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MANAGEMENT BRIEF

Effects of Fixed and Fluctuating Temperature on Hatch of Round Whitefish and Lake Whitefish Eggs

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Abstract
Temperature-response information for use in evaluating thermal discharges is often over 30 years old and in the nonpeer-reviewed literature, especially for Round Whitefish *Prosopium cylindraceum* and Lake Whitefish *Coregonus clupeaformis* exposed to nonlethal, elevated, and variable temperatures. Egg incubation experiments on Round Whitefish collected in Lake Ontario and Lake Whitefish collected in Lake Huron were carried out from December 13, 2011, to April 7, 2012. Experimental treatments included ambient baseline control conditions as well as fixed and fluctuating (variable) temperature increases of 1, 2, 3, and 5°C above ambient baseline conditions. For both species, the window for hatching for all experimental temperature treatments was variable (range, 10–38 d for Round Whitefish and 11–44 d for Lake Whitefish), and the hatching windows tended to be greater as temperatures increased. Our results indicated that both fixed and variable incremental increases in temperature above ambient baseline conditions have a statistically significant effect on 50% hatch, and hatch occurs earlier with higher incremental temperature increases. The ecological significance of advanced hatch, such as indirect mortality and food source availability, was evaluated.

The effect of temperature on incubation and development of eggs is known and well established in the literature for a wide variety of fish species (Wismer and Christie 1987; Casselman 1995; Sandström et al. 1997; Lukšiene et al. 2000). However, many of these studies focus on determining thermal tolerances and spawning successes and do not necessarily address fluctuating temperatures such as those associated with the natural environment or thermal discharges at industrial sites. Furthermore, there appears to be limited temperature information on coldwater species such as Round Whitefish *Prosopium cylindraceum* and Lake Whitefish *Coregonus clupeaformis* other than that in nonpeer-reviewed literature (Griffiths 1979, 1980). Few studies exist on the effect of fluctuating temperatures associated with thermal discharges on fish behavior and survival, and these involved primarily warmwater species (Kelso 1974; Ross and Siniff 1982; Sandström et al. 1995; Lukšiene et al. 2000; Smythe and Sawyko 2000). Even fewer studies discuss the issue of advanced hatch (e.g., Casselman 1995). Other studies (e.g., Sandström et al. 1995) have shown that spawning and subsequent hatching of fish from thermal discharge waters occurs earlier than in natural populations. There is a need to further refine thermal effect endpoints for fish species that occur in the vicinity of industrial plant discharges. Establishment of thermal preferences, tolerances, and regimes will permit accurate risk assessment evaluations by life stage for indicator fish species that frequent and spawn in the vicinity of thermal discharges. This is becoming increasingly important as natural water bodies heat up because of climate change (Casselman 2002).

The objective of the study was to determine whether, and to what extent, fixed and fluctuating (variable) incremental temperature increases above ambient temperature affect the timing of hatch for Round Whitefish and Lake Whitefish. In the Great Lakes region, Round Whitefish spawning occurs in the fall (November–December) at temperatures of 2.0–4.5°C

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and hatching occurs in the spring (April–May). Similarly, Lake Whitefish spawning occurs in the fall (October–December) at temperatures of 1–8°C and hatching occurs in the spring (April–May) (Wismer and Christie 1987). Advanced hatching of larval fish due to temperatures warmer than ambient may have ecological consequences. For example, food sources may not be readily available, resulting in impacts to survival and recruitment (e.g., Hoyle et al. 2011). The experiments for this current study were conducted in laboratory and field settings at the Wesleyville Hatchery and Aquatic Research Facility (WHARF) in Port Hope, Ontario, from December 2011 to April 2012.

METHODS

Egg collection.—Round Whitefish eggs were collected from fish gill-netted in Lake Ontario near Oshawa, Ontario, on December 14, 2011. The eggs were collected from females caught in a single gill net at the north end of the diffuser of the Darlington Nuclear Generating Station (DNGS) in 4.7°C water. Eggs were fertilized in four separate families, with two families containing eggs and milt from one female and one male each, and two families containing eggs and milt from two females and two males each, for a total of six females and six males. All fertilized eggs were pooled and then randomly distributed among the treatments. Eggs were fertilized using the dry fertilization technique following Ontario Ministry of Natural Resources (OMNR) protocols and guidelines (i.e., Hooper 2006; OMNR 2009, 2010). Eggs were transferred to the WHARF on the same day as collection and began incubation approximately 6–8 h after fertilization. Ambient water temperatures at WHARF at the start of incubation were within 0.2°C of the water temperature where the eggs were collected.

Lake Whitefish eggs were collected from fish gill-netted in Lake Huron (similar water temperatures to DNGS) on December 13, 2011, and were from one family with eggs from one female and milt from four males. Eggs were fertilized using the dry fertilization technique following OMNR protocols and guidelines (i.e., Hooper 2006; OMNR 2009, 2010). Eggs were transferred to the WHARF on the same day as collection and began incubation approximately 9–10 h after fertilization.

Egg incubation.—The OMNR egg incubation guidelines and protocols were followed (i.e., Hooper 2006; OMNR 2009, 2010). Eggs were incubated from December 13, 2011, to April 7, 2012, using 12 MariSource vertical stacked trays. Within each tray were four individual rows where eggs could be incubated as independent samples (i.e., eggs placed in each row constituted a replicate). Water was supplied from the forebay of a nonoperating power plant (connected to Lake Ontario), prefiltered, and passed through an ultraviolet treatment system for disinfection and as well as through off-gas chambers before use in ambient or experimental treatments.

Experimental design.—The eggs of Round Whitefish and Lake Whitefish were incubated in the vertical stacked trays using seasonal temperature regimes similar to those recorded from lakes receiving thermal discharges. The experiments focused on egg development from fertilization to hatching over the winter.

TABLE 1. Temperature increments above ambient for Round Whitefish and Lake Whitefish studies, December 2011 to April 2012. Round Whitefish eggs began incubation on December 14, 2011, and Lake Whitefish eggs began incubation on December 13, 2011.

Degrees (°C) above ambient baseline temperature	Treatment code	Round Whitefish (number of replicates)	Lake Whitefish (number of replicates)
Fixed increments			
0	A-F	8	
1	A-F + 1	8	
2	A-F + 2	4	
3	A-F + 3	6	
5	A-F + 5	6	
Variable (fluctuating) increments			
0	A-V	8	4
1	A-V + 1	4	4
2	A-V + 2	4	4
3	A-V + 3	8	4
5	A-V + 5	8	4

Eggs were incubated using different experimental treatments: baseline temperature (ambient), four treatments of fixed increments above ambient, and four treatments of variable or fluctuating increments above ambient (Table 1). Each treatment consisted of a minimum of four replicates. Natural variation in temperature occurred in ambient forebay conditions over the testing period. Eggs in the fixed increment temperature treatments were gradually acclimated to the higher fixed temperature (at 0.5°C/h until the desired constant temperature was reached). Similarly, eggs subjected to the variable increment temperature regime were also gradually acclimated to the higher temperature before they were subjected to continuous temperature fluctuations of 0.5°C/h over a 24-h period (defined as a cycle), which is consistent with temperature discharge fluctuations at some industrial plants. This design, however, did not address abrupt temperature changes of several degrees per hour, which was the focus of earlier experiments reported by Griffiths (1979, 1980).

The experimental treatments were as follows:

1. Ambient temperature (°C) (baseline control using actual lake temperatures from a forebay connected to Lake Ontario via a submerged intake pipe. There are two controls, one for the fixed increment regime, designated A-F, and one for the variable (fluctuating) increment regime, A-V).
2. Ambient + 1°C (fixed increment condition, A-F + 1, and variable increment condition [six cycles per day], A-V + 1).
3. Ambient + 2°C (fixed increment condition, A-F + 2, and variable increment condition [three cycles per day], A-V + 2).

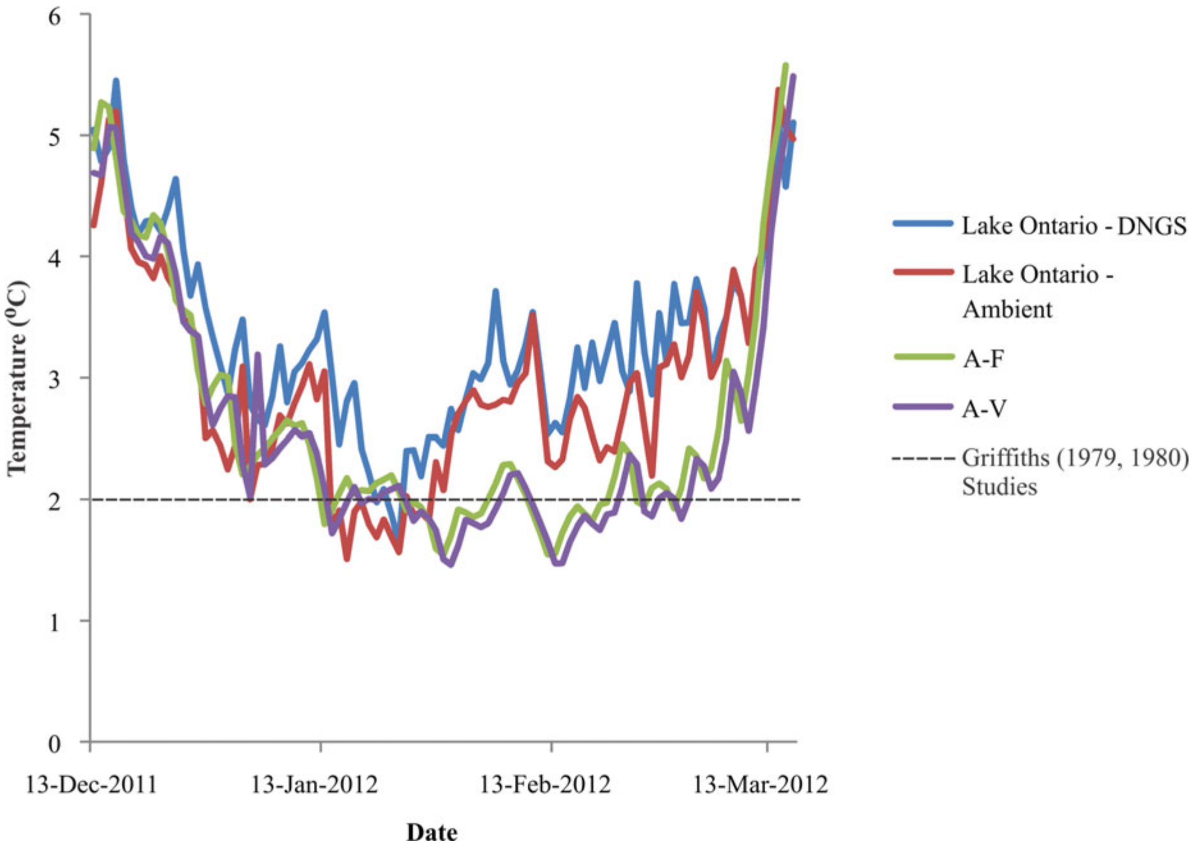

FIGURE 1. Mean daily temperatures for the experimental ambient controls (A-F and A-V). For the period of December 2011 to March 2012, mean daily temperatures for our ambient controls were compared with mean daily temperatures from two locations in Lake Ontario: in the vicinity of the Darlington Nuclear Generating Station (DNGS) discharge (Lake Ontario–DNGS) and 4 km west of DNGS (Lake Ontario–Ambient). A fixed "ambient" control temperature was used in past studies (i.e., Griffiths 1979, 1980).

4. Ambient + 3°C (fixed increment condition, A-F + 3, and variable increment condition [two cycles per day], A-V + 3).
5. Ambient + 5°C (fixed increment condition, A-F + 5, and variable increment condition [1.2 cycles per day], A-V + 5).

A major difference between the current experimental design and past studies (i.e., Griffiths 1979, 1980) is that naturally occurring variable ambient field temperatures were used in the current study as opposed to a fixed "ambient" temperature for the duration of the experiments (Figure 1). The temperature treatments used in this study allowed for the assessment of egg development under chronic exposure conditions (i.e., not rapidly lethal throughout the development period), and were consistent with temperature elevations at some discharges of industrial plants, especially within the thermal plume.

Round Whitefish eggs were subjected to all temperature treatments within the fixed increment and variable increment regimes (Table 1). For each treatment, four to eight replicates, each of which had approximately 300–600 eggs, were undertaken. The higher number of eggs per replicate allowed for improved survival estimates compared with earlier studies, which had lower numbers (i.e., Griffiths 1979, 1980). The eggs from each Round Whitefish family were arranged randomly in each tray.

Lake Whitefish eggs were subjected only to temperature treatments from the variable increment temperature regime (Table 1). Each treatment had four replicates, and each replicate had approximately 400–600 eggs. These eggs were not subjected to the treatments from the fixed increment temperature regime because fewer eggs were available.

Egg development and mortality.—Two temperature loggers (Onset TidbiT v2 Temp logger; accuracy, ±0.2°C at 25°C) were installed in each incubator with temperatures measured at 15-min intervals. Temperatures in each incubator were also measured "in-line" using temperature sensors (0.1°C accuracy) at 15-min intervals and relayed to a controller as a feedback to ensure proper temperatures for each treatment.

Hatching for each treatment and replicate was assessed daily. Stages of egg development were observed following Brooke (1975). Before the eye-up stage (i.e., stage 12), there was minimal handling of the eggs since this is the period when the eggs are considered to be the most delicate (i.e., egg membranes are soft and susceptible to breakage). Developing eggs were treated with the fungicide 35% Perox-Aid to further control fungal growth, and dead eggs were removed on a daily basis.

At weekly intervals, several eggs were removed randomly from each treatment and examined under a dissecting microscope (Konus 5424 Crystal-Pro 7X–45X stereoscopical trinocular microscope). Photographs and videos of egg development were taken using the Celestron Digital Microscope Imager. All eggs removed for developmental checks were discarded from the experiment and preserved in glass vials containing 3% buffered formalin solution.

Reference temperature locations.—Since ambient water used for the experiments was drawn from a forebay that had connections to Lake Ontario, additional data from thermistors was collected from two nearshore Lake Ontario sites for comparative purposes. The first field site was located in the vicinity of the DNGS thermal diffuser (6.5 m) (referred to as Lake Ontario–DNGS) and represents thermal discharge limits. The bottom temperature data from three temperature-collecting rigs was averaged to obtain mean daily temperatures. The second site was located less than 4 km west of the DNGS thermal diffuser in approximately 5.25 m of water and was assumed to be representative of ambient Lake Ontario conditions (referred to as Lake Ontario–Ambient). Temperature data for both sites were only available from December 13, 2011, to March 16, 2012, and for each site, the temperature data points collected at 15-min intervals were averaged to obtain mean daily temperatures.

Data analysis.—Temperature data collected from the temperature loggers were averaged to obtain mean daily temperatures for each of the experimental treatments. To ensure that mean daily temperatures above ambient and temperature fluctuations conformed well to the experimental plans, a plot was produced to display the mean daily temperatures for each of the experimental treatments for the fixed increment regimes (A-F, A-F + 1, A-F + 2, A-F + 3, and A-F + 5) and for the variable (fluctuating) increment regime (A-V, A-V + 1, A-V + 2, A-V + 3, and A-V + 5). Additionally, a one-way ANOVA and follow-up Tukey honestly significant difference multiple-range test were performed to compare the mean daily temperatures of the ambient baseline controls from this study (i.e., A-F and A-V) and those of the two reference locations (Lake Ontario–DNGS and Lake Ontario–Ambient). This comparison was made to illustrate that the ambient baseline conditions (i.e., A-F and A-V) used in our experiments were similar to those found in field Lake Ontario locations.

Hatching data (i.e., date and numbers hatched) were recorded for each of the experimental treatments in order to observe hatch distribution and the number of days required for 50% hatch for each of the experimental treatments in the fixed increment and variable increment regimes. Statistical significances of differences of the 50% percentile hatch between pairs of treatments were determined using a median test on the distribution of days to hatch. The median test is a standard nonparametric test that compares the values in each treatment against the overall values of the combined data. When there were sufficiently large departures for the treatments an assessment of statistically significant differences was completed (SAS version 9.3).

RESULTS

Temperature Comparisons

Mean daily temperatures above ambient and temperature fluctuations conformed well to the experimental plans (Figures 2, 3). Patterns of temperature fluctuation were consistent between each of the treatments and confirmed that eggs were subjected to temperature increases over the incubation period.

Water temperatures obtained from the intake forebay for the experimental ambient controls (i.e., A-F and A-V) matched reasonably well with the temperatures found in the nearshore Lake Ontario locations. The results of the ANOVA indicated that significant differences did occur ($F_{3,\,378} = 12.91$, $P < 0.01$). As expected, the follow-up multiple range test indicated that temperatures at the DNGS thermal discharge site (Lake Ontario–DNGS) were higher than those at the ambient Lake Ontario site (Lake Ontario–Ambient) and ambient experimental treatments for the fixed increment and variable increment regimes (A-F and A-V, respectively). Temperatures at the ambient Lake Ontario site and ambient control for the fixed increment regime (i.e., A-F) were similar. Similarly, the experimental ambient for the variable increment regime (A-V) was not different from that of the fixed increment regime (A-F) but was slightly lower than that of ambient Lake Ontario (i.e., Lake Ontario–Ambient) (Figure 1; Table 2).

Advanced Hatch

For both the fixed increment and variable increment temperature regimes for Round Whitefish, a general trend was observed where eggs subjected to increasingly higher temperatures hatched earlier (Figures 4, 5). For example, for the fixed increment temperature regime, 50% hatch occurred at 62 d for the A-F + 5 treatment, which was almost 6 weeks earlier than 50% hatch for the A-F treatment (103 d) (Figure 4). For the variable increment temperature regime, 50% hatch from the A-V + 5 treatment (70 d) occurred more than 1 month earlier than that from the baseline treatment (A-V) (103 d) (Figure 5). These

TABLE 2. Pairwise comparison of mean daily temperatures (°C) for Lake Ontario locations near the DNGS discharge (Lake Ontario–DNGS) and west of DNGS (Lake Ontario–Ambient) and the ambient baseline controls for the fixed increment (A-F) and variable increment (A-V) regimes, December 13, 2011, to March 16, 2012. Temperatures with the same letter are not significantly different at $P = 0.05$.

Variable	Mean daily temperature (°C)
Lake Ontario–DNGS	3.32 z
Lake Ontario–Ambient	2.97 y
A-F	2.64 yx
A-V	2.58 x

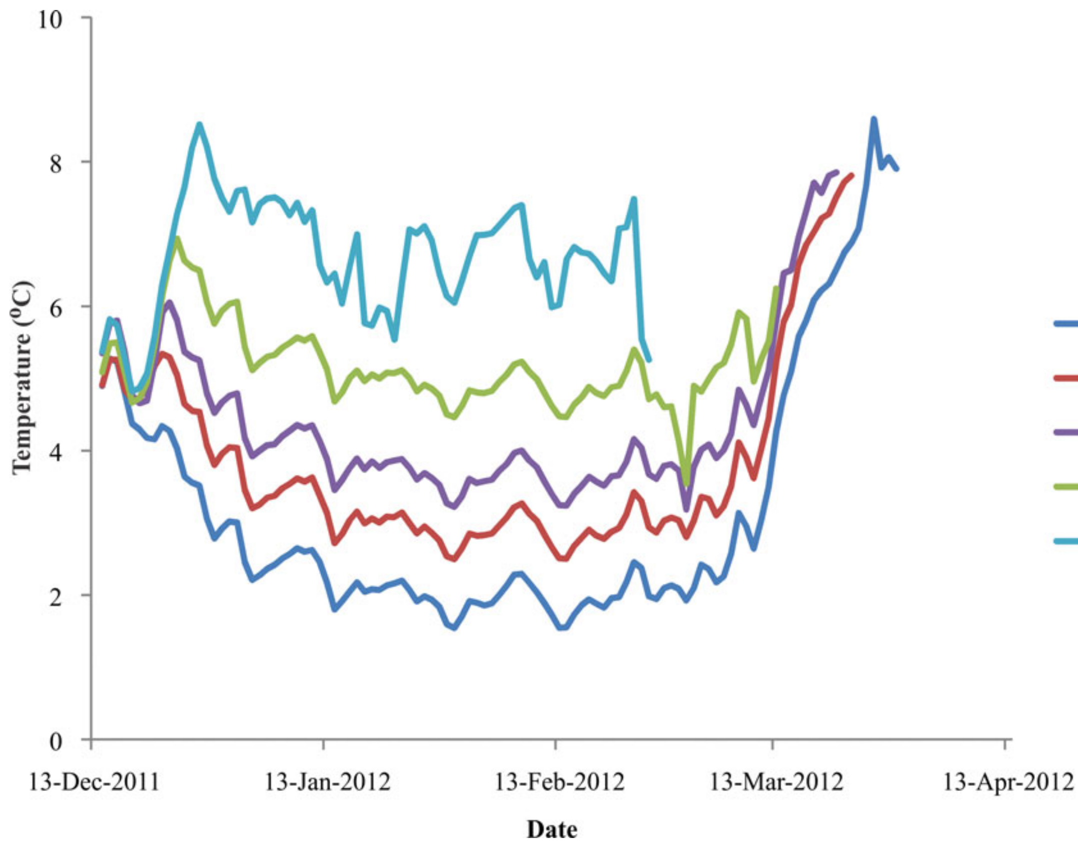

FIGURE 2. Mean daily temperatures for Round Whitefish eggs incubated at 0, 1, 2, 3, and 5°C fixed increments above ambient temperature (A-F control, A-F + 1, A-F + 2, A-F + 3, and A-F + 5, respectively) from December 2011 to April 2012. Eggs were gradually acclimated to the higher fixed temperature at 0.5°C/h until the desired constant temperature was reached.

results suggest that a stable or fluctuating increase in ambient water temperature of 5°C advances hatch by 1 month or more. For all treatments (fixed increment and variable increment), the hatching window, defined as the number of days from first hatch to complete hatch, were variable, ranging from 10 to 38 d.

Lake Whitefish eggs were subjected only to variable increment temperature treatments and not the fixed increment temperature treatments because of the limited number of eggs collected. Similar to the Round Whitefish results, a positive relationship was seen between timing of hatch and increased temperature treatments (Figure 6). Lake Whitefish eggs subjected to a fluctuating 5°C increase above ambient (i.e., A-V + 5) hatched the earliest compared with those subjected to the baseline (ambient) treatment (A-V). A 50% hatch for eggs subjected to the + 5°C treatment (A-V + 5) occurred approximately 5 weeks earlier than that of eggs from the baseline treatment (A-V) (76 versus 111 d, respectively). The window between first and last hatch for each treatment was variable, ranging over approximately 2–3 weeks (11–18 d) for all treatments, with the exception of the + 5°C treatment, where hatching occurred over a 6.5-week period (44 d).

Overall, statistical analysis of our hatching data (Table 3) indicated that

1. there is a decrease in hatching time with increased temperatures above ambient;
2. fixed (constant) increment temperature increases decrease the hatching time more than variable (fluctuating) increment temperature increases; and
3. the hatching window increases with increasing temperature.

The results of the median test indicated that all treatments were significantly different at $\alpha < 0.0001$. The large numbers of hatchlings provided the statistical power to determine statistically significant differences even with a small difference in days.

The treatments indicated a tendency of a greater hatching window as temperature was increased. A test for statistical differences of this dispersion was approximated by assuming that the days to hatch were approximately normally distributed and calculating the variance (Table 3). The *F*-statistic tests for differences in variance using the ratio of the large variance to the small variance (Snedecor and Cochran 1980). A treatment pairwise comparison was completed and those variances not significantly different at $\alpha = 0.05$ are shown with similar letters in Table 3. For example, for the Round Whitefish treatments of 5°C above ambient (fixed increment, A-F + 5, and variable increment, A-V + 5), the dispersion was not statistically significantly different

TABLE 3. Hatching summary and test for statistically significant differences in dispersion for all Round Whitefish and Lake Whitefish experimental temperature treatments (described in Methods). For both species, data are arranged in descending order for 50% hatch. Treatments for each species with the same letter are not significantly different at $\alpha = 0.05$. Treatments with no letters are dissimilar to all other treatments. All days to hatch are significant between treatments at $\alpha < 0.0001$.

Temperature treatment	Days to 50% hatch	Hatching window (days)	Variance of hatching window (days^2)	Number of larvae hatched	Not statistically significantly different dispersion
Round Whitefish					
A-F	103	10	2.2	2,660	z
A-V	103	17	6.9	2,701	x
A-V + 1	96	18	5.4	1,391	y
A-F + 2	94	11	5.3	2,056	y
A-F + 1	93	30	24.2	4,293	
A-V + 2	92	21	7.7	1,770	w
A-V + 3	86	38	32.1	2,353	
A-F + 3	82	28	10.0	2,885	
A-V + 5	70	23	15.5	2,568	v
A-F + 5	62	19	14.9	2,540	v
Lake Whitefish					
A-V	111	12	7.0	1,773	x
A-V + 1	104	12	2.2	2,264	z
A-V + 2	98	11	7.8	1,946	w
A-V + 3	96	18	6.6	1,891	x
A-V + 5	76	44	46.7	2,435	

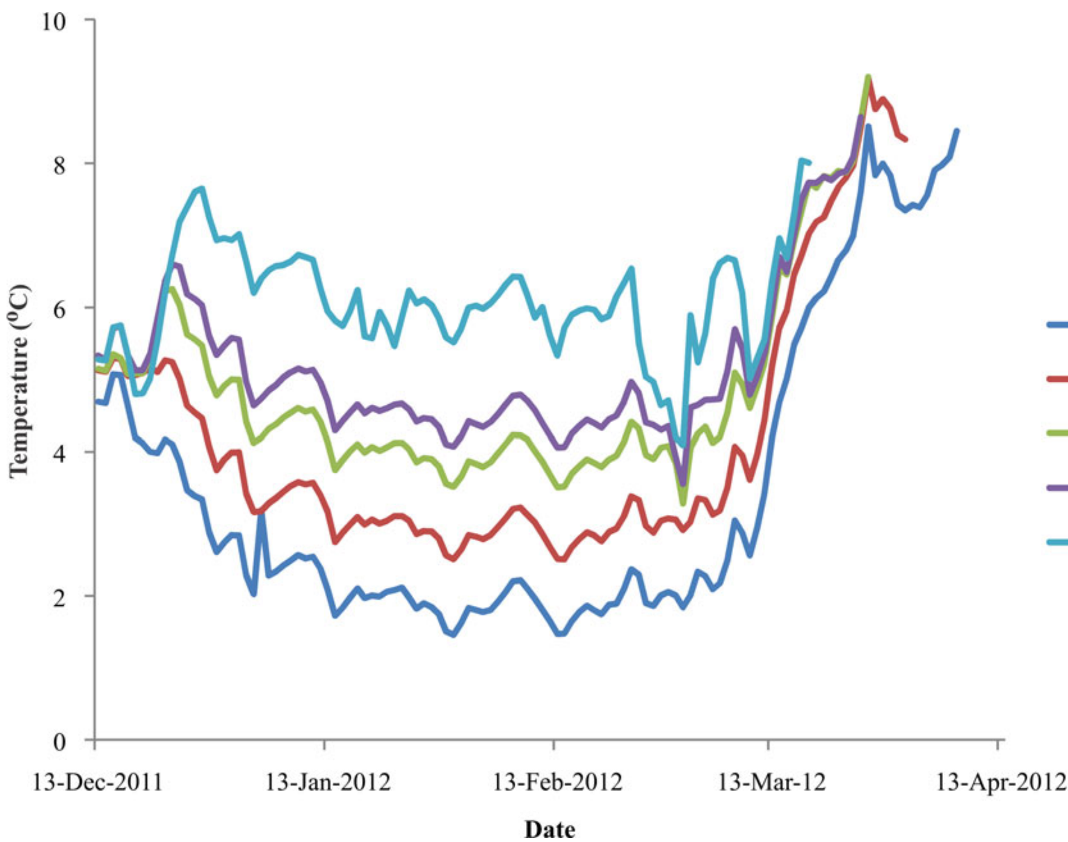

FIGURE 3. Mean daily temperatures for Round Whitefish and Lake Whitefish eggs incubated at 0, 1, 2, 3, and 5°C variable fluctuating increments above ambient temperature (A-V control, A-V + 1, A-V + 2, A-V + 3, and A-V + 5, respectively) from December 2011 to April 2012. Eggs were gradually acclimated to the higher temperature before they were subjected to continuous temperature fluctuations of 0.5°C/h over a 24-h period.

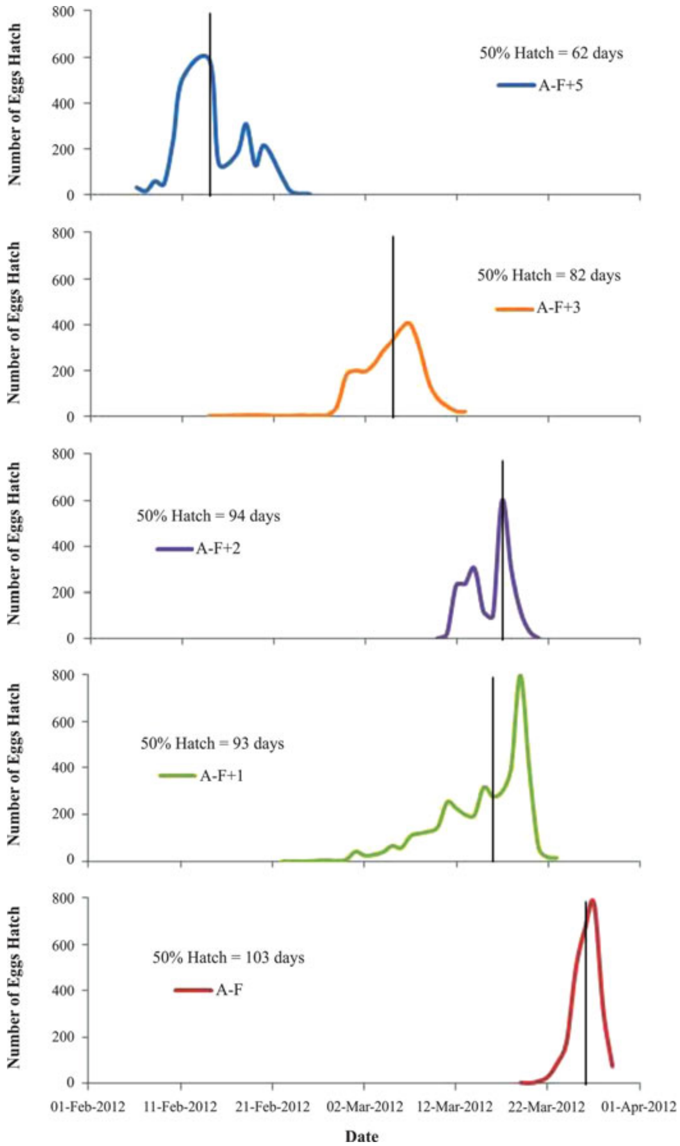

FIGURE 4. Round Whitefish hatching distribution for treatments of 0, 1, 2, 3, and 5°C fixed increments above ambient temperature (A-F control, A-F + 1, A-F + 2, A-F + 3, and A-F + 5, respectively). Vertical black lines indicate 50% hatch. Eggs began incubation on December 14, 2011.

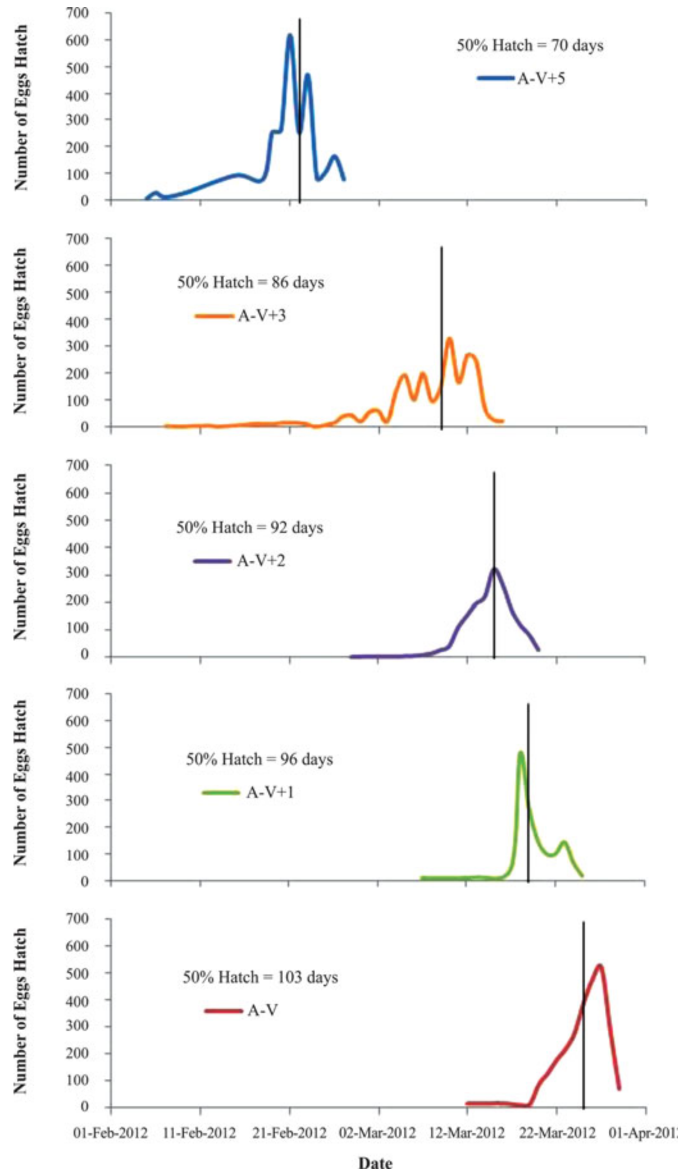

FIGURE 5. Round Whitefish hatching distribution for treatments of 0, 1, 2, 3, and 5°C variable (fluctuating) increments above ambient temperature (A-V control, A-V + 1, A-V + 2, A-V + 3, and A-V + 5). Vertical black lines indicate 50% hatch. Eggs began incubation on December 14, 2011.

from each other, but these treatments have a different dispersion in days to hatch compared with all other treatments (Table 3).

DISCUSSION

The results of our study showed that fixed and fluctuating increases in temperature above ambient baseline conditions have a statistically significant effect on 50% hatch, and days to 50% hatch occur earlier at higher temperature increases above ambient. In general, this advanced hatch is more pronounced with greater increases in temperature. Advanced hatch of Round Whitefish and Lake Whitefish may indirectly lead to mortality due to changes in food supply. In past studies, Griffiths (1979, 1980) had indicated that early hatch may be an issue since lake conditions may not be suitable for recently hatched larvae to survive. While not discussed by Griffiths (1979, 1980), his data indicated that early hatch was occurring at higher experimental temperatures above baseline. At a simulated fixed baseline temperature of approximately 2°C, 50% hatch of Round Whitefish eggs occurred at 155 d. At fixed temperatures of 4, 7, and 10°C, 50% hatch occurred at 106, 65, and 37 d, respectively. With fluctuating incremental temperature increases of 2, 5, and 8°C above the 2°C baseline, 50% hatch occurred at 131, 111 and 87 d, respectively (Griffiths 1980). Similar trends were seen for Lake Whitefish. At a simulated fixed baseline temperature of 2°C, 50% hatch occurred at 187 d. At fixed temperatures of

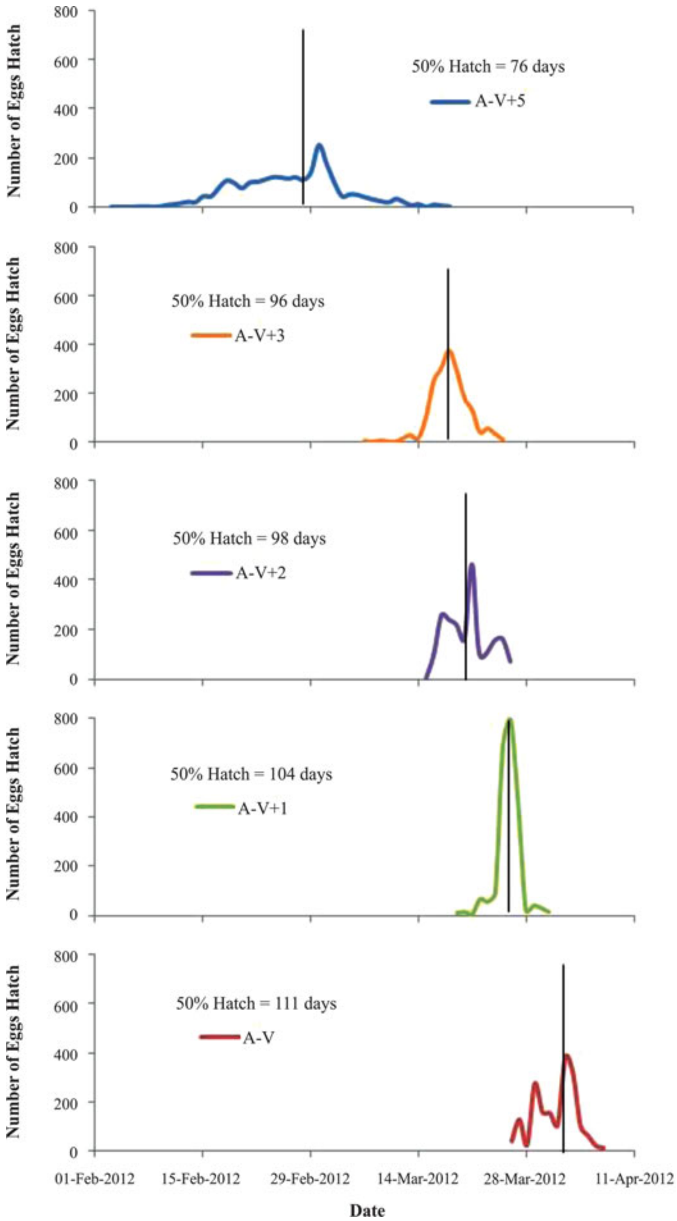

FIGURE 6. Lake Whitefish hatching distribution for treatments of 0, 1, 2, 3, and 5°C variable (fluctuating) increments above ambient temperature (A-V control, A-V + 1, A-V + 2, A-V + 3, and A-V + 5). Vertical black lines indicate 50% hatch. Eggs began incubation on December 13, 2011.

4, 7, and 10°C, 50% hatch occurred at 142, 79, and 42 d, respectively. With fluctuating incremental temperature increases of 2, 5, and 8°C above the 2°C baseline, 50% hatch occurred at 165, 139 and 98 d, respectively (Griffiths 1979). Hatching windows were variable for both whitefish experiments, generally spanning several weeks. In our current study, statistical analysis suggested that the hatching window or dispersion for each treatment was variable spanning 10–38 d for Round Whitefish treatments (fixed increment and variable increment) and 11–44 d for Lake Whitefish treatments, and there was a tendency of a greater hatching window as temperature increased. The hatching results of our current study cannot be directly compared with the Griffiths (1979, 1980) studies because of differences in the experimental design and temperature treatments. However, the observed trend of advanced hatch occurring with greater incremental temperature increases above baseline is similar.

Advanced hatching at higher temperatures has been shown for other species. Griffiths (1978) also examined the potential effects of unstable thermal discharge plumes on the eggs of Yellow Perch *Perca flavescens* and found that maximal hatch advancement (3.5 weeks) occurred for eggs exposed to a change in temperature (delta *T*) of + 10°C. Additionally, a delta *T* of + 2–6°C would generally advance hatch dates by 1 week or less. Casselman (1995) also noted that early hatch can be detrimental to the eggs of Lake Trout *Salvelinus namaycush*; however, the mortality of these Lake Trout eggs and larvae was also related to the interstitial water quality and depleted oxygen conditions. Although not directly related to early hatch, Sandström et al. (1995) reported that spawning and hatching of Eurasian Perch *P. fluviatilis* occur very early in discharge waters compared with reference waters and that this early spawning may explain the maturation of males during the first summer, while in reference waters eggs have yet to hatch or the Eurasian Perch are still in the larval stages.

A mismatch of hatching and food supply has been explored in other studies. Freeberg et al. (1990) reported that Lake Whitefish larvae survival in Lake Michigan was related to food availability especially during the first 7 weeks after hatch. Similarly, Hoyle et al. (2011) noted that the recruitment of larval Lake Whitefish to the juvenile stage was related to spring prey (e.g., zooplankton such as copepods) availability. An 89% decline in larval whitefish zooplankton prey appears to be causing decreased larval fish growth and survival to the juvenile life stage. Declines in zooplankton were attributed to dreissenid mussel establishment and the presence of a predatory zooplankton species, *Cercopagis pengoi*, but not related to temperature. In contrast, Claramunt et al. (2010) did not find a relationship between Lake Whitefish larval survival and prey availability. Instead, they concluded that larval Lake Whitefish density was not directly regulated by zooplankton density at the time of emergence or temperature and that a density-dependent regulation potentially exists with high larval emergence rates.

It is probable that prey species such as zooplankton will also be influenced by slight increases in temperature changes and experience higher growth and increased productivity. These conditions can exist within thermal discharges at industrial sites. The effects of temperature on invertebrate growth at lower temperatures are well documented (Dodson 2005). In addition to zooplankton, both Lake Whitefish and especially Round Whitefish also feed on chironomid larvae or pupae, which are benthic and not very mobile and, therefore, would probably be influenced by temperature. Nevertheless, future work should focus on food availability and larval presence and also on the effects of temperature increase on the development of food sources, which include both zooplankton and benthic invertebrate larvae.

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