 20 in Basque, 10 in Blanc, and 25 in Sauterelle in 1994. These stations were located in the most suitable area for spawning (i.e. riffles with gravel and rocks substrate; P. East and P. Hamel, personal observations). To avoid repeated sampling in a same parcel, we marked each parcel after sampling. To determine when the swim-up larvae drifted from the spawning grounds to the lakes, we

sampled the banks of the receptor lakes with dip nets in 1993. Transects of 10 m parallel to the shore were done at depths of 10-60 cm, on both sides of the mouth of spawning ground tributaries. Six transects were done for the Fernand, Prunier, and Basque spawning ground tributaries and 10 transects for that of Sauterelle. The sampling period extended from 21 June to 2 July on Fernand spawning ground, from 21 June to 21 July on Prunier spawning ground, from 1 to 18 June on Sauterelle spawning ground, and from 7 June to 16 July on Basque spawning ground (no larvae were caught at Blanc spawning ground). Samples were taken daily on Sauterelle spawning ground, and at 2-3 d intervals on the other spawning grounds. In 1994, the larvae were sampled by two drift nets in Sauterelle spawning ground. The nets were set side by side and almost completely covered the stream.

The water temperature on each spawning ground was recorded at 15 min intervals with an electronic thermograph located on the bottom of the stream bed within the collection sites of eggs, with the exception of Lake Basque inlet where water temperature was recorded with a mechanical thermograph every 3 h. The water depth was measured at all sampling sites except for Fernand and Prunier.

The eggs and larvae were kept in a 5% formalin solution for subsequent identification of the developmental stages in the laboratory. The determination of developmental stages followed McElman and Balon (1980). We grouped the developmental stages into five major phases: (1) egg cleavage, starting at fertilization; (2) organogenesis, starting with the elevation of the axial strand over the yolk, epiboly not complete; (3) eyed egg, starting with the appearance of lenses in the eyes; (4) hatching (hereafter called benthic larvae); and (5) swim-up larvae, starting with the inflation of the swim bladder.

Validation of the degree-day equations

The four degree-day equations built by Hamel et al. (1996) were of the form $y = k/(T-t_0)$, where y is the incubation time from fertilization to attainment of a given developmental phase,

k the sum of degree-days above t_0, T the water temperature (°C), and t_0 the water temperature at which no development occurs (developmental zero). The values of k and t_0 of each developmental phase are listed in Table 1. To assess the reliability of these equations, the predicted dates of attainment of organogenesis, eyed egg, hatching, and swim-up phases were compared with those observed on the six spawning grounds. We considered that the "observed" date of first spawning was the day preceding the first time the cumulative frequency of eggs in the cleavage phase represented at least 5% of all eggs found in that phase during the reproductive season. Similarly, the "observed" dates of attainment of the subsequent developmental phases were noted as the day that the cumulative frequency of eggs of a given phase represented at least 5% of all eggs found for that phase. The "predicted" date of the attainment of each phase was obtained by using the corresponding degree-day equation in conjunction with the mean daily water temperature measured on the spawning grounds. Starting with the day after the observed spawning date, we first calculated the incubation time (y) corresponding to the observed mean daily water temperature to obtain the proportion of the total development that occurred daily (1/y). We then summed these daily portions of development to predict the date of attainment of the phase studied, which corresponded to the day when this summation was nearest to 1.

Results

Factors determining the timing of spawning

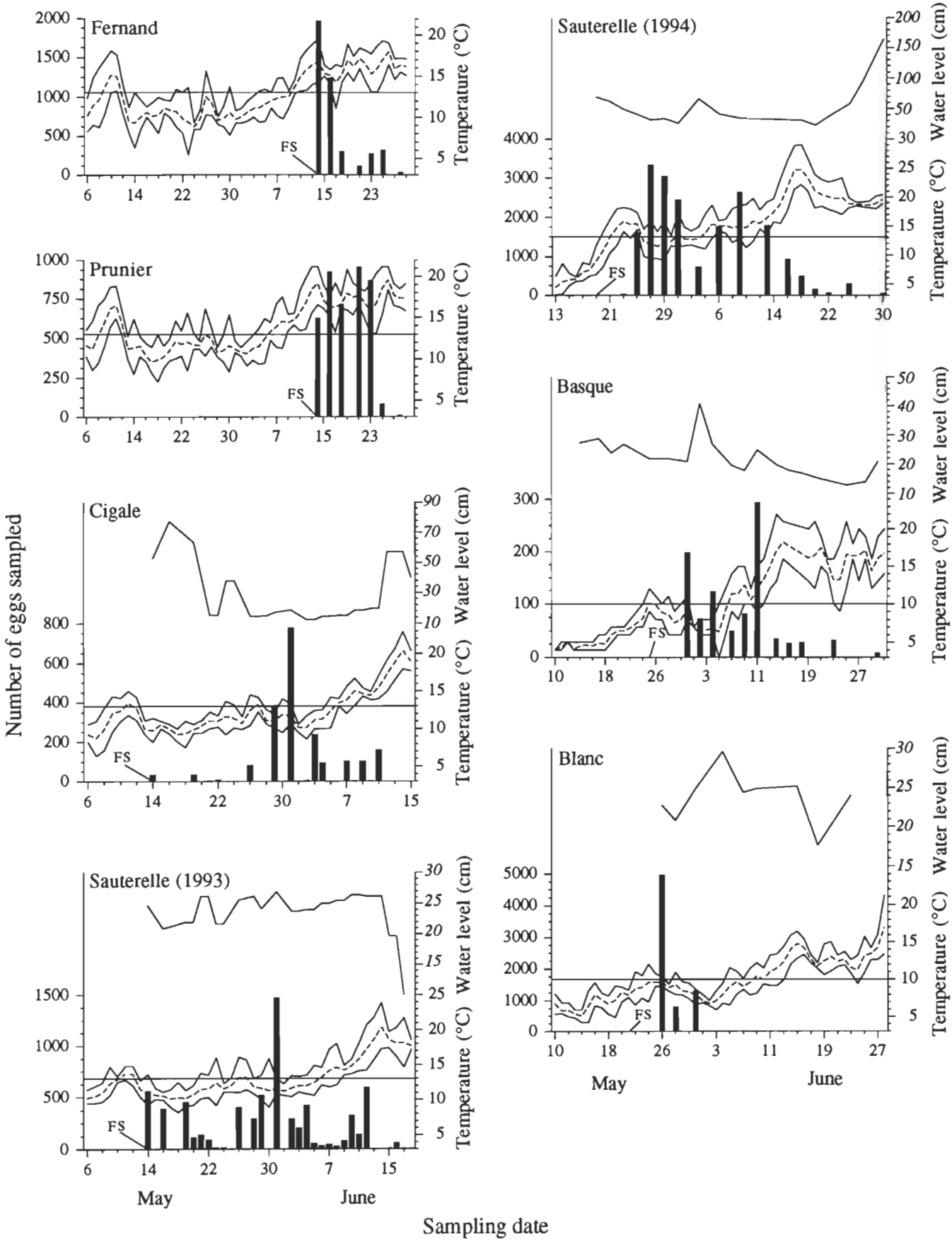
Spawning started from mid to late May on all spawning grounds studied in 1993 and 1994 (Fig. 1). Although not shown in Figure 1, evidence of some spawning was observed in early May in Fernand and Prunier before the beginning of the sampling period: on the Fernand spawning ground, approximately 1600 ripe spawners were present on 12 May, while approximately 5000 were present on 12 May on the Prunier spawning ground; also,

Table 1. Values of k and t_0 used for each developmental phase studied (from Hamel et al. 1996).

Developmental phase	k (degree-days)	t_0 (°C)
Organogenesis	34.247	5.272
Eyed egg	51.394	5.329
Hatching	130.323	4.935
Swim-up larvae	159.589	7.540

Figure 1

Spawning period of white sucker on the spawning grounds studied as determined by the number of eggs in the cleavage phase found in our samples. The water level, and maximum (——), mean (-----), and minimum (——) water temperature are also shown. First sampling (FS) began before or soon after the first spawners were seen on the spawning grounds. The horizontal solid line show the estimated threshold temperature for spawning.


Fernand
Prunier
Cigale
Sauterelle (1993)
Sauterelle (1994)
Basque
Blanc
FS
Number of eggs sampled
Temperature (°C)
Water level (cm)
May
June
Sampling date

eggs were found on 14 May at the only site sampled on the Prunier spawning ground. Logistical problems prevented us from starting the sampling at this time. The spawners were present on the spawning grounds for only a few days and soon returned to the lake following a decrease in water temperature on 13 May; they were seen again on the spawning grounds only after 7 and 11 June on the Fernand and Prunier spawning grounds, respectively.

The comparison of spawning activity (as determined by the number of eggs found in the cleavage phase) with water temperature suggests that the beginning of spawning in white sucker is related to a threshold temperature (Fig. 1). In all cases, the first spawning occurred only after a given temperature had been reached, whether or not the water temperature remained above or dropped below this threshold afterwards. However, in the cases where the water temperature dropped, additional spawning was observed when the mean water temperature again rose over the threshold temperature. On the Fernand, Prunier, Cigale, and Sauterelle spawning grounds, the threshold temperature was 13°C (mean water temperature). In Fernand and Prunier, the mean water temperature exceeded 13°C in early May, when some evidence of spawning was observed, and in the beginning of June, when spawning resumed. In Cigale and Sauterelle (in 1993) the onset of spawning and the peak spawning activity (from 28 May to 4 June) both followed a rise in mean water temperature over 13°C. A third spawning in Sauterelle began around 9-10 June, after the mean temperature again rose over 13°C. In 1994, the beginning of the two spawning periods observed in Sauterelle (around 25 May and 6 June) followed a rise of the mean water temperature over 13°C.

The white sucker of the inlets of lakes Basque and Blanc spawned at lower temperatures than those on the Fernand, Prunier, Cigale, and Sauterelle spawning grounds (Fig. 1). The threshold temperature for the onset of spawning at these two sites seemed to be near 10°C, since the first eggs were found only after the mean water temperature reached 10°C. A second spawning began near 8 June in Basque inlet, in agreement with the 10°C threshold. The spawning pattern at the inlet of Lake Blanc differed somewhat from those

observed on the other spawning grounds: only one spawning occurred even though the mean water temperature again rose over 10°C on 9 June.

At almost all study sites, spawning did not start immediately after the threshold temperature had been reached. A mean delay of 2.6 ± 1.9 d was observed between the time when this temperature was reached and the subsequent beginning of spawning (Table 2).

Finally, in contrast to the findings of Barton (1980) and Walton (1980), there was no evidence of a relationship between the stream water level (indicative of discharge) and spawning activity in our study: spawning occurred in the 15-50 cm range, i.e., at both low and high water levels (Fig. 1).

Validation of the degree-day equations

For embryos found on the Fernand, Prunier, and Sauterelle spawning grounds (Fig. 2), the degree-day equations predicted the attainment of organogenesis, eyed egg, hatching, and swim-up phases with an overall mean difference of 1.6 ± 1.7 d between predicted and observed incubation times. The results for the Cigale spawning ground were not considered here because they indicated that the organogenesis, eyed egg, and hatching phases all occurred on 29 May; this was possibly caused by the sampling difficulties encountered at this site (high water level, few eggs sampled). The equations were less accurate for Basque and Blanc inlets, where the overall mean difference was 6.4 ± 3.4 d. In these two cases, the predicted times were always greater than the observed times, meaning that the embryos developed much faster than predicted from the degree-day equations. To determine whether this inaccuracy was due to a faster embryonic developmental rate than in the population from the Sauterelle spawning ground (from which the parameters of the degree-day equations were established) or to the inadequacy of the degree-day model to predict the incubation times of fish eggs in the field, we compared the incubation times predicted with the degree-day equations to those predicted using the thermodynamic equations tested by Hamel et al.

Table 2. Number of days between the attainment of the threshold temperature and the observed spawning dates.

Spawning site	Spawning date	Delay (days)
Fernand [a]	12 June	2
Prunier	13 June	7
Cigale	13 May	2
	28 May	1
Sauterelle (1993)	13 May	2
	27 May	1
	9 June	3
Sauterelle (1994)	24 May	3
	2 June	2
Basque	30 May	5
	8 June	1
Blanc [a]	24 May	0
Mean ± 1 SD		2.6 ± 1.9

[a] For these sites, we considered that spawning occurred 2 d before we first found eggs because substantial number of eggs in the organogenesis phase were present in the first samples.

Figure 2

Embryonic development of white sucker on the spawning grounds studied. Observed (asterisks) and predicted (arrows) dates of attainment of each phase are indicated.

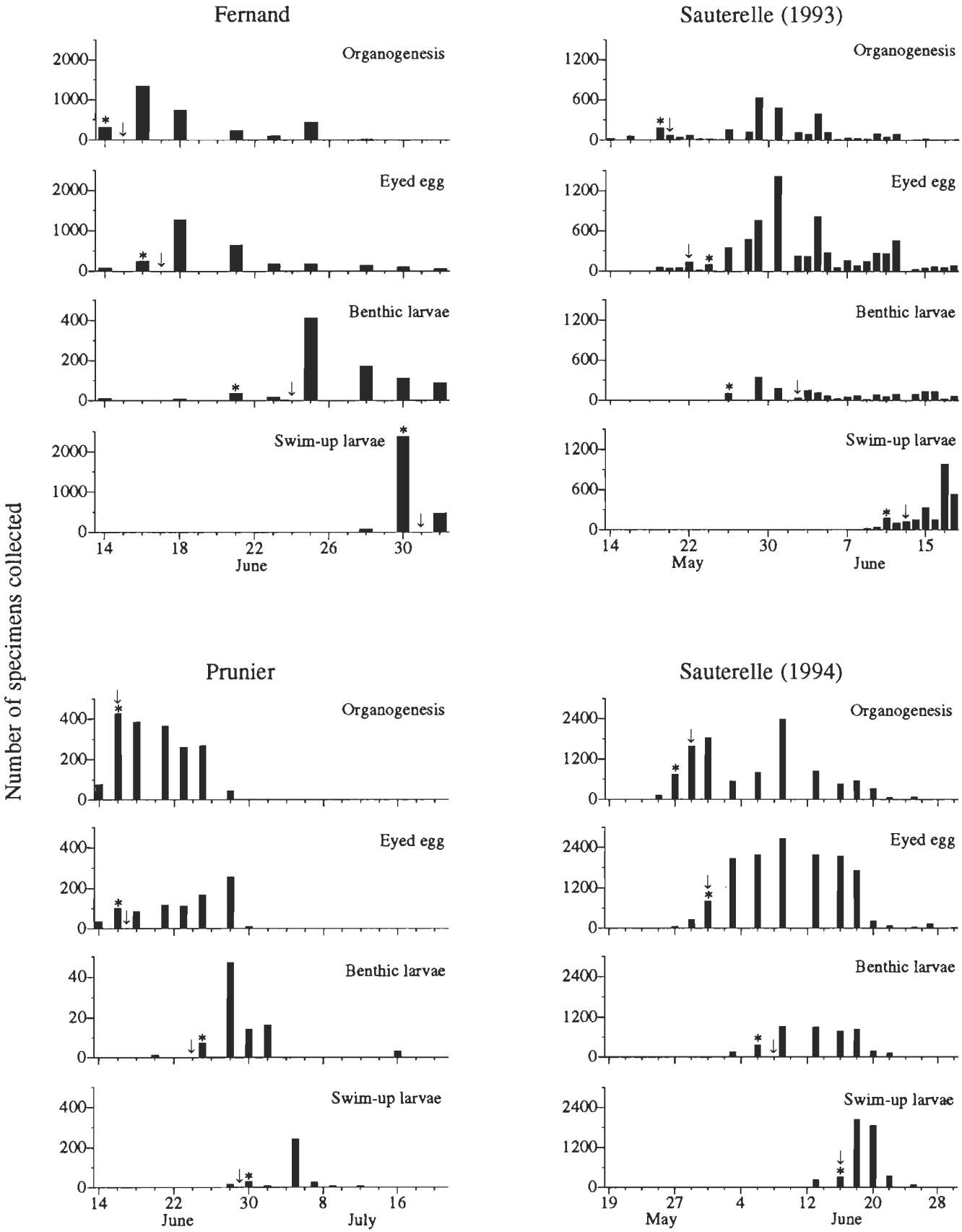
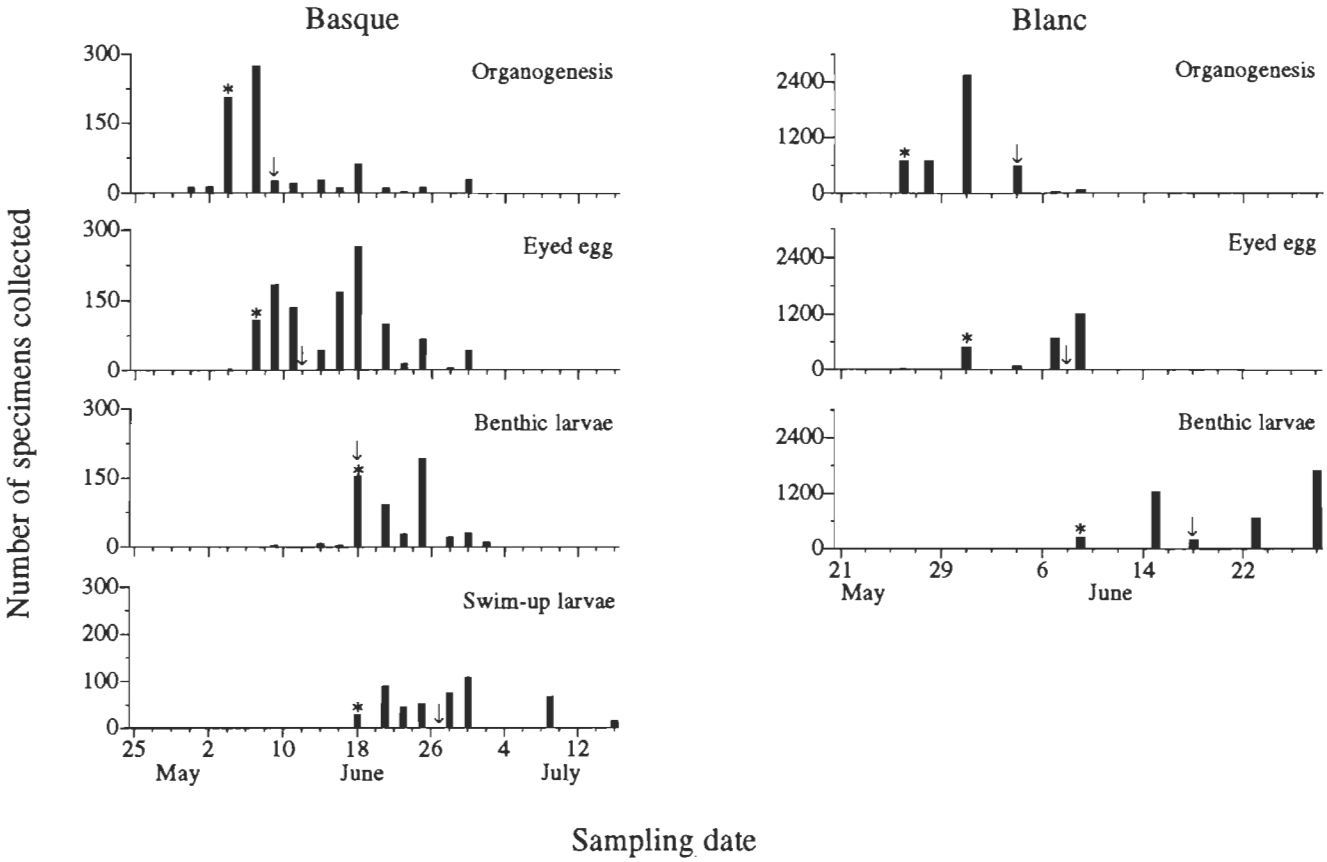

Fernand
Sauterelle (1993)
Prunier
Sauterelle (1994)
Organogenesis
Eyed egg
Benthic larvae
Swim-up larvae
Number of specimens collected
Sampling date
June
May
July

Figure 2 (continued)


Basque
Blanc
Organogenesis
Eyed egg
Benthic larvae
Swim-up larvae
Number of specimens collected
Sampling date
May
June
July

(1996), which account for the nonlinearity of the developmental rate (see Discussion). The incubation times predicted from the thermodynamic model were the same as those predicted from degree-days, indicating that the models' inaccuracy in predicting the embryonic developmental rate in Basque and Blanc inlets was due to interpopulation differences.

Finally, we observed a synchronization in the drift of swim-up larvae on Sauterelle spawning ground in 1994, where the swim-up larvae were caught in drift nets. The swim-up larval phase lasted only 6 d, from 16 to 22 June (Fig. 2), even though spawning was spread over 24 d, from 25 May to 18 June (Fig. 1). Water temperature is not sufficient to explain the reduced duration of the swim-up phase observed here: the degree-day equations used with the mean daily water temperature predicted a swim-up period of 12 d, twice longer than that observed.

We could not determine if a synchronization in drift occurred on Fernand and Sauterelle (in 1993) spawning grounds because swim-up larvae were still found in our samples when the sampling was stopped. No synchronization was evident on Prunier and Basque spawning grounds, where the duration of the swim-up phases were 2 d shorter and 3 d longer than the duration of the cleavage phase, respectively. However, this lack of evidence for a synchronization in the drift on the latter spawning grounds may have occurred because the sampling of the swim-up larvae was done in the receptor lakes rather than with drift nets. Once in the lake, the larvae possibly stayed near the banks for many days, which, in turn, biased our estimation of the duration of the swim-up phase.

Discussion

Factors determining the timing of spawning

Previous studies on white sucker reproduction found a major influence of water temperature on the initiation of the spawning migration (Raney and Webster 1942, Tremblay 1962, Geen

et al. 1966, Bond 1972, Walton 1980, Corbett and Powles 1983). Our results indicate that water temperature is also a primary factor in determining the timing of spawning (i.e. laying and fertilization of eggs). At all study sites, no spawning occurred before the threshold temperature was reached (10° or 13°C depending of the area) even though fish were on the spawning grounds. The threshold mean temperature observed in this study could be viewed as a synchronizing cue indicating to spawners the presence of adequate spawning conditions. In fish species where the final maturation of gametes is spontaneous (i.e. automatically following gamete growth), such synchronizing cues are needed only to initiate spawning itself (Munro 1990). In contrast, these cues activate the final maturation of gametes in other species, which is followed by spawning if mates are present. Since the final maturation of eggs in white sucker is not a spontaneous process (Stacey et al. 1984), the threshold temperature observed here seems to be a synchronizing cue activating the final maturation of eggs and not spawning itself. Furthermore, the average delay of 2-3 d observed between the attainment of the threshold temperature and the beginning of spawning is consistent with the 3-4 d delay observed by Stacey et al. (1984) between injection of human gonadotropin and ovulation in female white sucker (gonadotropin is responsible for final oocyte maturation). Therefore, the precise timing of spawning in white sucker appears to be determined by a critical threshold temperature initiating the final oocyte maturation (here 10° or 13°C), which is followed by mating approximately 2-3 d later, when maturation and ovulation are completed. The lower threshold temperatures of Basque and Blanc inlets are discussed below.

Validation of the degree-day equations

The degree-day equations tested in the present study closely predicted the incubation times to organogenesis, eyed egg, hatching, and swim-up phases of white sucker in the warmer spawning grounds (Fernand, Prunier, and Sauterelle; Fig. 2). In contrast, our models were

less accurate in the colder habitats Basque and Blanc (Fig. 2). We showed that the discrepancies observed between predicted and observed incubation times in the colder spawning grounds were not due to an inadequacy of the degree-day model to predict the incubation times of white sucker eggs in the field, but rather to a faster embryonic developmental rate of these populations. This faster rate, as well as the lower threshold temperature for spawning, could be adaptations to colder environments (Basque and Blanc inlets are located in colder areas than the other study sites). It is generally accepted that the timing of spawning has evolved to ensure a maximum survival of the offspring (Bye 1984, Munro 1990). As in other fish species (Conover 1992), white sucker populations living in colder environments face the pressure to spawn later in the spring than their southern counterparts to avoid cold temperatures that are lethal to the eggs. For example, although spawning migrations start at the same temperature (10°C), they occur in mid April near Peterborough, Ontario (Corbett and Powles 1983), and in mid to late May in Alberta (Bond 1972, Walton 1980). However, the outcome of later spawning is a reduction in the length of the growing season for the progeny. The length of the first growing season is of prime importance because survival of young-of-the-year through the first winter has been shown to be highly dependent on body size at first winter in some species (Conover 1992, Goodgame and Miranda 1993). Another consequence of reproduction in colder environments is the concurrent increase in the duration of the embryonic period. Finally, it has previously been suggested that intraspecific variations in embryonic developmental rate and early growth rate observed in fish and insects are adaptations to temperature. It has generally been found that development and growth are faster in colder environments (Campbell et al. 1974, Smoker 1986, Brännäs 1988, Conover and Present 1990, Dingle and Mousseau 1994). Thus, we suggest that the lower spawning temperature and increased developmental rate observed at the colder spawning grounds Basque and Blanc result from pressures for suitable

temperatures for the eggs on one hand, and for a long growing season for the progeny on the other hand.

In most areas of its geographical distribution the spawning migration of white sucker is reported to start only when the water temperature reaches 10°C (Geen et al. 1966, Bond 1972, Walton 1980, Corbett and Powles 1983). Furthermore, Bond (1972) and Stacey et al. (1984) have shown that white sucker spawners were not fully ripe when arriving on the spawning grounds. Similarly, we observed that some days elapsed between the arrival of white sucker on Fernand and Prunier spawning grounds and the onset of spawning. Thus, we suppose that the 13°C threshold for spawning probably applies over most of the species' range. For northern populations where climatic conditions are comparable to those found in Basque and Blanc inlets (mean water temperature over 10°C only in late May-early June), a threshold of 10°C would probably predict more closely the timing of spawning. Similarly, the values of the constant k in the degree-day equations should also be modified to obtain more realistic predictions of the attainment of each developmental phase. An a posteriori adjustment of these values, done by computing the mean number of degree-days required by the eggs to attain each developmental phase in Basque and Blanc inlets, gave 9.45, 22.88, 95.36, and 108.47 degree-days for organogenesis, eyed egg, hatching, and swim-up phases respectively. The use of these values in the equations (with t_0 unchanged) should give good predictions in colder environments.

Finally, a synchronization of hatching (and thus of the drift), similar to the one observed for the drift of swim-up larvae in the present study (Sauterelle, in 1994), was observed by Walton (1980) and Hamel et al. (1996). Hamel et al. (1996) suggested that white sucker embryonic developmental rate increases as daylength increases in spring, in response to the influence of photoperiod on the metabolic rate of fish embryos. This synchronization of the drift could be an adaptation to lower the risk of predation on individual

larvae. When entering in the lake, the larvae swim in the water column and are very susceptible to predation by larger fish. Being in the lake together over a short period of time could lower the risk of predation by a "dilution effect" (Pitcher and Parrish 1993). Given this synchronization, a control of white sucker directed on the drifting swim-up larvae (e.g. with electric fences in the streams) could shorten the duration of the control, and would allow the elimination of a greater proportion of the total recruitment at lower costs.

Our results emphasize that degree-day equations can effectively predict the incubation times of white sucker in nature. This contrasts with the conclusions of many authors, who warned against the use of the degree-day approach (see reviews of Andrewartha and Birch 1954, Bagenal and Braum 1971, Humpesch and Elliott 1980, Wagner et al. 1984, Highley et al. 1986). Laboratory experiments conducted on various species have shown that degree-day models are inaccurate at the low and high ends of the temperature range allowing development of poikilotherm eggs (the developmental rate decreases asymptotically rather than linearly with temperature and falls at higher temperatures). However, these extremes rarely occur in nature, especially during the spawning period of white sucker. In this context, it is quite conceivable that the degree-day approach is reliable in nature because of the selective pressure acting on fish to spawn only when optimal temperatures for egg development are present.

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CONCLUSION GÉNÉRALE

Les résultats des deux articles composant ce travail nous permettent de prédire précisément l'atteinte des principales phases du développement embryonnaire du meunier noir en nature. Dans le premier article, nous présentons quatre équations basées sur un modèle degrés-jours, permettant de prédire les durées d'incubation nécessaires jusqu'à l'atteinte des phases d'organogénèse, d'oeuf oeillé, d'éclosion et de larve pélagique (angl.: "swim-up"). Le modèle degrés-jours était quelque peu moins précis que le meilleur modèle (thermodynamique) parmi les sept testés en laboratoire, mais était au moins aussi précis que ce dernier lors de la validation in situ. Cette étude nous a aussi permis de découvrir qu'il existe un synchronisme de l'éclosion des oeufs de meunier noir in situ.

Dans le deuxième article, qui est complémentaire au premier, nous avons identifié les facteurs déterminant la date de ponte, afin de connaître le temps t_0 du développement embryonnaire, nécessaire à l'utilisation des équations degrés-jours. Nous avons également validé les équations degrés-jours avec les oeufs pondus naturellement sur six frayères. Nous avons découvert que la ponte du meunier noir ne survient que 2 à 3 d après qu'une température seuil soit atteinte (10° ou 13°C dépendant de la région). Les équations degrés-jours ont prédit l'atteinte des différentes phases de développement avec une précision moyenne de 1,6 d, excepté aux deux sites plus froids où le taux de développement a été plus rapide que prédit; nous avons cependant proposé a posteriori des équations degrés-jours modifiées qui devraient permettre de bonnes prédictions pour les populations de meunier noir retrouvées dans ces régions climatiques plus froides. Enfin, nous avons aussi observé un synchronisme de la dérive des larves à un des sites étudiés (la durée exacte de la dérive n'a pas pu être déterminée aux autres sites). Étant donné ce synchronisme, la durée d'un

contrôle visant les larves pélagiques pourrait être réduite, comparativement à un contrôle visant les autres phases de développement, ce qui permettrait d'éliminer une plus grande proportion du recrutement à moindres coûts.

En conclusion, nous avons mis en évidence qu'il est possible de prédire la date de ponte du meunier noir sur une frayère donnée en suivant uniquement la température de l'eau. Par la suite, il est possible de prédire précisément la date d'atteinte des principales phases du développement embryonnaire en se servant des équations degrés-jours, permettant ainsi de planifier le moment le plus propice à une intervention de contrôle.

ANNEXE A

Résumé long en français du chapitre 1.

Comparaison de différents modèles pour prédire le taux de développement embryonnaire des poissons in situ, avec référence particulière au meunier noir, *Catostomus commersoni.*

Introduction

La température exerce une influence majeure sur le taux de développement des oeufs des poïkilothermes. Bien qu'il y ait une abondante littérature concernant les modèles reliant la durée d'incubation des oeufs à la température, il n'existe pas de consensus quant au meilleur modèle à utiliser. Il est reconnu que l'utilisation des degrés-jours permet de décrire précisément le taux de développement dans la partie centrale de l'échelle de température permettant le développement chez une espèce donnée, mais non aux températures plus basses ou plus hautes où la relation devient curvilinéaire. Plusieurs modèles ont été proposés pour expliquer le manque de linéarité du taux de développement aux basses ou aux hautes températures: une fonction de puissance, l'équation de Bělehrádek, une équation quadratique, des modèles exponentiel et thermodynamique. Tous ces modèles sont habituellement basés sur des expérimentations faites en laboratoire à des températures constantes et peuvent donc mener à des estimations imprécises des durées d'incubation in situ, suite à l'influence d'autres facteurs tels l'intensité lumineuse, la photopériode, la quantité d'oxygène dissous, et les fluctuations de température.

Les études existantes portant sur le meunier noir, *Catostomus commersoni*, ne documentent pas la relation entre la durée d'incubation et la température pour les stades de développement autres que l'éclosion, pas plus qu'elles ne couvrent une étendue de températures. Les objectifs de cette étude étaient donc de (1) déterminer la durée d'incubation jusqu'à l'atteinte de différentes phases de développement du meunier noir à huit températures en laboratoire, (2) déterminer quel est le meilleur modèle, parmi les plus fréquemment utilisés dans la littérature, pour décrire la relation entre la durée d'incubation et la température pour différentes phases de développement, et (3) tester la précision du meilleur modèle en suivant le développement d'oeufs incubés sous des conditions naturelles.

Matériel et méthodes

Développement des oeufs en laboratoire et in situ

Au printemps 1993 nous avons incubé des oeufs en laboratoire à huit températures différentes allant de 8,5 à 21,2°C. De 300 à 500 oeufs ont été placés dans chacun des 48 incubateurs utilisés (six incubateurs par température). La température de l'eau était notée deux fois par jour (±0,5°C). À chaque jour, aux cinq températures les plus hautes et à tous les 2-3 d aux autres températures, 10 embryons étaient prélevés dans chaque incubateur pour faire le suivi du développement embryonnaire. Nous avons regroupé les différents stades de développement observés en cinq phases principales: segmentation, organogénèse, oeuf oeillé, éclosion, et larve pélagique (angl.: "swim-up"). Nous avons assumé qu'une phase donnée était atteinte la première journée où 90% ou plus des oeufs avaient atteint cette phase.

Nous avons aussi incubé des oeufs sur la rive d'une frayère située dans la Réserve Mastigouche (Québec). Les incubateurs consistaient en 15 gouttières de PVC (6 cm de profondeur X 12 cm X 2 m). Afin de simuler l'étalement de la période de ponte du meunier noir nous avons procédé à cinq incubations successives, soit les 12, 14, 17, 19, et 21 mai; environ 1500 oeufs ont été distribués dans chacun des incubateurs. La température de l'eau était enregistrée aux 15 min avec un thermographe électronique (± 0,01°C). Dix embryons vivants étaient prélevés quotidiennement dans chaque incubateur pour faire le suivi du développement embryonnaire.

Analyse des données

À partir des expérimentations faites en laboratoire nous avons modélisé la relation entre la durée d'incubation (y) et la température de l'eau (T). Sept modèles fréquemment utilisés dans la littérature pour prédire les durées d'incubation ont été ajustés à nos données:

1) Degrés-jours: $y = k / (T-t_0)$

2) Puissance: $y = aT^b$

3) Équation de Bělehrádek: $y = a / (T-t_0)^b$

4) Équation quadratique : $y = a + bT + cT^2$

5) Exponentiel: $y = ab^T$

6) Exponentiel (second degré): $y = ab^T c^{T^2}$

7) Thermodynamique:

$$y = \frac{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2_L}} - \frac{1}{T}\right)\right]}{\rho(25°C)\frac{T}{298}\exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right]}$$

où T est la température de l'eau (°C, excepté pour le modèle 7 où T est en Kelvin), et les autres paramètres des constantes (leur description est faite au chapitre 1).

Tous les modèles ont offert un ajustement aux données qui était comparable et hautement significatif (voir Résultats et Discussion). Nous avons donc comparé les durées d'incubation in situ aux durées prédites avec (1) le modèle degrés-jours, à cause de sa simplicité, et (2) le modèle thermodynamique, à cause de ses fondements théoriques comparativement aux autres modèles.

Résultats et Discussion

Développement des oeufs en laboratoire

Nos durées d'incubation jusqu'à l'éclosion et la larve pélagique étaient différentes de celles observées dans d'autres études, ce qui suggère une variabilité du taux de développement embryonnaire pour une température donnée. Il se peut que les disparités observées avec les études précédentes réflètent des différences dans la méthodologie utilisée pour l'incubation

des oeufs ou des différences dans la façon de déterminer la date d'atteinte d'une phase de développement. D'un autre côté, elles peuvent résulter de différences intraspécifiques dans le taux de développement des oeufs, ce qui a déjà été démontré par Brännäs (1988, pour les références complètes voir la section References du chapitre 1) pour les saumons keta, *Onchorynchus keta*, et Atlantique, *Salmo salar*. D'autres recherches seront nécessaires afin de déterminer jusqu'à quel point notre modèle prédictif est applicable à différentes populations de meunier noir.

Tous les modèles testés ont présenté un ajustement aux données qui était comparable et hautement significatif. Les valeurs de R^2 ajusté étaient toujours supérieures à 0,90, les résidus étaient toujours normalement distribués et une relation hautement significative a été observée entre la durée d'incubation et la température pour les modèles pouvant être linéarisés (test F, $p < 0,0001$). Le modèle exponentiel du second degré, le modèle thermodynamique et la fonction de puissance étaient un peu plus performants que les autres modèles: ce sont les seuls dont les valeurs de R^2 ajusté étaient toujours retrouvées à l'intérieur d'un écart d'environ 0.01 unité (1%) par rapport à la plus grande valeur observée pour chaque phase de développement. En se basant uniquement sur les résultats de l'analyse statistique il est impossible d'identifier lequel de ces trois modèles est le meilleur. Il n'existe aucun fondement théorique pour l'équation exponentielle du second degré, ni pour la fonction de puissance. Par contre, le modèle thermodynamique présente de meilleurs fondements biologiques parce qu'il est basé sur des principes thermodynamiques reconnus qui s'appliquent aux réactions biochimiques.

Par ailleurs, bien qu'il ait souvent été critiqué à cause de son manque de précision aux températures limites, on ne peut rejeter le modèle degrés-jours en se basant sur nos résultats. Le modèle degrés-jours a présenté un très bon ajustement aux données dans nos expériences en laboratoire. De plus, des études précédentes ont obtenu des résultats satisfaisants avec le

modèle degrés-jours sur le terrain (Bernal et González 1993, Bergh et Judd 1993, Judd et al. 1993).

Développement des oeufs in situ

Les modèles thermodynamique et degrés-jours ont tous les deux prédit avec précision les durées d'incubation observées en nature. Pour le modèle thermodynamique, la plus grande différence moyenne entre les durées prédites et observées était de 2,1 d, survenant à la phase d'organogénèse, et la différence moyenne globale (i.e. lorsque toutes les phases de développement sont regroupées) était de 1,4 ± 1,0 d. Le modèle degrés-jours était au moins aussi précis que le modèle thermodynamique pour prédire les durées d'incubation. La plus grande différence moyenne entre les durées prédites et observées était de 1,7 d, survenant à la phase d'organogénèse et la différence moyenne globale de seulement 1,2 ± 1,2 d. La précision élevée des modèles thermodynamique et degrés-jours contraste avec la plus faible précision à laquelle on aurait pu s'attendre d'après la littérature. Ainsi, il est souvent mentionné que les variations de température et de photopériode observées en nature diminuent la précision des modèles établis en laboratoire. La précision élevée de nos modèles suggère que ni les températures fluctuantes ni d'autres facteurs comme la photopériode ne semblent avoir une influence significative sur le taux de développement embryonnaire du meunier noir in situ et qu'en conséquence, les durées d'incubation peuvent être prédites avec précision à partir uniquement de la température moyenne quotidienne de l'eau. Nos résultats démontrent aussi que la simple approche des degrés-jours, souvent critiquée pour son manque de précision, était au moins aussi précise sous des conditions naturelles que le modèle thermodynamique plus complexe. Comme les températures de l'eau observées dans cette étude (étendue: 8,2°-21,8°C) ressemblent beaucoup à celles observées durant la période de fraie du meunier noir, nous nous attendons à ce que le modèle degrés-jours prédise précisément les durées d'incubation sur la plupart des frayères.

Enfin, bien que nous ayons fertilisé des oeufs durant une période de 10 d (du 12 au 21 mai), la période d'éclosion a duré seulement 5 d (du 4 au 8 juin). Parmi les hypothèses envisagées pour expliquer cette synchronisation de l'éclosion, la seule plausible suggère que l'allongement de la photopériode durant l'expérimentation in situ serait responsable de la réduction de la durée d'incubation jusqu'à l'éclosion observée pour les oeufs des dernières fertilisations. Les études de MacCrimmon et Kwain (1969) et de Brännäs (1987) ont démontré qu'une augmentation de l'intensité lumineuse ou de la photopériode accélérait le taux de développement embryonnaire des salmonidés, ce qui soutient l'hypothèse que l'accélération du taux de développement des oeufs de meunier noir a été causée par l'allongement de la photopériode.

Conclusion

Étant donné sa simplicité d'utilisation et la précision élevée obtenue en nature avec le modèle degrés-jours, nous concluons que les gestionnaires devraient employer ce modèle pour prédire les durées d'incubation du meunier noir. Le synchronisme de l'éclosion observé ici est intéressant lorsqu'on considère ses implications en aménagement de la faune. Ainsi, un contrôle des jeunes stades de développement du meunier noir visant les larves benthiques réduirait les coûts de l'opération car moins de traitements seraient nécessaires, comparativement à un contrôle visant les phases de développement plus précoces. Enfin, des recherches portant sur les facteurs déterminant la ponte seront nécessaires afin de déterminer à quel moment débuter le cumul des degrés-jours. La précision du modèle degrés-jours devra aussi être validée avec différentes populations de meunier noir afin de déterminer s'il existe une variation intraspécifique dans le taux de développement embryonnaire, telle que celle suggérée dans notre revue des durées d'incubation (chapitre 1).

ANNEXE B

Résumé long en français du chapitre 2.

Occurrence de la ponte et validation d'un modèle degrés-jours pour prédire le taux de développement embryonnaire du meunier noir, *Catostomus commersoni*, in situ.

Introduction

Le meunier noir, *Catostomus commersoni*, a été introduit dans plusieurs lacs à omble de fontaine, *Salvelinus fontinalis*, de l'est du Canada. Un des moyens envisagés pour réduire l'impact du meunier noir sur les populations d'omble de fontaine serait de compromettre le recrutement en contrôlant les larves benthiques par des traitements à la Roténone, ou les larves pélagiques par l'utilisation de la pêche électrique sur les frayères. De telles interventions nécessitent une connaissance du moment précis où ces stades de développement sont retrouvés en nature. Hamel et al. (1996, pour les références complètes voir la section References du chapitre 2) ont proposé quatre équations basées sur un modèle degrés-jours pour prédire la date d'atteinte des phases d'organogénèse, d'oeuf oeillé, d'éclosion, et de larve pélagique (angl.: "swim-up") in situ. Toutefois, pour utiliser ces équations correctement on doit pouvoir prédire avec certitude la date de ponte et valider les équations pour différentes populations de meunier noir. La majorité des études existantes concernent seulement la migration de reproduction de l'espèce sur les frayères; on retrouve très peu d'informations quant à la ponte elle-même. De plus, les équations degrés-jours proposées par Hamel et al. (1996) n'ont pas été testées pour des populations naturelles de meunier noir.

Les objectifs de cette étude étaient donc (1) d'identifier les facteurs déterminant la date de ponte du meunier noir en nature, et (2) de valider les équations degrés-jours proposées par Hamel et al. (1996) pour différentes populations de meunier noir.

Matériel et méthodes

Les six frayères étudiées sont deux tributaires du lac Cinq Doigts, dans la Réserve Rouge-Matawin (nommés ci-après frayères Fernand et Prunier, du nom des lacs sources de ces tributaires), deux tributaires du lac Sans-Nom, dans la Réserve Mastigouche (frayères Cigale

et Sauterelle), le tributaire du lac Basque dans la région du Saguenay, et celui du lac Blanc dans la Réserve de Rimouski. Les lacs Basque et Blanc sont situés dans une région climatique plus froide que ceux des Réserves Rouge-Matawin et Mastigouche.

Les oeufs et les larves benthiques de meunier noir ont été échantillonnés sur tous les sites d'étude au printemps 1993 et à la frayère Sauterelle au printemps 1994. Dix à 25 stations d'échantillonnage étaient visitées aux 2-3 d sur chaque frayère. Les larves pélagiques ont été échantillonnées dans les lacs récepteurs avec des filets troubleaux en 1993, et avec des filets de dérive placés en aval de la frayère en 1994. La température de l'eau sur les frayères était enregistrée à toutes les 15 min à l'aide de thermographes électroniques. La détermination des stades de développement atteints par les spécimens recoltés a été faite au laboratoire; nous avons regroupé les stades en cinq phases principales: segmentation, organogénèse, oeuf oeillé, éclosion, et larve pélagique.

Les équations degrés-jours testées étaient du type $y = k/(T-t_0)$, où y est la durée d'incubation de la fertilisation jusqu'à l'atteinte d'une phase de développement donnée, T la température de l'eau (°C) et k et t_0 des constantes. La valeur des paramètres k et t_0 pour chaque phase de développement est présentée au chapitre 2. Pour évaluer la fiabilité des équations degrés-jours pour les différentes populations, les dates d'atteinte de chaque phase, prédites d'après les dates de ponte observées et les équations degrés-jours, ont été comparées aux dates d'atteinte de chaque phase sur les six frayères.

Résultats

Facteurs déterminant la date de ponte

La ponte du meunier noir semblait reliée à une température seuil. Dans tous les cas, la ponte n'est survenue seulement après qu'une température seuil ait été atteinte, peu importe si la température de l'eau demeurait au-dessus ou baissait sous ce seuil par la suite. Aux frayères

Fernand, Prunier, Cigale et Sauterelle, la température seuil pour la ponte se situait à 13°C (température moyenne de l'eau). Pour les meuniers noirs des frayères Basque et Blanc, la température seuil se situait à environ 10°C. Sur la plupart des sites étudiés la ponte n'a pas débutée immédiatement après que la température seuil ait été atteinte; un délai de quelques jours a été observé entre la date d'atteinte de cette température et le début de la ponte (délai moyen de 2,6 ± 1,9 d). Finalement, nous n'avons observé aucune relation entre le niveau d'eau des ruisseaux et l'activité de fraie.

Validation des équations degrés-jours

Les équations degrés-jours ont prédit avec précision les dates d'atteinte de chaque phase de développement pour les embryons retrouvés sur les frayères Fernand, Prunier et Sauterelle, la différence moyenne entre les dates prédites et observées étant de seulement 1,6 ± 1,7 d. Par contre, les équations ont été beaucoup moins précises pour les frayères Basque et Blanc, où la différence moyenne était de 6,4 ± 3,4 d. Dans ces derniers cas les durées d'incubation prédites étaient toujours plus grandes que celles observées, ce qui signifie que les embryons se sont développés plus rapidement que prédit d'après les équations degrés-jours et qu'il existe des différences intraspécifiques dans le taux de développement embryonnaire du meunier noir.

Finalement, à la frayère Sauterelle (en 1994) la dérive des larves est survenue durant une période de 6 d, malgré que la ponte ait eu lieu durant 24 d (la durée exacte de la dérive n'a pas pu être déterminée aux autres sites).

Discussion

Facteurs déterminant la date de ponte

Nos résultats démontrent que la température de l'eau est le principal facteur déterminant la date de ponte. Sur toutes les frayères étudiées, aucune ponte n'a eu lieu avant que la température seuil ne soit atteinte (10° ou 13°C dépendant de la région) et ce, même si les géniteurs étaient déjà sur les frayères. La température seuil observée dans cette étude est interprétée comme un signal indiquant aux géniteurs l'arrivée de conditions de ponte adéquates, activant la maturation finale des oeufs. En effet, ce signal n'est pas le déclencheur de la ponte proprement dit parce que nous avons observé un délai entre l'atteinte de la température seuil et le début de la ponte. Le délai moyen de 2-3 d que nous avons observé concorde avec le délai de 3-4 d observé par Stacey et al. (1984) entre l'injection de gonadotropine et l'ovulation chez des meuniers noirs femelles. Nous concluons donc que la synchronisation de la ponte du meunier noir est déterminée par une température seuil de 10° ou 13°C amorçant la maturation finale des oocytes, qui est suivie par la ponte environ 2-3 d plus tard, lorsque la maturation et l'ovulation sont complétées.

Validation des équations degrés-jours

Les équations degrés-jours testées dans la présenté étude ont prédit avec précision les durées d'incubation jusqu'à l'organogénèse, l'oeuf oeillé, l'éclosion, et la phase de larve pélagique des meuniers noirs retrouvés aux frayères Fernand, Prunier et Sauterelle. Par contre, nos équations ont été moins précises aux frayères Basque et Blanc situées dans des habitats plus froids, le développement embryonnaire ayant été plus rapide chez ces populations. Ce développement plus rapide, ainsi que la température seuil plus basse pour la ponte, pourraient être des adaptations à un environnement plus froid. Ainsi, il est généralement accepté que la synchronisation de la ponte a évolué pour assurer une survie maximale à la progéniture (Bye

1984, Munro 1990). Comme pour d'autres espèces de poissons, les populations de meunier noir vivant dans des environnements plus froids sont confrontés à une pression favorisant une ponte plus tardive au printemps que les populations plus au sud, afin d'éviter des températures froides, létales pour les oeufs. Cependant, la conséquence d'une ponte plus tardive est une réduction de la saison de croissance pour la progéniture. La longueur de la première saison de croissance est d'une importance primordiale car la survie des jeunes de l'année durant le premier hiver est fortement dépendant de leur taille (Conover 1992, Goodgame et Miranda 1993). De plus, une conséquence supplémentaire de la reproduction dans des environnements plus froids est l'augmentation de la durée de la période embryonnaire. Nous suggérons donc que la température de ponte plus basse et l'augmentation du taux de développement observés aux frayères Basque et Blanc résultent d'une part des pressions pour des températures propices pour les oeufs et d'autre part, de celles favorisant une longue saison de croissance pour la progéniture.

Sur la majeure partie de l'aire de distribution du meunier noir, l'arrivée des géniteurs sur les frayères se produit seulement lorsque la température de l'eau atteint 10°C (Geen et al. 1966, Bond 1972, Walton 1980, Corbett et Powles 1983). Par conséquent, le seuil de 13°C pour la ponte s'applique probablement à la plupart des populations. Pour les populations situées plus au nord, là où les conditions climatiques sont comparables à celles retrouvées aux frayères Basque et Blanc, un seuil de 10°C prédirait probablement plus précisément la date de ponte. De la même façon, les valeurs de la constante k dans les équations degrés-jours devraient aussi être modifées pour prédire plus précisément l'atteinte de chaque phase de développement. Un ajustement a posteriori de ces valeurs nous a donné 9,45, 22,88, 95,36, et 108,47 degrés-jours pour les phases d'organogénèse, d'oeuf oeillé, d'éclosion et de larve pélagique respectivement. L'utilisation de ces valeurs (avec t_0 inchangé) devrait donner de bonnes prédictions dans les environnements plus froids.

Le synchronisme de la dérive, tel que celui observé à la frayère Sauterelle (en 1994), pourrait être une adaptation pour diminuer le risque de prédation des larves par un "effet de dilution". Étant donné ce synchronisme, un contrôle du meunier noir visant les larves pélagiques lorsqu'elles dérivent vers le lac pourrait réduire la durée du contrôle et permettrait d'éliminer une plus grande proportion du recrutement total, à moindres coûts.

Enfin, notre étude a démontré que les équations degrés-jours peuvent être très efficaces pour prédire les durées d'incubation du meunier noir en nature. Ceci contraste avec les conclusions de plusieurs auteurs qui ont déconseillé l'utilisation des degrés-jours parce qu'ils sont imprécis aux limites inférieures et supérieures de l'échelle de température permettant le développement des oeufs des poïkilothermes (Andrewartha et Birch 1954, Bagenal et Braum 1971, Humpesch et Elliott 1980, Wagner et al 1984, Highley et al. 1986). Cependant, ces températures extrêmes surviennent rarement en nature, surtout durant la période de ponte du meunier noir. Dans ce contexte, on peut concevoir que l'approche des degrés-jours soit fiable en nature étant donné la forte pression de sélection agissant sur les poissons pour que la ponte ne survienne seulement que lorsque des températures optimales pour le développement des oeufs sont présentes.