Effects of Constant and Rising Temperatures on Survival and Developmental Rates of Embryonic and Larval Yellow Perch, *Perca flavescens* (Mitchill)

K. E. F. Hokanson and Ch. F. Kleiner

INTRODUCTION

The yellow perch, *Perca flavescens* (Mitchill), is an important sport, commercial, and forage fish species indigenous to the eastern part of the United States and Canada. Available data on its thermal requirements consist of thermal tolerance and preference of juveniles. Hart (1947) reported that the ultimate upper incipient lethal temperature of yellow perch was 29.7°C when acclimated to 25°C. The final preferendum of young yellow perch was 24.2°C; older perch preferred 21°C (Ferguson, 1958). Mansueti (1964) described the egg strands of the yellow perch and the morphology and anatomy of embryonic, larval, and juvenile stages and noted the coincidence during development with the Eurasian yellow perch, *Perca fluviatilis* (Linnaeus). Swift (1965) published a table of percentage mortality and average time to hatch for *P. fluviatilis* at various temperatures. Kokurewicz (1969) also described the effect of constant temperature on developmental rate of *P. fluviatilis* up to the time of hatch.

The study reported here was conducted in the spring of 1971. It is part of the continuing program at the National Water Quality Laboratory to determine thermal requirements of aquatic organisms and to develop laboratory culture methods for toxicant bioassays. This study defines the thermal tolerance limits and optimal culture conditions of embryonic and larval stages, describes the effect of temperature on development and hatchability, and compares the physiological requirements of the North American and Eurasian yellow perch.

METHODS

Apparatus

The embryo-survival and developmental rate experiments were conducted in the apparatus described in detail by McCormick and Syrett (1970). One modification was the arrangement of three embryo- and larvae-rearing units, each 15 x 10 x 10 cm deep, in series (Fig. 1). A manifold provided triplicate series for a total of 9 incubation units at each temperature. Water flowed continuously through each unit at an average rate of 216 ml/min (SD = 21, range 114-354).

Several types of experimental chambers were required in this study; these allowed flow-through conditions, minimized handling of delicate life stages, and permitted observing development and vitality of embryonic and larval stages under a dissecting microscope. Eggs were incubated in chamber 1A which was placed inside 1B (Figs 1 and 2). Newly-hatched larvae fell through the coarse screen on the bottom
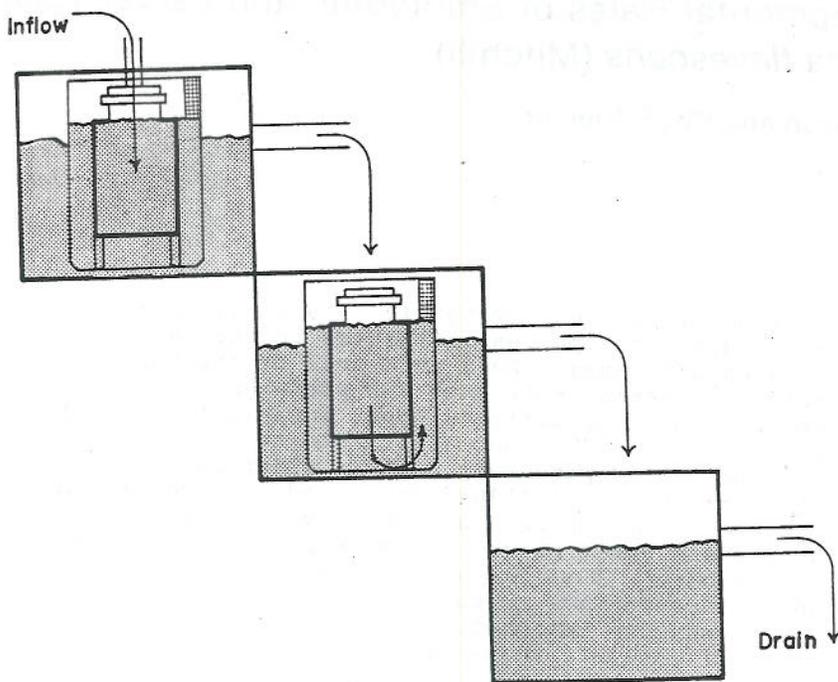
Inflow

Drain

Fig. 1. Side view of incubation units showing their stepwise arrangement and flow pattern through egg incubation chambers

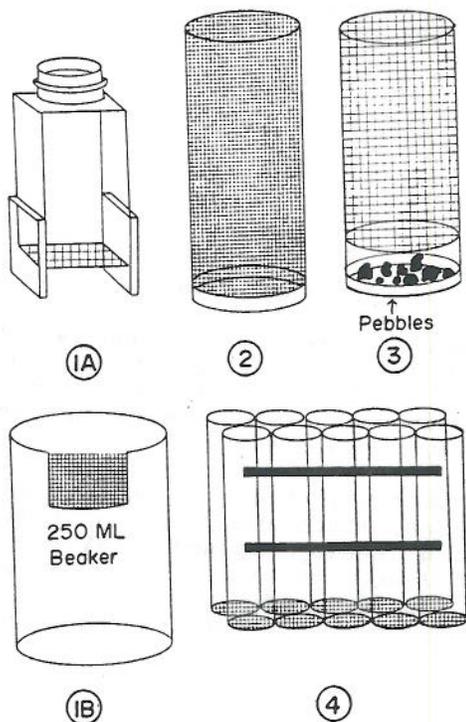Pebbles

(1A)　　(2)　　(3)

250 ML Beaker

(1B)　　(4)

Fig. 2. Experimental chambers for retaining yellow perch embryos (coarse screen) and larvae (fine screen). 1A embryo incubation, 1B outer chamber for 1A to retain larvae after hatching, 2 for newly hatched larvae, 3 for early embryo incubation, 4 for individual larval experiments (horizontal bar holds "cells" together)

(8 meshes/cm) of 1A and were retained by chamber 1B (Figs 1 and 2); they were transferred to chamber 2 until swim-up or 50% mortality of unfed larvae. Embryos incubated at 12°C to formation of the neural keel were retained in chamber 3 until they were transferred to test temperatures in chambers 1A and 1B. Pebbles in chamber 3 prevented embryos from settling in stagnant areas on the bottom of the container. Chamber 4 permitted observations on survival and activity of individual larvae. Coarse screens (8-12 meshes/cm) were used to increase water circulation past embryos (chambers 1A and 3, Fig. 2). Fine screens (16-20 meshes/cm) were used to retain free-swimming larvae (chambers 1B, 2, 4).

The temperature-controlling apparatus usually maintained the standard error of the mean (SE) temperature within ± 0.06°C and the range for each temperature within 0.9°C. The maximum SE was ± 0.12°C at 25.4°C and the maximum range was 1.5°C at 3.1°C. Temperature increased by 0.1 - 0.2°C from the upper to lower incubation units below 13°C. Daily temperatures of each unit were read to the nearest 0.1°C with a mercury thermometer and ranges were observed from recording thermographs.

Temperature-controlled untreated water from Lake Superior was vigorously aerated in the headbox to maintain dissolved gases near air saturation. The mean dissolved oxygen concentration was maintained at 97% (range 94-101%) air saturation at each temperature determined from bi-weekly samples. The range of pH values was 7.7 - 7.9. Other water quality characteristics of this supply have been described by Hokanson et al. (1973).

Experimental Procedure

Adult yellow perch were collected from Little Cut Foot Sioux Lake, Itasca County, Minnesota. Two lots of fish were collected and transported to the laboratory, one on 29 April and the other on 5 May 1971. The temperature of the water at the time of collection was 6° and 11°C, respectively. Fish were held at 12.0° - 12.6°C in the laboratory for 16 and 5 h, respectively, to increase egg fertility. Eggs were fertilized at 12°C in a constant temperature room. Females were killed, and egg strands were excised and fertilized by the dry method. Each egg strand was cut into subsamples of 93-293 eggs and distributed to 24 test chambers, each randomly assigned a treatment. One pair of fish from the first lot was used in the study of developmental rate, and 2 pairs from the second lot were used in the study of embryo survival through early larval stages.

Embryo-Survival Experiment. 24 treatments in 3 groups (Table 1) were used to determine the effects of constant or rising temperatures on survival of yellow perch embryos of known age to the larval swim-up stage. In the first group, eggs were exposed to temperature extremes soon after fertilization to include the most sensitive developmental stage (see Hokanson et al., 1973). Eggs were exposed to 9 constant temperatures from 3° to 22°C (2-3 deg C intervals). Egg subsamples were adjusted to test temperatures within 1 h of fertilization before they were placed under continuous-flow conditions. In the second group the survival of older embryos was observed. Egg subsamples were incubated at 12.0°C until the neural keel formed (63.5 h) before they were adjusted to 11 constant temperature levels from 3° to 26°C over a 1-h period. In the third group egg subsamples were exposed to 4 separate rising temperature regimes, since the thermal tolerance of

Table 1. Survival and hatchability of yellow perch embryos exposed to constant or rising temperatures - replicates combined. Groups 1 and 3 - fertilization to larval swim-up stage; group 2 - fertilization to neural keel at 12.0°C, neural keel to larval swim-up stage at test temperatures

Treatment group	Mean temperature (°C)	Total hatch (%)	Normal hatch (%)	Dead and abnormal hatch (%)	Swim-up larvae (%)	Duration of hatching (Days)
1	3.1	0	0	0	0	30.0[a]
	5.0	52	26	26	0	20.0
	7.1	75	44	31	24.5	13.5
	10.1	83.5	68	15.5	50	12.5
	13.1	84.5	81	3.5	75	8.5
	16.1	87	83.5	3.5	72.5	6.5
	18.2	75.5	67	8.5	53.5	6.0
	20.0	58	48	10	30.5	6.5
	22.1	7.5	1.0	6.5	0	2.5
2	3.3	61	2	59	0	30.5
	5.2	67	20	47	0.4	20.5
	7.2	74.5	50	24.5	28	23.5
	10.2	80.5	56.5	24	40	11.0
	13.1	81.5	77.5	4	70.5	8.0
	16.1	81.5	79.5	2	73.5	4.0
	18.2	68	65	3	61.5	2.0
	19.9	93.5	90.5	3	79.5	5.0
	22.1	81	69	12	58.5	5.0
	23.8	67.5	23.5	44	14.5	4.5
	25.4	24.5	0	24.5	0	2.5
3	4.9° + 0.5°/Day	80.5	76	4.5	66	2.0
	4.9° + 1.0°/Day	80.5	77.5	3	72	3.5
	6.9° + 1.0°/Day	84.5	82.5	2	71.5	3.0
	10.0° + 1.0°/Day	88	85.5	2.5	85	2.0

a   Developmental rate exposure at 3.1 °C.

successive developmental stages is known to increase for some species
(Hokanson et al., 1973). Eggs were incubated at 4.9°, 6.9°, and 10.0°C
for 24 h after fertilization; then they were increased by 2°-3°C at
an average rate of rise of 0.5° or 1.0°C/day. Two egg strands provided
common replicates for all groups to facilitate comparison of treatment
effects.

Three measured parameters used for this study were total hatch, normal
hatch, and swim-up larvae (attached below surface film) expressed as
percentages of the total number of eggs in each subsample. The numbers
of normal, dead, and abnormal yolk-sac larvae were recorded daily at
hatching. Total hatch is an·expression of embryo survival to hatch
regardless of the condition of the newly hatched yolk-sac larvae.
Normal hatch excludes dead and abnormal yolk-sac larvae that hatch.
The percentage of swim-up larvae gives a measure of the vitality of
newly-hatched larvae. Larvae were retained until the swim-up stage
or until death. Three endpoints are used in this paper to describe
yellow perch responses to temperature - optimum, optimum range, and
median tolerance limit (TL50); the distinction between egg and embryo
has been defined by Hokanson et al. (1973). The maximum total hatch
was adjusted to 100% for each egg strand, and the percentages of normal
hatch and swim-up larvae were normalized by the formula of Abbott (1925)
before derivation of the TL50 limits. The arcsin $\sqrt{\text{percentage}}$ transfor-
mation was used for the 2-way analysis of variance tests of treatment
differences (Steel and Torrie, 1960).

Embryonic and Larval Developmental Rates. This experiment was designed
to describe the median time to attain various morphological stages
and physiological events in the early life stages of yellow perch. Sub-
samples from one egg strand were adjusted to 8 constant temperatures
from 3.1° to 19.7°C within 1 h of·fertilization. The following 7 stages
and events, which could be readily recognized in living embryos and
larvae, were observed:

1. Neural keel; yolk plug large.

2. Heart beat.

3. Retinal pigmentation; eye appears totally black, including the
lens of the eye.

4. Branchial respiration; mouth movements synchronized with opercula.

5. Mass hatch; 50% of total hatch.

6. Swim-up larvae; 50% of normal hatch attached to surface film or
free-swimming.

7. Mortality of unfed larvae; 50% of normal hatch.

Observations were made twice a day and recorded to the nearest 0.5
day. Total lengths of normal larvae at mass hatch were measured with
an ocular micrometer to the nearest 0.1 mm.

The survival of newly-hatched larvae was observed at 12.0°C after
mass hatch at 5.4°, 7.3°, and 10.4°C. Twenty normal larvae were ad-
justed to 12.0°C at 2-3 deg C/day, and individual survival and acti-
vity were observed.

RESULTS

Embryo Survival

Different proportions of yellow perch embryos developed in the range
of 3.3° to 25.4°C, depending on their age and thermal history (Fig. 3).
The highest mean total hatch was 93.5% at 19.9°C in the second treat-
ment group; therefore, an average 6.5% of the eggs in all subsamples
were assumed to be infertile. The remaining proportion that failed
to hatch were assumed to be dead embryos. The proportions of dead and
abnormal larvae at hatch represent the differences between the percent-
age total hatch and normal hatch values. Common abnormalities included
spinal curvatures and edema as reported by Kokurewicz (1969). Percent-
age dead larvae represents the differences between the normal hatch
and swim-up larvae values. Differences in temperature response be-
tween egg strands were not significant (P >0.10, F-test); therefore
replicates were combined. The effects of temperature on the response
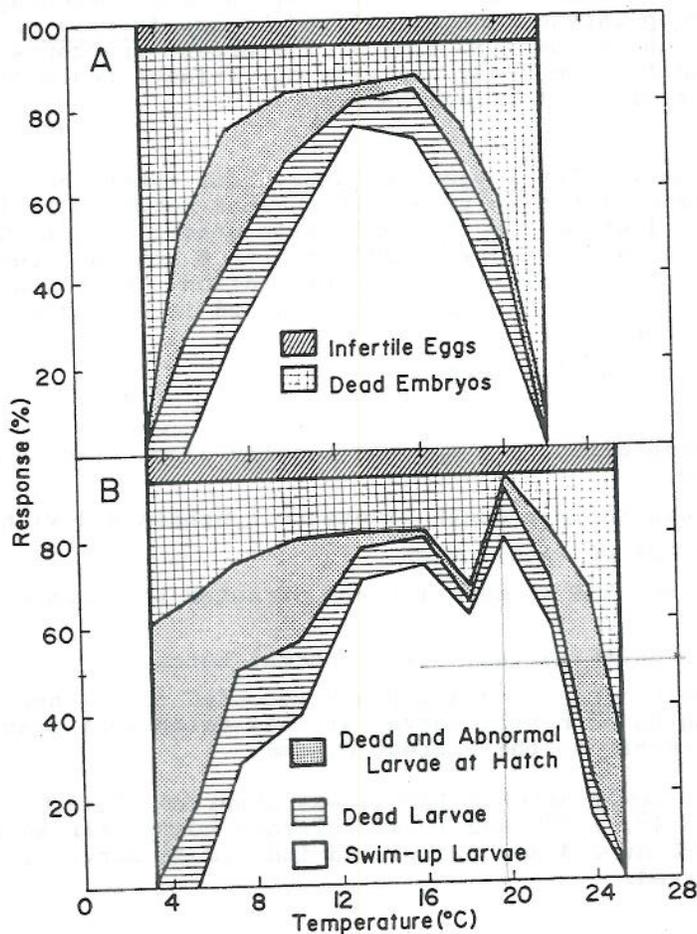of each treatment group are described below.

Fig. 3. Effect of constant incubation temperatures on percentage total
hatch, normal hatch, and swim-up larvae of known aged yellow perch
embryos-replicates combined. (A) Embryos incubated at test temperatures
from fertilization to larval swim-up stage; (B) embryos incubated at
12.0°C until neural keel formed, then at test temperatures to larval
swim-up stage. Fate of eggs shown as percentage differences

Group 1. Hatching occurred over a narrower range of temperatures when embryos were exposed to constant temperatures soon after fertilization (Table 1, Fig. 3A). The maximum mean total hatch was 87% at 16.1°C. Only 3.5% of these were dead or abnormal at hatch. The incidence of dead or abnormal larvae increased at temperature extremes. Greater than 67% normal hatch occurred in the optimum range of 10.1° to 18.2°C. Variations in normal hatch within the optimum range are considered similar to the optimum response (Table 2). Hatching occurred in the range of 5.0° to 22.1°C, but did not occur at 3.1°C. Only 1% normal hatch occurred at 22.1°C. The duration of the hatching period was about 6 days at 16°-20°C and 20 days at 5°C. The lower and upper TL50 define the range of temperatures for which survival is equal to or greater than 50% of the optimum response, and these limits were 6.8° and 19.9°C for normal hatch (Table 2).

A maximum of 75% of the eggs survived to the larval swim-up stage at 13.1°C (Table 1). More than 53% survived to the swim-up stage in the optimum range of 13.1° to 18.2°C. A relatively greater proportion of larvae that hatched at low temperatures failed to reach the swim-up stage than at high temperatures. Larvae were inactive at 5.0°C and all died. Survival of swim-up larvae at 22.1°C was limited by embryo survival. The lower and upper TL50 for embryo survival to the swim-up stage were 9.8° and 18.8°C (Table 2).

Table 2. Median tolerance limits (TL50) and optimum range of yellow perch embryos incubated at a series of constant temperatures

Treatment group	Response	TL50 ($x \pm$ SE) Lower	TL50 ($x \pm$ SE) Upper	Optimum range (°C) [a]
1 [b]	Total hatch	4.8 ± 0.20	20.5 ± 0.20	-
	Normal hatch	6.8 ± 0	19.9 ± 0.05	10.1 - 18.2
	Swim-up larvae	9.8 ± 0.80	18.8 ± 0.25	13.1 - 18.2
2 [c]	Total hatch	<3.3	24.6 ± 0.05	-
	Normal hatch	7.0 ± 0.05	22.9 ± 0.20	13.1 - 18.2
	Swim-up larvae	9.3 ± 0.05	22.5 ± 0.10	13.1 - 22.1

[a] Range of temperatures over which the response was not significantly different from the highest value (P = 0.05, Tuckey's multiple range test).

[b] Embryos reared from fertilization to larval swim-up stage.

[c] Embryos incubated at 12.0°C from fertilization to formation of neural keel, then exposed to test temperatures to swim-up stage.

Group 2. Hatching occurred over a wider range of temperatures when embryos were exposed to temperature extremes at an older stage of development (Table 1, Fig. 3B). The maximum mean total hatch for this group was 93.5% at 19.9°C. Relatively greater proportions of embryos survived to hatch at the temperature extremes from 3.3° to 25.4°C, but many were dead or abnormal at hatch. Only 2% normal hatch occurred at 3.3°C and none at 25.4°C. A total of 65-79.5% normal hatch occurred in the optimum range of 13.1° to 18.2°C. The duration of the hatching period was only 2.0 - 5.0 days above 16°C and required up to 30.5 days at 3.3°C.

Similar proportions of embryos survived to the swim-up stage below 18°C as in the first treatment group, but more survived at higher temperatures. A maximum of 79.5% of the eggs survived to the swim-up stage at 19.9°C. Greater than 58.5% survived in the optimum range from 13.1° to 22.1°C. The lower and upper TL50 for survival of older embryos to the larval swim-up stage were 9.3° and 22.5°C (Table 2).

Group 3. The responses to all rising temperature regimes were within the optimum range reported for constant temperature groups. A total of 76 - 85.5% normal hatch and 66-85% swim-up larvae were produced (Table 1). Incidence of dead and abnormal larvae were also low (2-4.5%) for this treatment group. Best results were obtained with an initial temperature of 10°C increasing by 1.0°C/day.

Hatching was generally completed in 2 - 3.5 days for rising temperature regimes (Table 1). Mass hatch was completed in 21 days at 16.1°C for the 4.9° + 0.5°C/day treatment and in 10 days at 20.0°C for the 10.0° + 1.0°C/day treatment. Larval swim-up was completed in 25 days at 16.2°C and in 14 days at 24.3°C for these respective treatments.

Embryonic and Larval Developmental Rates

The median time required for morphological differentiation of the embryo (stages 1-4) decreased exponentially with increasing temperature (Fig. 4). More than 80% of the eggs developed to the neural keel stage at 3.2°C, but most perished by the time the heart beat and circulation began. Median time to hatch ranged from 6 days at 19.7°C to 51 days at 5.4°C. Mass hatch occurred within a day after the start of branchial respiration above 7.3°C. At lower temperature levels hatching was premature and occurred before the heart beat started at 3.2°C. Larval swim-up occurred on the day of hatch above 13.1°C and 1-2 days later at lower temperatures. None reached the swim-up stage at 5.3°C. Feeding trials at higher temperatures suggested that feeding commenced once the larvae became free-swimming. Activity of larvae declined rapidly in the absence of food even though 50% survived for 15 days at 19.8°C and 65 days at 5.3°C. The median period between swim-up and mortality of unfed larvae
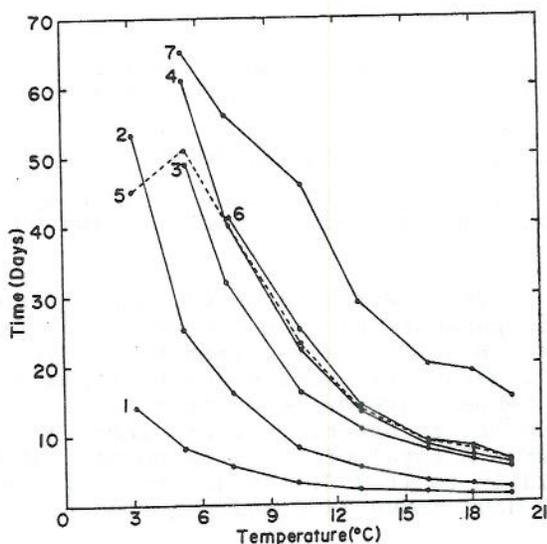

Fig. 4. Relationship between temperature and median time of development of yellow perch embryos and larvae. (1) Neural keel; (2) heart beat; (3) retinal pigmentation; (4) branchial respiration; (5) mass hatch; (6) swim-up larvae; (7) unfed larvae mortality

was 9 days at 19.8°C and 21 days at 10.5°C. At lower temperatures this period was shortened, and death occurred only 4 days after branchial respiration began at 5.3°C.

Larvae that hatch at low incubation temperatures have an increased chance for survival when transferred to a higher temperature. A total of 25%, 85%, and 90% reached the swim-up stage at 12°C after hatching at 5.4°, 7.3°, and 10.4°C, respectively.

P. *flavescens* vs P. *fluviatilis*

Thermal requirements for total hatch and time to mass hatch of *P. flavescens* and *P. fluviatilis* are shown in Fig. 5. The lower and upper TL50 for total hatch of *P. flavescens* were 4.8° and 20.5°C (Table 2). The calculated lower and upper TL50 for *P. fluviatilis*, from the data of Swift (1965), were 6.1° and 20.2°C. The median time to hatch was nearly identical for both species above 13°C. At lower temperatures *P. fluviatilis* tended to hatch about 3-6 days sooner.
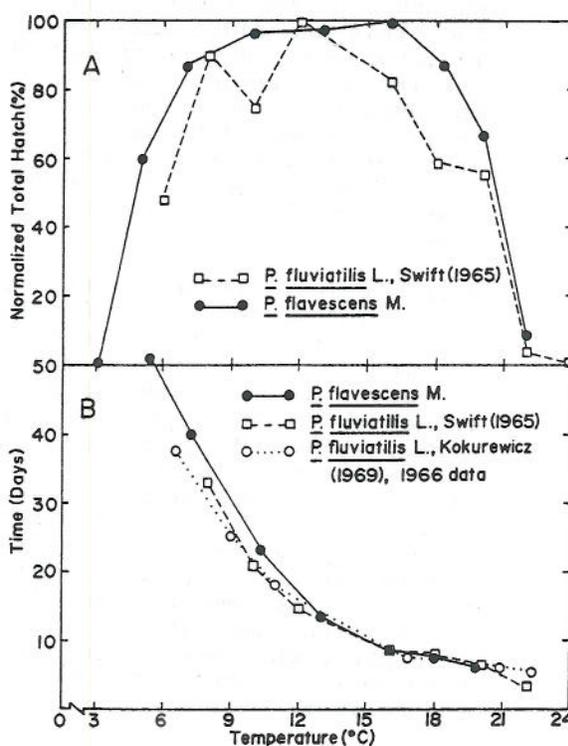

Fig. 5. Effects of constant incubation temperatures on *Perca flavescens* and *P. fluviatilis*. (A) Relative effects on total hatch; (B) time to mass hatch

The total length of *P. flavescens* larvae at mass hatch ranged from 4.7 to 6.6 mm. The mean lengths were maximal (6.1 - 6.3 mm) at 7.1° - 13.1°C, intermediate (5.6 - 5.8 mm) at 16.1° - 20.0°C, and minimal (5.1 - 5.2 mm) at 5.0° and 22.1°C. Newly-hatched larvae at 10°C appeared elongated with smaller yolk sacs and well-developed jaws, whereas those at higher temperatures were shorter with larger yolk sacs. Most larvae were premature when incubated below 7°C. This description of size and condition of newly-hatched yellow perch at various temperatures is identical to that of *P. fluviatilis* (Kokurewicz, 1969).

DISCUSSION

Thermal tolerance of successive embryonic and larval stages of yellow perch increased with morphological differentiation. Survival of early embryonic stages (before neural keel) was generally favored at 3.1° to 19.9°C. The lower and upper TL50 for normal hatch were 7.0° and 22.9°C for older embryonic stages (after neural keel). Newly-hatched larvae required temperature in excess of 9.8°C for normal activity and survival. Larval survival at high temperatures was limited only by embryo survival in this study. The optimum range for sustained growth and survival of feeding larval perch needs to be established. The optimum range (13.1° - 18.2°C) for embryo survival from fertilization to the larval swim-up stage was quite narrow at constant incubation temperatures which affected both embryo and larval requirements. In contrast, embryos exposed to rising incubation temperatures (range 4.9° - 24.3°C) had optimum survival to the larval swim-up stage.

The optimal thermal regime for culture of yellow perch was an initial exposure of fertilized eggs to 10°C and exposure to 20°C before hatching. This procedure was used successfully by Hale and Carlson (1972) in laboratory culture of larval perch. Larvae must be fed shortly after the larval swim-up stage. Larval survival thereafter will depend on the amount of food especially at elevated temperatures (Kudrinskaya, 1970). The period between larval swim-up and mortality of unfed larvae is progressively shortened at higher temperatures. The "critical period" for endogenous feeding of larval perch would be even shorter since starvation of larval fishes is evident before death occurs (Toetz, 1966).

Morphological differentiation of the embryo and hatching are independently influenced by incubation temperatures. Hatching is generally caused by the joint action of temperature on secretion of hatching enzymes and on enzyme and embryonic activity (Hayes, 1942). Hatching of yellow perch follows shortly after commencement of branchial respiration above 7°C, and it is morphologically premature at lower temperatures. Ishida (1944) reports in *Oryzias* that the initiation of respiratory movements appears to rupture the hatching glands which line the pharynx. At temperatures above 13°C hatching of yellow perch is probably favored by increased enzyme and embryonic activity. Hatching was especially favored by rising temperature regimes that produce more viable larvae, shorter hatching periods, and fewer abnormal larvae than constant temperatures. Lower temperatures often produce longer larvae with somewhat smaller yolk sacs at hatching (Blaxter, 1969). This phenomenon may be related to lower efficiencies of conversion from yolk to embryonic tissue in salmon at low temperatures (Hayes and Pelluet, 1945).

Premature hatch at low incubation temperatures has been reported in other species and is discussed by Kokurewicz (1969). The cause of premature hatch below 7°C is not clear since embryonic and enzyme activity would be minimal. It is doubtful that hatching glands were active by the time of hatch at 3°C. Mansueti (1964) observed that the yellow perch egg case tended to become thin as the embryo grew. A few days before hatching the egg case began to soften and take on a ragged appearance. The variability of the hatching period also increased at lower temperatures. In preliminary experiments we observed mass hatch of yellow perch 23 days sooner at 6°C and 16 days sooner at 8°C when egg subsamples were handled (pipette) daily for observations of development.

The apparent earlier hatching of P. fluviatilis at lower incubation temperatures (Fig. 5) may be caused by different degrees of handling of the egg strands. We designed incubation chambers (Figs 1 and 2) to minimize handling of P. flavescens eggs. Kokurewicz (1969) noted considerable variation among his experiments on P. fluviatilis in size and time to mass hatch at low incubation temperatures, but he did not mention the amount of handling his eggs received. The relative effects of temperature on total hatch and size at hatch of these two species are remarkably similar and tend to support the theory that P. flavescens and P. fluviatilis may be conspecific.

SUMMARY

1. The effects of 24 treatments of constant or rising temperatures (3.1° - 25.4°C) on survival of yellow perch embryos of known age were determined in continuous-flow incubators. The median times to attain 7 morphological stages and physiological events in living embryos and larvae were also observed at 8 constant temperatures (3.1° - 19.7°C).

2. Early embryonic stages (before neural keel) tolerated constant temperature exposures from 3.1° to 19.9°C. The median tolerance limits (TL50) for normal hatch of older embryonic stages (after neural keel) were 7.0° and 22.9°C. The lower TL50 of swim-up larvae was 9.8°C. The optimum range for swim-up larvae was only 13.1° to 18.2°C when embryos were reared at constant incubation temperatures after fertilization. Survival of swim-up larvae at higher temperatures was limited only by embryonic survival.

3. Optimum yields of swim-up larvae (66-85%) were produced when initial incubation temperatures (4.9° - 10.0°C) were increased 0.5° - 1.0°C/day (range 4.9° - 24.3°C). Rising temperature regimes also favored shorter hatching periods and lower incidence of abnormalities at hatch.

4. Mass hatch occurred in 6 days at 19.7°C and in 51 days at 5.4°C. Hatching followed commencement of branchial respiration above 7.3°C, but was morphologically premature at lower temperatures.

5. Larval swim-up occurred on the day of hatch above 13°C, and within 2 days at lower temperatures. Unfed larvae survived 15 days at 19.8°C and 65 days at 5.3°C. The median period between swim-up and mortality of unfed larvae was 9 days at 19.8°C and 21 days at 10.5°C.

6. Total length of normal larvae at mass hatch varied from 4.7 to 6.6 mm. Mean lengths were 6.1 - 6.3 mm at 7.1° - 13.1°C, 5.6 - 5.8 mm at 16.1° - 20.0°C, and 5.1 - 5.2 mm at 5.0° and 22.1°C.

7. Effects of incubation temperatures on total hatch, median time to hatch, and size at mass hatch of Perca flavescens were compared to P. fluviatilis. The data tend to support the theory that P. flavescens and P. fluviatilis may be conspecific.

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K.E.F. Hokanson, U.S. Environmental Protection Agency, National Water Quality Laboratory, Box 5oo, Monticollo, Minn. 55362/USA

Ch.F. Kleiner, U.S. Environmental Protection Agency, National Water Quality Laboratory, 6201 Congdon Boulevard, Duluth, Minn. 55804/USA

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