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Differences in Incubation Period and Survival of Embryos among Brook Trout Strains

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Abstract.—The incubation period and survival of brook trout *Salvelinus fontinalis* embryos were compared among four genetically different strains: Temiscamie (Quebec), Assinica (Quebec), Horn Lake (Adirondack), and Little Tupper Lake (Adirondack). Eggs were fertilized and then incubated under cold (mean, 5.1°C) and warm (mean, 9.4°C) thermal regimes, and the accumulated degree-days and days to 100% hatch were recorded. Within all strains, embryos incubated under the warm thermal regime accumulated more degree-days to 100% hatch than embryos incubated under the cold regime. Degree-days to hatch differed between the two thermal regimes, ranging from 457 to 672 ($P < 0.001$). Mean degree-days to hatch also differed among strains ($P < 0.001$). Under the cold regime, Assinica strain embryos developed the fastest and hatched after the fewest degree-days (457), whereas Temiscamie strain embryos developed the slowest (549 degree-days). The two Adirondack strains developed at similar rates (Horn Lake, 486 degree-days; Little Tupper Lake, 490 degree-days). Under the warm regime, Assinica and Temiscamie strains developed the slowest (672 and 654 degree-days, respectively), whereas the Adirondack strains developed the fastest and at similar rates (Little Tupper Lake, 588 degree-days; Horn Lake, 593 degree-days). The Assinica strain embryos incubated in cold and warm thermal regimes showed identical times to 100% hatch (91 d). The other three strains hatched from 8.5 to 12.5 d sooner in the warm regime than in the cold regime. Survival among the four strains was lower at 9.4°C (40–57%) than at 5.1°C (60–73%; $P < 0.001$). The differences in incubation period were likely caused by genetic differences among strains because the groups of embryos were incubated in physically identical environments with a common water source. The similarity in embryonic development between the two Adirondack strains may reflect an important local geographical adaptation different from that of the Quebec strains, which originated from more northerly populations.

For many freshwater fish species, adaptations that increase survival during early life history will result in improved year-class recruitment and fitness because the highest mortality usually occurs within the first year of life. The timing of egg hatch and fry emergence can enhance the probability of survival when synchronized with seasonal periods of high secondary production of food that maximize growth and survival of juvenile fish or optimal conditions for migration (Bams 1969; Northcote 1978). Phenotypic expression of hatch and emergence timing is controlled by genetic and environmental variables and their interactions (Falconer and Mackay 1996).

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The developmental rates to hatch and emergence have been shown to vary among genetically different salmonid populations. For example, populations of lake trout *Salvelinus namaycush* originating from the Great Lakes and one northern Wisconsin lake had different hatch and emergence times even though they were reared in the same environment, and these differences were presumed to be genetic in origin (Horns 1985). Similarly, embryo developmental rates varied among populations of several species of Pacific salmon *Oncorhynchus* spp. (e.g., Murray et al. 1990). However, differences in incubation times among populations have not always been observed when investigated. For example, embryo development rates were similar between autumn and spring spawning Arctic char *S. alpinus* from Lake Windermere (Swift 1965; Baroudy and Elliott 1994). When differences in embryonic development do exist, they probably reflect differences in selection pressures among populations and therefore represent an important adaptation for survival.

Water temperature is a key environmental var-

iable that influences when and where adult salmonids spawn and the rate at which their embryos will develop. Salmonid embryos typically hatch earlier with increasing water temperature (e.g., Embody 1934; Murray and McPhail 1988). Behavioral traits, such as the choice of spawning location (e.g., inlets or outlets of lakes; Burger et al. 1985) and redd site selection (e.g., areas of constant temperature groundwater upwelling; Curry et al. 1995; Baxter and McPhail 1999), and physiological traits, such as the timing of maturity and spawning (e.g., early versus late runs; Burger et al. 1985; Beer and Anderson 2001), may greatly influence the thermal characteristics of embryo incubation environments. The expression of behavioral and physiological traits, as controlled by the physical environment through temperature, ultimately determines the period required for embryos to hatch and fry to emerge.

Some brook trout *Salvelinus fontinalis* populations possess a life history strategy that uses both lake and stream habitats at different life stages. Lake habitats are used as primary areas for feeding and growth until just prior to maturity. Spawning, however, may occur on shoals within lakes or in lake outlets or inlets. For example, Temiscamie strain brook trout, which are native to Lake Albanel, Quebec, live in the lake for most of the year but spawn far upstream in the Temiscamie River, the lake's inlet. In contrast, the Assinica strain brook trout, which are native to Assinica Lake, Quebec, spawn in the lake's outlet (Flick 1977; Van Offelen et al. 1993). Other lacustrine brook trout, such as populations from Horn Lake and Little Tupper Lake in the Adirondack region of northern New York (Keller 1979), spawn on shoals within lakes.

Temperature regimes associated with each of these habitats (inlets, outlets, and shoals) will likely differ during the egg incubation period in winter. Inlets of lakes may be colder than outlets during the winter (Burger et al. 1985). Brook trout that spawn on lake shoals often spawn in areas of groundwater upwelling that is warmer and more stable than surface water, inlets, or outlets (Freeze and Cherry 1979). The choice of these locations, combined with the seasonal timing of spawning (early versus late fall), narrows the thermal regime experienced by embryos during incubation and helps to regulate the timing of fry emergence in the spring (e.g., Burger et al. 1985).

When embryos from different populations are reared in identical thermal environments, such as those experienced in a hatchery, genetic differences may cause some populations to express faster or slower developmental rates than others. From an ecological perspective, genetic differences in developmental rates may contribute to a suite of adaptations that synchronize fry emergence with food availability or other environmental variables linked to improved survival. However, these differences create problems in propagation, especially when the fish being reared are to be used in performance (e.g., survival) trials of strains after stocking. For example, a field comparison usually requires that strains have identical size distributions so that paired lots can be stocked concurrently. If gamete collections occur on approximately the same date, but time to hatch differs among strains, propagation of matched lots of fish for stocking becomes difficult and requires growth regulation by altering temperature and feeding. We noted this problem in our earlier performance comparisons of Assinica and Temiscamie strain brook trout that were evaluated after stocking into Adirondack ponds and streams (Cone and Krueger 1988; Van Offelen et al. 1993).

The purpose of this study was to compare the developmental and survival rates of Temiscamie, Assinica, Horn Lake, and Little Tupper Lake brook trout embryos at two thermal regimes. Each of the four strains are propagated and stocked into streams and lakes in New York and elsewhere, such as Michigan (Gowing 1986; Alexander et al. 1990).

Methods

Strain descriptions.—Assinica strain eggs originated from Lake Assinica near the headwaters of the Broadback River (50°30′N, 75°15′W) in the James Bay drainage of Quebec (Flick 1977; Van Offelen et al. 1993). In New York, the hatchery strain was founded with four females and three males captured near the outlet of Lake Assinica in September 1962 (Flick 1977). Fertilized eggs from these founders were transported to the Brandon Park Hatchery, located in the northern Adirondack Mountains near Paul Smiths, New York, where they were propagated and succeeding generations were maintained.

Temiscamie strain broodstock originated from the Temiscamie River (51°10′N, 75°10′W), a tributary to Lake Albanel in the Rupert River system, James Bay drainage, Quebec (Flick 1977; Van Offelen et al. 1993). Temiscamie adults were captured in 1965 and 1967 (20–30 adults each year) from a site located approximately 128 km upstream of Lake Albanel. The fertilized eggs were

TABLE 1.—Dates of gamete collection and fertilization locations of broodstock collection and number of parents used to produce embyros for comparison of incubation period and survival among four brook trout strains.

Strain	Gamete collection and fertilization date	Broodstock location	Number of males	Number of females
Temiscamie	29 Oct 1998	Black Pond, Cat Pond	5	4
Assinica	27 Oct 1998	Black Pond	10	19
Horn Lake	5 Nov 1998	Panther Lake	31	10
Little Tupper Lake	4 Nov 1998	Hyde Pond	12	31

transported to New York, where broodstocks were developed and maintained.

Assinica and Temiscamie broodstocks (>100 Assinica adults; >400 Temiscamie adults) have been propagated continuously from adult fish reared in small, reclaimed Adirondack ponds (Van Offelen et al. 1993). Allelic frequencies at allozyme loci differ greatly between the two strains (Perkins et al. 1993). In this paper, we refer to the Assinica and Temiscamie strains as the Quebec strains.

The Horn Lake strain originated from Horn Lake, a 15-ha lake in the southern portion of the Adirondack Mountains, Herkimer County, New York (Keller 1979; Perkins 1991). Horn Lake strain fish are shoal spawners (Keller 1979). The strain is propagated by the Warren County Hatchery and stocked into other New York waters. Based on allozyme analysis (Perkins 1991), the Horn Lake strain differs genetically from the Temiscamie, Assinica, and Little Tupper Lake strains.

The Little Tupper Lake strain originated from a 971-ha lake in Hamilton County, New York (Keller 1979). The strain is also propagated by the Warren County Hatchery and is stocked mostly into Adirondack waters of New York. Its genetic purity is unknown, as some domestic fish were stocked in Little Tupper Lake and its watershed within the past 20–30 years (Keller 1979). Like the Horn Lake strain, the Little Tupper Lake strain spawns on shoals in lakes. Based on allozyme analysis, the Little Tupper Lake strain differs genetically from the other three brook trout strains we studied (Perkins 1991). In this paper, the Horn Lake and Little Tupper Lake strains are referred to as the Adirondack strains.

Egg fertilization and incubation.—Gametes of the four strains were collected from adult brook trout captured in Adirondack lakes between 29 October and 4 November 1998 (Table 1). The Temiscamie and Assinica strains were captured from Black and Cat ponds, located near Paul Smiths, New York, the Little Tupper Lake strain was collected from Hyde Pond near Paul Smiths, and the Horn Lake strain was captured from Panther Lake, located near Old Forge, New York.

Eggs taken from each female were pooled and fertilized with sperm pooled from all males. Single lots of approximately 5,000 eggs of each strain were chosen randomly. Eggs were water-hardened, placed into bottles, and transported to the Little Moose Field Station, Old Forge, New York. At the field station, embryos from each strain were placed in four Plexiglas incubators that held 50 eggs each (Gunn and Keller 1984; modified from Kennedy 1980). The incubators held each egg in a separate compartment, thereby allowing the fate of each embryo to be determined and eliminating the need for removal of dead eggs. Embryos were not disinfected during incubation.

Eggs of each strain were held in incubators under cold (2.6–10.3°C; mean = 5.1°C) and warm (6.5–11.0°C; mean = 9.4°C) thermal regimes (Figure 1). Each thermal regime had two replicate incubators. Little Moose Lake supplied the water for incubation. Thus, the variation in the cold thermal regime followed the natural temperature variation of an Adirondack lake. Passive heat exchange from the heated air in the incubation room to water in tanks provided the warm thermal regime. Optic StowAway temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts) were used to record water temperature (accuracy, ±0.1°C) once every hour until all surviving eggs hatched. Oxygen concentrations were at saturation, and flow rates in the tanks holding the incubators were approximately equal in both thermal regimes.

The number of eggs that hatched each day was recorded until the hatch of all surviving eggs in an incubator was complete. The developmental rate for each strain at each thermal regime was calculated for each incubator as the accumulated temperature units (degree-days) for all eggs that survived to hatch. The number of days to 100% hatch was also recorded for each incubator.

Data analysis.—A fixed-effect analysis of var-

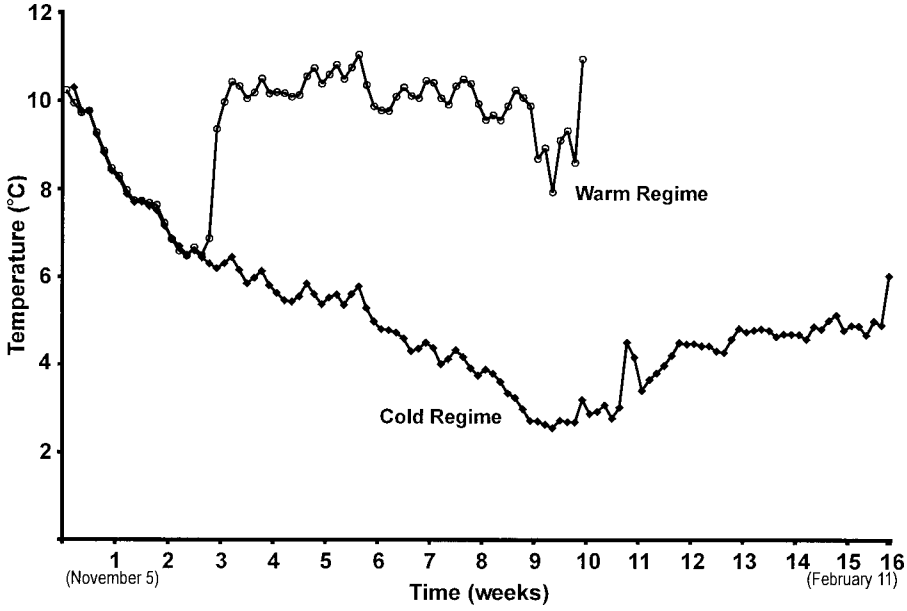

FIGURE 1.—Mean daily temperatures (beginning 29 October 1998) based on hourly measurements of the cold and warm thermal regimes used to incubate embryos of four brook trout strains. Water for incubation was obtained from Little Moose Lake in the Adirondack region of New York.

iance (ANOVA) model was used to analyze the rate of development for all four strains (Zar 1984). The model partitioned development, as measured in degree-days, into variation attributed to the main effects (strain and water temperature) or their interactions:

$$^{\circ}\mathrm{D} = \mu + S + W + (S \times W) + e,$$

where °D is the observed number of degree-days to 100% hatch for each strain, μ represents the overall mean number of degree-days to 100% hatch for all strains, S is a categorical variable that represents the strains (Temiscamie, Assinica, Horn Lake, and Little Tupper Lake), W represents the mean water temperature (°C) during development, $S \times W$ represents the interaction effect of water temperature on development in degree-days for each strain, and e is the residual error. When the overall model was significant ($P \leq 0.05$), Tukey's multiple comparison test was used to determine which strains differed (Zar 1984). Heterogeneity of survival rates among the four strains and between the two temperature regimes was tested with a log-likelihood ratio test (G-test; Zar 1984).

TABLE 2.—Results of the analysis of variance describing the effect of brook trout strain and mean incubation temperature on the number of degree-days to 100% hatch for Temiscamie, Assinica, Horn Lake, and Little Tupper Lake embryos (degree-days = μ + strain + mean temperature + strain × mean temperature).

Variable	df	F-value	P-value
Strain	3	95.7	<0.001
Temperature	1	1,841	<0.001
Strain × temperature	3	99.5	<0.001

Results

For all strains, embryos incubated under the warm thermal regime accumulated more degree-days to 100% hatch than embryos subjected to the cold regime. Degree-days to hatch differed between the two thermal regimes, ranging from 457 to 672 ($P < 0.001$; Tables 2, 3).

The developmental rates of embryos from fertilization until hatch, as measured by degree-days, differed among the four strains ($P < 0.001$; Table 2; Figure 2). Under the cold thermal regime, the mean degree-days to 100% hatch was fastest for the Assinica strain (456 degree-days), slowest for the Temiscamie strain (549 degree-days), and intermediate for the two Adirondack strains, Little Tupper Lake (490 degree-days) and Horn Lake (486 degree-days; Table 3). Under the warm thermal regime, the Quebec strains developed more slowly than did the Adirondack strains (Figure 2). A highly significant interaction between strain and mean temperature ($F = 99.5$, $P < 0.001$; Table 2)

TABLE 3.—Mean degree-days, mean days to hatch, and number of eggs surviving to hatch for four brook trout strains incubated at two thermal regimes. Two 50-egg incubators were used for each strain (total of 100 eggs) within each thermal regime.

Mean temperature (°C; ±SE)	Strain	Mean degree-days to 100% hatch (SE)	Mean days to 50% hatch (SE)	Mean days to 100% hatch (SE)	Number of eggs surviving to hatch
5.1 (0.16)	Temiscamie	549 (7.3)	101.5 (0.5)	107.5 (1.5)	70
	Assinica	456 (0.0)	85.0 (0.0)	91.0 (0.0)	73
	Horn Lake	490 (0.0)	93.5 (1.5)	99.0 (0.0)	60
	Little Tupper Lake	481 (9.6)	96.0 (0.0)	99.0 (2.0)	70
9.4 (0.15)	Temiscamie	653 (0.0)	90.0 (0.0)	95.0 (0.0)	40
	Assinica	672 (0.0)	89.0 (0.0)	91.5 (1.5)	57
	Horn Lake	593 (6.5)	83.5 (0.5)	88.5 (0.5)	40
	Little Tupper Lake	589 (2.0)	85.5 (1.5)	90.5 (0.5)	55

reflected the lack of a consistent developmental pattern between the two thermal regimes for the Assinica strain. The Assinica strain developed faster under the cold regime than under the warm regime. The developmental rates of the two Adirondack strains did not differ within either thermal regime (Figure 2). Tukey's multiple comparison tests showed that the development of the Assinica strain differed from that of the other three strains under both temperature regimes ($P < 0.05$).

The number of days from fertilization to 100% hatch varied among strains and between thermal regimes, except for the Assinica strain (Table 3). The Assinica strain showed identical days to 100% hatch in the cold and warm thermal regimes (91 d). The other three strains hatched from 8.5 to 12.5 d sooner in the warm regime than in the cold regime (Table 3). The Temiscamie strain displayed the most marked difference in days to hatch between the two thermal regimes (12.5 d). The same pattern among strains was also evident for the number of days to 50% hatch.

Survival was lower for embryos incubated under the warm regime (40–57%) than for those incu-

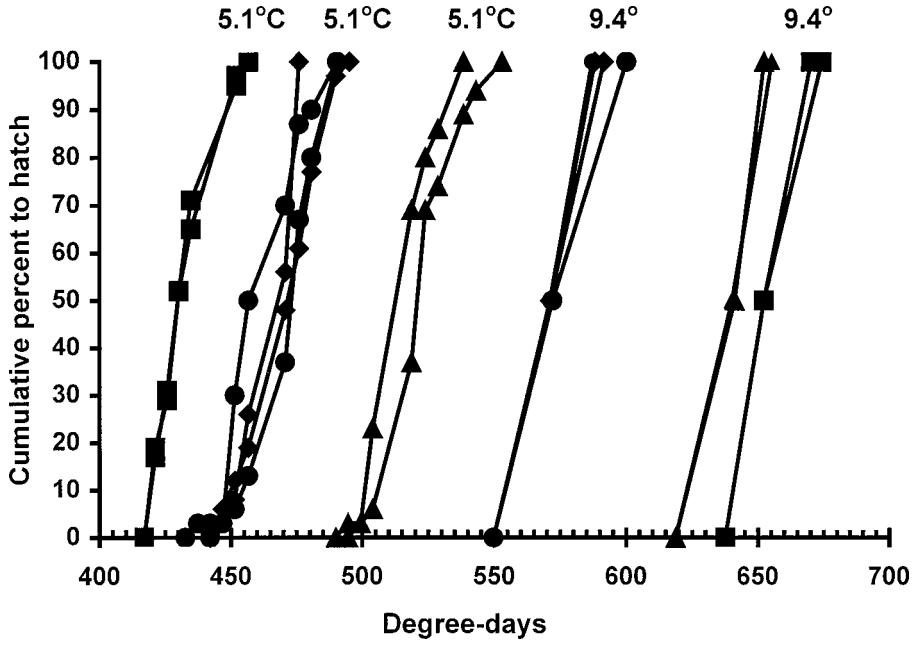

FIGURE 2.—Cumulative percentage hatch and accumulated degree-days of embryos of four brook trout strains incubated under cold (mean temperature = 5.1°C) and warm (mean = 9.4°C) thermal regimes. Each line represents one incubator containing 50 eggs. The Assinica strain is symbolized by squares, the Temiscamie strain by triangles, the Horn Lake strain by circles, and the Little Tupper Lake strain by diamonds.

TABLE 4.—Likelihood ratio (*G*-test) comparison of egg survival rates of four brook trout strains incubated at two temperatures.

Comparison	df	*G*	*P*-value
Among strains	3	35.51	<0.0001
Between temperatures	1	32.15	<0.0001
Among strains, within temperatures			
5.1°C	3	4.38	0.22
9.4°C	3	10.38	0.02
Between temperatures, within strains			
Assinica	1	5.66	0.017
Temiscamie	1	18.48	<0.001
Little Tupper Lake	1	8.05	0.005
Horn Lake	1	4.82	0.028

bated under the cold regime (60–73%; $P > 0.001$; Table 4). Survival to hatch differed among strains for the warm regime ($P = 0.02$) but not for the cold regime ($P = 0.22$; Table 4). At warm temperatures, the Assinica and Little Tupper embryos had the highest survival rates (57% and 55%, respectively) and the Temiscamie and Horn Lake strains had the lowest rates (40%).

Discussion

Embryos of the two Quebec strains of brook trout differed in developmental rate from each other and from the two Adirondack strains when incubated under the cold thermal regime. The cause of the differences was most likely genetic in origin. Eggs of the four strains were held in physically identical incubators with a common water source, which minimized environmental sources of variation. Differences among populations in the developmental rate of embryos have also been reported for other *Salvelinus* species (lake trout; Horns 1985). Differences among populations of other salmonid species have also been reported, namely, chum salmon *Oncorhynchus keta* (Beacham and Murray 1986; Smoker 1986), coho salmon *O. kisutch* (Murray et al. 1990; Konecki et al. 1995), pink salmon *O. gorbuscha* (Beacham and Murray 1986), chinook salmon *O. tshawytscha*, and sockeye salmon *O. nerka* (Beacham and Murray 1989).

The differences we found in incubation period among brook trout strains represent genetic differences observed among the source stocks currently used for propagation purposes in New York. Developmental differences among these strains may not accurately reflect the incubation period expressed by the original wild populations because selection and genetic drift may have altered the broodstocks used in this study. For example, the incubation period that we reported for the Assinica strain may not correctly characterize the source population due to the small number of founders used to propagate this strain.

The developmental differences among brook trout strains were large relative to the differences reported for populations of most other salmonid species. For example, at a mean temperature of 5.1°C, the Temiscamie strain required 93.0 degree-days more than the Assinica strain to attain 100% hatch and 16.5 d more to reach 50% hatch (Table 3). In contrast, the mean time to 50% hatch at 4°C among seven chum salmon stocks from the Fraser River varied 3.5 d at most (Beacham and Murray 1986). Similarly, incubation rates among lake trout populations from the Great Lakes basin differed by less than 50 degree-days (Horns 1985). Large incubation differences comparable to those reported here for brook trout strains have been observed among British Columbia coho salmon populations, for which time to 50% hatch varied by as much as 18 d at 3.8°C (Murray et al. 1990).

The increase in degree-days required to hatch under the warm regime indicates that the development rate slowed in response to increased incubation temperature. Embody (1934) reported that the development of brook trout embryos reached a threshold at 10°C, such that further increases in temperature failed to accelerate hatch nearly as much as they did at lower temperatures. Marten (1992) reported that days to hatch for a domestic strain of brook trout varied as a function of the mean temperature at fertilization and the mean temperature from fertilization to 50% hatch over 15 temperature combinations. Conversion of Marten's (1992) tables to degree-days and weighted mean temperatures revealed that degree-days to 50% hatch linearly increased as mean temperatures increased. Physiological processes, such as metabolic rates, increase as temperature increases (e.g., Diana 1995), and embryo development rates might be expected to increase with temperature, with a resulting decline in the accumulation of degree-days to 100% hatch. Though such a relationship has been reported for Atlantic salmon *Salmo salar* (Gunnes 1979), our study indicates the opposite situation for brook trout. Brook trout embryo development neither increased nor remained constant, as measured by degree-days, but instead appeared to slow in the warm regime, requiring an increase in degree-days. Mean days to hatch declined only modestly with the increase in temperature between the cold and warm regimes, but mean degree-days to hatch increased significantly.

A similar response to temperature has been noted for embryo development among coho salmon populations from Washington (Tang et al. 1987; Konecki et al. 1995).

The developmental response to temperature reported here for brook trout could be adaptive by modulating developmental rates such that fry emerge at approximately the same time each year, irrespective of incubation temperatures. For example, in some years, fall-spawned embryos may be exposed to unusually warm temperatures, especially in the first part of the incubation period in October or November. The developmental rates of embryos may need to decrease in high water temperatures to permit an increase in the accumulation of degree-days so that hatching and emergence will be delayed until environmental conditions are favorable for survival in the spring. Without a compensating adjustment, fry could develop too rapidly and hatch prematurely in late winter or early spring. Interestingly, the mean number of days to 100% hatch for the Assinica strain was approximately the same (91 d) under both thermal regimes (Table 3), indicating that developmental rates were completely compensated.

Compensation in developmental rates has been reported for chum and pink salmon populations investigated under natural thermal variations. Fry emigration reflects the integration of the time required for all earlier developmental stages, from egg fertilization through the initiation of downriver migration. Henderson et al. (1995) found that the number of days to 50% emigration for pink salmon fry in the Fraser River varied little, though the cumulative degree-days from the peak of spawning to the point of 50% fry emigration varied between 460 and 770. Smoker (1986) reported that putatively cold-adapted Puget Sound chum salmon developed as quickly from fertilization to migration as did stocks spawning in warmer rivers.

Survival differences comparable to those reported here for brook trout strains at cold and warm temperatures have been observed among populations of other salmonid species. Low (e.g., 2°C, rainbow trout *O. mykiss*; Stonecypher et al. 1994) and high (14°C, coho salmon; Murray et al. 1990) incubation temperatures have been shown to reduce the survival of embryos and alevins. Among coho salmon populations, Vancouver and Queen Charlotte Island stocks had lower embryo survival rates at 1.5°C and 2°C than did mainland British Columbia stocks (Murray et al. 1990). Survival of embryos differed between two Washington coho salmon stocks incubated over a range of temperatures from approximately 0°C to 17°C (Tang et al. 1987). Survival differences have also been observed among chum salmon populations for embryos incubated at 4, 8, and 12°C (Beacham and Murray 1986) and among sockeye and chinook salmon populations for embryos incubated over a range of temperatures from 2°C to 15°C (Beacham and Murray 1989).

The similar developmental rates of the Adirondack strains within both thermal regimes may reflect a regional adaptation different from the more northerly populations originating from Quebec. Such an adaptation could be important for fry survival and for the timing of emergence in the thermal regimes likely to be experienced by eggs incubating in Adirondack waters. Thus, the differences among strains may be important to consider for management of brook trout introduced into Adirondack waters. The success or failure of introduced populations depends, in part, on how well the adaptations of the strain match the environmental characteristics of the receiving waters (Krueger et al. 1981). Ideally, a strain considered for introduction should originate from a location with a thermal regime comparable to that of the proposed site of introduction. This approach should increase the probability that fry will emerge when conditions are favorable for survival.

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