Pacific Salmon in Hot Water: Applying Aerobic Scope Models and Biotelemetry to Predict the Success of Spawning Migrations

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ABSTRACT

Concern over global climate change is widespread, but quantifying relationships between temperature change and animal fitness has been a challenge for scientists. Our approach to this challenge was to study migratory Pacific salmon (*Oncorhynchus* spp.), fish whose lifetime fitness hinges on a once-in-a-lifetime river migration to natal spawning grounds. Here, we suggest that their thermal optimum for aerobic scope is adaptive for river migration at the population level. We base this suggestion on several lines of evidence. The theoretical line of evidence comes from a direct association between the temperature optimum for aerobic metabolic scope and the temperatures historically experienced by three Fraser River salmon populations during their river migration. This close association was then used to predict that the occurrence of a period of anomalously high river temperatures in 2004 led to a complete collapse of aerobic scope during river migration for a portion of one of the sockeye salmon (*Oncorhynchus nerka*) populations. This prediction was corroborated with empirical data from our biotelemetry studies, which tracked the migration of individual sockeye salmon in the Fraser River and revealed that the success of river migration for the same sockeye population was temperature dependent. Therefore, we suggest that collapse of aerobic scope was an important mechanism to explain the high salmon mortality observed during their migration. Consequently, models based on thermal optima for aerobic scope for ectothermic animals should improve predictions of population fitness under future climate scenarios.

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Introduction

Environmental temperature is a key determinant of the distributions and abundances of biota (Parmesan and Yohe 2003; Perry et al. 2005) through a profound effect on their physiology. For fishes, it is well established that extreme temperatures limit energy allocation (Brett 1971; Neill and Bryan 1991; Claireaux and Lagardere 1999; Claireaux et al. 2000; Lefrancois and Claireaux 2003), which then restricts whole-animal tolerance to temperature extremes (Pörtner 2002). Nevertheless, quantifying the relationship between animal fitness and temperature change has proved to be difficult for scientists interested in predicting effects of climate change. An emerging and promising approach for such predictions is the use of aerobic scope (the difference between basal and maximal metabolic rates; Fry 1971; Priede 1977). Aerobic scope, like other physiological functions, has a temperature optimum (T_{opt}), and so scope decreases at temperatures (termed *pejus temperatures*) above and below T_{opt} (Pörtner 2002; Pörtner and Knust 2007). In the case of temperatures above T_{opt}, not only does basal oxygen demand continue to increase exponentially with temperature, but cardiac pumping capacity plateaus and then collapses (Brett 1971; Farrell 1997, 2002; Lee et al. 2003*a*). A critical temperature is reached (T_{crit}) when aerobic scope is minimal. Insufficient aerobic scope then leads to the use of anaerobic metabolism, exhaustion, and even death (Pörtner and Knust 2007). Thus, whole-animal tolerance to extreme temperatures becomes restricted as energy allocation to essential tissues becomes limited.

We reasoned that a linkage between aerobic scope and lifetime fitness should be much easier to establish for adult Pacific

salmon (genus *Oncorhynchus*) because of the relative short-term needs for exercise during their river migration for spawning, which may last several days to a month. Pacific salmon spawn once, and so failure to complete the return migration to natal spawning grounds results in zero lifetime fitness. Annually, tens of millions of adult salmon leave the Pacific Ocean to complete a spawning migration to their natal spawning grounds. During these river migrations of varying length and hydraulic difficulty, salmon often encounter turbulent river reaches that probably require maximum swimming effort (Rand and Hinch 1998; Hinch and Bratty 2000; Hinch et al. 2002) for varying periods of time. The empirical observation that fish passage is prevented in years when there is extreme river flow or extreme water temperature (Rand et al. 2006), sometimes resulting in the "disappearance" of many thousands of fish during their river migration, points to aerobic scope being a critical determinant of successful upstream river migration. Thus, there could be natural selection for individuals with high aerobic scope, high T_{opt}, or both.

Experimental support for this line of logic comes from the variation among salmon populations observed for aerobic scope, swimming performance, and body form. For example, Fraser River (British Columbia, Canada) sockeye salmon that migrate up to 1,000 km upstream experience harsher hydraulic conditions and warmer river temperatures than do coastal spawners. Correspondingly, these long-distance migrants have a greater aerobic scope, critical swimming speed, and T_{opt} (Tsuyuki and Williscroft 1977; Lee et al. 2003a, 2003b), as well as a smaller body size, a more fusiform shape, and a proportionally smaller total egg mass (Crossin et al. 2004).

The importance of aerobic scope for river migration is further emphasized by the continuous nature of upstream migration. Biotelemetry studies clearly show that once individual sockeye salmon (*Oncorhynchus nerka*) enter the Fraser River, they normally migrate upstream in a sustained fashion, maintaining land speeds (swimming speed minus river speed) of 20–40 km/d (e.g., English et al. 2005), thus enabling certain populations to cover up to 1,000 km in 20–30 d (Crossin et al. 2007). This is a remarkable feat of aerobic swimming when one considers some of the high-velocity river sections that are negotiated and that may require bursts of anaerobic activity (Hinch and Rand 1998; Hinch et al. 2002). Consequently, while swimming activity can be powered anaerobically, there is still a requirement to tap into a substantial portion of aerobic scope during periods of recovery (for examples of excess postactivity oxygen consumption, see Lee et al. 2000b; Wagner et al. 2006). The feat of river migration is made even more remarkable because salmon stop feeding before they enter the river and fuel all metabolic activities during this period, including locomotion, solely with somatic energy stores (typically lipid) accrued during the ocean phase of their life cycle. Therefore, there is also a challenge of fuel management because, in addition to swimming upstream, salmon also divert some of this stored energy to develop distinctive secondary sexual charac-

teristics and to produce sperm and eggs before they arrive at spawning grounds.

Our research group has been studying the physiological ecology of Fraser River salmon for nearly a decade. Here, we highlight some recent results, including biotelemetry tracking studies of individual sockeye, as well as data on the temperature limits for exercise. The purpose for this integration is to provide novel evidence for a tight linkage between migration success and the temperature experienced during migration, with special reference to Fraser River salmon. We also show population-specific associations between the aerobic scope temperature profile and historic river temperatures experienced during migration, and we suggest that mortality during upstream migration occurs when aerobic scope completely collapses and approaches zero at T_{crit}.

Salmon Migration and River Temperature

Climate change is driving species' ranges toward the poles (Parmesan and Yohe 2003). Fraser River sockeye salmon are near the southern boundary of their postglacial geographic distribution (Burgner 1991) and therefore are particularly susceptible to any increases in river temperature (Beamish et al. 1997; Schindler 2001; Rand et al. 2006). Most Fraser River sockeye salmon populations make their upstream migrations when the river temperature is around its seasonal maximum (Fig. 1B), and so the progressive increase in peak summer temperature by approximately 1.8°C during the past 50 yr, as shown in Figure 1C, is alarming. Two important facts are readily apparent from the summer temperature profile of the Fraser River in relation to sockeye salmon migration dates (Fig. 1B). First, different sockeye salmon populations experience different river temperatures during their migration. For example, summer-run (so called by fisheries managers as these populations enter the Fraser River in midsummer) sockeye typically encounter peak summer temperatures, while late-run populations (entering in late summer and early autumn) typically experience cooler temperatures. Second, year-to-year variation in migration temperature is significant given the temperature spread between the 50-yr maxima and minima (Fig. 1B). Notably, river temperature during the summer of 2004 was anomalously high and, as shown in Figure 2D and 2E, new historic maxima (>21°C) were recorded, the significance of which will become apparent later.

Coincident with anomalously high river temperatures in 2004 was the premature entry into the Fraser River of the Weaver Creek sockeye salmon population, which belongs to the late-run group (Fig. 1B). For almost a decade, variable portions of this and other late-run populations have unaccountably entered the river 4–8 wk prematurely (Cooke et al. 2004, 2006). This alteration in river entry time is a very unusual behavior for salmon as migration times are highly conserved (Hodgson and Quinn 2000). Historically, late-run populations have stopped at the cool coastal and estuarine waters near the Fraser River mouth (the Strait of Georgia) for anywhere from
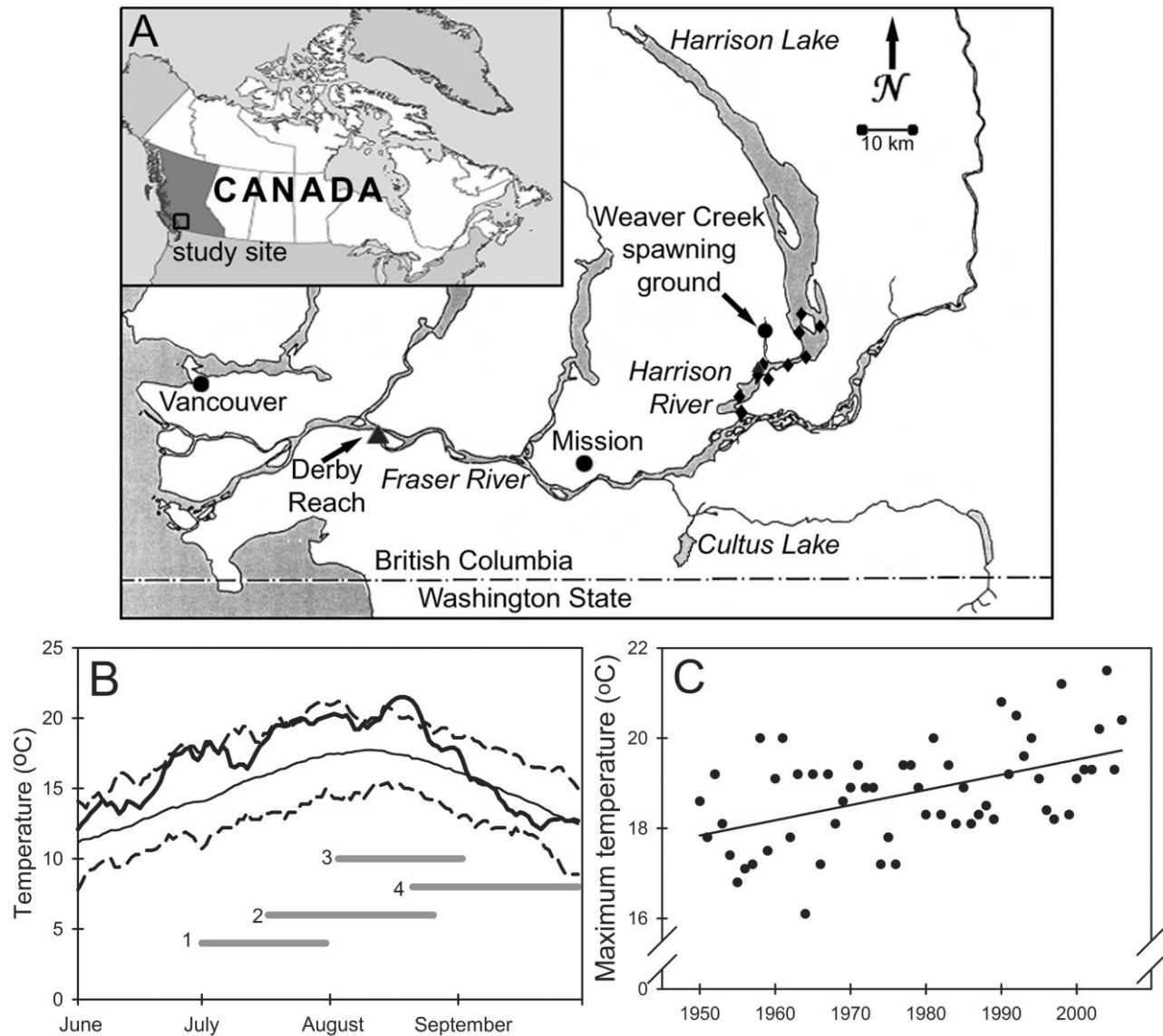
Figure 1. *A*, Location of the field study site for tracking Weaver Creek sockeye salmon that migrate through the Fraser River, British Columbia, Canada, and into the Harrison River. The location of fish capture and release sites (*triangles*), telemetry receiver stations (*diamonds*), and the Weaver Creek spawning site (*circle*) are indicated. Gates Creek is located 250 km farther upstream from the confluence of the Harrison and Fraser rivers. *B*, Water temperature of the main stem Fraser River during the annual upstream migration of sockeye salmon. The continuous heavy line represents the daily water temperatures for 2004. Daily average (*continuous light solid line*) and the daily maximum and minimum (*continuous broken lines*) water temperatures were based on 57 yr of data from temperature loggers. Different populations of sockeye enter the river over a period that can last more than 1 mo (the migration window), and the horizontal bars represent the approximate migration windows for the four major run-timing groups of sockeye in the Fraser River (1 = early Stuart [population from the Stuart Lake system]; 2 = early summer, which includes Gates Creek sockeye; 3 = summer; and 4 = late summer, which includes Weaver Creek sockeye). *C*, The progressive increase ($P < 0.05$) in peak summer water temperature in the Fraser River over the past 57 yr.

4 to 6 wk before initiating upstream migration. In 2004, late-run populations left the marine area early and experienced river temperatures that were warmer than those in their historical experience (figs. 1*B*, 2*D*). Thus, this early-entry behavior moved salmon from the relatively cool Strait of Georgia (~11°–13°C) into a river whose temperature was above the historic maximum (Fig. 1*B*). This aberrant behavior appears to have been a catastrophe because the majority of more than 120,000 Weaver Creek sockeye salmon "disappeared" and did not reach the spawning grounds.

The disappearance of Weaver Creek sockeye in 2004 is not the first example of massive salmon losses associated with high river temperatures in the Fraser River. In fact, several Canadian federal government inquiries about such losses have concluded
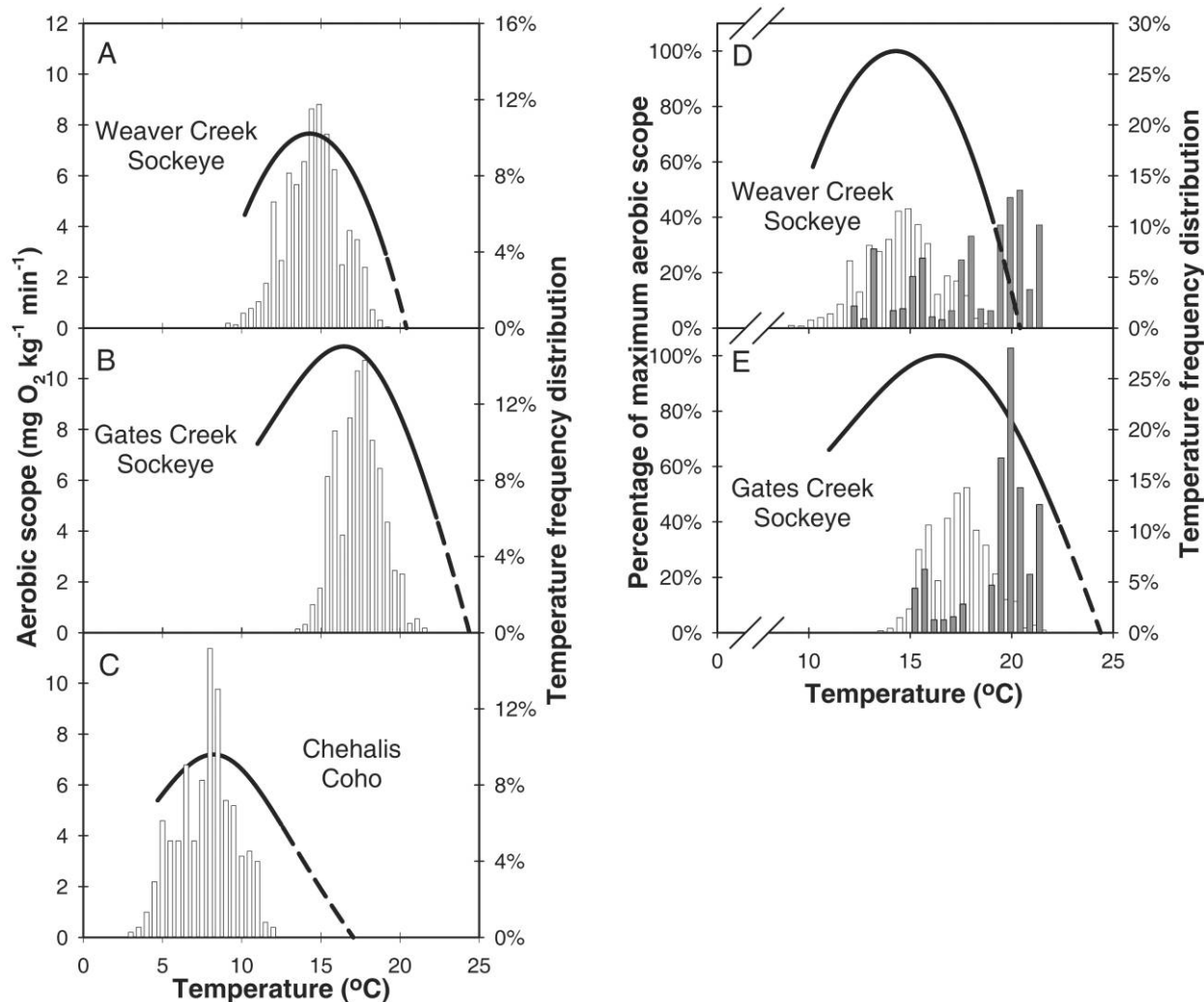
Figure 2. Estimates of aerobic scope (*solid line*; calculated from data on routine and maximum oxygen uptake of adult salmon; Lee et al. 2003*a*) in relation to acclimation temperature for Weaver Creek sockeye (*A*), Gates Creek sockeye (*B*), and Chehalis coho (*C*), with a frequency histogram overlay of the historic river temperatures that each population would have encountered during their migration before 2004. Each curve for aerobic scope was extrapolated (*broken line*) to derive the critical temperature when aerobic scope is zero. Aerobic scope was reexpressed for Weaver Creek (*D*) and Gates Creek (*E*) sockeye, as a percentage of the maximum, and the temperature data for 2004 are added as a separate overlay (*solid bars*). Note that the Chehalis coho are a fall/winter-migrating salmon, which corresponds with their lower temperature.

that anomalously high river temperatures probably contributed to the mortality of millions of migrating salmon in recent years (Fraser 1995; Williams 2005), placing the sustainability of Canada's largest salmon-producing river system in jeopardy (Cooke et al. 2004). Such temperature concerns extend beyond the Fraser River to the Columbia River in neighboring Washington, Idaho, and Oregon (Quinn et al. 1997), where there are reports of sockeye salmon temporarily ceasing their migration when river temperature increased to >21°C after migration had begun (Hyatt et al. 2003; Goniea et al. 2006; Keefer et al. 2007). It has been claimed that no sockeye population in the world has successfully established a river migration period when the historic mean water temperature exceeds 19°C (Hodgson and Quinn 2002). Despite this collection of suggestive evidence for

delays in salmon migration and of salmon disappearances, convincing evidence to link water temperature and migration success is lacking at the level of an individual fish in the Fraser River. Serendipitously, while we were performing biotelemetry studies on Weaver Creek sockeye salmon in 2004, we were able to generate this missing evidence. But before describing these biotelemetry results, it is essential to first erect a theoretical physiological framework to aid in the interpretation of the fish behaviors.

Aerobic Scope and T_{opt} for Fraser River Salmon

Fry (1971) first used aerobic scope to conceptualize environmental effects, including temperature, on fish metabolism and

activity (i.e., lethal, controlling, limiting, masking, and directive effects). Indeed, temperature optima for fish metabolism and swimming performance vary considerably among species (Brett 1971; Beamish 1978; Randall and Brauner 1991; Johnston and Ball 1997; Taylor 1997; Claireaux et al. 2006). Brett (1971) first characterized temperature profiles for adult sockeye salmon, showing that the temperature optima for aerobic scope, cardiac output, and critical swimming speed (U_{crit}) were all around 15°C. Lee et al. (2003a, 2003b) greatly extended this knowledge by swimming adult salmon at field locations where tests could be performed using natal river water and ambient or near-ambient temperatures (Farrell et al. 2003). Figure 2 displays the derived lines for the aerobic scope data from these experiments for two populations of sockeye salmon and a population of coho salmon (*Oncorhynchus kitsuch*). The T_{opt} for aerobic scope was clearly population specific and approximated the ambient river temperature during the migration. The Gates Creek sockeye population makes a longer and more arduous inland migration in early summer and has a greater aerobic scope and a higher T_{opt} (Fig. 2B) compared with the Weaver Creek sockeye population (late run; Fig. 2A), which has a shorter and less difficult coastal migration in early autumn. Chehalis River coho salmon, like Weaver sockeye, are coastal spawners that migrate in late fall and early winter and have a correspondingly lower T_{opt} for aerobic scope (Fig. 2C).

Given the importance of a high aerobic scope for successful river migrations, an important and novel discovery is a tight correspondence between T_{opt} and the modes of the frequency distributions for the historic river migration temperatures (also presented in Fig. 2). To derive these associations, we accessed temperature archives that were based on temperature loggers located in the main stem of the Fraser River. We assumed a 50% population arrival on these dates: September 14 for the Weaver sockeye, August 6 for the Gates Creek population, and November 1 for the Chehalis coho. We also assumed that the temperature experienced by the Weaver sockeye for a given day at Mission was identical to that measured at Hell's Gate on the same day since both are in the main stem. We then estimated the historic river temperature experienced by a given salmon stock and in a given year for the 15 d preceding and following the above entry dates. Temperature bin sizes were roughly 0.5°C for the histogram. The 2004 frequency histogram was calculated using hourly temperature data. Although a close correspondence between migration water temperature and physiological capacity has been implied (Lee et al. 2003b), it has never been delineated as shown in Figure 2.

These striking associations suggests that temperature profiles for aerobic scope are population specific and adaptive. Thus, adult salmon may have evolved an adaptive aerobic scope relative to the river temperature historically encountered most frequently by its population.

The T_{crit} for aerobic scope represents the temperature when salmon can only support their routine metabolism. T_{crit} has not been measured in adult Pacific salmon but can be estimated by extrapolating the lines presented in Figure 2 beyond T_{opt} to the intercept with the X-axis (i.e., the dashed lines in Fig. 2). Adult salmon would find it impossible to swim upstream in the Fraser River at T_{crit}. Therefore, T_{crit} probably represents an absolute upper temperature threshold for upstream migration for a given salmon population.

Analysis of T_{crit} and T_{opt} with respect to the historic migration temperatures (Fig. 2A–2C) reveals three important points. First, the high-temperature window between T_{opt} and T_{crit} is surprisingly narrow (6°–7°C for all three populations). Second, migration temperatures have clearly exceeded T_{opt}, presumably forcing some of the population to migrate with a suboptimal aerobic scope. Third, river temperature has rarely reached T_{crit} for these three populations during the past 50 yr.

In the summer of 2004, a major temperature anomaly occurred during the migration of the Weaver Creek sockeye population (hence, the separate presentations of data in Fig. 2D and 2E), and this was associated with high migration mortality. Our analysis (Fig. 2D) predicts that 30% of the Weaver population experienced river temperatures that exceeded T_{crit} (20.4°C), which leads to our suggestion that migration was prevented because of a complete collapse of aerobic scope and subsequent death, resulting in zero lifetime fitness for 30% of the population (i.e., nearly 38,000 adult salmon in 2004).

This analysis represents a best-case scenario because the functional thermal barrier for river migration must lie somewhere in the temperature window between T_{crit} (20.4°C) and T_{opt} (14.3°C). The precise temperature for the functional T_{crit} will depend on both the difficulty of the swimming challenge (which will change with the flow conditions from year to year) and the fish's maximum aerobic scope (which will show individual variation as well as being population specific). (Note here that while fish could potentially still swim maximally using anaerobic metabolism, any limitation on aerobic scope would affect the recovery process, perhaps prolonging the duration of recovery.) Therefore, the exact percentage of the Weaver Creek sockeye salmon that did not complete their migration in 2004 because of reduced aerobic scope is unknown. Nevertheless, the data presented in Figure 2 can be used to estimate the potential effect of reduced aerobic scope even though the exact proportion of aerobic scope that is needed for any salmon migration, including Weaver Creek, is unknown. To illustrate our point, we assume that Weaver sockeye need at least 25% of maximum aerobic scope for their short migration. For this hypothetical scenario, the functional T_{crit} would become a river temperature of 19.6°C, which would narrow the temperature window above T_{opt} to a functional 5.3°C. Then, applying 19.6°C as the upper temperature for successful migration to the frequency histogram of exposure temperatures for Weaver Creek sockeye in 2004 (Fig. 2D), it is evident that only 50% of the entire population experienced a mainstem river temperature of 19.6°C or lower. This would then lead to a prediction that 50% of the population had an unsuccessful migration due to insufficient aerobic scope. If Weaver Creek sockeye required either more or less than 25% of aerobic scope, then the percentage of the population failing to reach the spawning grounds would

be correspondingly higher or lower than 50%. To the best of our knowledge, this is the first attempt to directly associate the temperature dependence of a physiological capability with the failure of an animal migration. More importantly, we were able to corroborate this association with our field biotelemetry results, as shown in the next section.

Compared with Weaver Creek sockeye salmon, Gates Creek sockeye clearly evolved to migrate upstream earlier, when river temperatures are warmer. They also evolved a higher aerobic scope to contend with the significant swimming challenges imposed en route by a long, steep canyon and a fishway at a hydroelectric dam. Correspondingly, their maximum aerobic scope, T_{opt} (16.3°C), T_{crit} (24.4°C), and temperature window between T_{opt} and T_{crit} (7.1°C) are greater relative to Weaver Creek sockeye. We similarly discovered that T_{crit} lies above the historic temperatures, but unlike for the Weaver sockeye, the extreme temperatures encountered in the main stem of the Fraser River during 2004 were not above the T_{crit} for Gates Creek sockeye (Fig. 2E). This finding allows us to predict that Gates Creek sockeye salmon, unlike Weaver Creek sockeye, did not experience a complete collapse of aerobic scope in the main stem of the Fraser River in 2004. However, we do not have biotelemetry results to validate this suggestion. Interestingly, the highest temperature historically encountered by Gates Creek sockeye salmon in the mainstem is 21.7°C (Fig. 2E), which could be speculated to be the functional T_{crit} for Gates Creek sockeye salmon. This temperature corresponds to about 50% of maximum aerobic scope, and the temperature is consistent with the empirical observation that sockeye ceased migration in the Columbia River system (Hyatt et al. 2003) and showed en route mortality (Keefer et al. 2007). Alternatively, higher temperatures encountered by this population farther upstream (for which we have no historic data) could act as a selective force.

Biotelemetry Studies on Weaver Creek Sockeye Salmon

Historically, the Weaver Creek population has migrated into the Fraser River between mid-September and mid-October, with a median spawning date of October 15. These fish are now migrating between mid-August and late-September/mid-October (Fig. 1B), but the median spawning date has not changed. The result is a protracted period of freshwater residence. For a number of years, we have successfully used and validated radio and acoustic biotelemetry on adult Fraser River salmon (see Cooke et al. 2005, 2006; Crossin et al. 2007). Therefore, the acoustic biotelemetry studies we performed in 2004 on Weaver Creek sockeye to examine the double jeopardy created by a premature return and a thermal anomaly were done with a good measure of confidence in our methodological approach.

We captured Weaver sockeye with a beach seine on the Harrison River (a tributary of the Fraser River) as they were migrating to their natal spawning stream. The point of capture was near the confluence with the Fraser River, 10 km down-

stream from Weaver Creek (Fig. 1A). Captured fish were transferred and held overnight at the Chehalis Hatchery (located ~5 km from the capture site), while scale analyses were conducted to determine population identity (Gable and Cox-Rogers 1993). Population identity was later confirmed by DNA analyses (Beacham et al. 1995, 2004; Wood 1995). Fish sex was determined at time of capture by visual inspection or later by the ratio of plasma 17β-estradiol to testosterone, which is higher in females. Once Weaver Creek fish were identified, they were transported back to the initial capture site and released. Therefore, from capture to release, individuals were held for no longer than 24 h. Before being returned to the Fraser River, 39 fish were implanted intragastrically with an acoustic transmitter (V16-3H-R04K coded pingers, 16 mm in diameter and 56 mm in length that weigh approximately 25.0 g in air; Vemco, Shad Bay, Nova Scotia, Canada), and 45 fish were implanted with a radio transmitter (16 mm diameter, 46 mm length, with a 460-mm-long antenna that weighs approximately 16.1 g in air; model MCFT-3A, Lotek Wireless, Newmarket, Ontario) in the stomach, and a 2-mL blood sample, adipose fin clip, and gill tissue biopsy were collected, procedures that took <3 min total (Cooke et al. 2006). Migration behavior was tracked with 14 acoustic receivers (VR2, Vemco, Shad Bay, Nova Scotia) and four radio receivers strategically deployed along the migratory route, near the spawning areas, and in adjacent Harrison Lake (Fig. 1A). Receivers located below the release site determined fish fallback. The time of first detection at each receiver was recorded for each fish.

We tracked 83 individual Weaver sockeye salmon during five study periods that spanned the migration window (Fig. 3). Given the extreme river temperatures in 2004, we were not surprised by the low (30%) overall migration success of these fish. What was more informative was that individual migration success increased as river temperature decreased (Fig. 3). In fact, none of the eight salmon tracked in the first sample group survived when river temperature was >19.5°C. Also, only 10 out of 37 salmon in the second sample group survived when river temperature was between 18.0° and 19.5°C. Conversely, migration success was highest at 78% for the salmon from the last sample group, which were fish that had migrated into the Fraser River later than the other groups after holding in the cooler Georgia Strait for several weeks. Thus, the Weaver Creek sockeye that entered the river system the earliest, and at its warmest, suffered a disproportionately higher mortality rate than those entering later when the river had cooled. Those individuals that entered the system later during the last week of September experienced temperatures near the historic norm for the Weaver Creek population (14.0°C), their T_{opt} was 14.3°C, and they had excellent migration success (~70%). Conversely, salmon tagged at a temperature near their T_{crit} (20.4°C) failed to reach the spawning area. This clear inverse relationship between river temperature and migration success suggests that individual decisions regarding the timing of river entry have important consequences, especially in this unusually warm-temperature scenario.
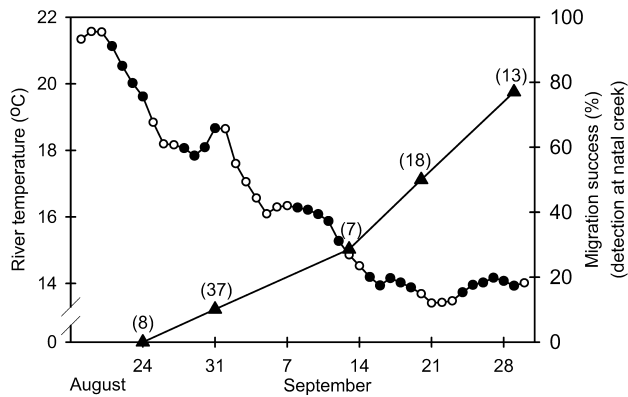
Figure 3. Inverse relationship between water temperature in the Harrison River in 2004 (*continuous line, circles*) and the survival to spawning areas (*lines and triangles*) for individual Weaver Creek sockeye salmon. The number of fish tagged and released for each of the five release dates is shown in parentheses. The five shaded regions (*solid circles*) are estimates of the thermal experiences in the Fraser and Harrison Rivers for the five sets of fish before interception (exact date is indicated by a triangle) in the Harrison River near the confluence with the Fraser River (see Fig. 1A). We estimated the mean ($\pm$ 95% CI) entry date into the Fraser River based on telemetry results showing migration rates for acoustic-tagged Weaver Creek sockeye of 25–36 km/d.

Some individuals migrated successfully and were tolerant of high temperatures in the main stem of the river. This result pointed to important differences in either individual upper temperature tolerances (something that is expected but not studied by us) or individual behaviors that allowed some salmon to avoid the temperature extreme. Adult Pacific salmon can temporarily (hours to months) seek cold-water refugia in tributaries and deep portions of lakes (Hodgson and Quinn 2000; Hyatt et al. 2003; Newell and Quinn 2005) when temperatures are high along the migration route, presumably to limit high-temperature exposure (Newell and Quinn 2005; Goniea et al. 2006). Accordingly, we were interested in confirming whether this type of behavioral strategy conferred a fitness advantage to Weaver Creek sockeye by improving migration success during the extremely warm periods.

Before September 14, Fraser River temperatures encountered by these salmon ranged from 15°C to 21°C, levels above long-term averages for that time of year (Fig. 1B). From the biotelemetry data, we identified two contrasting freshwater migration behaviors, which lasted until the salmon either moved into the spawning grounds 1 mo later or died prematurely. Of the 48 salmon tagged before September 14, one group ($N = 19$ salmon) milled about in the warm Harrison River (Fig. 1A), experiencing temperatures between 16°C and 20°C. None of this group successfully completed the migration. The other group ($N = 29$ salmon) sojourned in the adjacent, deep, oligotrophic Harrison Lake (Fig. 1A) and 16% reached the spawning area. Because some of these fish were bearing acoustic transmitter tags that reported water depth, we could reconstruct the

temperature experiences during lake residency for a subset of fish. Temperature loggers were deployed at various depths in the lake and residency was converted to percent time at a certain depths (<20 m, 20–40 m, 40–50 m, and >50 m) that corresponded to given thermal ranges. Time started with the first detection by a VR2 receiver and ended with the fish either returning to Harrison River being and detected on the spawning grounds (successful migrants; $N = 3$) or remaining in Harrison Lake (where it was assumed the fish had died; $N = 2$). To calculate residence times and depths of Weaver sockeye in Harrison Lake, mean depths per hour (minimum of 1 detection per hour and maximum of 55 detections per hour) were assessed for five sockeye. Overall, we estimated that these five sockeye spent more than 60% of the time below the thermocline (7°C at about 50 m; Fig. 4). The three sockeye that left the lake ascended to the lake surface 7 h before reentry into the Harrison River, a behavior that accounted for much of the surface residency of these fish. Thus, seeking refuge in the cool water of Harrison Lake improved the migration success of Weaver sockeye when faced with unusually high river temperatures.

Though compelling, these associations between migration temperatures and migration success are still correlative. Consequently, we sought direct evidence that survival and migration success were affected by the temperature experience. To do this, we intercepted Weaver Creek sockeye salmon in late summer around the historic date for 50% migration, but as in the previous study, we transferred the fish after biopsy directly to large freshwater aquaria at a research facility at Cultus Lake (Fig. 1A), where holding temperatures were manipulated (Crossin et al. 2008). These sockeye were captured and then held for 24 d at either 10°C ($N = 50$) or 18°C ($N = 50$), that is, approximately 4°C above or below their T_{opt}.

Survival of salmon held at 10°C (62%) was almost double that of salmon held at 18°C (32%), suggesting that the high holding temperature caused some mortality. Five days before
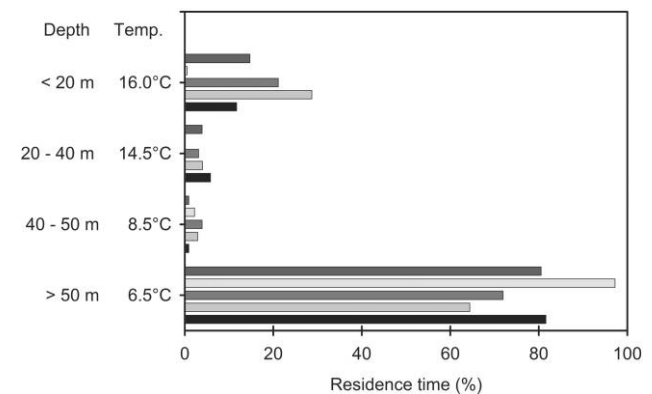

Figure 4. Percentage of time spent at given depth and temperature ranges by five (separate bars, with each gray scale corresponding to one individual) Weaver sockeye residing in Harrison Lake before their spawning date, as revealed from acoustic depth tags (an average for each hour).

their historic date for peak spawning, all surviving fish were biopsied, fitted with an acoustic biotelemetry tag, and released into the Fraser River at Derby Reach (Fig. 1A) to complete their migration. At release, the river temperature was 14°C, and the subsequent salmon migration was followed with the receiver array. Of the 31 surviving salmon released after being held at 10°C, 68% reached the spawning areas. A similar migration success (62%) was obtained for 13 additional control fish that were tagged a few days after this release date and at the same river temperature; that is, they were released immediately and without being experimentally held at a controlled temperature. In contrast, migration success was only 35% for the 17 surviving salmon released after being held at 18°C. Migration time from release to the spawning areas (3–4 d) was independent of the holding temperature and also was within the period observed for naturally migrating individual sockeye in the Fraser River (English et al. 2005). To the best of our knowledge, these are the first experiments to directly manipulate the temperature experience of an adult migrating fish and effect a change in subsequent migration success.

Thus, we have generated three separate lines of evidence that are consistent with temperature (in this case, an exceedingly high but natural temperature) having a significant and direct effect on migration success and hence lifetime fitness of wild adult sockeye salmon. What makes these observations more compelling is that we are able to place them in a theoretical physiological framework using the dependence of aerobic scope on water temperature. For example, Weaver sockeye experimentally held at a temperature 4.3°C below their T_{opt} had twice the migration success compared with fish held 3.7°C higher than their T_{opt} (Crossin et al. 2008).

In addition, there was an excellent agreement between the biotelemetry data and the aerobic scope model for T_{opt} and T_{crit}. Both sets of data suggest that disproportionate mortality occurred among Weaver Creek sockeye salmon that entered the system earliest and when it was warmest. The model predicted that few fish entering the river at >21°C would reach the spawning grounds (because T_{crit} is 20.4°C), and this prediction was corroborated with individual biotelemetry (Fig. 3). The biotelemetry results also revealed a 78% migration success after the river had cooled to the T_{opt} of 14.3°C for Weaver Creek sockeye (Fig. 2A), which is not an unreasonable survival rate given the other potential sources of mortality on the salmon in the Harrison River (e.g., predation by seals, unreported fishing). Likewise, for a river temperature of 18°C, the aerobic scope model predicts a 35% survival for Weaver Creek sockeye (Fig. 3D), which is similar to the poor survival (37%) found for the salmon experimentally held at 18°C and returned to the river.

Fishery managers use a split-beam hydroacoustic facility to estimate salmon migration numbers in the Fraser River (~126,000 Weaver Creek sockeye were estimated to have entered the Fraser River in 2004), but they have no direct way of accurately estimating mortality during the migration to spawning grounds. Mortality cannot be visually confirmed in the silt-laden Fraser River because dead salmon naturally sink, resulting in few observations of carcasses (Patterson et al. 2007). However, the spawning ground assessments estimated that only 29,000 sockeye reached the Weaver Creek spawning areas, suggesting that 97,000 salmon may have died en route. Extrapolating our biotelemetry results (a 30% overall migration success) to the Weaver Creek population, suggests that nearly 90,000 salmon did not reach the spawning grounds and, of these mortalities, around 38,000 (30% of the population) could be ascribed to the complete collapse of aerobic scope at or above the absolute T_{crit}.

Until we know exactly what proportion of aerobic scope is needed for successful migration, we cannot precisely ascribe mortality to an insufficient aerobic scope for upstream migration and other necessary activities. High temperature also contributes to salmon mortality through other mechanisms (by accelerating fungal and bacterial infections on skin and gills (Tierney and Farrell 2004) and, in the case of the Fraser River, a kidney parasite (Wagner et al. 2005), but quantitative relationships between temperature and infection-related mortality are lacking. Thus, we conclude that a complete collapse of aerobic scope induced by exposure to a high temperature, corresponding to an unusually warm river temperatures combined with aberrant migration behavior, contributed almost half of the predicted river mortality among the 2004 spawning sockeye population in Weaver Creek.

Discussion

We predicted that the exceptionally warm river temperatures experienced in 2004 by Weaver sockeye reduced aerobic scope in a portion of the population to a level that prevented successful upstream migration and resulted in zero lifetime fitness. These results greatly extend recent findings that suggest models based on T_{opt} for aerobic scope will improve predictions of population fitness under global climate change scenarios (Pörtner and Knust 2007). Wang and Overgaard (2007) comment on the persuasive nature of this correlative evidence, which involved comparisons of aerobic scope thresholds for field and laboratory data, to support the idea that thermal constraints on oxygen transport are responsible for the observed population decline for eelpout, *Zoarces viviparus*, in the Wadden Sea over the past 50 yr.

The mechanistic basis for the mismatch between an animal's demand for oxygen and the limited capacities of the circulatory and ventilatory systems to supply oxygen to tissues with increasing temperature has received much debate (Brett 1971; Randall and Brauner 1991; Farrell 1997; Johnston and Ball 1997; Taylor et al. 1997). A prevailing idea (Farrell 2002; Pörtner et al. 2002; Pörtner and Knust 2007; Wang and Overgaard 2007) is that the fish's cardiovascular system, and the heart in particular (Farrell 2007), can no longer ensure sufficient aerobic scope above T_{opt}. Likewise, cardiac adaptations have been implicated in niche expansion for salmon sharks (*Lamna ditropis*) into the subarctic seas (Weng et al. 2005) and the Thunnus lineage into colder deep-ocean waters (Blank et al. 2004). In

both salmon shark and tunas, increased expression of proteins required for cardiac excitation-contraction coupling, such as SERCA2, is regarded as an important adaptation for maintaining cardiac contractility in cold water.

More broadly, this article provides compelling evidence regarding the mechanisms by which large-scale animal migrations may fail in response to climate change (McCarty 2001; Walther et al. 2002) and provides opportunities for using physiological tools to enhance the conservation and sustainable management of fish and wildlife during periods of environmental uncertainty. Collectively, these insights represent a breakthrough for scientists who have sought a unifying mechanistic understanding of climatically induced population shifts in fitness of ectothermic animals (Pörtner and Knust 2007). Thus, fisheries managers, who must develop population-specific management strategies during periods of climate change, may find models of temperature dependence of aerobic scope, such as the one presented here, to be useful predictive tools. At present, the only experimental data available for assessing the effects of high river temperature on adult Pacific salmon come from a single time-to-lethality study on resting adult sockeye salmon that shows an exponential relationship between mortality with water temperature above 21°C (Servizi and Jensen 1977). Our findings suggest that more powerful and more precautionary predictive models can probably be constructed using T_{opt} and T_{crit} values for aerobic scope that are population specific.

Still ahead is the need to define these population-specific temperature profiles for aerobic scope and identify functional T_{crit} values that reflect the degree of difficulty for the upstream migration (i.e., fish with more difficult migrations may need a higher proportion of maximum aerobic scope as well as a greater absolute aerobic scope). Temperature exposure experiments incorporating postexposure biotelemetry, similar to the one we have described here (Crossin et al. 2008), might help calibrate population-specific aerobic profiles against actual migration success. It is also unclear whether the correspondence between T_{opt} and the mode for historically encountered temperatures represents a heritable trait or phenotypic plasticity. Therefore, additional research is needed to quantify temperature resilience and adaptability within a population. What remains a mystery is the apparently fatal biological drive of some sockeye populations to prematurely enter the Fraser River (Cooke et al. 2004) and attempt to migrate upriver at temperatures that are not only higher than those experienced by their predecessors but incompatible with successful spawning. For over 15 yr, fisheries managers have observed varying percentages of the late-run populations Fraser River sockeye salmon entering the river early: the earlier the fish enter, the greater the proportion that die before spawning. There has been much speculation about and some study of the reasons for early entry. One suggestion involves the decadal shifts in the North Pacific sea temperature and productivity (Hodgson et al. 2006); another is that late-run stocks chose to stay with the larger schools of summer-run stocks that normally enter earlier (Fig. 1B). Our studies have discovered that fish that enter the

Fraser River early, compared with fish with normal entry times, do so with a lower somatic energy store and at a more advanced reproductive state (these two states are probably inversely related because these salmon fuel reproductive development with somatic stores having stopped feeding; Cooke et al. 2006). Both early- and late-entry fish are apparently prepared for the osmotic switch to freshwater well in advance of river entry on the basis of biopsy assessments of gill Na^+, K^+-ATPase levels and comparison with known changes in enzyme activity during the migration (Shrimpton et al. 2005; Cooke et al. 2006).

Simplistic Prognoses

The progressive warming of the mainstem of the Fraser River truly has survival consequences for the populations of sockeye salmon that invaded this freshwater system when glaciers retreated some 10,000 yr ago. Over the past 50 yr, the difference between the average summer temperature and the maximum summer temperature has been about 2.5°C. With a warming of about 1.8°C during this period, much of this difference has disappeared, and therefore, it is not surprising that historic temperature maxima were set in 2004. What we now understand is that this climatic change will have differential effects on different sockeye populations if this warming trend continues, as it is predicted to do (Morrison and Foreman 2005). For the Weaver Creek sockeye salmon population, their apparently fatalistic behavior of early river entry is currently threatening the sustainability of the population. Thus, despite a 6.1°C temperature window between T_{opt} and T_{crit}, this population has high-temperature problems, given the possibility that the functional T_{crit} is 19.6°C. If the aberrant behavior has a genetic basis, the imminent threat of further warming may be postponed for a while through natural selection.

For the Gates Creek sockeye salmon population, with their adaptations for a warmer temperature and a more arduous migration than Weaver Creek sockeye, the prognostication is a little simpler. They migrate at the peak summer temperature and their T_{opt} of 16.3°C closely corresponds to the peak average mainstem river temperature, which is now 1.8°C warmer. Their functional T_{crit} is 21.7°C, if we accept that their temperature window between T_{opt} and T_{crit} is 7.1°C and assume that they need 50% of their aerobic scope for successful migration. Their temperature buffer for aerobic scope (5.4°C) would be exhausted in a little less than 150 yr, assuming the same rate of climatic warming. This period represents enough time for about 40 generations of the 2004 Gates Creek population to either adapt or face extinction.

With such a bleak prognosis, practical management options are few. One imperative is that fish migrating upstream at particularly high water temperatures should not be harassed by fishing activities or the like, which unnecessarily stress fish and thereby elevate their routine metabolic rate, reduce aerobic scope, and lower T_{crit}. The Fraser River is a large, high-volume, fast-flow system that does not lend itself to engineering solutions. Fish ladders could be built to reduce the swimming effort

(i.e., perhaps lower the proportion of aerobic scope needed for migration), but there may be far too many river reaches that represent an energetic challenge for some sockeye populations to make this approach feasible. Lowering the water temperature in the Fraser River would be a desperate management measure. There are presently no dams on the Fraser River. In the nearby Snake River, sockeye salmon take advantage of cold refugia created by some of the eight dams that they must negotiate to reach their spawning grounds (Keefer et al. 2007), but creation of local cold-water refugia or water channels in the Fraser River would probably have to take advantage of cold, deep refugia in feeder lakes such as the Harrison Lake. Ultimately, the ability of salmon to hold in cold water is limited by the finite somatic energy stores, which varies considerably among sockeye salmon populations (Crossin et al. 2004). Consequently, any management solutions that are adopted will have to be population specific, even within a watershed.

Acknowledgments

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