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Energy Depletion and Stress Levels in Sockeye Salmon Migrating at the Northern Edge of their Distribution

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Abstract

 The physiological challenge for anadromous fish to migrate upriver is influenced by river temperature, but the impacts of river temperature can be difficult to predict due to an incomplete understanding of how temperature influences migration costs, especially in high-latitude (>60°N) ecosystems. To assess temperature influences on migrating Pacific salmon *Oncorhynchus* spp., we measured heat shock protein 70 (HSP70), as an indicator of cellular stress, and energy content of Sockeye Salmon *Oncorhynchus nerka* throughout their upriver migration in the Pilgrim River, Alaska. Although HSP70 was elevated as fish moved to the spawning grounds and was higher in fish with low energy content, HSP70 did not increase with warmer river temperatures. We verified in an experiment that HSP70 abundance in Sockeye Salmon does respond to temperatures above 20.5°C. Over the 4 years of sampling, energy content decreased at similar rates as Sockeye Salmon moved upstream. We expected Sockeye Salmon energy levels would be lower when migrating in warmer river temperatures; however, we found higher energy levels occurred with higher temperatures in the Pilgrim River. We hypothesize that the relationship between temperature and energy content is due to river temperatures often occurring below optimal temperatures for migration. Lower temperatures could be energetically costly or reduce migration rates, both of which would result in lower energy content with cooler temperature. Understanding interactions between environmental drivers and physiological responses will help managers anticipate future changes for Sockeye Salmon at the northern edge of their distribution.

River temperature can be a major driver of Pacific salmon *Oncorhynchus* spp. populations by influencing spawning migrations (Donaldson et al. 2009; Rogers and Schindler 2011; Jefferies et al. 2014; Bowerman et al. 2017). How the thermal regime of the river relates to both the migration timing (Rand et al. 2006; Donaldson et al. 2009; Hinch et al. 2012) and the migration rate (Quinn et al. 1997; Wagner et al. 2005; Mathes et al. 2010; Keefer et al. 2017) constrains the conditions experienced by migrating salmonids. Warm river temperatures can induce heat stress and alter the energetic cost of reaching the spawning grounds, thereby influencing spawning success for salmonids (Rand et al. 2006; Donaldson et al. 2009; Rogers and Schindler 2011; Hinch et al. 2012). The negative consequences of migrating during warm river temperatures can be lethal (e.g., Mathes et al. 2010; Hinch et al. 2012) or sublethal for Pacific salmon, and sublethal effects can include infectious disease (Wagner et al. 2005; Teffer et al. 2018) and low energetic condition for spawning (Rand et al. 2006; Keefer and Caudill 2016). Understanding if and how temperature influences stress and energetic conditions of migrating adults is a major need, as fish populations are increasingly at risk of enduring changes in river temperature (Isaak et al. 2012).

Across the range of Sockeye Salmon *Oncorhynchus nerka*, members of the species are adapted to their natal river and thus their thermal optimum is adaptive for river migration at the population level (Lee et al. 2003; Farrell et al. 2008; Eliason et al. 2011; Raby et al. 2015). How the thermal experience of migrating salmonids relates to their thermal optima for aerobic and metabolic scope influences the metabolic costs and energetic condition of the fish and ultimately the outcome of spawning (Lee et al. 2003; Farrell et al. 2008; Mathes et al. 2010; Eliason et al. 2014; Jefferies et al. 2014). Thus, due to the physiological challenge of migrating upriver to spawn and completing their life cycle, Sockeye Salmon are susceptible to changes in river conditions (Rand et al. 2006; Donaldson et al. 2009; Schindler and Rogers 2009; Snyder et al. 2015). In the Fraser River, British Columbia, near the southern end of their range, Sockeye Salmon were unable to swim upstream at temperatures above 20°C and even temperatures above 18°C caused physiological stress (Brett 1952, 1971; Donaldson et al. 2009). Similarly, at the southern edge of their distribution, Sockeye Salmon ceased migration at temperatures above 21°C in the Columbia River watershed (Farrell et al. 2008). Higher energy demands from warmer temperatures during the spawning migration have caused mortality due to physiological stress (Rand et al. 2006; Donaldson et al. 2009; Hinch et al. 2012). In addition to en route mortality, another potential consequence of prolonged high-temperature exposure in the river is prespawn mortality (Hinch et al. 2012). Prespawn mortality is the failure to spawn (e.g.,

failure to deposit eggs), despite reaching the spawning grounds, due to a lack of energy (Quinn et al. 2007) and/or infectious diseases (Wagner et al. 2005; Miller et al. 2014; Teffer et al. 2017, 2018; Bass et al. 2019), both of which have been linked to changing temperature.

There is limited information linking variability in river conditions with energy demands of Sockeye Salmon during spawning migrations in arctic and subarctic ecosystems (Rand et al. 2006; Lennox et al. 2016). From the few studies in high (>60°N) latitude systems, temperature has been found to influence migration timing, and more research is needed on how temperature affects energy and stress levels during spawning migrations (Mundy and Evenson 2011; Lennox et al. 2016; Carey et al. 2017). Moreover, exploring the influence of river temperatures in subarctic watersheds will help generalize the impact of in-river temperature to other Sockeye Salmon populations and help managers anticipate which environmental factors will influence energetic conditions of Sockeye Salmon during spawning migrations.

To understand how temperature influences the energetic conditions and spawning success of migrating adult Sockeye Salmon at the northern edge of their distribution, our objectives were to (1) measure energy depletion in Sockeye Salmon during their spawning migration, (2) investigate physiological stress from temperature in Sockeye Salmon, and (3) relate energy content of Sockeye Salmon at different points of the migration to their thermal experience. We measured energy content of fish with a nonlethal energy meter that estimates somatic energy levels and has been used previously on wild migrating adult Sockeye Salmon (Crossin and Hinch 2005). We used heat shock proteins to assess heat stress in the fish. Heat shock proteins are a group of highly conserved proteins that help maintain cellular function and increase in concentration with exposure to stressors, especially warm temperatures (Basu et al. 2002). Heat shock protein 70 (HSP70) increases in concentration in all tissues in response to thermal stress within hours and remains elevated for 5 to 7 d (Ackerman and Iwama 2001; Lund et al. 2003; Chadwick and McCormick 2017). Significant correlations have been found between higher gill HSP70 levels and stream temperature in wild Atlantic Salmon *Salmo salar* (Lund et al. 2003) and Brook Trout *Salvelinus fontinalis* (Chadwick et al. 2015). While heat shock proteins have been established as a useful marker for thermal stress, their application to salmonids in the wild is limited.

METHODS

Study area.— We examined the influence of water temperature on the energetic costs of migration and spawning success of Sockeye Salmon returning to the Pilgrim River (65.196°N, –165.409°W), Port Clarence District, near

Nome, Alaska. The distance from the mouth of the river to the spawning grounds on Salmon Lake is ~180 km, with an elevation gain of about 150 m. Sockeye Salmon spawn in Salmon Lake and upriver of the lake in the Grand Central River (Figure 1). Salmon Lake is a small lake (surface area = 7.49 km^2) with a maximum depth of 40 m near the headwaters of the Pilgrim River (Todd and Kyle 1997; Keith 2016).

Temperature.— Temperature was recorded at seven stations spread out from the mouth of the Pilgrim River to the headwaters in 2013, 2014, 2015, and 2016 (Figure 1). Temperature was recorded every 15 min from late June through August using TidbiT v2, HOBO Water Temp Pro v2 (Onset Computer Corporation 2013). Stream temperature data collection followed the standards suggested by Mauger et al. (2015). In the river, temperature loggers were secured to the river bottom and we assumed the river water was well mixed. In the lake, temperature loggers were at 1 m off the bottom (~25 m) and 1 m below the surface. Temperature profiles of the lake were also measured in July and August each year of the study (Keith 2016). Average, minimum, and maximum water temperatures during the spawning migration (day of year [DOY] 184–243; Carey et al. 2017) were compared among years at each temperature station along the migration route (Snyder et al. 2015; Tsang et al. 2016). Similarly, average temperatures for the total migration route were compiled across locations from the mouth of the river to the outlet at Salmon Lake.

Fish collection and measurements.— We collected Sockeye Salmon from three locations (Grantley Harbor, a weir, and Salmon Lake) in 2013, 2014, 2015, and 2016 on the Pilgrim River, except no fish were collected in Grantley Harbor in 2016 (Figure 1). In Grantley Harbor, Sockeye Salmon ($N = 41$) were collected in cooperation with subsistence harvesters using floating gill nets in late June and early July. At river kilometer (rkm) 100 of the Pilgrim River (measuring from its mouth in Grantley Harbor), Sockeye Salmon ($N = 352$) were collected at a fish-counting weir. The fish weir was operated during the summer by the Norton Sound Economic Development Corporation with assistance from the Alaska Department of Fish and Game (Keith 2016). The fish weir was operated from ice-out in late June until early September and was monitored 24 h/d and checked regularly. Sockeye Salmon begin passing through the fish weir at the end of June or early July and finish by late August (Carey et al. 2017). At the fish weir, we sampled Sockeye Salmon at multiple times in July and early August in 2013 (sampling events = 2), 2014 (sampling events = 4), 2015 (sampling events = 4), and 2016 (sampling events = 3). We collected Sockeye Salmon ($N = 247$) at the end of the spawning migration by beach seine in Salmon Lake in mid to late August of each year. Length (mideye fork length), sex, and energy content were
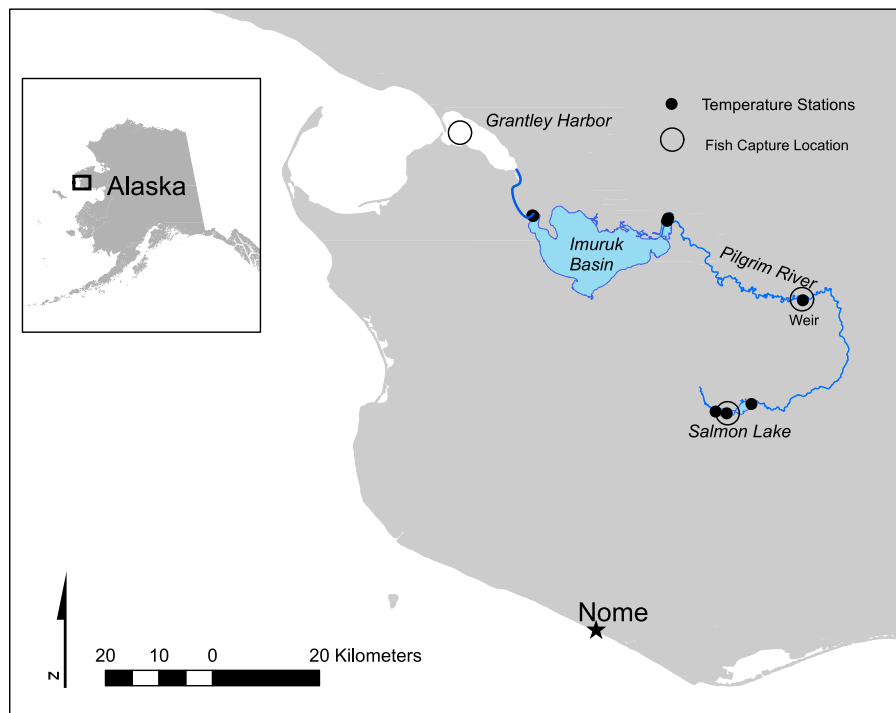

FIGURE 1. Map of the area of the spawning migration for Sockeye Salmon in the Pilgrim River, Alaska, indicating fish capture locations and water temperature monitoring stations. The airport in Nome is where air temperature data was recorded. [Color figure can be viewed at afsjournals.org.]

measured for all Sockeye Salmon. All data that support the findings of this publication can be found in Carey et al. (2019).

Physiological stress.— We used heat shock proteins (specifically HSP70) as a biomarker for cellular stress in Sockeye Salmon. To measure heat shock proteins, a muscle plug (6-mm dermal punch) was taken from the dorsal muscle (Crawford et al. 1977; Hanisch et al. 2010) of the fish at each collection site and immediately frozen in a dry nitrogen shipper. Additionally, a controlled laboratory experiment was conducted at the Trail Lakes Hatchery (Cook Inlet Aquaculture Association, Moose Pass, Alaska) to determine the temperature threshold for induction of HSP70 leading to increases in HSP70 abundance. Water temperature was controlled using Eheim Jager Tru-Temp 200 Watt Fully Submersible UL Approved Heaters. Two heaters were used per tank with an aerator for water circulation. Juvenile Sockeye Salmon individuals (87–114 mm fork length) underwent a temperature increase (1°C per hour) from 3.7°C to target temperatures. Temperature in each tank fluctuated slightly and the maximum recorded temperature was used as the treatment (12.0, 20.8, 21.8, and 24.0°C) for all subsequent analyses. A control with water temperature at a constant 3.7°C was also maintained to create five treatment levels. We conducted the experiment with five individual fish per aquarium and had at least two aquaria at each temperature. Temperature was monitored every 15 min using TidbiT v2, HOBO Water Temp Pro v2 (Onset Computer Corporation 2013). Fish were held at each treatment-level temperature for 4 h and then rapidly euthanized after temperature exposure. Entire fish were immediately frozen in a dry nitrogen shipper. Subsequently, fillets of dorsal muscle tissue were removed from individuals for analysis of HSP70.

Samples from the field collection and controlled experiment were analyzed at the U.S. Geological Survey S. O. Conte Anadromous Fish Research Laboratory, Turners Falls, Massachusetts. For the field (dermal punch) and experimental (fillet) samples, the muscle was separated from subdermal fat and skin and weighed to the nearest milligram. The muscle tissue was thawed and homogenized with Kontes Pestle Pellet handheld homogenizer (Thermo Fisher Scientific, Hampton, New Hampshire) in 10 volumes of SEID (150 mM sucrose, 10 mM EDTA, and 50 mM imidazole; pH 7.3 plus 0.1% deoxycholic acid). Homogenates were centrifuged at $3,000 \times g$ for 7 min at 4°C. A portion of the resulting supernatant was immediately diluted with an equal volume of 2× Laemmli buffer, heated for 15 min at 65°C, and stored at −80°C. A small volume of supernatant was used to determine total protein concentration in quadruplicate using the Pierce BCA Protein Assay kit (Thermo Fisher Scientific). Thawed samples were run on a 7.5% SDS-PAGE gel at 10 μg per lane with 5 μg Precision Plus protein standards

in a reference lane (Bio-Rad Laboratories, Hercules, California). Two lanes were reserved on each gel for a standard consistent tissue preparation reference to control for blot-to-blot variation. Following electrophoresis, proteins were transferred to Immobilon polyvinylidene difluoride transfer membrane (Millipore, Bedford, Massachusetts) at 30 V overnight in 25 mmol l-1 Tris, 192 mmol l-1 glycine buffer, pH 8.3. Immobilon polyvinylidene difluoride membranes were blocked with 5% nonfat dry milk in phosphate buffered saline plus 0.1% Triton X-100 (PBST) for 1 h at room temperature, rinsed in PBST, and exposed to primary polyclonal antibody specific for the inducible form of salmonid HSP70 (AS05061; Agrisera, Vannas, Sweden) at 1:25,000 dilution in PBST/tween with 5% nonfat dry milk for 1 h at room temperature. After rinsing in PBST, blots were exposed to goat anti-rabbit IgG conjugated to horseradish peroxidase diluted 1:10,000 in PBST and 5% nonfat dry milk for 1 h at room temperature. Blots were washed in PBST and incubated for 1 min in a 1:1 mixture of enhanced chemiluminescent solution A (396 μmol l-1 coumaric acid, 2.5 μmol l-1 luminol, 100 mmol l-1 Tris, pH 8.5) and enhanced chemiluminescent solution B (0.018% H_2O_2, 100 mmol l-1 Tris, pH 8.5) and then digitally imaged and quantified (Syngene PXi, GeneTools, Frederick, Maryland). All blots were normalized to the internal standard consistent tissue preparation and are represented as a ratio to the mean standard value that we refer to as HSP70 abundance.

To analyze the HSP70 abundance in the field, we plotted HSP70 abundance from Sockeye Salmon captured at the weir to the maximum temperature of the previous 5 d in the river and HSP70 from fish captured on the spawning grounds to the maximum temperature of the previous 5 d in the lake. Similarly, we plotted the relationship between HSP70 abundance and energy content (MJ/kg; see below) of individual fish at the midpoint of the migration (rkm 100) and on the spawning grounds. Next, we tested for presence (1) of elevated HSP70 abundance versus absence (0) using logistic regression with maximum 5-d temperature or energy content as a predictor variable. The HSP70 abundance in the field was considered elevated if the signal was >0.5 HSP70 abundance. Logistic regression models were fit using the glm function with a logit link assuming a binomial distribution in the Program R (R Development Core Team 2018). We assessed overdispersion and tested for the importance of maximum temperature using the chi-square (χ^2) statistic. If maximum temperature or energy content was significant in the logistic regression, we interpreted the log-odds ratio and calculated the probabilities of elevated HSP70 across the response variable. In the controlled experiment, the mean HSP70 abundance for Sockeye Salmon was compared across the maximum temperatures that occurred across treatment levels.

Energy content.— We determined the whole-body energy content of each fish using a Distell Model 692 Fish Fatmeter (Distell, West Lothian, Scotland). This hand-held energy meter emits a low-powered wave (frequency = 2 GHz, power = 2 mW) that interacts with water in the somatic tissues to estimate gross somatic energy and lipid levels. Microwave transmission is used commonly in the aquaculture industry for assessing the lipid content of finfish (Crossin and Hinch 2005) and has been used as a nonlethal tool in field studies (e.g., Cooke et al. 2006; Keefer et al. 2017). The energy meter has provided accurate estimates of somatic energy levels observed in wild migrating adult Sockeye Salmon (Crossin and Hinch 2005). The consistency across populations emphasizes the robustness of the calibration as populations differed in size, shape, rate of migratory energy use, and initial energy content.

Upon capture, we took readings on Sockeye Salmon at four spots along the dorsal surface just above the lateral line (Colt and Shearer 2001; Crossin and Hinch 2005). For the analysis, we focused on two measurements: (1) directly behind the opercular flap and (2) centered beneath the anterior insertion of the dorsal fin, as suggested by Crossin and Hinch (2005). Using relationships described by Crossin and Hinch (2005), we log-normally transformed all energy meter data and converted the energy meter readings (x) to estimates of gross somatic energy ($1.7338x + 5.4886$), an approach that has been applied successfully in other studies (Roscoe et al. 2010). We compared our energy content readings to the range found by Crossin and Hinch (2005) and Roscoe et al. (2010) to ensure our values on average were within the range found in other systems. The calibration of the energy meter is applicable to Sockeye Salmon throughout its range, and the relationship between lipid percentage, gross energy content, and energy meter readings did not differ among years, sex, or populations of Sockeye Salmon in the Fraser River (Crossin and Hinch 2005).

For all analyses, we considered males and females separately, as males develop a pronounced hump on their back, allocating energy differently during the spawning migration (Groot et al. 1995). We analyzed the energetic condition of Sockeye Salmon at the beginning, middle, and end of their migration across years. First, we used an analysis of covariance (ANCOVA) to determine if the rate of energy depletion differed among annual maximum temperature by testing for differences in the slopes of the energy depletion from the mouth of the river to the spawning grounds (Crossin et al. 2004b). Annual maximum temperature was included in the ANCOVA as a factor along with location. We did not include 2016 in the ANCOVA due to missing data at the mouth of the river. Next, we examined whether the energy content of Sockeye Salmon at the midpoint of the migration (rkm 100) was related to the maximum water temperature observed during the migration from the mouth of the river to rkm 100 using linear regression. The migration rate was assumed to be ~25 km/d (English et al. 2005; Gilk et al. 2011), suggesting that Sockeye Salmon would take ~5 d to swim from the mouth of the river to the midpoint of the migration and ~10 d to reach Salmon Lake. We also considered migration times of 3, 7, and 10 d to the weir. For the linear regression models, we tested the assumptions of independent values and normally distributed errors with residual plots. All statistical analyses were conducted in the Program R (R Development Core Team 2018).

RESULTS

Pilgrim River Water Temperature

River temperatures had similar maximum and minimum values across years, and temperatures were warmer in the lower river, with the warmest location for average and maximum temperatures in Imuruk Basin (Table 1; Figure 2). For all years, the lowest minimum temperatures occurred higher in the migration route, and the coldest location was above Salmon Lake in the Grand Central River. The seasonal patterns of temperature varied among years, with peak temperatures occurring at different times during the migration (Figure 2). Within a year, seasonal patterns of average daily temperature were similar across locations. In 2013, temperatures increased at the start of the migration, peaking in mid-July (DOY = 193) and then dropping slightly. In 2014, the thermal regime was more dynamic, with an initial increase in water temperature at all locations followed by a drop back to initial values in late July (DOY = 226). The thermal regime in 2015 was similar to 2013 in that there was an initial increase in temperature to reach the maximum value of the season in mid-July. The maximum temperature for 2016 in the migration route was recorded in early July, with temperatures then fluctuating ~5°C through the end of August.

Heat Shock Protein 70 Abundance

No fish at the mouth of the river were found to have elevated HSP70 abundance. At the midpoint of the migration (rkm 100), only 3 out of 66 had elevated levels of HSP70 (Figure 3A), while on the spawning grounds 21 out of 36 samples had elevated levels of HSP70 (Figure 3B). A logistic regression comparing elevated (>0.5 HSP70 abundance) to nonelevated individuals across the maximum 5-d temperatures in the lake was significant ($\chi^2 = -2.5$, df = 1, $P = 0.01$). An increase in temperature reduced the odds of elevated HSP70 by 51% (log-odds ratio = −0.7). Overdispersion was not indicated; however, the logistic model had a high response variance (residual deviance/residual degrees of freedom = 1.23). For

TABLE 1. The average (Avg), minimum (Min), and maximum (Max) river temperatures (°C) during the spawning migration across locations in the Pilgrim River, Salmon Lake (primary spawning area), and Grand Central River in 2013, 2014, 2015, and 2016.

| Location	2013			2014			2015			2016		
	Avg	Min	Max	Avg	Min	Max	Avg	Min	Max	Avg	Min	Max
Pilgrim River												
Grantley Harbor	13.6	9.8	15.7				14.0	11.7	17.0	14.6	12.8	17.8
Tusuk Channel	14.5	11.7	16.1	13.8	11.5	16.6	14.5	12.1	16.4	14.9	13.4	17.3
Imuruk Basin	14.8	11.8	17.3	14.9	9.9	18.7	15.2	12.3	17.4	15.2	12.8	18.3
Weir	12.4	8.4	15.8	12.6	8.3	15.6	13.0	9.9	15.1	13.4	10.6	16.5
Outlet Salmon Lake	12.5	8.4	14.4	13.3	9.5	17.0	13.4	9.7	15.9	14.5	13.1	17.3
Salmon Lake												
Surface	11.9	7.4	14.6	12.9	9.6	16.4	13.4	9.7	15.9	13.8	12.8	15.2
Bottom	3.2	2.9	3.3	3.7	3.4	3.9	4.4	4.4	4.4	5.6	5.7	5.4
Grand Central River	8.5	4.4	11.4	9.1	5.7	12.0	10.0	6.9	11.8	10.2	8.8	12.7
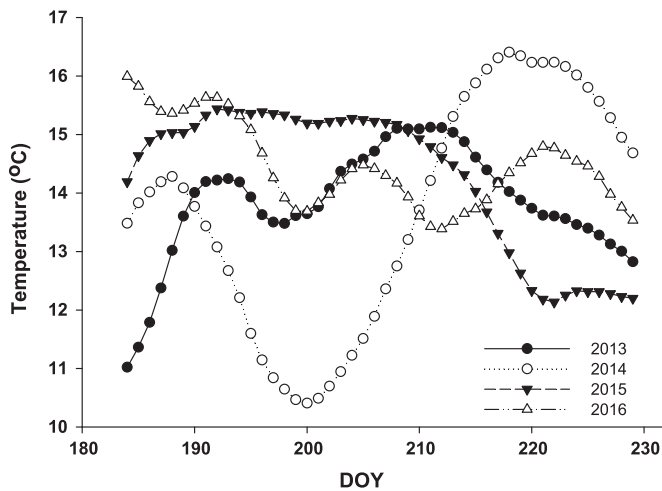
FIGURE 2. The 7-d moving average of river temperature during the spawning migration averaged across all locations of the migration route in the Pilgrim River to the spawning grounds on Salmon Lake. River temperature data includes measurements from 2013, 2014, 2015, and 2016 across days of the year (DOY).

carcasses in the lake, we found 38 out of 48 carcasses had elevated levels of HSP70 (Figure 3C). Using a logistic regression, we found no relationship between maximum 5-day temperature in the lake and elevated levels of HSP70 abundance in carcasses ($\chi^2 = -0.61$, $P = 0.54$).

The few fish with elevated HSP70 abundance had lower energy content at the midpoint of the migration (Figure 3D). On the spawning grounds in Salmon Lake, energy content of the fish was significant in predicting elevated HSP70 abundance in live fish ($\chi^2 = -2.5$, $P = 0.01$). An increase in energy content reduced the odds of elevated HSP70 by 93% (log-odds ratio = −2.68). The logistic model had a high response variance; however,

overdispersion was not indicated (residual deviance/residual degrees of freedom = 1.18). The logistic regression was not significant between energy content and elevated HSP70 abundance in carcasses ($\chi^2 = -0.61$, $P = 0.54$).

Laboratory Experiment

In the laboratory, HSP70 abundance did not exceed 0.5 in the cooler treatments (4°C and 12°C; Figure 4). Temperatures above 21°C resulted in higher HSP70 abundance. Heat stress occurred in Sockeye Salmon in the warmer treatments in which the maximum temperatures fluctuated to above 21°C (Figure 4). Thus, the threshold for the induction of HSP70 is between 13°C and 21°C for juvenile Sockeye Salmon.

Energy Content of Sockeye Salmon

The length of Sockeye Salmon averaged 539 mm (range = 450–640 mm) for females and 580 mm (range = 485–650 mm) for males across years in the Pilgrim River. Energy at the freshwater entry ranged from 7.00 to 9.78 MJ/kg for females and from 7.08 to 10.29 MJ/kg for males (Figure 5). At the freshwater entry and midpoint of the migration (rkm 100), females had a higher average energy level than males within each year, but they had similar energy levels within and across years in the spawning area of Salmon Lake. Variation in energy content among individuals occurred at all points along the migration route each year (Figure 5). Fish caught as they entered the river in Grantley Harbor had energy content values above 7 MJ/kg. The largest range in energy content occurred at the midpoint of the migration (rkm 100) for females and males. At rkm 100, the majority of fish were above 6 MJ/kg, with the highest values measured in 2013 and lowest values in 2016. On the spawning grounds, the range of energy levels was smaller than the energy values
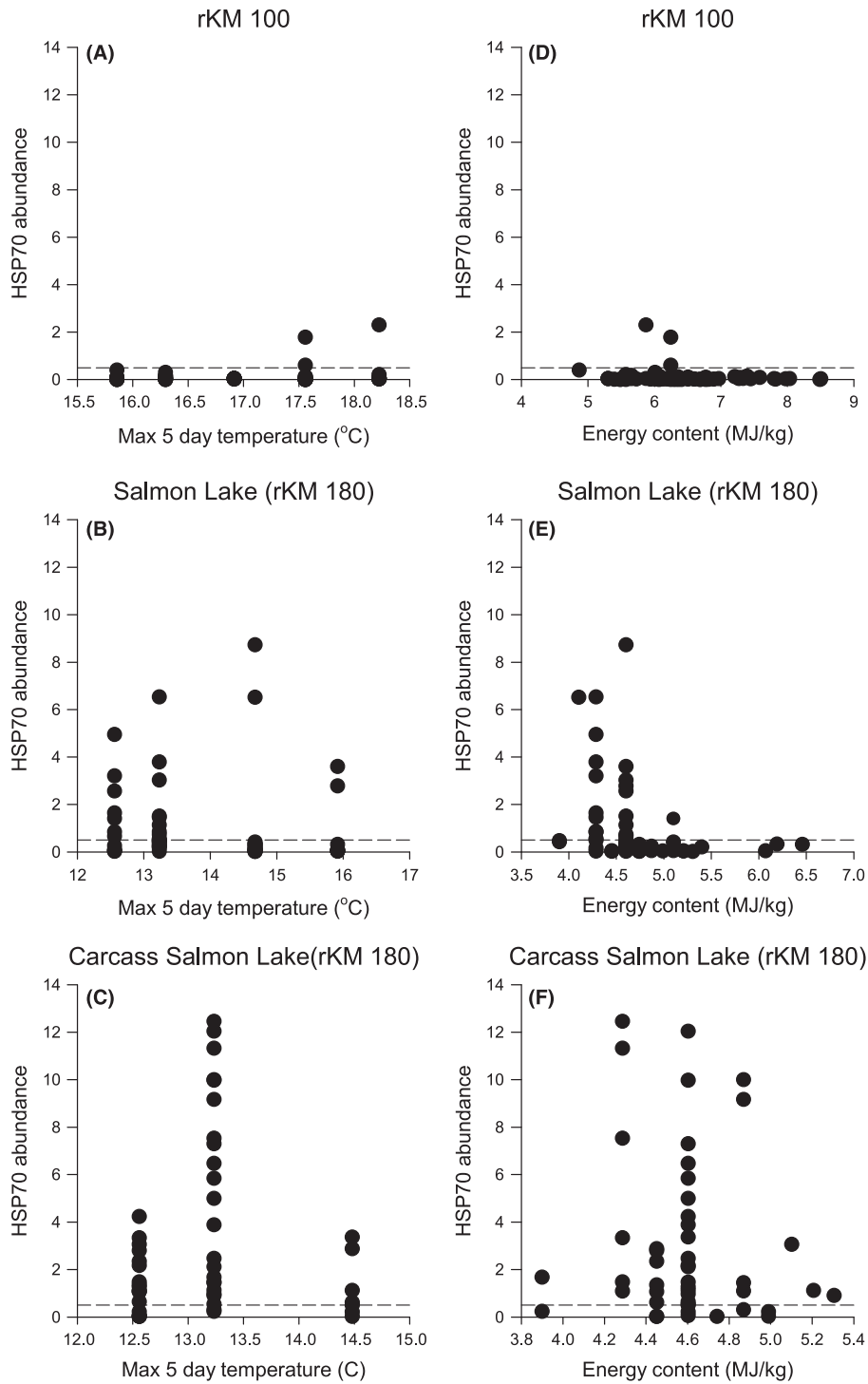
FIGURE 3. Muscle HSP70 abundance plotted against maximum 5-d temperature **(A)** in the river at the midpoint of the migration (rkm 100), **(B)** in the lake for live fish, and **(C)** in the lake for carcasses. Muscle HSP70 abundance is also plotted against energy content **(D)** of the fish at rkm 100, **(E)** for live fish in the lake, and **(F)** for carcasses in the lake. The dashed line indicates the value (>0.5) above which HSP70 abundance was elevated in the muscle tissue.

observed at the midpoint of the migration and the majority of fish occurred below 6 MJ/kg. In 2013 and 2016, several individuals had energy values near 4 MJ/kg on the

spawning grounds. No differences were found in the slopes of the energy depletion with river distance across annual maximum temperature for females (ANCOVA: $F = 0.32$,
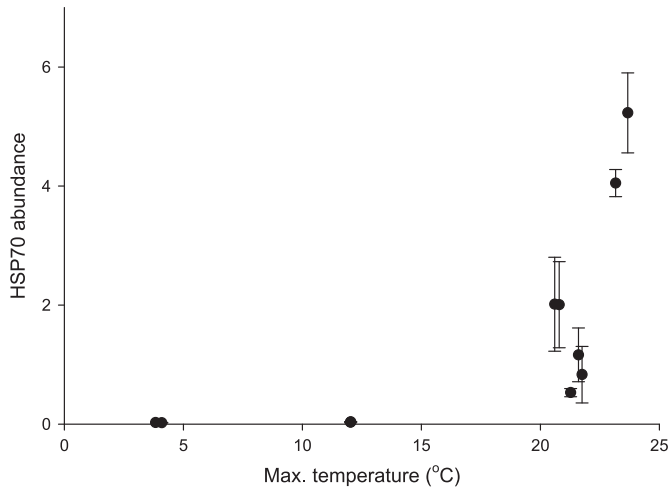
FIGURE 4. The mean (error bars show SE) of the HSP70 abundance for juvenile Sockeye Salmon plotted against maximum temperature in tank experiments at 4.1°C ($N = 6$), 12.0°C ($N = 4$), 20.8°C ($N = 8$), 21.8°C ($N = 9$), and 23.7°C ($N = 9$).

df = 2, $P = 0.75$) or males (ANCOVA: $F = 0.81$, df = 2, $P = 0.52$). Energy levels were significantly different across locations for females ($F = 26.9$, df = 1, $P = 0.01$) and males ($F = 97.01$, df = 1, $P = <0.01$), but no differences were found among annual maximum temperatures for females ($F = 0.69$, df = 2, $P = 0.57$) or males ($F = 3.70$, df = 2, $P = 0.16$).

There was a positive relationship between higher somatic energy levels for females with maximum river temperature at rkm 100 for migration timing of 3 d ($R^2 = 0.56$, $P = 0.03$), 5 d ($R^2 = 0.62$, $P = 0.02$; Figure 6), 7 d ($R^2 = 0.66$, $P = 0.01$), and 10 d ($R^2 = 0.66$, $P = 0.02$). Similarly, the energy content of males had a positive relationship with maximum river temperature for all migration rates of 3 d ($R^2 = 0.51$, $P = 0.05$), 5 d ($R^2 = 0.56$, $P = 0.03$; Figure 6), 7 d ($R^2 = 0.55$, $P = 0.03$), and 10 d ($R^2 = 0.54$, $P = 0.04$).
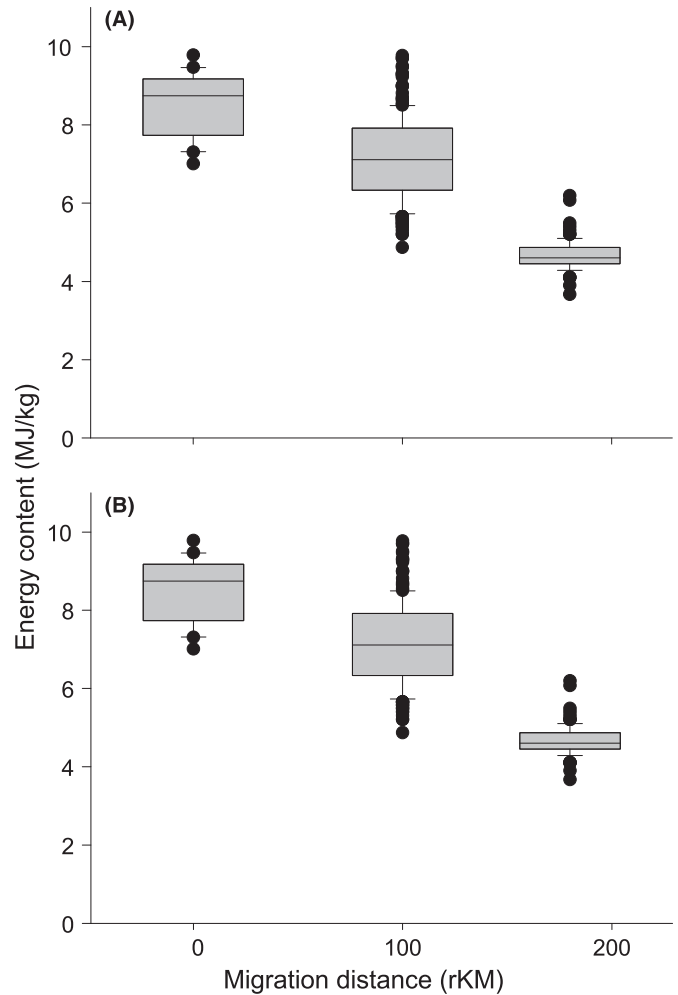

FIGURE 5. Box and whisker plots of energy content for (A) female Sockeye Salmon and (B) male Sockeye Salmon at freshwater entry (rkm 0), at the midpoint of the migration (rkm 100), and on the spawning grounds (rkm 180) in the Pilgrim River. The horizontal line in each box represents the median, the box dimensions represent the 25th to 75th percentile ranges, the whiskers show 10th to 90th percentile ranges, and the black dots are outliers.

DISCUSSION

Energy levels of Sockeye Salmon had similar values and rates of decline during the spawning migration among sampling years. The energetic conditions of Sockeye Salmon at the mouth of the Pilgrim River were similar to Sockeye Salmon entering other freshwater systems in lower latitudes (Crossin et al. 2004a, 2004b; Crossin and Hinch 2005). Conditions in the ocean during the marine phase of their life history influence the energetic condition of the fish at their freshwater entry (Kovach et al. 2015). The largest range of energy content was found at the midpoint (rkm 100) of the migration, and no fish were found below 4 MJ/kg, the threshold of energy content below which the spawning migration will be unsuccessful for

Sockeye Salmon (Crossin et al. 2004a). The energy values of Sockeye Salmon caught on the spawning grounds of Salmon Lake were similar to salmonids collected on spawning grounds in other systems with energy densities nearing 4 MJ/kg. Also, we found no relationship between body length and energy content at any point during the migration in concordance with other studies (Hendry and Berg 1999).

The temperatures observed in the Pilgrim River did not induce a strong response in HSP70 abundance of Sockeye Salmon as the temperatures observed mostly fall below the expected threshold for thermal stress of Sockeye Salmon (Brett 1952, 1971; Donaldson et al. 2009). In the laboratory, Sockeye Salmon had elevated HSP70 abundance
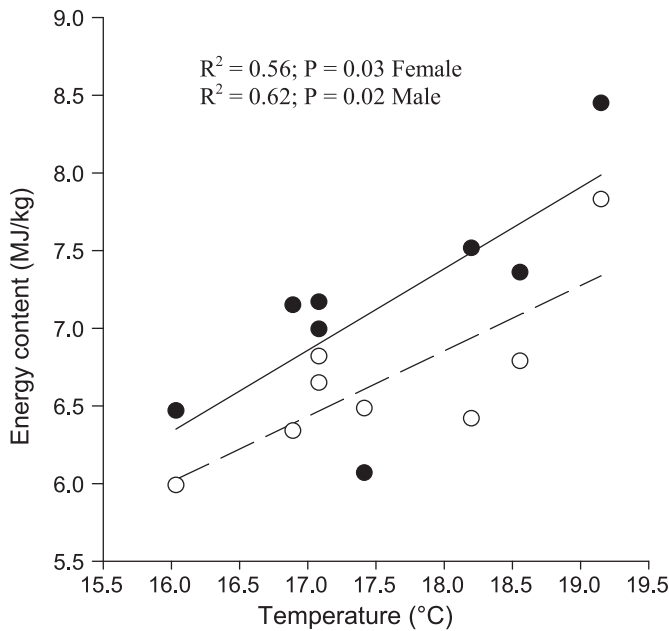
FIGURE 6. The energy content (MJ/kg) as a function of maximum temperature (°C) calculated for Sockeye Salmon females (filled dots) and males (open dots) migrating from the mouth of the river to the midpoint (rkm 100) of the migration. Migration rate was estimated at 5 d from freshwater entry to rkm 100 of the migration route.

when exposed to water temperatures above 21°C. Determining more precisely the temperature that induces heat stress in Sockeye Salmon in a controlled environment is a necessary next step and will increase the value of this biomarker to be broadly applicable across Sockeye Salmon populations in arctic and subarctic ecosystems. There is also a need to explore other biomarkers (e.g., Teffer et al. 2017) in understanding heat stress in adult salmonids and test heat responses at all life history stages. A limitation of the controlled experiment is the use of juvenile Sockeye Salmon to assess HSP70 responses of migrating adults as juveniles may have a different HSP70 response to high temperature given their preferred temperature range.

Interestingly, the energy content of individuals had a relationship with HSP70 abundance in Sockeye Salmon from the field collection. Individuals with elevated levels of HSP70 were at the lower end of the range of energy densities observed at each stage of the migration. On the spawning grounds, the energy content level corresponding to a probability of elevated HSP70 was similar to the energy level of ~4 MJ/kg needed for spawning success (Crossin and Hinch 2004). It should be noted that there was substantial variation of HSP70 abundance on the spawning ground, with many fish having low baseline levels. In a captive, aquaculture population of Sockeye Salmon on Vancouver Island maintained at temperatures less than 16°C, we observed more fish with elevated

HSP70 as reproductive migration progressed, but not all mature fish had elevated HSP70 abundance even at the peak of spawning (S. D. McCormick, J. M. Shrimpton, J. W. Heath, and A. M. Regish, U.S. Geological Survey, Leetown Science Center, unpublished results). These results and the present study suggest that sexual maturation in salmonids does not in and of itself result in increased HSP70 abundance but may increase its propensity for induction by other factors. There has been surprisingly little work done on cellular stress and oxidative damage during upstream migration, spawning, and senescence of Pacific salmon (Jefferies et al. 2014). Higher oxidative cardiac DNA damage was observed in Pink Salmon *O. gorbuscha* on the spawning ground compared with river entry, but no difference was seen in the white muscle (Wilson et al. 2014). Previous research on Rainbow Trout *O. mykiss* indicates that social interactions can result in increased HSP70 for both dominant and subordinate fish (Currie et al. 2009). We hypothesize that the increased HSP70 abundance observed in the present study may be due to social interactions or other stressors experienced by individuals during migration and on the spawning grounds, and that these responses are greater in fish with lower energy content. There is a clear need for increased research on the impact of sexual maturation and senescence on HSP70 levels in Pacific salmon.

Temperature can be a major driver of salmonid population dynamics by determining the success of spawning migrations through condition-dependent mortality (Donaldson et al. 2009; Rogers and Schindler 2011); however, water temperatures remained below 19°C during the spawning migration in the Pilgrim River from 2013 to 2016. The observed water temperatures were below the range of temperatures linked to Sockeye Salmon mortality in other systems, such as the Fraser River, British Columbia (Donaldson et al. 2009; Hinch et al. 2012). Warm temperatures have reduced the number of Sockeye Salmon returning to successfully spawn in the Fraser River by increasing the energetic costs of migration (Rand et al. 2006; Hinch et al. 2012). Sockeye Salmon in the Fraser River are unable to swim upstream in temperatures above 20°C (Donaldson et al. 2009). In the Columbia River watershed at the southern edge of their distribution, 20–21°C is the temperature threshold for blocking migration (Keefer et al. 2008). As temperatures remained below stressful thresholds found in other systems and migrating adults did not indicate elevated levels of HSP70 abundance, it is not surprising that rates of energetic decline for Sockeye Salmon we observed during the spawning migration were similar among years and across annual maximum temperatures during the migration period.

When we examined the thermal regime experienced by migrating Sockeye Salmon, we found a positive relationship

with maximum temperature indicating higher somatic energy occurred with higher temperatures in males and females. The unexpected result of a positive relationship for Sockeye Salmon energy content with temperature is possibly due to the influence of temperature on migration rate. Previous research on the large Fraser River indicates that cooler temperature results in slower migration rates that lead to greater time spent in the river prior to spawning (Hanson et al. 2008). If applicable to more northern rivers such as the Pilgrim River, then colder water temperatures may reduce migration rates leading to more time for energy depletion as fish migrate to the spawning grounds more slowly. Testing the influence of temperature on migration rate and their connection to differences in energy use will be an important next step for understanding the impact of temperature on migration and spawning success throughout the range of Sockeye Salmon.

The positive relationship between energy content of Sockeye Salmon and temperature could also be caused by the bell-shaped curve for the thermal optimum of aerobic scope (Lee et al. 2003; Farrell et al. 2008; Lea et al. 2016; Sinclair et al. 2016; Speers-Roesch and Norin 2016). Physiological function, such as aerobic scope, decreases above and below an optimal temperature (Farrell et al. 2008; Eliason et al. 2014). Across the range of Sockeye Salmon, aerobic scope peaks around modal river temperatures encountered during upriver migration, suggesting species are adapted to their natal river, and thus thermal optimum for aerobic scope is adaptive for river migration at the population level (Lee et al. 2003; Farrell et al. 2008; Eliason et al. 2011; Raby et al. 2015). Our expectation was that Sockeye Salmon would be adapted to river conditions of the Pilgrim River, and they seem to do well at the average temperatures of the river during the spawning migration. The unexpected result was that Sockeye Salmon are energetically challenged at the low end of the temperature range observed at this high latitude. Therefore, the Pilgrim River appears to range below the optimal temperature for Sockeye Salmon migration, resulting in a positive effect on somatic energy of increasing temperature.

At the southern distribution of Sockeye Salmon, the collapse of aerobic scope due to warmer river temperature is an important mechanism leading to high mortality in the Fraser River from warm temperatures (Lee et al. 2003; Farrell et al. 2008). Lee et al. (2003) demonstrated the metabolic optima for two different stocks (17.5°C for Gates Creek and 15.0°C for Weaver Creek) of Sockeye Salmon within the Fraser River at the southern end of their distribution with scopes for activity of 13.9–19.3°C (Gates Creek) and 12.8–16.2°C (Weaver Creek). Eliason et al. (2011) identified the Weaver Creek Sockeye Salmon, the population experiencing the coldest temperatures in their data set of the Fraser River, with a thermal optimal temperature of 14.5°C. During our sampling years, Sockeye Salmon often experience values below these optimal temperatures in the Pilgrim River. There is a need to specify the thresholds of negative effects from warmer temperatures for Sockeye Salmon in this high-latitude river.

Another process by which temperature and stress could influence energy content of migrating Sockeye Salmon is by delaying maturation. Stress from warm temperatures delaying maturation has been suggested as a mechanism to create higher nongonadal energy content by delaying conversion of stored energy into secondary sexual characteristics and gonads at the southern distribution of Sockeye Salmon (Bass et al. 2018). It is possible that colder temperature (that less than optimal for reproduction) could have a similar impact to delay maturation and alter the timing of energy conversion. To understand interannual variability in spawning success, there is a need to understanding how temperature in the Pilgrim River influences energy conversion during the migration to the spawning grounds. Beyond temperature, other factors that can cause stress should also be evaluated for high-latitude systems.

The influence of spawning lake temperature and residence time in the lake is another research gap for understanding spawning success of Sockeye Salmon. The thermal regime and residence time in spawning lakes is a determinant of spawning success in lower latitude systems such as the Fraser River (Wagner et al. 2005; Hinch et al. 2012). The residence time in Salmon Lake will influence the thermal regime fish are exposed to; however, temperatures in the lake apparently did not reach stressful levels during our sampling years. Across years, the surface temperature remained below 16.5°C. A better understanding of how returning adults use the lake habitat is necessary to improve our understanding of spawning success at the northern edge of their distribution.

Summary

Water temperature appears to influence the energy content of Sockeye Salmon but has not warmed enough to increase the energetic costs of migration. Rather, Sockeye Salmon that migrate during warmer periods of the migration have a higher energy content. Survival and fitness consequences of the exposure to different temperatures are ongoing management issues (Keefer and Caudill 2016). In the Pilgrim River, a better understanding of temperature experience along the migration route, migration rates, and behavioral thermal regulation is needed to determine the influence of river temperature on migrating Sockeye Salmon. Understanding the status of interactions between environmental drivers and biological responses will help managers anticipate future changes and make informed decisions about development that could influence the sustainability of Sockeye Salmon populations.

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