microbial community. Coevolution altered ecological population dynamics and resulted in bacteria adapted to phages in time and phages adapted to bacteria in space. Unlike coevolution in high-nutrient broth, coevolutionary dynamics in soil appear to be driven by fluctuating selection—a form of coevolution that can potentially continue indefinitely. These results suggest that rapid bacteria-phage coevolution, and not just purely ecological interactions, are likely to be crucial in explaining the structure, population dynamics, and ultimately the function of natural microbial communities.

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Differences in Thermal Tolerance Among Sockeye Salmon Populations

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Climate change–induced increases in summer water temperature have been associated with elevated mortality of adult sockeye salmon (*Oncorhynchus nerka*) during river migration. We show that cardiorespiratory physiology varies at the population level among Fraser River sockeye salmon and relates to historical environmental conditions encountered while migrating. Fish from populations with more challenging migratory environments have greater aerobic scope, larger hearts, and better coronary supply. Furthermore, thermal optima for aerobic, cardiac, and heart rate scopes are consistent with the historic river temperature ranges for each population. This study suggests that physiological adaptation occurs at a very local scale, with population-specific thermal limits being set by physiological limitations in aerobic performance, possibly due to cardiac collapse at high temperatures.

Warming oceans and rivers are affecting fish species worldwide (*1–4*). In particular, elevated temperatures in streams and rivers are creating lethal conditions for the migration of Pacific salmon to their spawning grounds, raising conservation concerns for these ecologically, economically, and culturally important fish species (*5–7*). Because physiological processes are critical in defining temperature-induced mortality (*8*), we investigated whether thermal limits are set at a local level and by physiological limitations in aerobic performance due to cardiac collapse.

The lifetime fitness of millions of sockeye salmon (*Oncorhynchus nerka*) that annually return to the Fraser River (British Columbia, Canada) depends on a physically demanding upriver migration. During this once-in-a-lifetime event, fish swim continuously against a fast flowing river for several weeks at ground speeds of 20 to 40 km day^{-1} (*9*). Feeding ceases in the ocean, and upriver swimming is fueled entirely by endogenous energy stores. Because sockeye salmon return to natal spawning grounds with remarkable fidelity, the Fraser River is home to more than 100 genetically and geographically distinct populations (*10*), each of which expe-

riences variable upriver migration conditions, depending on when they enter the river and where they spawn. Thus, populations vary in migration distance (100 to 1100 km), elevation gain (10 to 1200 m), river temperature (9° to 22°C), and river flow (2000 to 10,000 m^3 s^{-1}) (Fig. 1B and table S1). Reproductively isolated populations can potentially adapt to the environmental conditions that induce maximal aerobic challenges, which for sockeye salmon likely occur during their upriver spawning migration. Indeed, local migratory conditions apparently exert strong selective pressure for adaptation because morphological and behavioral characteristics (gross somatic energy, body morphology, egg number, and swimming behavior) do correlate with river migration distance, elevation gain, and/or work (distance × elevation gain) in sockeye salmon (*11, 12*). Therefore, we hypothesize that physiological adaptation in sockeye salmon occurs locally at the population level, reflecting upriver migration conditions.

We apply an established conceptual and mechanistic framework for understanding temperature effects on aquatic ectotherms, the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis (*13–15*). OCLTT attributes the decline in aerobic scope (the difference between resting and maximal oxygen consumption rates) above an animal's optimal temperature (T_{opt}) to capacity limitations of the organ systems that deliver oxygen to tissues. Here, we focus on heat tolerance, given the prevailing warming trend for the Fraser River (fig. S1). The expectation is that local adaptations should extend to multiple levels of the cardiorespiratory system, explaining intraspecific variation in thermal tolerance and aerobic scope.

Our study included eight populations of wild-caught Fraser River sockeye salmon, spanning

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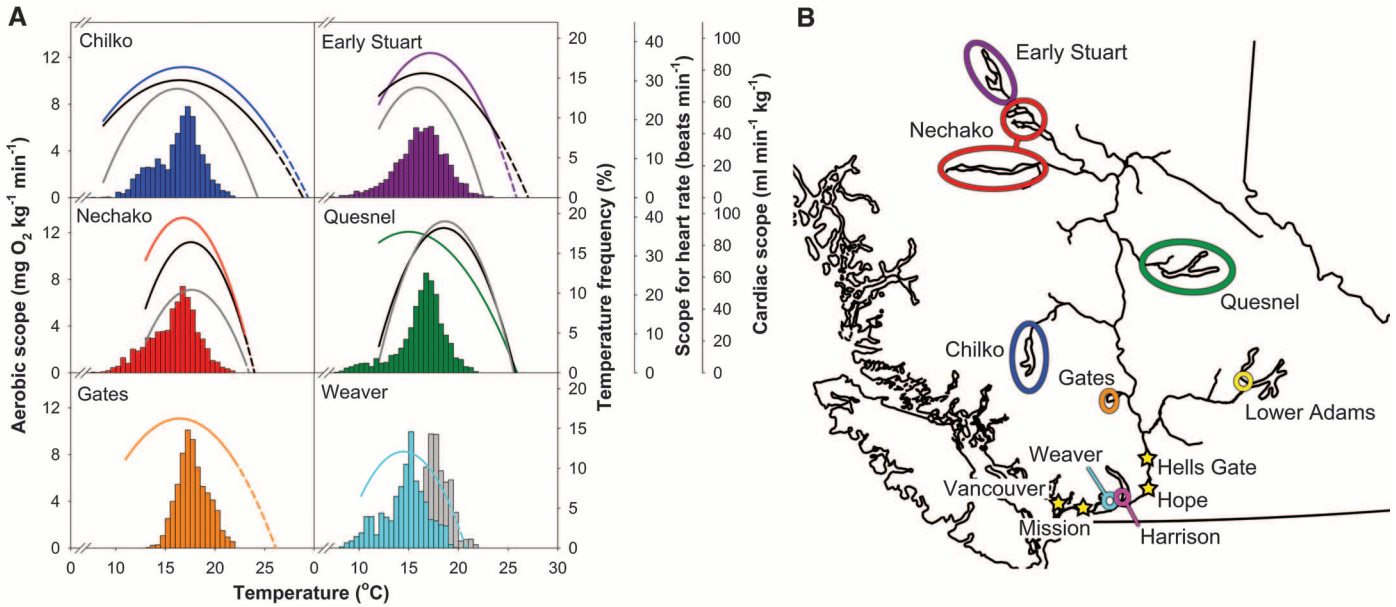
Fig. 1. (**A**) Population-specific estimates of aerobic (colored lines), cardiac (black lines), and heart rate (gray lines) scopes in relation to water temperature. The frequency histogram shows simulated distributions of average river temperatures encountered by individual modeled fish from each population during their upriver migration from 1995 to 2008. For Weaver fish, two temperature histograms are presented, one for the historical river entry (blue), the other for the current early entry phenomenon (gray) (16). Aerobic scope data for Gates and Weaver sockeye salmon provided by (17). (**B**) Map of the Fraser River, British Columbia, Canada, indicating the spawning locations for the eight sockeye salmon populations included in this study.

a range of river migration difficulties. Populations were first categorized into those that pass through Hells Gate, a hydraulically challenging river segment (upriver populations) and those that do not [coastal populations (table S1)]. Migration difficulty was further quantified using various environmental characteristics: distance, elevation gain, temperature, migration rate, duration, work, river slope, and migration effort (Fig. 1B and table S1). We predicted that migration distance, elevation gain, and work would exert the strongest selection pressure on aerobic scope, given their importance in selecting for morphological traits (12). We measured individual cardiorespiratory performance ($N = 97$) as a function of temperature in four populations (16). Many fish could not swim at the highest test temperatures, presumably reflecting a collapse of aerobic scope above T_{opt} (Fig. 1A and fig. S2). Moreover, aerobic scope curves for each population were significantly related to the historic range in river temperature they experienced (table S2), a finding consistent with two additional Fraser River sockeye salmon populations (17) (Fig. 1A and table S2). The coastal Weaver sockeye salmon experience the coldest temperatures and had the lowest T_{opt} (14.5°C), whereas the upriver populations experience similar river temperatures and accordingly had a similar T_{opt} [range 16.4° to 17.2°C (Fig. 1A and tables S1 and S3)]. The Chilko population displayed an unusually broad optimal thermal range (Fig. 1A and table S3) that corresponded with the lower temperatures encountered during their difficult migration in the Chilcotin water-

shed. In addition, significant differences in maximum aerobic scope among the populations (table S4) were positively correlated with the distance to the spawning ground (Fig. 2A and table S5). These results suggest population level adaptation of maximum aerobic scope to the selection imposed by river conditions encountered during migration (18–20).

Given that cardiac capacity and aerobic scope are tightly related (21), we expected populations with the greatest migratory demands to display similar adaptations in cardiac morphology and performance. Relative ventricular mass (RVM), percentage compact myocardium (% compact; the proportion of the ventricle supplied with coronary blood flow), and relative dry compact mass (RDCM) significantly differed among populations (table S4). All three morphological parameters were significantly greater for upriver compared with coastal populations ($P < 0.01$; t test), suggesting that the hydraulically challenging sections of the river impose selection on heart morphology. In addition, correlations between cardiac morphology and migration difficulty (Fig. 2, B to D, and table S5), and maximum aerobic scope with RDCM (table S5), provide promising evidence for local adaptation to river conditions on an even finer scale (18–20). Furthermore, aerobic scope, cardiac scope, and scope for heart rate were all positively correlated (fig. S3) and varied in parallel with river temperature (Fig. 1A), suggesting that the temperature dependence of cardiac performance is linked to that of aerobic capacity at the population level. Corroborating earlier work (21, 22), scope for

heart rate collapsed at a lower temperature than aerobic scope in two populations (Fig. 1A), suggesting that reduced scope for heart rate above T_{opt} may limit maximum cardiac output and the capacity of the cardiorespiratory system to transport oxygen. Interestingly, neither maximum cardiac scope nor maximum scope for heart rate differed significantly among the upriver populations tested (table S4). Therefore, future studies should examine cardiovascular function in coastal populations and consider the possibility of population differences in arterial oxygen-carrying capacity and tissue oxygen extraction ability to provide greater insight into local adaptation of cardiovascular performance.

Next, we sought a mechanistic explanation for the observed intraspecific variation in thermal tolerance. Cardiac adrenergic stimulation protects salmonid cardiac function at low temperatures (23, 24) and against the negative effects of acidosis and hypoxia during exercise (25), but protection diminishes at high temperatures associated with declining aerobic scope (23–25). Therefore, we hypothesized that the unusually broad and high thermal tolerance of the Chilko population would reflect a greater density of adrenaline-binding ventricular β-adrenoceptors compared with the comigrating Nechako population that has a narrower and lower thermal tolerance (Fig. 1A and table S3). We determined ventricular β-adrenoceptor density (B_{max}) and binding affinity (K_d) in fish that had been held for 4 days at 13°, 19°, or 21°C. At all three temperatures, Chilko had a significantly higher B_{max} compared with Nechako sockeye salmon
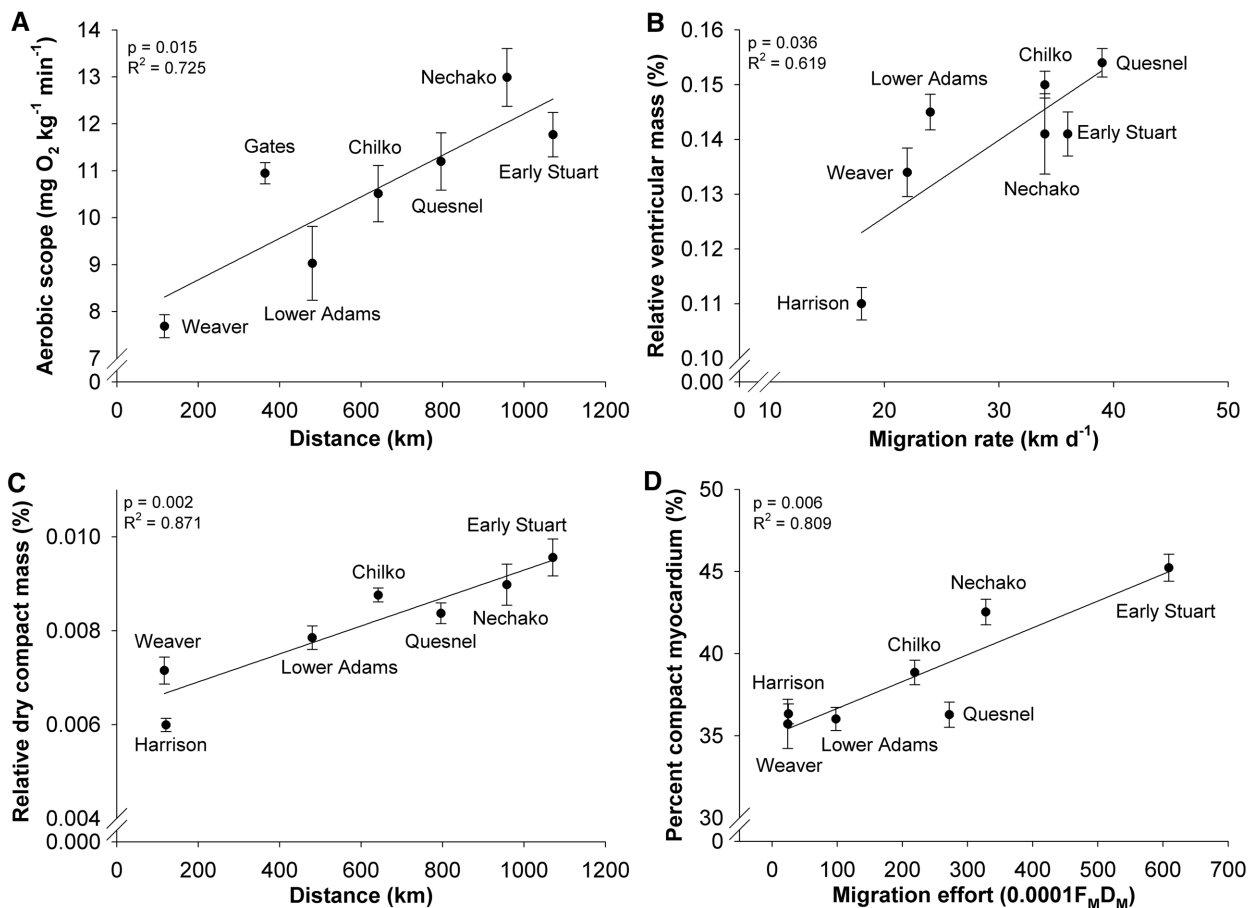
Fig. 2. Linear regressions between migration difficulty indices and (**A**) aerobic scope at T_{opt}, (**B**) relative ventricular mass, (**C**) relative dry compact mass, and (**D**) percentage compact myocardium (tables S1, S3, and S4). Population means ± SEM are presented. The migration difficulty indices with the strongest Pearson correlation coefficient are presented (table S5). F_M, Fraser River discharge; D_M, distance to spawning grounds. Only female sockeye salmon were compared for heart morphology (16).

(Fig. 3) [K_d did not differ (fig. S4)] and more than twice that previously measured for salmonids. In contrast to rainbow trout (24), B_{max} increased significantly when Chilko sockeye salmon were warmed to 19° and 21°C from 13°C. Consequently, elevated ventricular β-adrenoceptor expression for Chilko sockeye salmon may provide greater cardiac capacity and protection at temperature extremes, expanding their thermal tolerance compared with the Nechako population.

Our results support the hypothesis that continued increases in summer river temperatures will result in population-specific responses of sockeye salmon (5). Comparison of temperature profiles for aerobic scope (as a percentage of maximum) among six populations (Fig. 4) reveal clear differences across populations in T_{crit} (when aerobic scope is zero and fish survival is passive, time-limited, and supported by anaerobic metabolism). Although upstream migration is clearly impossible at T_{crit}, exactly how much aerobic scope is required for successful river migration is unknown. A biotelemetry study with Weaver sockeye salmon suggests that at least 50% of aerobic scope is needed [<10% of fish

Fig. 3. Ventricular β-adrenoceptor density (B_{max}). Significant differences between populations are indicated by * ($P < 0.001$). Significant differences between temperature treatments existed only for Chilko sockeye salmon and are indicated by differing letters (i.e., a and b; $P < 0.001$, 2-way analysis of variance). Rainbow trout were included as a reference group to confirm the assay technique.
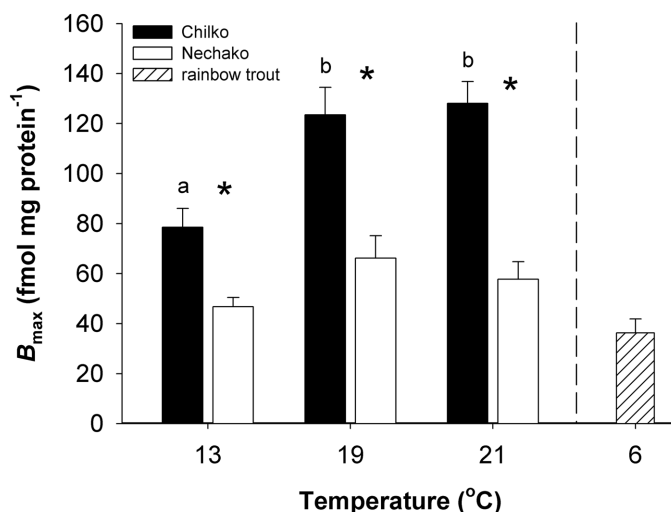
reached their spawning area at 18° to 21°C when aerobic scope is 0 to 68% of maximal (5, 26)]. However, given that all the upriver populations studied here have 89 to 97% of maximum aerobic scope at the upper 90th percentile of his-

toric temperatures encountered (table S3), we suggest that perhaps ~90% of aerobic scope is necessary over a broader time scale for upriver populations experiencing greater migration difficulty. Accordingly, temperatures exceeding the

Fig. 4. Percentage of maximum aerobic scope available for each population in relation to temperature. Dashed line at 21.5°C indicates the maximum Fraser River water temperature measured near Hells Gate since the 1940s. Although it is unknown what proportion of aerobic scope is required to successfully ascend the river, 90% and 50% are indicated as guidelines (dotted lines).
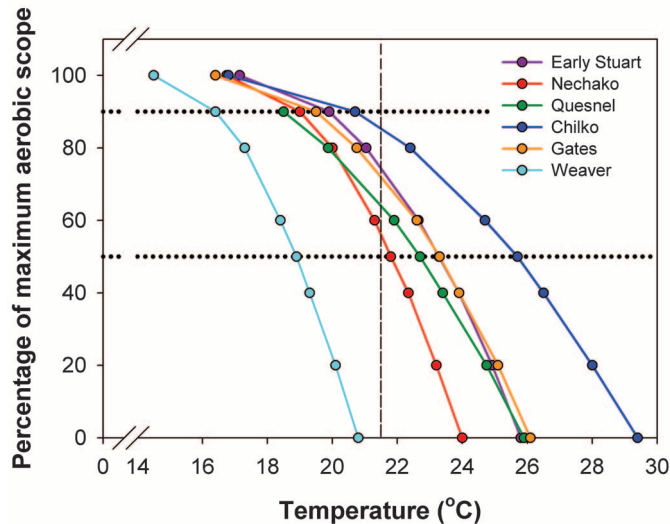
population-specific upper T_p [temperature corresponding to 90% of maximum aerobic scope, which includes current temperature maxima of 21.5°C (Fig. 4 and table S3)], could limit successful migrations due to a functional collapse in aerobic scope. Empirically, no sockeye salmon population has initiated river migration at a temperature exceeding 21°C (*27*), nor has a historic mean migration temperature been above 19°C (*6*). However, Chilko sockeye salmon may emerge as "superfish" with greater resilience to climate change by being able to maintain cardiorespiratory performance at higher temperatures. Conversely, Weaver and Nechako populations are especially susceptible to high temperature. If Weaver sockeye salmon continue to enter the Fraser River up to 6 weeks earlier than normal (*28*), exposing themselves to such high temperatures (Fig. 1A), high mortality en route will continue (*5, 26, 28*).

Although warming water temperatures are undoubtedly a global issue for fishes at the species level, we propose a concern at the population level for Fraser River sockeye salmon. Because current warming trends in the Fraser River (1.9°C during the past 60 years) (fig. S1) are expected to continue (*29*), survival of sockeye salmon populations will require some combination of behavioral adaptations (to avoid high temperatures by entering the river when it is cooler) and physiological adaptations (a higher T_p to increase high temperature tolerance). Substantial shifts in entry timing are unlikely due to energy and time constraints to achieve highly conserved spawning dates. On the other hand,

warming river temperatures could exert strong selective pressure for physiological adaptation. Physiological adaptation requires trait heritability, trait variability, and differential fitness. Evidence of all three have been presented here: local adaptation of cardiorespiratory traits, individual variability in these traits, and zero lifetime fitness for fish failing to complete their upriver migration. The salmonid genome clearly has the capacity for higher thermal tolerance [current thermal extremes are documented for redband trout that experienced 15° to 27°C diurnally, acutely tolerated 29°C, and demonstrated a plateau in aerobic scope at 26°C (*30*)], suggesting that there is potential for future physiological adaptation in Fraser River sockeye salmon. We suggest that adaptations at the level of the heart that sustain cardiac performance at high temperatures, such as the increased ventricular β-adrenoceptor density displayed in Chilko sockeye salmon, could be beneficial in this regard. The current challenge is determining whether the rates and extents of physiological adaptation for Fraser River sockeye salmon will allow them to adapt quickly enough to cope with the current warming trend.

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