

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

Patrice Hamel, Pierre Magnan, Michèle Lapointe, and Pierre East

Abstract: We sampled eggs and larvae of white sucker, *Catostomus commersoni*, on six spawning grounds to (i) determine the influence of water temperature and discharge on spawning and (ii) assess the reliability of four degree-day equations developed to predict the attainment of organogenesis, eyed egg, hatching, and swim-up phases. We estimated a threshold temperature for spawning of 13°C at four sites and 10°C at two colder sites. A delay of 2 or 3 days was observed between the threshold and the onset of spawning. On average, the degree-day equations predicted the attainment of the developmental phases with an accuracy of 1.6 days, except at the two colder sites, where developmental rates were faster than predicted. 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 over a 6-day period even though spawning lasted 24 days; it was not possible to determine the exact duration of drift at the other sites. This synchronization could be an adaptation lowering the risk of predation on individual larvae, 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 (i) déterminer l'influence de la température de l'eau et du débit sur la ponte et (ii) évaluer la fiabilité de quatre équations degrés-jours prédisant la date d'atteinte des phases d'organogénèse, d'oeuf ocellé, d'éclosion, et de larve pélagique. Nous avons estimé une température seuil pour la ponte de 13°C à quatre sites, et de 10°C à deux sites plus froids. Un délai de 2 ou 3 jours a été observé entre ce seuil et le début de la ponte. En moyenne, les équations degrés-jours ont prédit l'atteinte des phases de développement avec une précision de 1,6 jours, excepté aux deux sites plus froids, où les taux de développement ont été plus rapides que prédit. 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 jours, malgré que la ponte ait eu lieu durant 24 jours; il n'a pas été possible de déterminer la durée exacte de la dérive aux autres sites. Cette synchronisation pourrait être une adaptation pour diminuer le risque de prédation des larves, toutes les larves arrivant dans le lac dans un délai de quelques jours.

Introduction

The white sucker, *Catostomus commersoni*, has been introduced into many lakes of eastern Canada, where it is often considered a pest species by fisheries managers because of its impact on exploited fish species (Johnson 1977; Barton 1980; Magnan et al. 1990; Hayes et al. 1992; Magnan et al. 1994). For example, the mean annual yield of brook trout, *Salvelinus fontinalis*, decreased by 50–80% when in sympatry with white sucker in these lakes (Magnan 1988, 1989). Given their strong impact on brook trout populations and the concurrent socio-economic losses, fisheries managers are interested in developing management tools to control white sucker populations. One means of lowering the impact of white sucker on brook trout populations is to decrease their recruitment by controlling

benthic larvae with rotenone or drifting swim-up larvae with electrofishing on the spawning grounds (Magnan et al. 1997). 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. (1997) evaluated four degree-day equations for their ability to predict the timing of organogenesis, eyed egg, hatching, and swim-up larvae phases. To use these equations properly, one must know the timing of white sucker spawning as precisely as possible and assess the reliability of these equations in natural populations. Most studies on the reproductive period of white sucker have dealt mainly with their migration to the 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 that adequate water discharge is encountered (Barton 1980; Walton 1980). In contrast, little information exists on the timing of spawning itself (laying and fertilization of the eggs). Anecdotal information suggests that spawning occurs between 9 and 15°C (Stacey et al. 1984). Lalancette (1973) reported that spawning occurred between 13 and 15°C and that no spawning occurred at higher temperatures.

Received April 29, 1996. Accepted February 25, 1997.
J13451

P. Hamel, P. Magnan,¹ M. Lapointe, and P. East.
Département de chimie-biologie, Université du Québec à
Trois-Rivières, C.P. 500, Trois-Rivières, QC, G9A 5H7,
Canada.

¹ Author to whom all correspondence should be addressed.

The degree-day equations used by Hamel et al. (1997) have not been tested on natural populations of white sucker. Inter-population variation in the embryonic response to temperature has 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. 1997), suggesting interpopulation differences in the embryonic response to temperature.

The objectives of this study were (i) to determine the influence of water temperature and stream water discharge on the timing of white sucker spawning in the field and (ii) to assess the reliability of the degree-day equations used by Hamel et al. (1997) on natural populations of white sucker. To do so, we sampled eggs and larvae on six spawning grounds and followed the embryonic development while monitoring water temperature and stream water discharge.

Materials and methods

Study sites

The six spawning grounds were located in Québec (Canada), along a 485 km east–west axis crossing the Saint Lawrence 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 upstream 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 (upstream 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 (1997), 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 subjected to colder annual temperatures and to more precipitation than the five other 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 subjected to colder climates than those of lakes Cinq Doigts and Sans-Nom (which was supported by mean water temperatures measured on these spawning grounds; Fig. 1).

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 cm²) at all sites in spring 1993 and at Sauterelle in spring 1994. The beginning of egg sampling is shown on Fig. 1. Samples were taken every 2 or 3 days 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; a station was defined as an area suitable for spawning (i.e., riffles with gravel and rock substrate; P. East and P. Hamel, personal observations). At a given station, all suitable spawning areas were considered so that each station varied in surface area. We marked each quadrat (Surber sampler) after sampling to avoid repeated sampling of the same quadrat. 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 inlets. Six transects were done for the Fernand, Prunier, and Basque spawning ground inlets and 10 transects for that of Sauterelle. The samples were taken regularly, starting before the period when swim-up larvae would be present (Table 1). In 1994, the larvae were sampled with two drift nets in Sauterelle spawning ground. The nets were set side by side and almost completely covered the stream.

Water temperature was recorded at 15-min intervals with an electronic thermograph on each spawning ground with the exception of Lake Basque inlet, where water temperature was recorded with a mechanical thermograph every 3 h. The thermographs were located on the bottom of the stream bed within the egg collection site. Given the small size of the streams studied and the good water flow, we assumed that the water temperature at the thermograph location was representative of that of the whole spawning ground. 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 according to the description for white sucker given by McElman and Balon (1980). We grouped the developmental stages into five major phases: (i) egg cleavage, starting at fertilization; (ii) organogenesis, starting with the elevation of the axial strand over the yolk, epiboly not complete; (iii) eyed egg, starting with the appearance of lenses in the eyes; (iv) hatching (hereafter called benthic larvae); and (v) swim-up larvae, starting with the inflation of the swim bladder.

Assessment of the degree-day equations

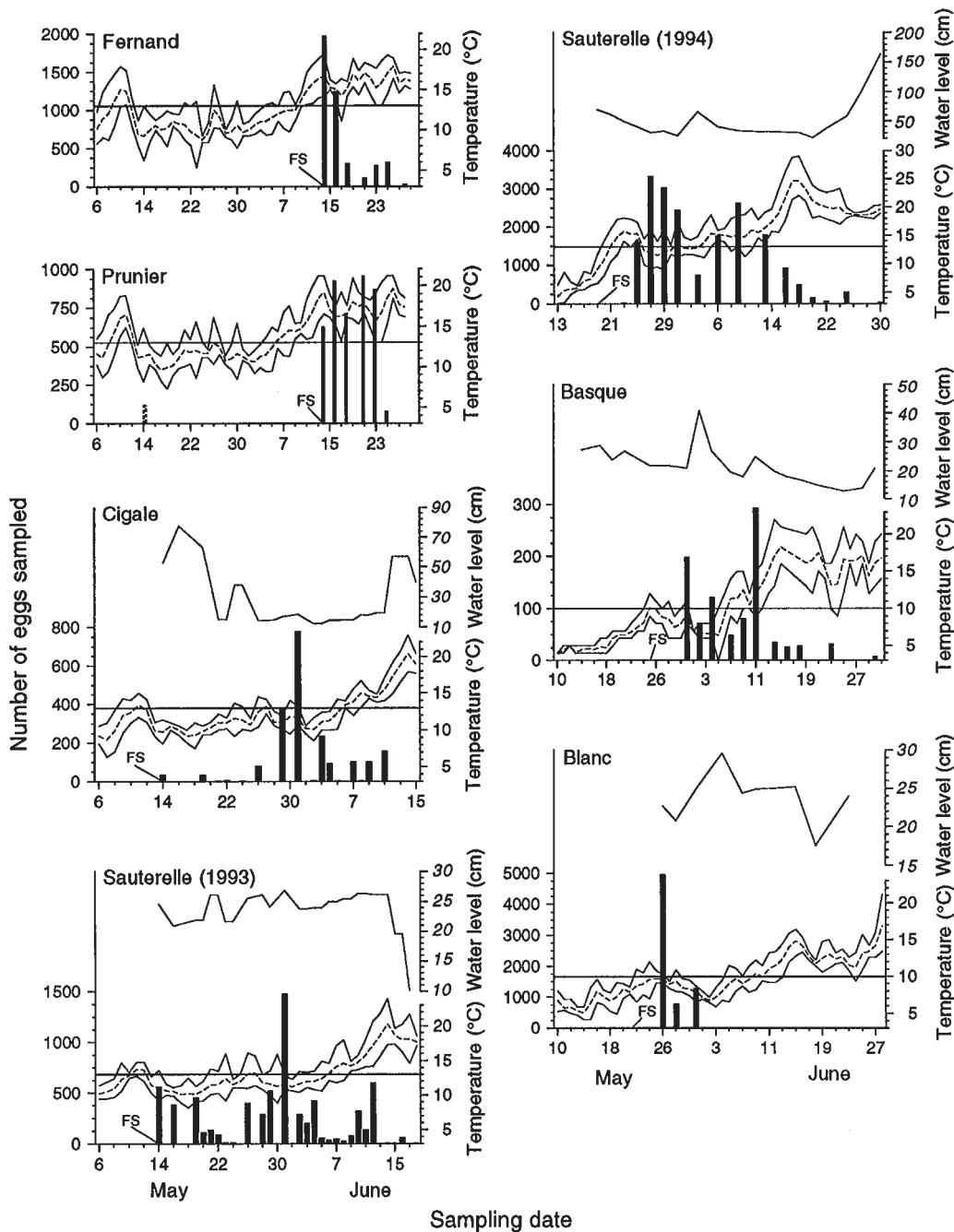
The four degree-day equations examined by Hamel et al. (1997) were of the form $y = k/(T - t_0)$, where y is the incubation time from fertilization to attainment of a given developmental phase, k the sum of degree-days, T the water temperature (°C), and t_0 the water temperature at developmental zero (i.e., temperature at which no development occurs). The values of k and t_0 of each developmental phase are listed in Table 2. 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. Because females spawn for protracted periods, we determined arbitrarily 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 specimens found for that phase. For consistency, the "observed" dates of attainment of the subsequent developmental phases were noted as the day that the cumulative frequency of specimens of a given phase represented at least 5% of all specimens 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 middle to late May on all spawning grounds studied in 1993 and 1994 (Fig. 1). On Sauterelle (1994), Basque, and Blanc spawning grounds, no spawning occurred before the beginning of sampling (Fig. 1). Although not shown in Fig. 1, evidence of some spawning in early May existed for the Fernand and Prunier spawning grounds before

Fig. 1. Spawning period of white sucker as determined by the number of eggs in the cleavage phase found in our samples (solid bars; hatched bar represents eggs found in the single Surber sample taken on 14 May on Prunier). Daily water levels and daily maximum (—), mean (---), and minimum (—) water temperatures are also shown. First sampling (FS) began before or soon after the first spawners were seen on the spawning grounds. The horizontal solid line shows the estimated threshold temperature for spawning.



the beginning of the sampling period. Visual observations and restricted sampling of spawners done at 2- or 3-day intervals revealed that approximately 1600 ripe spawners were present on 12 May on the Fernand spawning ground and that approximately 5000 were present on 12 May on the Prunier spawning ground. Also, eggs were found on 14 May at the only site sampled on the Prunier spawning ground (Fig. 1). Logistical problems prevented us from starting the sampling at this time. However, 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. Finally, although recently laid eggs (cleavage phase) were found on the first day of sampling on Cigale and Sauterelle (1993) spawning grounds, the absence of eggs in the later stages at this time suggests that little, if any, spawning occurred in the days preceding the beginning of sampling.

Table 1. Sampling period of swim-up larvae in the receptor lakes.

Sampling period	Spawning ground			
	Fernand	Prunier	Sauterelle and Cigale	Basque
Beginning	21 June	21 June	1 June	7 June
Ending	2 July	21 July	18 June	16 July
Frequency	2 or 3 days	2 or 3 days	Daily	2 or 3 days

Note: No larvae were caught at Lake Blanc.

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).

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

Assessment 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 days (mean \pm SD) between predicted and observed incubation times. For the Cigale spawning ground, the egg sampling indicated that the organogenesis, eyed egg, and hatching phases all occurred on 29 May (Fig. 2). Given this atypical result, we did not compare these observed dates with dates predicted from the degree-day equations.

The degree-day equations were less accurate for Basque and Blanc inlets, where the overall mean difference was 6.4 ± 3.4 days between predicted and observed incubation times. In these two cases, the predicted times were always greater than the observed times, meaning that the embryos developed 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 with those predicted using the thermodynamic equations tested by Hamel et al. (1997), 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 likely due to interpopulation differences.

Finally, we observed a certain synchronization in the drift of swim-up larvae on the Sauterelle spawning ground in 1994, where they were caught in drift nets. The swim-up larval phase lasted only 6 days, from 16 to 22 June (Fig. 2), even though spawning was spread over 24 days, 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 days, twice as long as the observed period.

Table 2. Values of k and t_0 used for each developmental phase studied (from Hamel et al. 1997).

Developmental phase	k (degree-days)	t_0 ($^{\circ}$ C)
Organogenesis	34.247	5.272
Eyed egg	51.394	5.329
Hatching	130.323	4.935
Swim-up larvae	159.589	7.540

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

Discussion

Factors determining the timing of spawning

Previous studies on white sucker reproduction found that water temperature influences the initiation of the spawning migration (Raney and Webster 1942; Tremblay 1962; Geen et al. 1966; Bond 1972; Walton 1980; Corbett and Powles 1983).

After gonad maturation, the onset of spawning could result either from the attainment of a given cue (like the attainment of a given temperature) or from a physiological consequence of temperature (i.e., a cumulative effect of temperature). An a posteriori examination of our data suggests that spawning of 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 above the threshold temperature. On the Fernand, Prunier, Cigale, and Sauterelle spawning grounds, the threshold was considered to be 13° C (mean water temperature). Indeed, in Fernand and Prunier, the mean water temperature exceeded 13° C in early May, when some evidence of spawning was observed, and at the beginning of June, when spawning resumed. In Cigale and Sauterelle (in 1993), both the onset of spawning and the peak spawning activity (from 28 May to 4 June) followed a rise in mean water temperature above 13° C. A third spawning began in Sauterelle around 9 or 10 June, after the mean temperature again exceeded 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. In the Basque and Blanc spawning grounds, the threshold mean temperature for the onset of spawning seemed to be near 10° C. A second spawning began around 8 June in Basque inlet, in agreement with the 10° C threshold. The spawning pattern at the inlet of Lake

Fig. 2. Embryonic development of white sucker on the spawning grounds studied. Observed (asterisks) and predicted (arrows) dates of attainment of each phase are indicated. The degree-day model was not tested for Cigale spawning ground (see Results section).

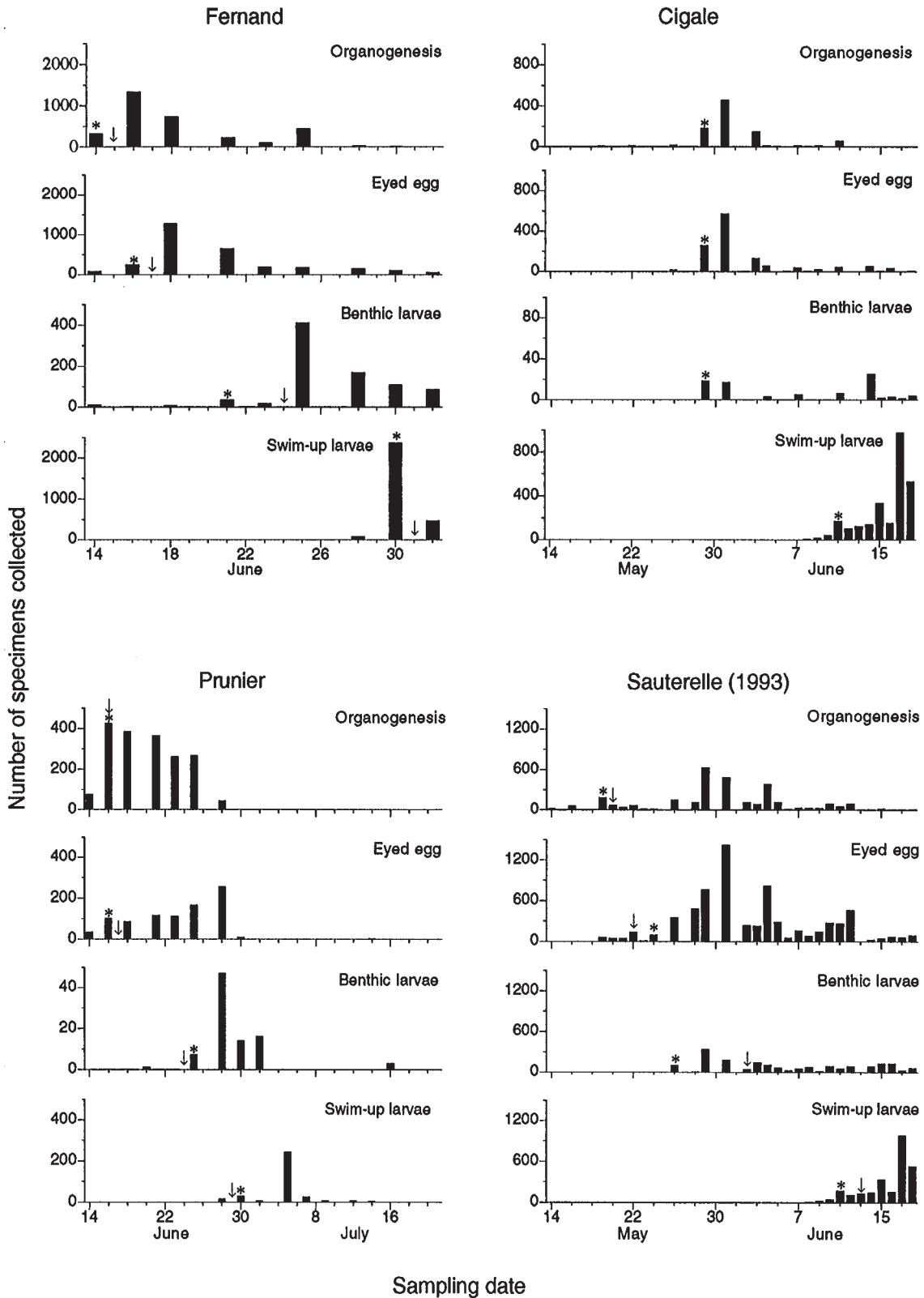
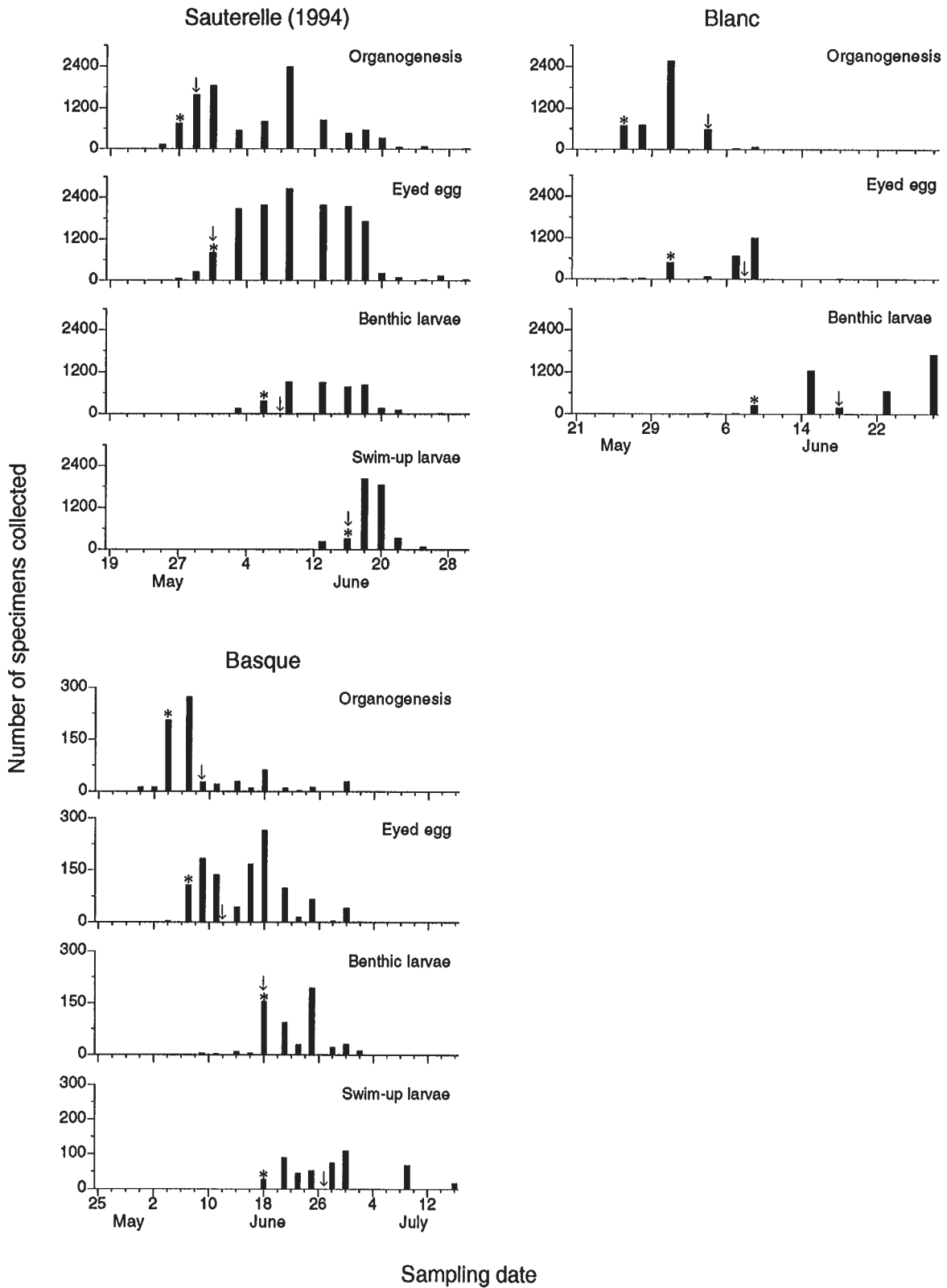


Fig. 2 (concluded).



Blanc differed somewhat from those observed on the other spawning grounds: only one spawning occurred even though the mean water temperature again rose above 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 ± 2.0 days was observed between the time when this

Table 3. 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
	25 May	—
Sauterelle (1994)	9 June	3
	24 May	3
	2 June	2
Basque	30 May	5
	8 June	1
Blanc ^a	24 May	0
Mean ± 1 SD		2.6±2.0

Note: All dates are in 1993 except where noted.

^aFor these sites, we considered that spawning occurred 2 days before we first found eggs because a substantial number of eggs in the organogenesis phase were present in the first samples.

temperature was reached and the beginning of spawning (Table 3). The only case where the threshold temperature hypothesis failed was in Sauterelle (1993), where the second spawning began before the 13°C threshold had been reached. However, the most intense period of this second spawning occurred 4 days after the threshold temperature had been reached (Fig. 1).

The hypothesis that spawning would occur only after the accumulation of a certain amount of degree-days could not explain the occurrence of more than one spawning on the same spawning ground nor the different amount of degree-days required to initiate spawning or successive spawnings on the sites studied. Alternatively, one could hypothesize that spawning occurs as soon as a substantial increase in mean temperature is followed by a decrease in mean temperature, regardless of the absolute temperature level. However, this hypothesis fails to explain the first spawning on the Fernand (12 June), Prunier (13 June), and Blanc spawning grounds and the second spawning on the Basque spawning ground, where no decrease in mean temperature had occurred at the time of spawning.

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. Because 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 or 3 days observed between the attainment of the threshold temperature and the beginning of spawning is consistent with the 3- or 4-day delay observed by Stacey et al. (1984), between injection of human gonadotropin and ovulation in female white sucker. 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 or 3 days later, when maturation and ovulation are completed. The lower threshold temperatures of Basque and Blanc inlets are discussed below.

Assessment of the degree-day equations

The degree-day equations we tested 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) but 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 probably 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; see Study Sites section). It is generally accepted that the timing of spawning has evolved to maximize survival of offspring (Bye 1984; Munro 1990). As in other fish species (Conover 1992), white sucker populations living in colder environments must 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, Ont. (Corbett and Powles 1983), and in middle 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 duration of the first growing season may be of prime importance because survival of young-of-the-year through the first winter is highly dependent on body size by 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 been suggested that intraspecific variations in embryonic developmental rate and early growth rate observed in fish and insects are adaptations to temperature. It has been shown that development and growth are generally faster in populations from colder environments (Campbell et al. 1974; Smoker 1986; Brännäs 1988; Conover and Present 1990; Dingle and Mousseau 1994). Thus, the lower spawning temperature and increased developmental rate observed at the colder spawning grounds Basque and Blanc could result from pressures for suitable temperatures for the eggs on one hand and for a longer growing season for the progeny on the other hand.

The arrival of white sucker on the spawning grounds in most areas of its geographical distribution is reported to occur only when the water temperature reaches 10°C (Geen et al. 1966; Bond 1972; Walton 1980; Corbett and Powles 1983). Similarly, it is likely that a singular threshold temperature for spawning apply over most of the species range. Moreover, given that early spawners are usually not fully ripe upon arrival on the spawning grounds (Bond 1972; Barton 1980; Walton 1980), the 13°C threshold for spawning probably applies in most populations. In contrast, for northern populations, where climatic conditions are comparable with 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 k values (done by computing the mean number of degree-days needed 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. However, our data do not allow one to determine if the differences between warm and cold populations correspond to discrete classes of thermal environments or to a continuum of environments. Also, any adjustment of t_0 would have to be determined experimentally with fish from the northern strains.

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. (1997). 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). Besides adaptation, the apparent synchronization of swim-up larval drift may also have other causes. Egg mortality may be a function of spawning date and therefore cause the appearance of synchronization, especially if early-spawned and late-spawned eggs suffer higher mortality than eggs spawned in the middle of the reproductive season. 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.

The degree-day equations were reliable on four of the six spawning grounds studied here. These results emphasize that the degree-day model 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 that allows 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. This restricted temperature range may explain the reliability of the degree-day model observed in our study.

Acknowledgements

We thank P. Lemay, G. Lacroix, Y. Paquette, C. Ste-Marie, S. Verville, and all of the people from the ministère de l'Environnement et de la Faune du Québec (MEF) for their invaluable field assistance in collecting samples. Dr. Chris Chambers and two anonymous referees gave very helpful comments on

earlier versions of this paper. The MEF and the Fondation de la faune du Québec provided financial support for this research. P.H. was supported by a postgraduate fellowship from le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche, gouvernement du Québec.

References

- Andrewartha, H.G., and Birch, L.C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Ill.
- Bagenal, T.B., and Braum, E. 1971. Eggs and early life history. In *Methods for assessment of fish production in fresh waters*. 2nd ed Edited by W.E. Ricker. Blackwell Scientific Publications, Oxford, U.K. pp. 166–198.
- Barton, B.A. 1980. Spawning migrations, age and growth, and summer feeding of white and longnose suckers in an irrigation reservoir. *Can. Field-Nat.* **94**: 300–304.
- Bond, W.A. 1972. Spawning migration, age, growth, and food habits of the white sucker, *Catostomus commersoni* (Lacépède), in the Bigoray River, Alberta. M.Sc. thesis, University of Alberta, Edmonton.
- Brännäs, E. 1988. Emergence of Baltic salmon, *Salmo salar* L., in relation to temperature: a laboratory study. *J. Fish Biol.* **33**: 589–600.
- Bye, V.J. 1984. The role of environmental factors in the timing of reproductive cycles. In *Fish reproduction: strategies and tactics*. Edited by G.W. Potts and R.J. Wootton. Academic Press, London. pp. 187–205.
- Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., and Mackauer, M. 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* **11**: 431–438.
- Conover, D.O. 1992. Seasonality and the scheduling of life history at different latitudes. *J. Fish Biol.* **41**(Suppl. B): 161–178.
- Conover, D.O., and Present, T.M.C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, **83**: 316–324.
- Corbett, B., and Powles, P.W. 1983. Spawning and early-life ecological phases of the white sucker in Jack Lake, Ontario. *Trans. Am. Fish. Soc.* **112**: 308–313.
- Dingle, H., and Mousseau, T.A. 1994. Geographic variation in embryonic development time and stage of diapause in a grasshopper. *Oecologia*, **97**: 179–185.
- Duchesne, J.-F., and Magnan, P. 1997. The use of climate classification parameters to investigate geographical variations in the life history traits of ectotherms, with special reference to the white sucker (*Catostomus commersoni*). *Écoscience*, **4**: 140–150.
- Environment Canada. 1982. Canadian climate normals: temperature and precipitation, 1951–1980; Quebec. Environment Canada, Ottawa, Ont.
- Geen, G.H., Northcote, T.G., Hartman, G.F., and Lindsey, C.C. 1966. Life histories of two species of catostomid fishes in Sixteen-mile Lake, British Columbia, with particular reference to inlet stream spawning. *J. Fish. Res. Board Can.* **23**: 1761–1788.
- Goodgame, L.S., and Miranda, L.E. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. *Trans. Am. Fish. Soc.* **122**: 131–138.
- Hamel, P., Magnan, P., East, P., Lapointe, M., and Laurendeau, P. 1997. Comparison of different models to predict the in situ embryonic developmental rate of fish, with special reference to white sucker, *Catostomus commersoni*. *Can. J. Fish. Aquat. Sci.* **54**: 190–197.
- Hayes, D.B., Taylor, W.W., and Schneider, J.C. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. *Trans. Am. Fish. Soc.* **121**: 36–53.
- Highley, L.G., Pedigo, L.P., and Ostlie, K.R. 1986. DEGDAY: a

- program for calculating degree-days, and assumptions behind the degree-day approach. *Environ. Entomol.* **15**: 999–1016.
- Humpesch, U.W., and Elliott, J.M. 1980. Effect of temperature on the hatching time of eggs of three *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and an English stream and river. *J. Anim. Ecol.* **49**: 643–661.
- Johnson, F.H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota Lake, 1966. *J. Fish. Res. Board Can.* **34**: 1633–1642.
- Lalancette, L.-M. 1973. Studies on the growth, reproduction and diet of the white sucker, *Catostomus commersoni commersoni* (Lacépède), of Gamelin Lake, Chicoutimi, Québec. Ph.D. thesis, University of Waterloo, Waterloo, Ont.
- Litynski, J.K. 1984. The numerical classification of the world's climate. *World Clim. Programme No. WCP/PMC-63*. World Meteorological Organization, Geneva, Switzerland.
- Litynski, J.K. 1988. Les climats du Québec d'après la classification numérique. Éditions Gamma, Montréal, Que.
- 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.
- Magnan, P. 1989. The impact of cyprinid and catostomid introductions on brook charr, *Salvelinus fontinalis*, populations: a review. *Physiol. Ecol. Jpn. Spec. Vol. No. 1*. pp. 337–356.
- Magnan, P., East, P., and Lapointe, M. 1990. Modes de contrôle des poissons indésirables: revue et analyse critique de la littérature. *Rapp. Tech. Université du Québec à Trois-Rivières, pour le ministère du Loisir, de la Chasse et de la Pêche du Québec et la Fondation de la faune du Québec*. Available from Ministère de l'Environnement et de la Faune, Direction du marketing et des communications, Centre de documentation, 150 boul. René-Lévesque Est, Québec, QC G1R 4Y1, Canada.
- Magnan, P., Rodríguez, M.A., Legendre, P., and Lacasse, S. 1994. Dietary variation in a freshwater fish species: relative contribution of biotic interactions, abiotic factors, and spatial structure. *Can. J. Fish. Aquat. Sci.* **51**: 2856–2865.
- Magnan, P., East, P., and Lapointe, M. 1997. Guide d'intervention pour le contrôle du meunier noir dans les lacs à omble de fontaine. *Rapp. Tech. Université du Québec à Trois-Rivières, pour le ministère de l'Environnement et de la Faune du Québec et la Fondation de la faune du Québec*. Available from Ministère de l'Environnement et de la Faune, Direction du marketing et des communications, Centre de documentation, 150 boul. René-Lévesque Est, Québec, QC G1R 4Y1, Canada. In press.
- McElman, J.F., and Balon, E.K. 1980. Early ontogeny of white sucker, *Catostomus commersoni*, with steps of saltatory development. *Environ. Biol. Fishes.* **5**: 191–224.
- Munro, A.D. 1990. General introduction. *In Reproductive seasonality in teleosts: environmental influences. Edited by A.D. Munro, A.P. Scott, and T.J. Lam*. CRC Press, Boca Raton, Fla. pp. 1–12.
- Pitcher, T.J., and Parrish, J.F. 1993. Functions of shoaling behavior in teleosts. *In Behavior of teleosts fishes*. 2nd ed. Fish Fish. Ser. No. 7. *Edited by T.J. Pitcher*. Chapman & Hall, New York. pp. 363–440.
- Raney, E.C., and Webster, D.A. 1942. The spring migration of the common white sucker, *Catostomus c. commersonii* (Lacépède), in Skaneateles Lake inlet, New York. *Copeia*, 1942: 139–148.
- Smoker, W.W. 1986. Variability of embryo development rate, fry growth, and disease susceptibility in hatchery stocks of chum salmon. *Aquaculture*, **57**: 219–226.
- Stacey, N.E., MacKenzie, D.S., Marchant, T.A., Kyle, A.L., and Peter, R.E. 1984. Endocrine changes during natural spawning in the white sucker, *Catostomus commersoni*. *Gen. Comp. Endocrinol.* **56**: 333–348.
- Tremblay, L. 1962. Température de l'eau d'un lac et la migration de frai du catostome, *Catostomus c. commersoni*. *Nat. Can.* **89**: 119–128.
- Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., Schoolfield, R.M., and Coulson, R.N. 1984. Modeling insect development rates: a literature review and application of a biophysical model. *Ann. Entomol. Soc. Am.* **77**: 208–225.
- Walton, B.D. 1980. The reproductive biology, early life history and growth of white suckers, *Catostomus commersoni*, and longnose suckers, *C. catostomus*, in the Willow Creek – Chain Lakes system, Alberta. *Fish. Res. Rep. No. 23*. Alberta Department of Energy and Natural Resources, Fish and Wildlife Division, Fisheries Research Section, Edmonton.