Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington

Andrew P. Hendry, Jay E. Hensleigh, and Reg R. Reisenbichler

Abstract: Sockeye salmon (*Oncorhynchus nerka*) introduced into Lake Washington in the 1930s and 1940s now spawn at several different sites and over a period of more than 3 months. To test for evolutionary divergence within this derived lineage, embryos that would have incubated in different habitats (Cedar River or Pleasure Point Beach) or at different times (October, November, or December in the Cedar River) were reared in the laboratory at 5, 9, and 12.5°C. Some developmental variation mirrored predictions of adaptive divergence: *(i)* survival at 12.5°C was highest for embryos most likely to experience such temperatures in the wild (Early Cedar), (*ii*) development rate was fastest for progeny of late spawners (Late Cedar), and (*iii*) yolk conversion efficiency was matched to natural incubation temperatures. These patterns likely had a genetic basis because they were observed in a common environment and could not be attributed to differences in egg size. The absolute magnitude of divergence in development rates was moderate (Late Cedar embryos emerged only 6 days earlier at 9°C) and some predictions regarding development rates were not supported. Nonetheless our results provide evidence of adaptive divergence in only 9–14 generations.

Résumé : Le saumon rouge (*Oncorhynchus nerka*) introduit dans le lac Washington dans les années 30 et 40 fraye maintenant à plusieurs endroits différents et sur une période de plus de 3 mois. Pour établir s'il y a eu divergence évolutionnaire chez cette lignée dérivée, des embryons qui auraient été incubés dans des habitats différents (rivière Cedar ou plage Pleasure Point) et à des périodes différentes (octobre, novembre ou décembre dans la rivière Cedar) ont été élevés en laboratoire à 5, 9 et 12,5°C. Certaines variations dans le développement correspondaient aux prédictions de divergence adaptative, notamment : *(i)* la survie à 12,5°C était plus élevée chez les embryons les plus susceptibles d'être exposés à une telle température dans le milieu d'origine (ponte hâtive, rivière Cedar), (*ii*) le taux de développement était plus élevé chez la progéniture des géniteurs tardifs (ponte tardive, rivière Cedar) et (*iii*) l'efficacité de conversion du vitellus concordait avec les températures d'incubation dans le milieu. Ces tendances sont probablement d'origine génétique parce qu'elles ont été observées dans un environnement commun et ne pouvaient être attribuées à des différences dans la taille des oeufs. L'ampleur absolue de la divergence au plan des taux de développement était modérée (les embryons tardifs de la rivière Cedar ne sont sortis de l'oeuf que 6 jours plus tôt à 9°C) et certaines prédictions concernant le taux de développement n'ont pas été confirmées. Néanmoins nos résultats fournissent l'évidence de la divergence adaptive dans seulement les neuf à quatorze générations.
[Traduit par la Rédaction]

Introduction

Studies of introduced populations have yielded important insights into evolution, particularly in regard to rates and mechanisms of population divergence (Stearns 1983; Reznick et al. 1990; Svensson 1997; Hendry and Kinnison 1998). Pacific salmon (*Oncorhynchus* spp.) provide opportunities to study incipient population divergence because they have been successfully introduced into new locations, such as New Zealand, the Great Lakes, and Lake Washington. Studies within these systems have shown that salmon introductions can give rise to a suite of new breeding groups, some of which become reproductively isolated from the others (Gharrett and Thomason 1987; Hendry et al. 1996; Quinn et al. 1996). These new populations are often exposed to different habitats and have diverged phenotypically in adult life history and morphology following colonization (Hendry and Quinn 1997; Kinnison et al. 1998). What remains ambiguous, however, is the extent to which such divergence is genetically based, as opposed to environmental effects expressed through phenotypic plasticity.

The present study tests for genetic divergence in the developmental biology of Lake Washington sockeye salmon (*Oncorhynchus nerka*). From 1937 to 1945, hatchery-produced sockeye salmon were transferred from Baker Lake (Fig. 1) to Lake Washington (reviewed in Hendry 1995). The largest population established by these introductions was in the principal tributary to the lake, the Cedar River. Then, in 1957, sockeye salmon were first observed spawning at certain beaches along the shores of Lake Washington (Woodey 1966). The largest of these beach-spawning aggregations was at

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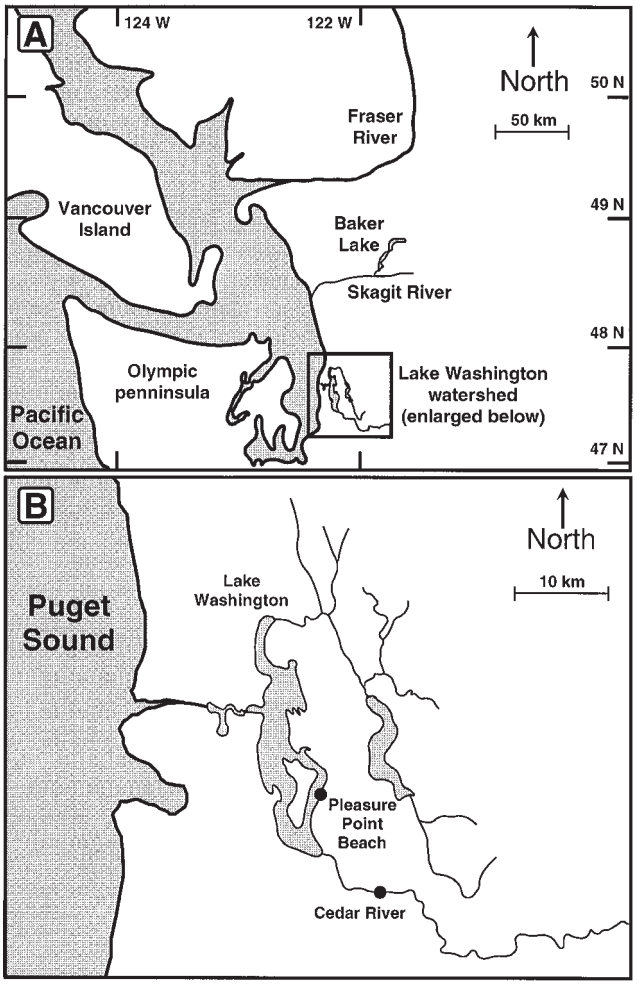
Fig. 1. Locations of (A) Lake Washington and Baker Lake and (B) the Cedar River and Pleasure Point Beach. Solid circles indicate collection locations.



Pleasure Point, a site about 7 km north of the Cedar River. Allelic variation at allozyme and microsatellite loci has revealed that the Pleasure Point population is also of the Baker Lake lineage and was most likely colonized by straying from the Cedar River (Hendry et al. 1996; J.K. Wenburg and A.P. Hendry, unpublished data). Since the founding event, however, Pleasure Point spawners have become at least partially reproductively isolated from Cedar River spawners (J.K. Wenburg and A.P. Hendry, unpublished data), enhancing the potential for their adaptive divergence.

River and beach spawning areas differ markedly in environmental features that influence salmonid evolution (Blair et al. 1993; Wood 1995; Taylor et al. 1997). Adult salmon spawning in the Cedar River experience strong currents and their embryos are exposed to frequent scouring events (Thorne and Ames 1987). In contrast, adults at Pleasure Point spawn in the near absence of current and their embryos incubate in stable substrates (Woodey 1966). These dramatic habitat differences suggest that selection should contribute to adaptive divergence of the two populations. In a pattern consistent with beach–river divergence in other lake systems, Cedar River females were longer than Pleasure Point females, and Pleasure Point males were deeper bodied (for their length) than Cedar River males (Hendry and Quinn 1997). These findings implied adaptive divergence owing to some combination of plasticity and genetic change since the beach site was colonized.

Examining variation in developmental characteristics under controlled conditions allows a test for divergence that is not confounded by phenotypic plasticity. Such a comparison within Lake Washington should prove informative because beach and stream incubation environments often differ in incubation temperature, which can lead to adaptive differentiation (Brannon 1987). For Lake Washington, we predicted that, in comparisons at a common temperature, embryos from populations that naturally incubate in warm water should take longer to develop than those from populations that naturally incubate in colder water. Such divergence would reduce hatching and emergence asynchrony caused by the otherwise positive correlation between incubation temperature and development rate (Brannon 1987). We also predicted that yolk conversion should be most efficient at laboratory temperatures approximating those that embryos would have experienced in the wild (Beacham and Murray 1987, 1989).

Selective regimes can also differ among fish that spawn or incubate at different times, even if they do so at the same location (e.g., Taylor 1980). Accordingly, some rivers accommodate seasonally distinct conspecific populations (Gharrett and Smoker 1993; Tallman and Healey 1994) that have adapted to their specific incubation conditions (Tallman 1986; Tallman and Healey 1991). Although the Cedar River does not contain discrete seasonal runs, the spawning period stretches from early October through early January. Because the tendency to spawn at a particular time is inherited (Gharrett and Smoker 1993), the extent of gene flow within populations such as the Cedar River should be negatively correlated with the spread in spawning time (isolation-by-time).

Thus, the embryos of fish that spawn at different times should be able to adapt, at least in part, to their specific thermal regimes (adaptation-by-time). For the Cedar River, we predicted that embryos likely to experience high temperatures in the wild should be those demonstrating the best survival at such temperatures in the laboratory. We also predicted that embryos beginning incubation late should take less time to develop than those beginning incubation early, when compared at a common temperature (Brannon 1987; Tallman and Healey 1991). We tested our predictions by incubating the embryos of spawning sockeye salmon that were collected at different times or places within Lake Washington at each of three different temperatures.

Methods

Study sites, temperature regimes, and gamete collection

The Cedar River is the largest tributary to the Lake Washington watershed and anadromous salmonids spawn in its lower 34.8 km. Most spawning takes place from late September through late December, with the peak in late October, and the annual number of spawners from 1967 to 1991 ranged between 76 000 and 350 000 (R. Egan, Washington Department of Fish and Wildlife, Mail Stop 43151, 600 Capitol Way N., Olympia, Wash., unpublished data). Cedar River water temperatures were obtained for October 1 – May 16 for each of the last 16 years (1980–1995) from the U.S. Geological Survey (1201 Pacific Avenue, Suite 520, Tacoma, Wash.). These data had been recorded at a gauging station 2.7 km upstream from the river mouth. At Cavanaugh Pond (a side channel–pond beside the Cedar

Table 1. Incubation temperatures in the laboratory and in the wild, and the predicted and observed days spent in each developmental stage at each laboratory temperature.

	Fertilization to hatching				Hatching to emergence			
	Early Cedar	Middle Cedar	Late Cedar	Pleasure Point	Early Cedar	Middle Cedar	Late Cedar	Pleasure Point
Laboratory, 5°C								
Mean temperature	5.0	5.0	5.0	4.9	5.0	5.2	6.0	5.2
Predicted days	123	123	123	123	66	64	—	64
Observed days	123	124	120	124	60	55	—	53
Laboratory, 9°C								
Mean temperature	9.0	8.9	8.8	8.9	8.7	8.6	9.1	8.5
Predicted days	77	78	78	78	45	45	44	45
Observed days	76	77	74	76	40	39	36	38
Laboratory, 12.5°C								
Mean temperature	12.2	12.2	12.4	12.2	12.3	12.6	12.3	12.6
Predicted days	57	57	56	57	31	30	—	30
Observed days	54	54	51	53	24	25	—	26
Wild								
Mean temperature	6.8	6.0	6.4	9.9	6.5	8.6	9.9	9.9
Min. temperature	1.5	1.0	1.0	9.8	1.0	5.5	6.5	9.8
Max. temperature	12.0	9.5	11.5	9.9	10.0	13.0	15.5	9.9

Note: Predicted number of days in each period at each temperature were calculated using the Salmonid Incubation Program (Jensen 1988). Predicted days from hatching to emergence were invariably longer than those observed because Jensen's (1988) model uses maximum alevin wet weight, which typically occurs slightly after emergence. Degree-days can be calculated simply by multiplying the days in a given time period by the average temperature over that period.

River at river km 10.3), a HOBO temperature logger (Onset Computer Corp., Pocasset, Mass.) was buried 30 cm in the gravel in the center of the main spawning area (January 8 – March 27, 1996).

The Pleasure Point Beach lies about 7 km north of the Cedar River (Fig. 1) and has about 700 m^2 of spawning area (A.P. Hendry, unpublished data). Annual escapements at Pleasure Point have been estimated at 100–1000 (1963–1965, Woodey 1966) and 520–8180 (1976–1991, R. Egan, unpublished data). Estimates for the more recent of these two periods include several other beach sites near Pleasure Point, but spawners at these other sites are much less abundant. Spawning at Pleasure Point typically takes place between early November and early January, with the peak in late November (R. Egan, unpublished data), and the embryos incubate in upwelling groundwater (Woodey 1966). To record incubation temperatures at Pleasure Point, two HOBOs were buried 30 cm below the surface of the gravel, 5 m away from each other and near the center of the spawning area (November 1, 1995 – March 28, 1996).

Cedar River sockeye salmon were collected from a weir at river km 10.4 (as part of a hatchery program that began in 1991, Seiler and Kishimoto 1996). We obtained gametes from adults collected at this weir in 1995 and spawned on either October 21 (Early Cedar) or November 20 (Middle Cedar). The weir was removed in early December and the river remained very high and turbid throughout that month. Therefore, our final Cedar River collection (December 21, Late Cedar) was made using landing nets in Cavanaugh Pond, which joins the river about 100 m downstream from the weir. Cavanaugh Pond embryos incubate in Cedar River water that seeps through a berm separating the pond from the main river. At Pleasure Point, spawning fish were collected using a beach seine on November 18 (1995), gametes were squeezed gently from six males and six females, and all fish were then released. The number of females in each collection (six) was chosen to minimize potential impacts on the small Pleasure Point population.

Laboratory rearing

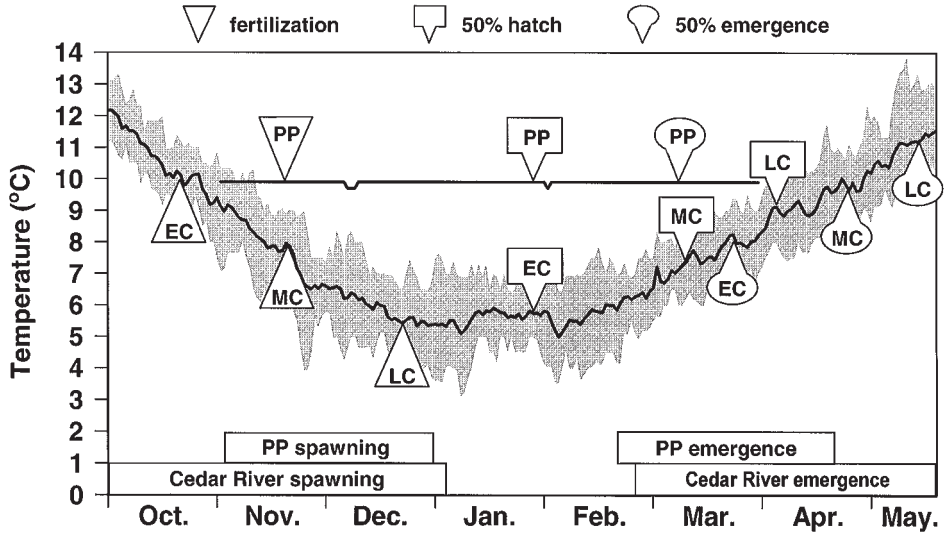
Gametes were transported in coolers to the laboratory within 2 h of their collection. For each female, a sample of about 50 eggs was blotted dry, weighed, and counted to determine average egg weight. The remaining eggs for each female were then fertilized (each by a separate male), giving rise to six full-sib families for each of the four collections. Three Heath stacks were plumbed so that one received 12.5°C water, one 9°C water, and one 5°C water (Table 1). Water flowed through the stacks at a rate of 11.4 $L \cdot min^{-1}$ and each incubation tray held six PVC egg cups (internal diameter = 8 cm). Eggs from each of the 24 experimental families were divided into six lots of 100, and these lots were randomly assigned to egg cups (two separate egg cups for each family at each of the three temperatures). The stacks were draped with black plastic to eliminate light.

At 55, 33, and 30 days postfertilization (at 5, 9, and 12.5°C, respectively), all dead eggs were counted and removed from each egg cup. Eggs were checked periodically thereafter and mortalities removed and counted. Survival from fertilization to hatching (percent) was calculated for each family at each temperature as the mean of its survival in the two egg cups. After hatching commenced, the numbers of live and dead eggs and alevins in each cup were counted daily. The mean and median dates of hatching were calculated for each cup and then averaged for the two cups from each family, at each temperature.

On the first day that at least 95% of the embryos had hatched within a family, 100 of them (randomly chosen from the two egg cups) were transferred to PVC emergence chambers maintained at the same temperature that each family had experienced prior to hatching (Table 1). Alevins incubated in a substrate of glass marbles and, at emergence, swam upward through 16 cm of water, exiting the chamber through a notch at the top and falling a short distance into a surrounding tub (see Hendry 1995 for details on the emergence chambers). Emergence chambers were shielded with a translucent cover that permitted diffuse light on a natural photoperiod to reach the upper layer of the marble substrate. The tubs surrounding each emergence chamber were checked daily for newly emerged fry, which were removed, counted, killed with an overdose of MS 222, and preserved in 10% buffered formalin. The mean and median dates of emergence were calculated for each family.

After about 100 days of preservation, every 10th fry to have emerged was measured (fork length to the nearest 0.1 mm) and weighed (wet weight to the nearest milligram), and the yolk was removed and weighed (wet weight to the nearest milligram). Family

Fig. 2. Temperature profiles for Pleasure Point (upper line) and the Cedar River (lower line and shaded area); fertilization dates for the Early Cedar (EC), Middle Cedar (MC), Late Cedar (LC), and Pleasure Point (PP) collections; hatching and emergence dates for the embryos of each collection if they had incubated in the wild (predicted using Jensen's 1988 model); and periods of natural spawning and emergence (boxes along the *x*-axis). Temperature records for the Cedar River depict the 16-year average (line), the 10th percentile (lower boundary of the shaded area), and the 90th percentile (upper boundary of the shaded area). Natural spawning times are from stream surveys (R. Egan, unpublished data), emergence times for the Cedar River are the period during which 90% of the fry emigrate to the lake (Seiler and Kishimoto 1996), and emergence times for Pleasure Point were estimated from spawning times and natural incubation temperatures.



means were calculated for fry length, fry weight (with yolk), tissue weight (without yolk), and proportion yolk (percent) at each temperature.

Statistical analysis

Median values for days to hatching and emergence were not analyzed further because they were nearly identical to the mean values. All statistical analyses were based on family means (the mean value for the offspring of each full-sib mating) at each temperature because this was the appropriate unit of replication for comparing the development of embryos from the four collections. The effects of temperature, collection, and their interaction were analyzed using split-plot ANOVA models (SPSS version 7.5) because each full-sib family had been divided among three temperatures. Egg size varied among the four collections (see Results), so it was added as a covariate to the ANOVA models. When an effect of egg weight was detected, the trait was compared among groups at a common egg weight (i.e., comparison of adjusted means, Huitema 1980). Tukey tests were used for post hoc pairwise comparisons among collections within temperatures, when such interpretations were necessary to evaluate our predictions.

Late Cedar fry were excluded from the split-plot ANOVAs associated with emergence (days to emergence, fry length, fry weight, tissue weight, and proportion yolk) because they experienced higher temperatures after hatching (in the cold treatment) and because many escaped from the chambers during an overflow (in the warm treatment). However, one-way ANOVAs and Tukey tests were used to compare fry among all four collections at 9°C, where such problems did not occur. One Middle Cedar family experienced 100% mortality at all temperatures and was excluded from the analyses. Hypothesis testing was conducted at $\alpha = 0.05$, but interactions were considered significant at $P < 0.10$ (a conservative approach to the interpretation of main effects).

Results

Natural temperature regimes

Cedar River temperatures (monitored over the past 15 years) decreased through the spawning season and increased through the hatching and emergence period (Fig. 2). No information is available on spatial variation in Cedar River temperatures, but there are no major tributaries and the vast majority of spawning takes place in the lower main stem of the river. During the incubation period, average daily temperature did not differ between the Cavanaugh Pond collection site and the Cedar River gauging station (average difference = 0.09°C, paired *t*-test, two-tailed $P = 0.40$). At Pleasure Point, temperatures were effectively isothermal (9.8–9.9°C), and nearly identical thermal regimes were recorded by the two different temperature loggers. Embryos from the different collections would have experienced dramatically different temperature regimes if they had incubated in the wild (Fig. 2).

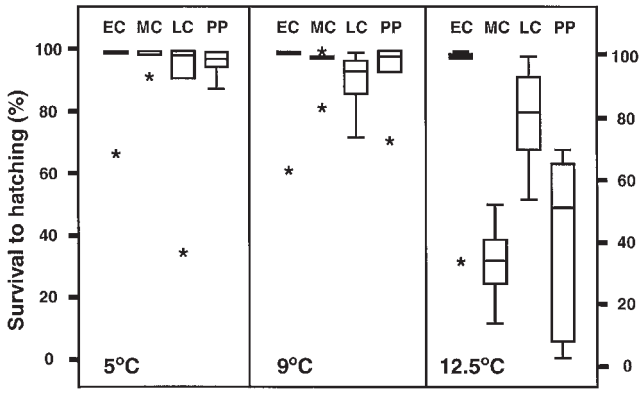
Developmental biology

Average egg weight differed slightly among the four collections (one-way ANOVA, $P = 0.03$). When added as a covariate to the ANOVA models, egg weight did not significantly influence survival to hatching ($P = 0.07$), days to hatching ($P = 0.12$), days to emergence ($P = 0.10$), or proportion yolk at emergence ($P = 0.51$). In contrast, fry length, fry weight, and tissue weight at emergence were positively correlated with egg weight ($P < 0.001$, $P = 0.01$, and $P = 0.007$, respectively).

Split-plot ANOVAs indicated that survival to hatching (arcsine transformed) was considerably higher at 5 and 9°C than at 12.5°C ($P < 0.001$; Fig. 3) but that survival did not differ consistently among the four collections ($P = 0.38$). There was, however, a significant interaction between temperature and collection ($P < 0.001$) because Early Cedar embryos had higher survival than Middle Cedar embryos ($P = 0.01$) and Pleasure Point embryos ($P = 0.02$) at 12.5°C (Fig. 3).

Days from fertilization to hatching were negatively correlated with water temperature ($P < 0.001$) but did not differ consistently among the four collections ($P = 0.10$) and there

Fig. 3. Survival from fertilization to hatching at the three incubation temperatures for embryos from the Early Cedar (EC), Middle Cedar (MC), Late Cedar (LC), and Pleasure Point (PP) collections. The data are shown as the median, quartiles, and extreme values (asterisks) for family means.



was no interaction effect ($P = 0.22$). Within each temperature, Late Cedar embryos tended to hatch slightly earlier (Fig. 4A), but the only significant difference was at 12.5°C, where they hatched 3 days earlier than Early Cedar embryos ($P = 0.043$).

Days from fertilization to emergence were negatively correlated with water temperature ($P < 0.001$; Fig. 4B) but did not differ consistently among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.12$). There was no interaction between temperature and collection ($P = 0.11$). At 9°C, Late Cedar alevins emerged 4–6 fewer days after fertilization than alevins from the other collections (one-way ANOVA, $P < 0.001$; $P < 0.008$ for each pairwise Tukey comparison). Although we excluded Late Cedar fry at 12.5 and 5°C from the emergence analysis (see Methods), qualitative observations indicated that they also emerged early at these temperatures, relative to other collections.

Fry length varied with incubation temperature ($P < 0.001$) and among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.02$), but there was a strong interaction between temperature and collection ($P = 0.007$). This interaction arose because Pleasure Point fry were their longest at 9°C whereas fry from the other collections were their longest at 5°C (Fig. 5A). At 9°C (including the Late Cedar), Early Cedar fry were longest, Late Cedar and Middle Cedar fry were shortest, and Pleasure Point fry were intermediate in length ($P = 0.003$). If egg weight was included in the models, fry length did not differ among the collections ($P = 0.13$), except at 9°C, where Pleasure Point fry were largest at a standard egg weight ($P = 0.01$).

Fry emerging at 12.5°C weighed less (including yolk) than those at either 5 or 9°C ($P < 0.001$; Fig. 5B) and this trend was consistent for the different collections (no interaction, $P = 0.51$). Considering all three temperatures, fry weight did not differ consistently among the Early Cedar, Middle Cedar, and Pleasure Point collections ($P = 0.06$). At 9°C, however, Early Cedar fry were heavier than Late Cedar and Middle Cedar fry, and Pleasure Point fry were intermediate in weight ($P = 0.003$). When egg weight was included as a covariate, the collections no longer differed in fry weight ($P = 0.70$). The same trends were evident when tissue weight was used in the models instead of overall fry weight.

Proportion yolk at emergence (arcsine transformed) did not differ between 5 and 9°C but was greater overall at 12.5°C ($P < 0.001$). Proportion yolk differed among Early Cedar, Middle Cedar, and Pleasure Point fry ($P = 0.03$), but this difference varied somewhat with temperature (interaction, $P = 0.06$; Fig. 5C). At 9°C (including the Late Cedar), no differences were detected among the collections ($P = 0.08$).

Discussion

We investigated population divergence on a short time scale by quantifying developmental variation for introduced sockeye salmon that now incubate at different times or places within the Lake Washington watershed. Observed divergence was *(i)* consistent with our predictions based on incubation temperature, (*ii*) documented in a common laboratory environment at three different temperatures (reducing the likelihood that genetic effects were confounded by phenotypic plasticity), and (*iii*) not strongly influenced by differences in egg size (the most obvious maternal effect). We conclude that certain developmental features of sockeye salmon embryos can evolve in an apparently adaptive fashion in less than 9–14 generations (since 1957, when fish were first observed at Pleasure Point, or since 1937, when the introductions into Lake Washington began).

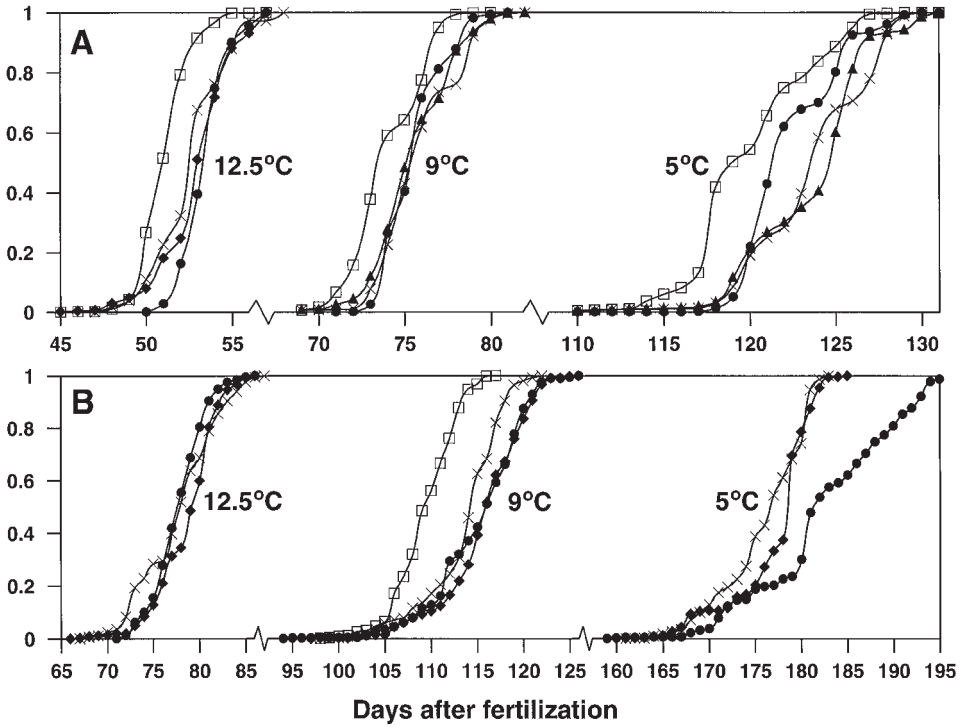
Temporal patterns of divergence

Cedar River fish that spawn in either mid-October, mid-November, or mid-December experience very different incubation conditions (Fig. 2). Genetic exchange would be limited among the fish that spawn at these different times because nuances of spawning behavior limit mixing within a breeding season (Hendry et al. 1995), and the high heritability of spawning date maintains much of the isolation across generations (Gharrett and Smoker 1993). Predictions for how developmental divergence might occur within the Cedar River population with respect to spawning date (and therefore, incubation time) were supported to varying degrees.

Survival from fertilization to hatching was high for most of the experimental families at both 5 and 9°C, but declined precipitously at 12.5°C for embryos from all collections except Early Cedar (Fig. 3). This pattern was consistent with the prediction that embryos from populations likely to experience high temperatures prior to hatching in the wild (see Early Cedar in Fig. 2 and Table 1) should be those most tolerant of such temperatures in the laboratory. Thus, evolutionary divergence in the ability to withstand high temperatures has taken place within Lake Washington.

Evidence for divergence in development rate within the Cedar River was mixed. In other studies, the embryos of early spawners often develop slowest whereas the embryos of late spawners develop fastest, presumably to increase synchrony of developmental events (Tallman 1986; Beacham and Murray 1987, 1988; Brannon 1987). For Lake Washington, Early Cedar and Middle Cedar embryos hatched and emerged after about the same number of days, but Late Cedar embryos required fewer (Fig. 4). Early emergence by Late Cedar embryos in the laboratory was due to accelerated development prior to hatching, and between hatching and emergence (Table 1). Thus, divergence in development rates within the Cedar River

Fig. 4. Cumulative (A) hatching and (B) emergence curves for all fry from each collection at each incubation temperature. Points depict the cumulative proportion of fry that had hatched or emerged on a given day for Early Cedar (solid circles), Middle Cedar (solid triangles), Late Cedar (open squares), and Pleasure Point (crosses). Data were not available for the Late Cedar emergence at 5 or 12.5°C.



was evident for Late Cedar embryos but not for Early Cedar embryos.

Spatial patterns of divergence

The Pleasure Point and Cedar River populations are at least partially reproductively isolated from each other (J.K. Wenburg and A.P. Hendry, unpublished data) and they experience very different incubation environments (Fig. 3). Embryos incubating at Pleasure Point do so in nearly isothermal water (about 10°C) whereas Cedar River embryos incubate in a colder and more variable thermal regime. We tested predictions for divergence between these populations with respect to development rate and yolk conversion efficiency.

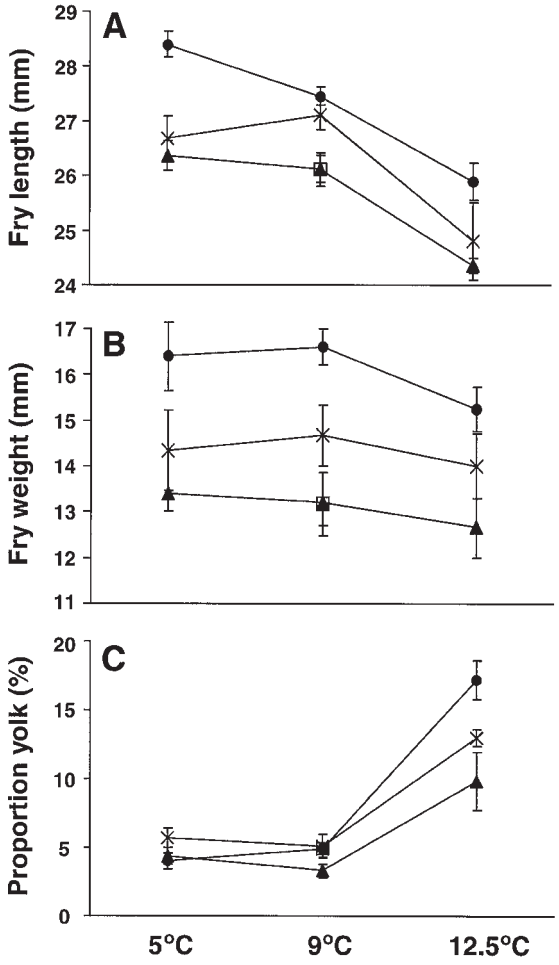
Pleasure Point embryos naturally incubate in warmer water than their contemporary Cedar River embryos (Middle Cedar), and hence, the former would be expected to hatch and emerge much earlier in the wild (Fig. 2). We had predicted that the Pleasure Point embryos should therefore delay hatching and emergence to bring their timing closer to the Cedar River peak (sensu Brannon 1987; Tallman and Healey 1991). Contrary to this prediction, hatching and emergence trajectories were nearly identical for Pleasure Point and Middle Cedar embryos at each of the three laboratory temperatures (Fig. 4). In a pilot study 2 years earlier, Pleasure Point embryos also did not delay hatching and emergence relative to Cedar River embryos (Hendry 1995). Divergence in development rate does not appear to have occurred for Pleasure Point and Cedar River embryos beginning incubation at a comparable time.

Embryos from the two locations demonstrated their highest yolk conversion efficiency (i.e., greatest body length at emergence) at laboratory temperatures that corresponded to their natural incubation environments. Similar patterns have been reported in laboratory studies of developmental variation among other sockeye salmon populations (Beacham and Murray 1987, 1989). The matching of yolk conversion efficiency to natural conditions is important because small size and excessive yolk reserves (reflecting incomplete yolk to tissue conversion) increase the susceptibility of newly emerged salmon fry to predators (Taylor and McPhail 1985; Fresh and Schroder 1987). Selection for predator avoidance may be important within Lake Washington because predation rates on sockeye salmon fry can be very high (Beauchamp 1995; Seiler and Kishimoto 1996). Such selection may have led to the evolutionary divergence in yolk conversion efficiency that has taken place within Lake Washington sockeye salmon.

Factors constraining adaptive divergence

The observed divergence in survival rate and yolk conversion efficiency was substantial and has clear fitness advantages. In contrast, the greatest divergence in development rate resulted in only a 6-day difference in time to emergence at 9°C, which would reduce emergence asynchrony only slightly. Other studies comparing embryos that naturally incubate in similar temperatures but at different times have documented greater differentiation. For example, time to yolk absorption for the progeny of different beach spawners from Cultus Lake (lower Fraser River, B.C.) declined by more that 10 days over a 6-week period (at 5°C, Brannon 1987). Similarly, time to emergence differed by about 10 days between embryos of chum salmon (*Oncorhynchus keta*) from Bush Creek (Vancouver Island, B.C.) that spawned a month apart (at about 5°C, Tallman and Healey 1991).

Fig. 5. (A) Fry length, (B) fry weight, and (C) proportion yolk at emergence for Early Cedar (solid circles), Middle Cedar (solid triangles), Late Cedar (open squares), and Pleasure Point (crosses). Error bars represent 1 SE around the mean. Data were not available for Late Cedar at 5 or 12.5°C.



There are several reasons why development rates may not have diverged much despite some restriction on gene flow and large differences in incubation conditions. First, synchronization can also be achieved through spawning time (Brannon 1987), and peak spawning at Pleasure Point is later than in the Cedar River (late November versus late October). This difference has been evident since at least the mid-1960s (Woodey 1966) and would reduce emergence asynchrony between these sites. Second, selection for synchronized emergence may be less strong than in other sockeye salmon lake systems because Lake Washington provides ample feeding opportunities for juveniles throughout the spring (Eggers 1978). The protracted spawning and emergence periods in the Cedar River (Seiler and Kishimoto 1996) may be the result of relaxed selection for synchronized emergence. Third, accelerated development in the Late Cedar embryos may have evolved for avoidance of high spring temperatures rather than for synchronization.

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