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[Article]

Effects of Temperature on Survival and Development of Early Life Stage Pacific and Western Brook Lampreys

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Abstract.—We examined the effects of temperature (10, 14, 18, and 22°C) on survival and development of Pacific lampreys *Lampetra tridentata* and western brook lampreys *L. richardsoni* during embryological and early larval stages. The temperature for zero development was estimated for each species, and the response to temperature was measured as the proportion of individuals surviving to hatch, surviving to the larval stage, and exhibiting abnormalities at the larval stage (i.e., malformations of the body). The estimated temperature for zero development was 4.85°C for Pacific lampreys and 4.97°C for western brook lampreys. Survival was greatest at 18°C, followed by 14, 10, and 22°C, significant differences being observed between 22°C and the other temperatures. Overall survival was significantly greater for western brook lampreys than for Pacific lampreys; however, the overall difference in proportion of individuals surviving was only 0.02. Overall survival significantly decreased from the time of hatch (proportion surviving = 0.85) to the larval stage (0.82; i.e., during the free-embryo stage). The proportion of individuals exhibiting abnormalities at the larval stage was greatest at 22°C, followed by 18, 10, and 14°C, significant differences being observed between 22°C and the other temperatures. These data provide baseline information on the thermal requirements of early life stage Pacific and western brook lampreys and will aid in assessment and prediction of suitable spawning and rearing habitats for these species.

Because of the great importance of temperature to aquatic life, understanding how temperature affects individuals is crucial to understanding the basic ecology of a species. Accordingly, the role of temperature in influencing the biology of fishes has been widely demonstrated. For example, water temperature can greatly influence community structure and interactions (Beschta et al. 1987), habitat selection and partitioning (Magnuson et al. 1979; Hofmann and Fischer 2002), physiological rates (Holmes 1990), reproductive timing (Brett 1970), and survival and fitness of individuals (Elliott 1981). While fish taxa can be categorized on the basis of general patterns of thermal tolerance and preference (Hokanson 1977; Magnuson et al. 1979; Elliott 1981), regional adaptations to thermal regimes are not uncommon (Hall et al. 1978; Beschta et al. 1987), and the effects of temperature may differ among ontogenetic stages (Magnuson et al. 1979; Elliott 1981; Sanders 1993). Because of this, generalizations about the thermal requirements of a species or groups of species must be broad. More specific information is often needed to elucidate the basic biology of a species or to provide guidance for activities such as determining the suitability of available habitat or developing water quality criteria for species of interest. Addressing these issues often requires species-specific information and may require examination of multiple life history stages or of those stages that are potentially most sensitive.

Aside from the fundamental influence of temperature on the biology of individuals, populations, and species, current interest in the effects of temperature has been driven by broad-scale and regionally localized perturbations to thermal conditions within aquatic systems. Because thermal conditions can greatly influence the quantity and quality of habitat available to aquatic organisms, recent alterations to the thermal regime of the Columbia River (northwestern United States and southwestern Canada)—specifically, increases in spring and summer temperatures (Quinn and Adams 1996)—have prompted interest in the habitat requirements and thermal ecology of aquatic species within the Columbia River basin. Among these are two native species of lampreys, the Pacific lamprey *Lampetra tridentata* and the western brook lamprey *L. richardsoni*. Both Pacific and western brook lampreys have broad geographic distributions within North America, the Pacific

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TABLE 1.—Sex, sample size (*N*), mean total length, and mean wet mass of Pacific and western brook lampreys that provided gametes for experiments in 2001 and 2002.

Species	Sex	Year	*N*	Length (mm; ±SD)	Mass (g; ±SD)
Pacific lamprey	Female	2001	5	459 ± 42	318.4 ± 65.4
		2002	6	446 ± 28	292.0 ± 42.0
	Male	2001	6	508 ± 41	287.5 ± 87.9
		2002	6	480 ± 37	267.6 ± 69.5
Western brook lamprey	Female	2001	31	122 ± 5	4.236 ± 0.656
		2002	29	122 ± 10	4.545 ± 1.130
	Male	2001	19	127 ± 7	3.938 ± 0.668
		2002	28	124 ± 9	3.758 ± 0.995

lampreys inhabiting Pacific coastal streams from Baja California northward to Alaska and the western brook lampreys inhabiting Pacific coastal stream systems from California northward to southeastern Alaska (Moyle 2002).

Like most other fishes, lampreys are obligate poikilotherms and therefore are directly affected by the temperature of their environment (Brett 1970; Elliott 1981). In general, little is known about the thermal requirements of lampreys, except for the well-studied sea lamprey *Petromyzon marinus* (Piavis 1961; McCauley 1963; Potter and Beamish 1975; Beamish 1980; Manion and Hanson 1980; Swink 1995; Rodríguez-Muñoz et al. 2001). Given the varied life history patterns and distributions among and within species, lampreys may experience a broad range of thermal conditions. However, the influence of temperature on survival during early life stages is of particular interest. The thermal requirements of early life stages are generally believed to be among the most narrow (Elliott 1981; Rombough 1988), and thermal exposure during early life development may potentially affect later life stages (Atkinson 1996); therefore, this period may be a critical determinant of recruitment for many fish populations (Houde 1987).

We examined the effects of four temperatures (10, 14, 18, and 22°C) on survival and development of early life stage Pacific and western brook lampreys. Lampreys were reared in the laboratory under controlled conditions from fertilization until individuals reached the larval stage (Piavis 1961). Lampreys were examined daily, and species-specific development rates, temperatures for zero development, and effective temperatures were calculated. Survival of lampreys was compared between two distinct time periods (95% hatch and fully developed larvae). This allowed us to examine the effects of temperature on survival, changes in survival over time, and differences among species. We also examined the effects of temperature on the occurrence of larval abnormalities.

Methods

The following procedures were replicated in 2001 and 2002. In the spring, subadult Pacific and western brook lampreys were collected from the wild, transported to the U.S. Geological Survey, Columbia River Research Laboratory, Washington, and held until sexually mature (May–June) to provide gametes for experiments. Pacific lampreys were collected from the Columbia River at the Bonneville Dam north shore fish ladder (Skamania County, Washington), and western brook lampreys were collected from Gibbons Creek (Clark County, Washington) and Yellowhawk Creek (Walla Walla County, Washington). Lengths and masses of lampreys used to provide gametes for experiments in 2001 and 2002 are summarized in Table 1. Pacific lampreys were held in 1400-L circular tanks and provided with a continuous inflow of water (approximately 0.3 $L \cdot min^{-1} \cdot kg^{-1}$). Western brook lampreys were held in 38-L aquaria provided with burrowing substrate and a continuous inflow of water (approximately 0.3 L/min). Water provided to all lampreys was from the Little White Salmon River (Skamania County, Washington). Water was treated with sand filters and heated to simulate seasonal thermal trends at Bonneville Dam (University of Washington 2001). All lampreys were exposed to a simulated natural photoperiod provided by 25-W incandescent lights on timers with 0.5 h of increasing and decreasing illumination at the beginning and ending of each light phase, respectively.

Before spawning, mature lampreys were anesthetized in 250 mg/L of tricaine methanesulfonate (MS-222) buffered with an equal concentration of sodium bicarbonate and rinsed in freshwater to remove traces of anesthetic. Female lampreys were

TABLE 2.—Temperature and mean dissolved oxygen (DO), pH, and total dissolved gasses (TDG) in lamprey experiments. Variables were measured once daily in each water bath for the duration of the experiment. Dissolved oxygen was converted from mg/L to a percentage following Lind (1985).

Year	Temperature (°C)	DO (%; ±SD)	pH (±SD)	TDG (%; ±SD)
2001	10	108.15 ± 8.11	7.62 ± 0.13	101.89 ± 1.02
	14	104.85 ± 9.40	7.66 ± 0.10	101.26 ± 0.45
	18	103.70 ± 7.64	7.72 ± 0.11	101.52 ± 0.45
	22	103.73 ± 8.47	7.72 ± 0.14	102.50 ± 0.48
2002	10	103.22 ± 5.24	7.39 ± 0.18	101.14 ± 0.76
	14	103.13 ± 5.19	7.44 ± 0.18	100.66 ± 0.54
	18	104.61 ± 5.00	7.48 ± 0.12	101.27 ± 0.41
	22	106.76 ± 6.48	7.47 ± 0.18	102.08 ± 0.37

positioned over a glass bowl filled with approximately 2 L of freshwater at the same temperature as the animal. Eggs were forced out the vent by squeezing the abdomen in a downward motion. This was repeated until blood appeared with the gametes. Sperm was removed from males in a similar fashion. Gametes were mixed with a gentle flow of water from a large pipette for 5 min and allowed to rest undisturbed for 30 min to allow fertilization to occur. After 30 min the fertilized eggs were divided into four glass bowls and the water temperature of each bowl was gradually adjusted through the addition of cool or warm water until reaching the target temperatures of 10, 14, 18, and 22°C (approximately 30 min). Once target temperatures were reached, fertilized eggs were transferred to flow-through hatching jars (6.86-L McDonald type) of the appropriate temperature (one hatching jar per temperature).

After fertilization, zygotes were incubated at 10, 14, 18, and 22°C for 15 temperature units (degrees above 0°C × days), after which 100 viable embryos were placed into each of 10 rearing vessels per temperature. A lag of 15 temperature units between the time of fertilization and the time of selecting experimental individuals was used to allow development to reach a point where fertilization could be confirmed. Each rearing vessel had a volume of approximately 60 mL and was constructed with a screen bottom to allow water to flow through. Rearing vessels were placed into a water bath at the appropriate rearing temperature (10, 14, 18, and 22°C), and each vessel was supplied with freshwater inflow at a rate of 0.05 L/min. Water supplied to rearing vessels and illumination was similar to above, with the addition of water treatment by ultraviolet sterilizers. Water supplied to rearing vessels was monitored daily for dissolved oxygen content, pH, and total dissolved gasses (Table 2).

Individuals in each rearing vessel were examined daily for the duration of the experiment, which lasted from the time that individuals were assigned to a rearing vessel until the individuals had reached the larval stage (i.e., stage 18; for a comprehensive descriptions of developmental stages referenced in this study, see Piavis 1961). The larval stage is marked by differentiation of all systems (except genital) and the extrusion of yolk from the gut (Piavis 1961). Because of increased locomotor activity as lampreys approached the larval stage, the timing of the larval stage was determined through qualitative observations. For daily examinations, each rearing vessel was removed from the incubation bath, placed in a petri dish with water of the appropriate temperature, and examined under a stereomicroscope at 10× to 40×. The number of individuals hatched and not hatched, the number of surviving individuals, and the number of abnormal larvae were recorded. Dead individuals were removed from rearing vessels daily. Larval abnormalities were traits considered to have a potential negative effect on survival or fitness in conditions less favorable than a laboratory setting, such as malformations of the body (Piavis 1961).

All statistical analyses were performed at $\alpha = 0.05$ using SAS software (SAS version 8.01; SAS Institute Inc., Cary, North Carolina). Fewer than 10 replicates were available for some treatment combinations because of mechanical trauma that resulted from improperly adjusted freshwater inflow. Given that the data were unbalanced, we estimated degrees of freedom following Satterthwaite (1946). Using the number of individuals hatched and not hatched for each rearing vessel, we used logistic regression to estimate the number of days to 50% hatch (D_{H50}) and the number of days to 95% hatch (D_{H95}; this terminology follows Rodríguez-Muñoz et al. 2001). For each species,

TABLE 3.—Effective temperature (E_T), days required to reach 50% hatch (D_{H50}), days required to reach 95% hatch (D_{H95}), and days to the larval stage (D_L) for Pacific and western brook lampreys reared at four temperatures. The values of D_{H50} and D_{H95} were estimated independently for each replicate by means of logistic regression.

Species	Temperature (°C)	E_T (°C)	D_{H50} (±SE)	D_{H95} (±SE)	D_L
Pacific lamprey	10	5.15	26.22 ± 0.57	29.26 ± 0.50	56
	14	9.15	16.95 ± 0.20	18.85 ± 0.36	35
	18	13.15	11.10 ± 0.03	12.22 ± 0.10	23
	22	17.15	8.38 ± 0.05	9.08 ± 0.08	17
Western brook lamprey	10	5.03	26.93 ± 0.53	29.34 ± 0.60	56
	14	9.03	15.82 ± 0.18	17.00 ± 0.19	33
	18	13.03	10.84 ± 0.10	11.90 ± 0.06	23
	22	17.03	8.05 ± 0.10	9.03 ± 0.09	17

a linear regression model was fit to describe the effects of temperature on the development rate to 50% hatch. We then estimated the temperature for zero development (T_0), the effective temperature ($E_T = T—T_0$), and the accumulated degree-days to which individuals were exposed (DD = $E_T \times$ days). Degree-days were calculated to provide a standardized measure for the effects of time and temperature on development. The number of days individuals were held under experimental conditions (see above) was the number required to reach the larval stage (D_L). A repeated measures factorial analysis of variance (ANOVA) was used to examine the effects of species and rearing temperature on the proportion of individuals surviving to hatch (S_H = proportion of individuals surviving to D_{H95}), the proportion of individuals surviving to the larval stage (S_L = proportion of individuals surviving to D_L), and interactions among the main factors (PROC MIXED; SAS Institute 1989). A factorial ANOVA was used to examine the effects of species and rearing temperature on the proportion of abnormal individuals at the larval stage (A_L = proportion of abnormal larvae at D_L) and interactions between the main factors (PROC MIXED; SAS Institute 1989). Similar trends in main effects were observed for both years, including a slightly higher proportion of western brook lampreys surviving than Pacific lampreys, low survival at 22°C compared with that at the other temperatures examined, a slight decrease in survival from hatch to the larval stage, and a greater occurrence of larval abnormalities at 22°C that at the other temperatures. Preliminary examination indicated that year (2001 and 2002) did not have a significant effect on the overall survival ($F_{1,123} = 1.02$, $P = 0.31$) or proportion of abnormalities ($F_{1,118} = 0.75$, $P = 0.39$); therefore, data for both years were combined and the variable year was included in the final models as a random blocking effect (Kuehl 1994) to account for systematic variation associated with the time when the experiment was performed (Sokal and Rohlf 1995). Variance in response variables was stabilized by using an arcsin transformation for S_H and S_L and a square-root transformation for A_L. When main factors had an overall significant effect, Bonferroni *t*-tests were used to make pairwise comparisons between treatment combinations. Statistical comparisons are based on transformed data; however, reported mean values are based on the original measurement scale (Kuehl 1994).

Results

Mean D_{H50} and D_{H95} (Table 3) varied greatly among temperatures, and temperature accounted for a large proportion of the observed variance in developmental rate ($1/D_{H50}$) for Pacific ($r^2 = 0.9864$) and western brook ($r^2 = 0.9828$) lampreys. T_0 estimates from linear regression models were 4.85°C and 4.97°C for Pacific and western brook lampreys, respectively, and were used to calculate effective temperatures (Table 3).

Interaction was not significant between species and temperature ($F_{3,117} = 1.19$, $P = 0.32$), species and development stage ($F_{1,120} = 1.90$, $P = 0.17$), or temperature and development stage ($F_{3,120} = 1.56$, $P = 0.20$); therefore, these data were combined to examine the effects of main factors on survival. There was a significant difference in survival among temperatures ($F_{3,117} = 201.98$, $P < 0.0001$) and species ($F_{1,117} = 5.34$, $P = 0.02$) and in survival at hatching and at the larval stage ($F_{1,120} = 53.77$, $P < 0.0001$). Survival was greatest at 18°C, followed by 14, 10, and 22°C (Figures 1, 2), and mean comparisons indicated that survival was significantly less at 22°C than at 10°C ($t = 19.46$, df = 117, $P < 0.0001$), 14°C ($t = 16.49$, df = 117, $P < 0.0001$), or 18°C ($t = 21.47$, df =

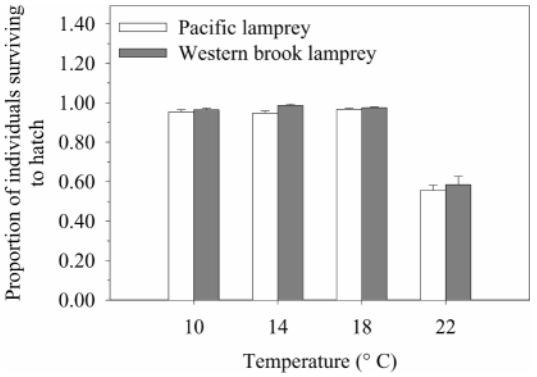

FIGURE 1.—Proportion of Pacific and western brook lampreys surviving from fertilization to hatch; whiskers are SEs. Overall, survival was significantly less at 22°C than at the other temperatures.

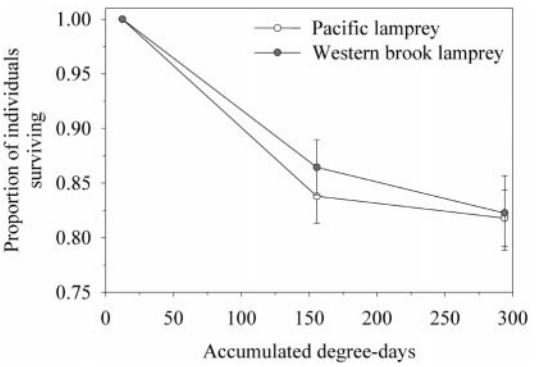

FIGURE 3.—Trends in the proportion of Pacific and western brook lampreys surviving from the initiation of experiment (12.5 degree-days [DD]) to hatch (155.6 DD) and from hatch to the larval stage (294.0 DD); whiskers are SEs. A slight but significant decrease in survival was observed from the time of hatch to the larval stage.

117, $P < 0.0001$). Survival differences between other temperatures were not significant ($P > 0.05$).

Survival was significantly greater for western brook lampreys than for Pacific lampreys ($t = -2.31$, df = 117, $P = 0.02$); however, this difference may be due to the small degree of variability in the transformed data, because the difference in the proportion of individuals surviving between the species was only 0.02. Similarly, a significant decrease in survival occurred after hatch ($t = 7.33$, df = 120, $P < 0.0001$), with a difference between S_H and S_L of 0.03 (Figure 3).

Species and temperature did not interact significantly to affect the proportion of individuals exhibiting abnormalities at the larval stage ($F_{3,111} = 2.30$, $P = 0.08$). The occurrence of abnormalities differed significantly among temperatures ($F_{3,111} = 127.22$, $P < 0.0001$) but not among species ($F_{1,111} = 0.31$, $P = 0.58$). The occurrence of abnormalities was greatest at 22°C, followed by 18, 10, and 14°C (Figure 4). Significant differences in the occurrence of abnormalities were observed between 22°C and 18°C ($t = -16.36$, df = 111, $P < 0.0001$), between 22°C and 14°C ($t = -13.57$, df = 112, $P < 0.0001$), and between 22°C and 10°C ($t = -15.38$, df = 111, $P < 0.0001$); however, no significant differences between other temperatures were observed ($P > 0.05$).

Discussion

Many factors have been used to explain the variation in early life stage survival and development of fishes, most notably photoperiod and temperature (Brett 1970). While photoperiod often stim-

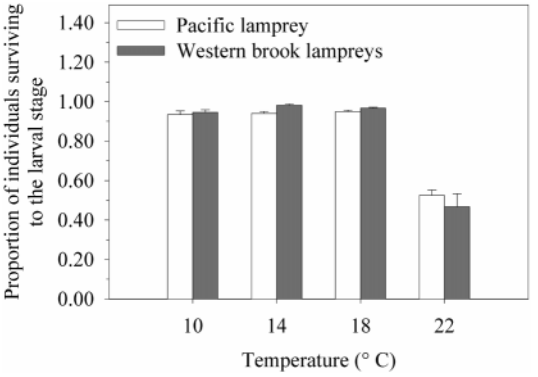

FIGURE 2.—Proportion of Pacific and western brook lampreys surviving from fertilization to the larval stage; whiskers are SEs. Overall, survival was significantly less at 22°C than at the other temperatures.

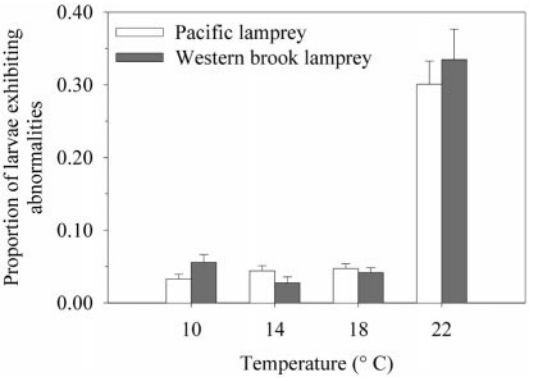

FIGURE 4.—Proportion of Pacific and western brook lamprey larvae exhibiting abnormalities; whiskers are SEs. Significantly more larvae exhibited abnormalities at 22°C than at the other temperatures.

ulates the onset of events related to reproduction, such as migratory behavior, temperature often dictates the conditions necessary for embryogenesis. Overall, Pacific and western brook lampreys responded similarly to temperature. Estimated days to 50% and 95% hatch were very consistent among species (Table 3), as were the estimated temperatures for zero development. And although a systematic difference was observed in the overall proportion of individuals surviving between the two species, the biological significance associated with the small magnitude of this difference is questionable. The scale at which we examined temperature in this experiment did not allow us to isolate the temperature at which survival was maximized during early life stages of these species; however, survival appeared to be optimal over the range of 10–18°C with a sharp decline in survival at 22°C. Correspondingly, we observed a low occurrence of abnormalities at 10, 14, and 18°C, and a significant increase in abnormalities at 22°C. Similarly, Piavis (1961) and Rodríguez-Muñoz et al. (2001) reported optimal temperatures of 18.3°C and 19°C, respectively, for survival of early life stage sea lampreys.

Our data indicate that, with respect to early life stages, Pacific and western brook lampreys have a broader zone of thermal tolerance than sea lampreys do. Although survival of Pacific and western brook lampreys was significantly reduced at 22°C, the proportion of individuals surviving to the larval stage was more than 0.50 over the entire range of temperatures examined (range of 12°C; Figure 2). Comparatively, Piavis (1961) observed no survival to the burrowing stage (stage 17) for sea lampreys at temperatures below 15.6°C or above 21.1°C. This corresponds to a temperature range of less than 4.5°C in which early life stage sea lampreys can survive. Alternatively, McCauley (1963) suggested that sea lamprey eggs could hatch over a temperature range of 10°C (15–25°C); in that study, however, the low percent hatch (<30%) at temperatures greater than or equal to 20°C and less than or equal to 15°C suggests that much of the reported hatching range included suboptimal temperatures. More recently, Rodríguez-Muñoz et al. (2001) reported high survival rates (>58%) from fertilization to the burrowing stage for sea lampreys reared at 16, 19, and 23°C, with no survival to the burrowing stage for individuals reared at 11°C or lower. Rodríguez-Muñoz et al. (2001) also reported an estimated temperature for zero development of 6.93°C, warmer than that estimated for lamprey species examined in this experiment, which may further restrict the range of potential temperatures available for embryogenesis of sea lampreys in comparison with Pacific and western brook lampreys.

The relationship between stream temperature and reproductive timing is poorly understood for the species examined in this study. Within the Columbia River basin, temperature data are available for several main-stem and high-order stream systems; however, low-order tributaries are not well represented. Most documented occurrences of lamprey spawning activity in this region have been in low-order streams and the frequency with which lampreys use main-stem and high-order stream habitat for spawning is unknown. Close et al. (2003) reported that stream temperatures ranged from 7.5°C to 14.9°C during the main spawning period for Pacific lampreys (May 28–June 13) in Meacham Creek (Umatilla County, Oregon). Claire (2004) sampled potential Pacific lamprey spawning sites in the South Fork Clearwater Drainage, Idaho, during the spring and summer of 2000–2002. Stream temperatures in this area typically exceed 20°C during the summer; they exceeded 26°C in 2000 (Claire 2004). Although lampreys are known to occur in this area, no signs of spawning activity were observed. Lê et al. (2004) observed Pacific and western brook lamprey spawning activity over the period of April 16–July 14, 2003, in Cedar Creek (Clark County, Washington), during which time stream temperatures ranged from 10°C to 22°C. Spawning activity of Pacific and western brook lampreys appears to be most frequent during times when stream temperatures should be suitable for embryogenesis and early larval stage development; however, spawning may occur under conditions that are potentially detrimental to early life stage survival (e.g., 22°C; Lê et al. 2004).

The similarity in response to temperature by Pacific and western brook lampreys in this experiment suggests similar reproductive timing and thermal habitat requirements for early life stage development. Under conditions of sympatric distributions, this may result in interspecific competition and partitioning of thermal resources for spawning and rearing habitat (Magnuson et al. 1979). Although anecdotal data are abundant, quantitative distribution data for Pacific lampreys within the Columbia River basin are limited to fish passage data collected at hydroelectric projects along the main-stem Columbia and Snake Rivers and in a small number of localized studies (e.g., Close et al. 2003; Cochnauer and Claire 2003;

Claire 2004; Lê et al. 2004), and distribution data for western brook lampreys within the Columbia River Basin are essentially nonexistent. Therefore, the degree to which these species exhibit a sympatric distribution is unknown; however, both species have been observed concurrently within the same Columbia River tributary (Gibbons Creek, Washington, personal observation).

The relationship between temperature and reproductive timing may also have an effect on growth and long-term survival of fish. In general, the thermal tolerance zone for embryological development of fish is believed to be narrow; however, there is less agreement on the temperature sensitivity of other life stages and fish sizes (Brett 1970; Elliott 1981; Rombough 1988). For example, the most stenothermic life stage for sea lampreys appears to be the embryo, with the range of thermal tolerance being broader and more variable for larvae, juveniles, and adults (see Rodríguez-Muñoz et al. 2001). Therefore, spawning generally occurs within a specific range of temperatures suitable for embryological development (Brett 1970), and often occurs under thermal conditions that maximize survival, energy conversion (Blaxter 1969), and individual size at specific developmental stages (Atkinson 1994). However, thermal conditions that are optimal for embryological development may result in hatching when thermal conditions are suboptimal for later life stages (Brett 1970).

In this experiment, survival from the time of hatch (155.6 ± 10.8 DD) to the time that individuals reached the larval stage (294.0 ± 10.2 DD) differed significantly, indicating that mortality continued after hatch. However, a change in the trend of individuals surviving over the two time periods is apparent when survival is plotted against degree-days (Figure 3). From fertilization to hatch the overall proportion of individuals surviving decreased from 1.00 to 0.85 (approximately 143.1 DD), whereas the proportion of individuals surviving from hatch to the larval stage decreased from 0.85 to 0.82 (approximately 138.4 DD). Because lampreys exposed to 10°C, 14°C, and 18°C exhibited high survival rates throughout the duration of the experiment, individuals exposed to 22°C probably had the greatest influence on the observed trend (Figures 1, 2). Nevertheless, because no interactions were observed among the factors examined, changes in survival rates were statistically systematic among temperatures. The decreasing trend in mortality may be the result of selective mortality over time within the treatments. Alternatively, the effects of temperature on survival may be variable through ontogeny; however, a more complex experimental design would be required to address these questions.

Temperature can significantly influence the biology of fishes. Regarding early life stages, temperature can influence the timing of reproduction, development rates, survival, and the quantity and quality of habitat available for spawning and rearing. Categories that group species based on general trends in thermal preference and tolerance (e.g., thermal guilds; Magnuson et al. 1979) provide information useful for determining broad-scale distributions; however, inclusion of a species in these types of categories may be based on the thermal requirements of closely related taxa and often do not take into account fine-scale differences between species and ontogenetic stages or the effects of local adaptation (Hall et al. 1978; Magnuson et al. 1979; Elliott 1981; Beschta et al. 1987; Sanders 1993). Therefore, empirical evidence should be used to provide more specific information when necessary, such as for comparative purposes, or to provide a basis for management strategies. Compared to sea lampreys, Pacific and western brook lampreys were less stenothermic over the period of development examined, with a lower temperature for zero development; however, thermal requirements of other life stages should be defined before generalizations can be made. The differences between the response to temperature by the two species examined in this study and that of sea lampreys indicate the need for species-specific biological examinations before initiation of management or conservation efforts. Further work is needed to examine the response of these species to a more dynamic thermal environment, at isolated ontogenetic stages, and to other habitat components; however, the data we report provide baseline information that will be useful for predicting reproductive timing, developmental rates, and the suitability and distribution of spawning and rearing habitat available to Pacific and western brook lampreys.

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