

Expanded, compressed, or equal? Interactions between spawning window and stream thermal regime generate three responses in modeled juvenile emergence for Pacific salmon

Luca A. Adelfio^{a,b}, Steven M. Wondzell^c, Nathan J. Mantua^d, and Gordon H. Reeves^c

^aUSDA Forest Service, Chugach National Forest, Cordova Ranger Station, P.O. Box 280, Cordova, AK 99574, USA (former affiliation);

^bUSDA Forest Service, Huron-Manistee National Forests, Mio Ranger Station, 107 McKinley Road, Mio, MI 48647, USA (current affiliation); ^cUSDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA; ^dSouthwest Fisheries Science Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA

Corresponding author: Luca A. Adelfio (email: luca.adelfio@usda.gov)

Abstract

Climate warming poses challenges to native fish, particularly at high latitudes. We used incubation models to explore how interactions between spawning timing and daily varying water temperature affected emergence timing for five species of Pacific salmon in 33 thermally diverse streams in south-central Alaska. Interactions between spawning timing and stream thermal regime led to three different emergence timing responses: (1) “expanded” by typically 2–3 times the duration of the spawning window for summer spawning salmon at streams with a large annual water temperature range; (2) “equal” in duration to the spawning window, regardless of spawning timing, at streams with upwelling groundwater; and (3) “compressed” for late-spawning salmon where water temperature was cooler at spawning than at emergence. Across all sites, a ± 15 -day range in spawning timing had influence similar to anomalously warm winters ($+2$ °C to $+3$ °C) on the emergence timing window. Differences among species, spawning timing, and thermal regimes suggest that a range of adaptations in spawning behavior will likely enable Pacific salmon populations to accommodate shifting thermal regimes during their early life history.

Key words: Pacific salmon, egg incubation, spawning timing, stream temperature

1. Introduction

Climate change is affecting phenology, the seasonal timing of life-history events, profoundly altering interactions between biota and their habitat (Inouye 2022). Shifts in phenology may be adaptive, maintaining synchrony during a period of change, or maladaptive, creating a trophic mismatch that decreases fitness (Parmesan 2006; Ohlberger et al. 2014; Woolway et al. 2021). As the climate continues to warm rapidly, understanding linkages between habitat, temperature, and phenology will be increasingly important to better anticipate the effects of climate change on organisms and ecosystem services.

Pacific salmon (*Oncorhynchus* spp.) are ecologically, socially, and economically valuable fishes that inhabit broad native and introduced ranges (Quinn 2007). They exhibit complex life histories that appear highly synchronized with local environmental conditions (Crozier et al. 2008). The ability to rapidly develop local adaptations in phenology has, historically, allowed them to thrive throughout periods of environmental change and after sudden introductions into novel

habitat (Quinn et al. 2000; Gharrett et al. 2013). Rising water temperature associated with global climate change poses substantial challenges and threats to Pacific salmon throughout their life cycle (Bryant 2009; Mantua et al. 2010; Isaak et al. 2012). Shifts in phenology are anticipated to be increasingly important for self-sustaining Pacific salmon populations as the climate warms (Crozier et al. 2008; Manhard et al. 2017).

The embryo, immotile amongst the streambed gravel of the natal stream, is perhaps the Pacific salmon life phase that is most sensitive to climate change (Martin et al. 2020). Water temperature is the major driver of the egg-development rate, largely controlling the duration of incubation and heavily influencing egg-to-fry survival and juvenile size-at-emergence (Murray and McPhail 1988; Beachum and Murray 1990). Spawning phenology has generally been adapted to the seasonal cycle in local freshwater temperature, known as the stream thermal regime, to help synchronize it with egg development and the emergence-timing window such that all life stages experience favorable environmental conditions (e.g.,

food resources, flow regime, and habitat accessibility) to promote survival of juvenile offspring (Holtby et al. 1989; Quinn et al. 2000; Granath et al. 2004; Campbell et al. 2019; Kaylor et al. 2021). Under rapid environmental change, spawning timing can adapt much faster than egg characteristics (Quinn et al. 2002; Dickerson et al. 2005; Tillotson et al. 2019), so the range of spawning timing and the adaptive capacity currently present within a population are likely important components of resilience in the face of rapid climate-driven environmental changes (Crozier et al. 2008).

Stream thermal regimes typically vary greatly within the streambed incubation environment, within a stream network, and between adjacent watersheds, providing a complex mosaic of incubation water temperatures across the spawning areas of even a single salmon population (Steel et al. 2012; Adelfio et al. 2019; Kaylor et al. 2022). It is generally understood that a thermally complex landscape with different water sources (e.g., meltwater vs. rain) and residence time in the ground (e.g., shallower precipitation-fed vs. deeper groundwater flows) may increase diversity in early life-history phenology within a population, potentially increasing adaptive capacity in the face of environmental change (Sparks et al. 2019).

Further, interannual and decadal variation observed in water temperature can have substantial effects on the duration of egg incubation. Even seemingly small increases in mean water temperature during the incubation period (e.g., 1 °C) can accelerate development by weeks (Beacham and Murray 1990). Temporal variability in freshwater temperature and flow is experienced by both the spawning adults and the developing embryos, requiring plastic responses by individuals (Beechie et al. 2008). Clearly, spawning salmon cannot forecast the temporal variations in water temperatures that their offspring will experience over the duration of the egg-incubation period. At the population level, individuals spawning over a window of time may promote population persistence by expanding the window of emergence, increasing the likelihood that at least a subset of the cohort will emerge into favorable environmental conditions (Rooke et al. 2019; Sparks et al. 2019).

As the climate warms, the impacts on stream thermal regime are highly heterogeneous, even on watershed and stream-reach scales, owing to interactions between the geologic, topographic, and hydrologic drivers that affect water temperature (e.g., Arismendi et al. 2013; Ficklin et al. 2014; Lisi et al. 2015). For example, water temperature during the typical incubation period for coho salmon (*Oncorhynchus kisutch*) was considerably more sensitive to climate variation in streams fed by precipitation through shallow, near-surface flow pathways as compared to adjacent streams fed by deeper upwelling groundwater (Adelfio et al. 2019). Modeling predicted that warmer, rainier winter conditions would shorten egg development for coho salmon by up to 3 months in the precipitation-fed streams but would have little effect on egg development in the adjacent groundwater-fed streams. This suggests substantial variability in the potential impacts of climate change on egg development, even on a small spatial scale. The diversity in emergence phenology within a population may be particularly important to resilience in the early

life stages; however, the mechanisms underlying emergence variability remain understudied.

Beer and Steel (2018) showed that the duration of the emergence timing window is influenced by interactions between spawning timing and water temperature. For salmon that spawn in summer or early autumn, water temperatures are usually warmer at the beginning of the incubation period than at the end of the incubation period the following spring. As a result, an embryo must incubate for several more days at the end of the incubation period to accumulate the same thermal energy gained on a single day near the beginning of the incubation period. Thus, a one-day change (delay or advance) in spawning timing can change (lengthen or shorten, respectively) the duration of incubation by more than one day. For salmon that spawn in late autumn, water temperatures are often colder at the beginning of the incubation period than at the end of the incubation period (the following spring), so developing embryos can accumulate more thermal units in a single day at the end of the incubation period than over several days at the beginning of the incubation period.

Beer and Steel (2018) recognized this phenomenon and identified an “expansion-compression threshold date (E-C threshold).” Spawning before the E-C threshold results in an “expanded” emergence timing window, whereas spawning after the E-C threshold results in a “compressed” emergence timing window (Fig. 1). As a result of expansion and compression effects, spawning timing can be an important driver of emergence timing variability; however, it remains unclear how the magnitude of effects may vary within and among streams and across species life histories.

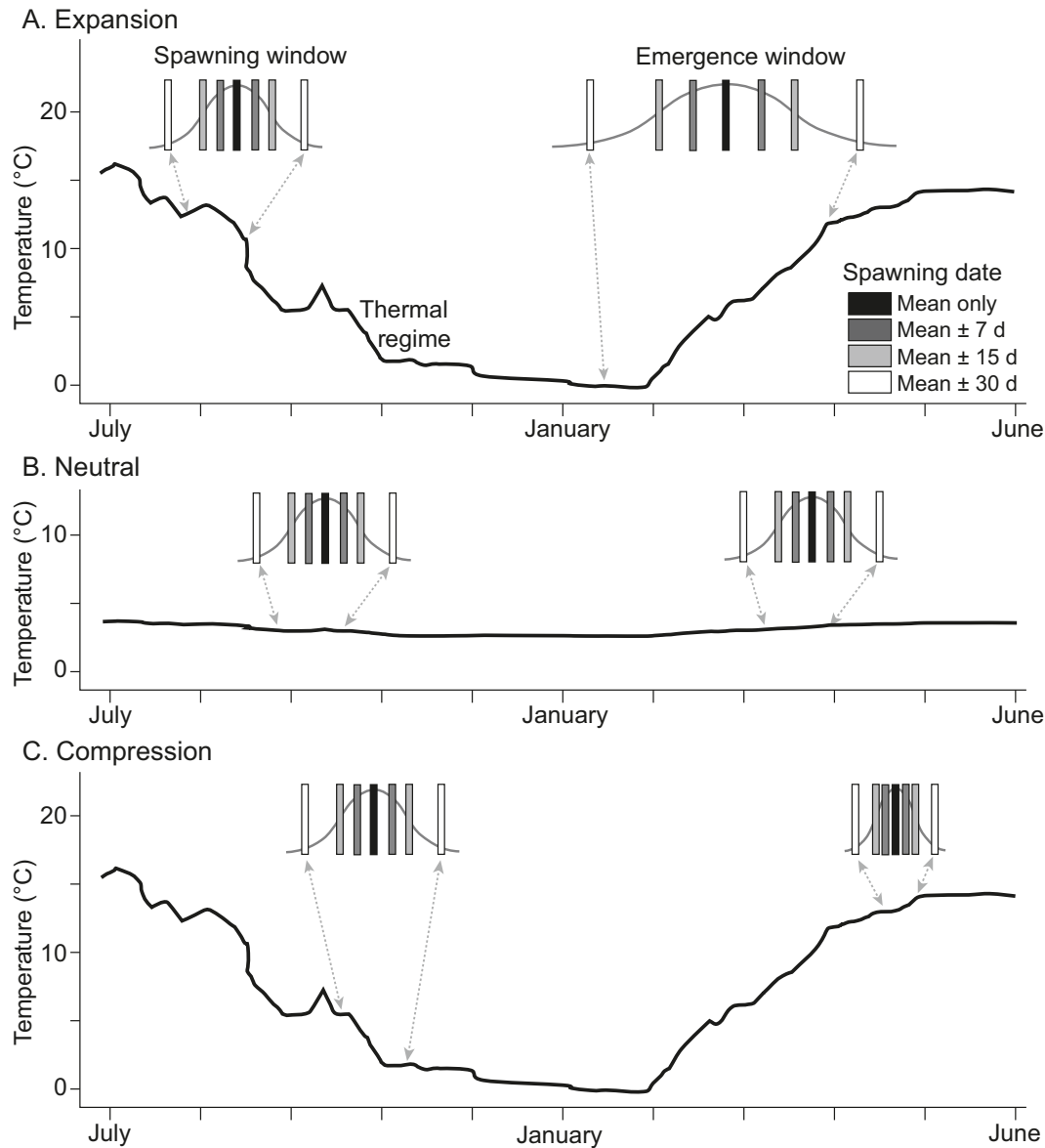
Here, we used incubation models for Pacific salmon as a tool to explore how interactions between spawning timing and stream thermal regimes can drive variability in modeled emergence timing for five species of Pacific salmon. Specifically, we used water-temperature observations collected at 33 spawning sites in southcentral coastal Alaska and seven spawning-timing scenarios as inputs for empirically derived incubation models that estimate duration of incubation and emergence dates. We address two primary questions: (1) How do variations in the spawning-timing window affect the emergence-timing window across a wide range of stream thermal regimes? (2) What proportion of the predicted variability in emergence date can we attribute to spawning timing as compared to other potential sources of variation stemming from differences in thermal regimes (a) among the geographic subregions, (b) among streams, (c) between the shallow streambed and the surface (stream) water, and (d) with interannual differences in prevailing weather?

2. Methods

2.1. Study area

The study was conducted across a 300 km long swath of coastal south-central Alaska, spanning three geographic subregions on the Chugach National Forest: Kenai Peninsula, Prince William Sound, and Copper River Delta (Fig. 2). The area’s mountainous coastal landscape has been greatly influenced by glaciation. Salmon spawn in streams and lakes

Fig. 1. Example of hypothetical spawning and emergence windows for a given thermal regime (solid black line) for a stream with seasonal temperature variations (A and C) and a groundwater-dependent stream with little seasonal variation (B). At streams with a seasonally variable thermal regime, the emergence window for salmon spawning in late summer or early autumn is longer in duration than the spawning window (expansion; Panel A). For salmon spawning later in the season at the same site, the emergence window is shorter in duration than the spawning window (compression; Panel C). At a spawning site with stable water temperature owing to strong upwelling of groundwater, the spawning window and the emergence window are of the same duration (neutral; Panel B).



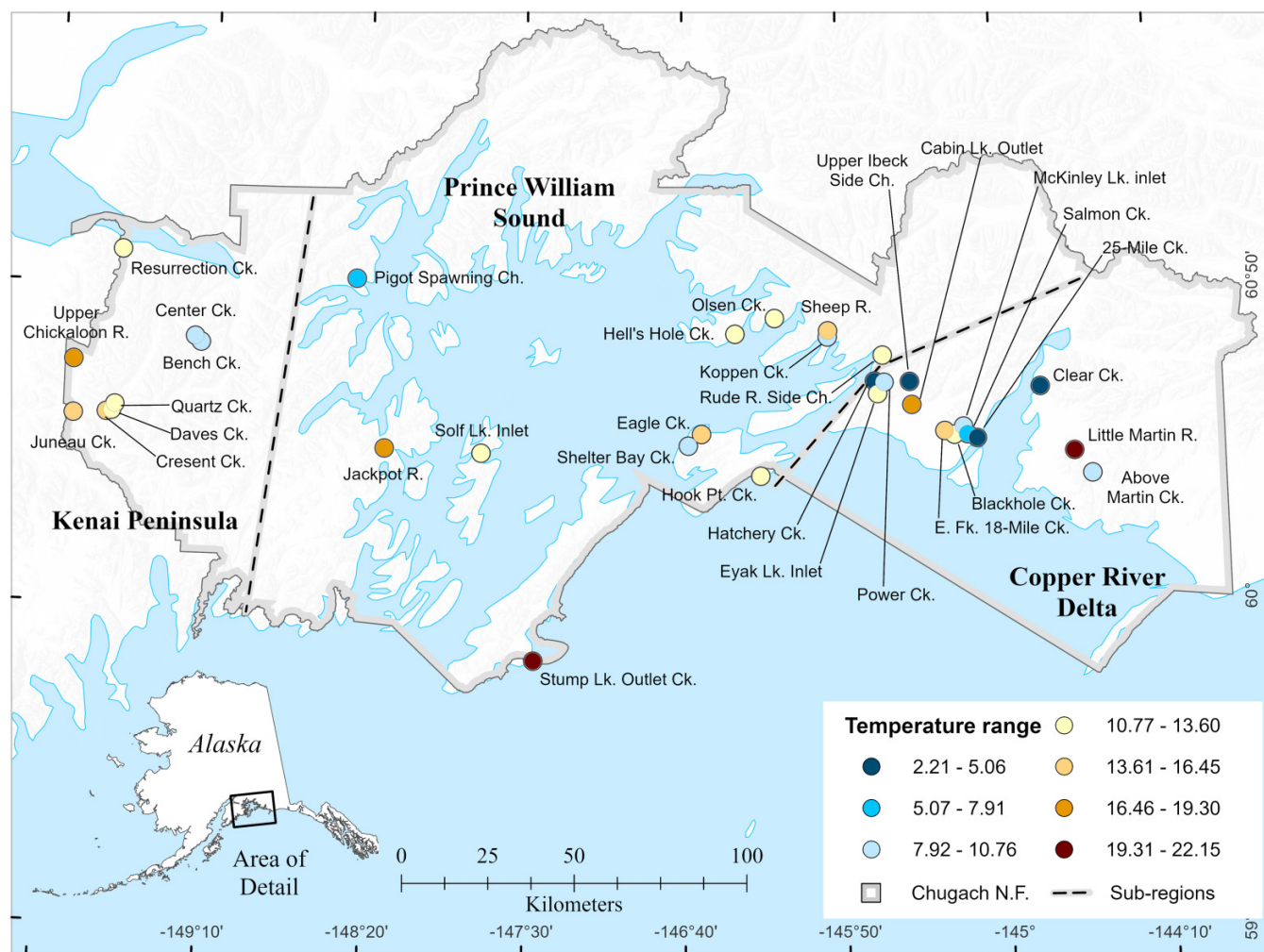
in valley bottoms, on alluvial fans, and on glacial outwash plains. Rainfall, snowmelt, glacier melt, and groundwater can be important water sources at salmon-spawning sites, contributing to high spatial variability in stream thermal regimes.

The study area has a subarctic maritime climate characterized by cool temperatures and a relatively small annual temperature range (Bieniek et al. 2012). During the 1981–2010 climate period, the mean annual sea-level air temperature was 4 °C. Most watersheds received around 200 cm of precipitation at sea level in an average year, with over three times as

much precipitation falling at higher elevations (Hayward et al. 2017).

Five months of below-freezing monthly mean air temperatures are currently common in the winter across the study area, even at sea level, resulting in persistent winter snowpack and ice cover on lakes and streams. The prevailing winter climate varies by region and even on a local scale in the study area. The influences of mountains, continental air masses, proximity to the ocean, and glaciers can create sharp gradients in temperature and precipitation, particularly in the autumn and winter months. There is a pro-

Fig. 2. Study sites ($n = 33$) and the three geographic subregions within the study area. Point color denotes the average annual range in water temperature ($^{\circ}\text{C}$) for each site. The projected coordinate system is North American Datum 1983 UTM zone 6 N. Base map credits: ESRI, NASA, and U.S. Geological Survey. Data source credit: U.S. Department of Agriculture Forest Service.



nounced rain shadow in the Kenai Mountains on the Kenai Peninsula, where the annual temperature is 3°C and annual precipitation ranges from 50 cm in the valley bottoms to around 200 cm at higher elevations (Hayward et al. 2017), so the winter weather conditions at sites in the Kenai Peninsula subregion are typically cooler and drier as compared to Prince William Sound and the Copper River Delta. Similarly, in the Copper River Delta subregion, sites located close to the Copper River are often exposed to frigid wintertime air masses blowing down the Copper River Canyon resulting from arctic high pressure in interior Alaska. In contrast, sites only a few kilometers away are sheltered from these winds and often have milder winter air temperatures owing to a stronger maritime influence.

Coastal south-central Alaska experienced substantial inter-annual variation in air temperature during the study period (2013–2019). Although the average annual air temperature was within 0.4°C of the 1981–2010 normal temperature for most of the study period, the air temperatures were exceptionally warm ($+2$ – 3°C mean annual) during the two-year period from autumn 2014 through summer 2016. During these

two winters, the prevailing weather was cool and rainy, little snow accumulated at sea level, and most coastal streams remained ice-free for much of the winter, an unusual occurrence (Adelfio 2016). Global projections suggest that the air temperatures and conditions observed during these winters may become the new climate “normal” in the study area during the 2050s (Walsh et al. 2017).

2.2. Water temperature data collection

Hourly water temperature data were collected year-round in the stream (“surface water”) and within the shallow streambed at 33 known salmon spawning sites. Salmon spawning sites were identified by local knowledge or the state of Alaska Anadromous Waters Catalog (Giefer and Graziano 2023). At each site, 3–5 temperature dataloggers with $\pm 0.2^{\circ}\text{C}$ accuracy (Onset Computer Corporation, Bourne, MA, USA) were installed within a single stream reach, typically measuring less than 50 m in length. One datalogger, shielded from direct solar radiation and protected from physical damage inside a piece of galvanized steel pipe measuring 15 cm long and 4.1 cm in diameter, rested on top of the substrate

and measured the surface (stream) water temperature. The remaining 2–4 temperature dataloggers were buried approximately 50 cm into the streambed gravels using field methods modified from Zimmerman and Finn (2012). These streambed temperature loggers measured water temperatures likely to be experienced by buried salmon eggs.

The monitoring network was installed between 2009 and 2014, but here, we use all the data collected from 1 October 2013 (beginning of water year 2014) through 30 September 2019 (end of water year 2018). This 5-year period was selected for analysis because the temperature records are mostly complete across all the sites in the monitoring network. The monitoring network included 13 sites on the Copper River Delta, 12 in Prince William Sound, and 8 sites on the Kenai Peninsula. The study watersheds were located within 1.0 degree of latitude, but varied by longitude, catchment area, lake and perennial ice cover (glaciers and snow fields), and mean elevation (Supplementary materials A, Table S1).

2.3. Modeling duration of incubation

We calculated the duration of incubation using a model developed by Beacham and Murray (1990) and modified by Sparks et al. (2019). The modified model, the inverse of the original function, calculates the daily advancement toward complete embryo development, called the relative daily “effective value” (E_i):

$$E_i = \frac{1}{\exp[\ln(a) + b \times \ln(T - c)]}$$

where T is daily mean water temperature and a , b , and c are empirically derived coefficients for each species. We used eq. 4 from Beacham and Murray (1990) (Supplementary materials A, eq. S1) and the associated coefficients for fry emergence (Supplementary materials A, Table S2) from Beacham and Murray (1990). We used the coefficients for coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), chum salmon (*O. keta*), Chinook salmon (*O. tshawytscha*), and for even-year and odd-year pink salmon (*O. gorbuscha*).

Pink salmon have a two-year life cycle resulting in genetic isolation between even- and odd-year populations that have co-evolved differences in egg characteristics and phenology. The temporal distribution of spawning activity within the spawning window can differ between even- and odd-year populations and can adapt over time (Kovach et al. 2012). Further, the spatial distribution of spawning activity in the same stream reach can differ between even-year and odd-year populations (Helle 1966). We treated the even- and odd-year populations as if they were independent species and modeled duration of incubation and emergence dates for all study years (disregarding whether the year was odd-numbered or even-numbered).

We applied the effective value model to hindcast dates of fry emergence based on water temperatures recorded by each datalogger, the species that spawn at the site, and seven spawning-timing scenarios: the specified mean spawning date and 7, 15, and 30 days before and after. Salmon may spawn over several days, weeks, or even months at a site, and the duration of spawning varies by species, site, and

year (e.g., Helle 1966; Tallman and Healey 1991; Lang et al. 2006). Unfortunately, the duration of the spawning window and the distribution of spawning activity within the spawning window have not been rigorously documented at all of these temperature monitoring sites for all species. We estimated the likely mean date of spawning (Table 1) based on site notes, agency records of regional averages, and the observations and professional opinions of fisheries biologists who conduct escapement counts on some of these streams and adjacent river systems (Personal communications S. Haught, Alaska Dept. of Fish and Game and J. Lang, U.S.D.A. Forest Service). The spawning scenarios we developed were not intended to exactly capture spawning duration at each site for each species but reflected a range of possible spawning timings. The spawning scenarios were useful for exploring patterns in interactions between spawning timing and stream thermal regimes across sites and species, not for accurately hindcasting emergence, as we describe in Discussion.

We calculated the duration of incubation for each site and spawning-timing scenario by summing E_i from the date of spawning until $E_i = 1$, the calculated date of fry emergence from the gravel. For odd-year pink salmon, the c coefficient was positive (0.153), resulting in an unsolvable logarithmic function on days when water temperatures were below 0.16 °C. For those days, we set the daily accumulation of E_i to zero, a reasonable assumption because development rates approach zero at water temperatures near the freezing point (Alderdice and Velsen 1978). We performed the incubation modeling in R version 3.4.3 (R Core Team 2017). We used the ggplot2 package (Wickham 2016) in R for preliminary figure preparation and to compute and draw a kernel-density estimate.

2.4. Analysis of components of variance

We used Proc Mixed in the SAS 9.4 software to evaluate the proportion of the total variation in predicted incubation duration and emergence timing related to each random effect variable, accounting for repeated measures over time. Only random effects (Table 2; Region, Site, Location, Type, Spawn Year, and Timing) were included in the model—no direct effects were specified—and we modeled the covariance structure to estimate the variance associated with each random effect and then calculated the proportion of the total variance contributed by each random effect variable.

The variation in the dataset reflected both the underlying environmental heterogeneity in stream temperature as well as the total number of sites and the types of sites selected for monitoring. The Copper River Delta subregion had the most sites ($n = 13$) and the most heterogeneous thermal regimes in the study area, including groundwater-dominated sites and sites with substantial lake effects. The Kenai Peninsula subregion had the fewest sites ($n = 8$), and we observed less heterogeneity in thermal regimes. The distribution of the five species of Pacific salmon was also variable across sites. Coho salmon had the highest frequency of occurrence across the monitored sites, spawning at 85% of the sites. Chum salmon had the lowest frequency of occurrence, spawning at only 24% of the sites. Species presence also differed among the three subregions (Table 1).

Table 1. Likely mean spawning timing estimated for each salmon species by study site and subregion.

Region	Name	Coho	Chinook	Chum	Pink	Sockeye
Copper River Delta	Blackhole Ck.	1 October				
	Cabin Lk. Outlet Ck.	1 October				
	Clear Ck.	1 November			15 August	15 July
	Hatchery Ck.	1 November				1 August
	Upper Ibeck Side Ch.	15 September				
	Little Martin R.	15 October				1 August
	Above Martin Ck.	1 November				15 July
	McKinley Lk. Inlet	1 November				1 August
	Eyak Lk. Inlet	15 October				1 July
	Power Ck.	1 November			15 August	1 August
	Salmon Ck.	1 November				15 August
	E. Fk. 18-Mile Ck.	1 October			15 August	
	25-Mile Ck.	15 November				15 August
Prince William Sound	Eagle Ck.			1 August	15 August	
	Hell's Hole Ck.	1 October				
	Hook Point Ck.	1 October				
	Jackpot R.	15 September	10 August		15 August	1 August
	Koppen Ck.			1 August	15 August	
	Olsen Ck.			1 August	15 August	
	Pigot Spawning Ch.			1 August	15 August	
	Rude River Side Ch.	15 October		1 August	15 August	15 August
	Sheep R.			1 August	15 August	15 August
	Shelter Bay Ck.	15 October		1 August	15 August	
	Solf Lk. Inlet	15 October				1 August
	Stump Lk. Outlet Ck.	1 October			15 August	1 August
Kenai Peninsula	Bench Ck.	1 October	1 August			
	Center Ck.	1 October	1 August			
	Upper Chickaloon R.	1 October	15 August		1 August	15 August
	Crescent Ck.	1 October	15 August		1 August	15 August
	Daves Ck.	10 October	15 August			15 August
	Juneau Ck.	10 October	15 August		1 August	10 September
	Quartz Ck.	1 October	15 August		1 August	15 August
	Resurrection Ck.	15 October	1 August	15-Aug	1 August	15 August

Table 2. The data structure of the simulated incubation-duration and emergence-timing dataset.

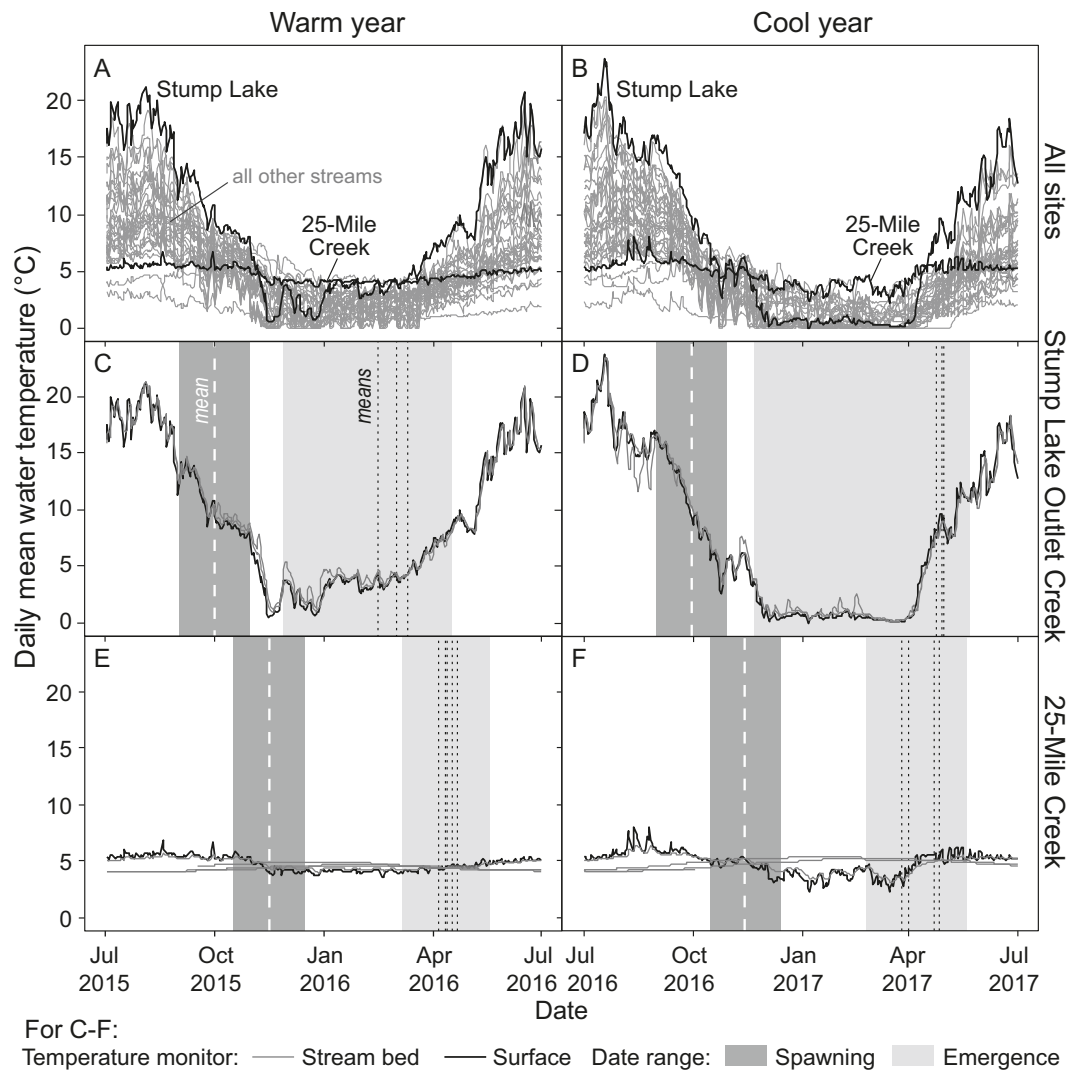
Random effect	Number of values	Definition
Region	3	Copper River Delta (CRD), Prince William Sound (PWS), and Kenai Peninsula (KP)
Site	33	Individual stream reaches, number in each region—CRD: $n = 13$; PWS: $n = 12$; KP: $n = 8$.
Location	2	Temperature logger either located in the surface stream or buried in the streambed
Type	5	USCZ, DSCZ, Surface, USPZ, DSPZ
Spawn year	6	2013 through 2018; number of sites varies by spawn year
Timing	7	30, 15, or 7 days before mean; mean; 7, 15, or 30 days after mean

Note: The table gives the number of values for each variable within each random effect. These are listed in the order in which they nested, with the lowest-listed effect (Timing) nested within the next higher level, and so on, up to the highest level (Region).

The unbalanced nature of the dataset makes drawing comparisons within and among species difficult—that is, the total amount of variance in predicted incubation duration or emergence timing is partly a function of the number of sites and spawning years included in the analysis. To limit the chance that the unbalanced data would create artifacts in our results, we limited comparisons to subsets of sites and/or species in

which the data were well balanced. Thus, we conducted one analysis using data from only those sites where coho salmon spawned, examining how the relative amount of variability in emergence timing changed under different spawning-timing windows. We conducted a second set of analyses focusing on spawning sites used by the three most common species (coho, sockeye, and pink salmon) under a 60-day spawning-

Fig. 3. Daily mean water temperature presented by “spawning year” (1 July–30 June) for all sites ($n = 33$, A and B), the site with the largest average annual range in water temperature (Stump Lake Outlet Ck., tiles C and D), and the site with the smallest average annual range in water temperature (25-Mile Ck., E and F). The columns compare water temperatures during the warmest year (A, C, and E) and the coolest year (B, D, and F) of the study period. Spawning timing and predicted emergence timing mean scenarios (dashed lines) and total windows (background shading) are shown (tiles C, D, E, and F).



window scenario (± 30 days), first conducting analyses for each species over all 33 sites in which at least one of these species spawned and then conducting another set of analyses for each species over just the 10 sites in which all three species co-occur. Note that we conducted a separate analysis for each species in each set of analyses—that is, species was never included as a factor in the statistical analyses. To facilitate comparisons among species, we plotted the results of these independent analyses together in a single graph.

3. Results

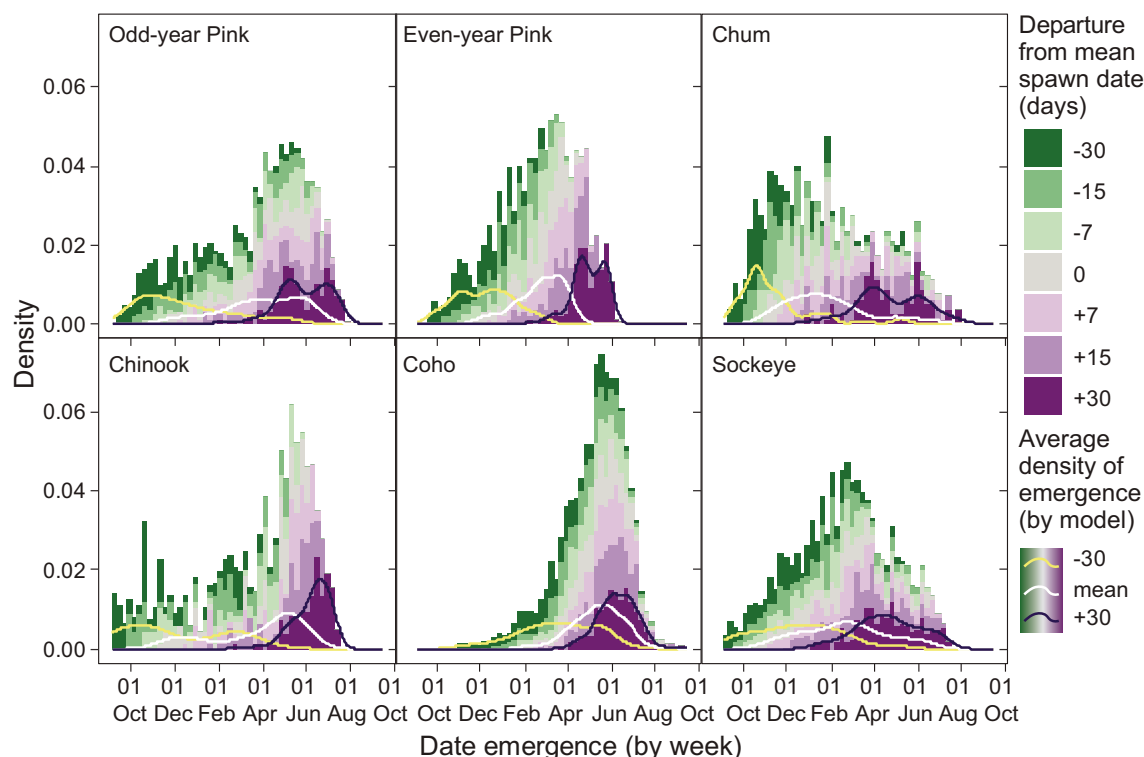
3.1. Water temperatures during the incubation period varied across sites and study years

Winter air temperatures varied greatly among the years of this study. During the winters of 2014–2015 and 2015–2016,

air temperatures averaged 2–3 °C warmer than the 30-y climate normal for the region. In comparison, air temperatures were more typical during the winters over the remainder of the study period (winters 2016–2017 through 2018–2019). Stream thermal regimes varied greatly across the 33 study sites, reflecting inherent differences among the watersheds, and these differences also determined each stream’s sensitivity to changes in prevailing weather conditions. As a result, we observed a mosaic of temperature conditions for spawning salmon and their incubating eggs across the study area (Figs. 3a and 3b).

The sites with the largest annual temperature range were also the most responsive to interannual differences in air temperature. Water temperature was most variable at sites downstream from shallow lakes, such as Stump Lake Outlet Creek, where the warmest daily mean temperatures were 20–24 °C and the annual range in water temperature exceeded 20

Fig. 4. The density of modeled juvenile emergence (bars) during each week of the year for all study sites and spawning years. Species and odd-year and even-year pink salmon are separated by tile. The seven spawning scenarios (+30, +15, +7, mean, -7, -15, and -30 days) are denoted by fill color. Lines show kernel density estimates of emergence modeled from the mean spawning scenario (white), 30 days earlier spawning (yellow), and 30 days later spawning (black).



°C. We observed interannual variability in winter water temperatures and the duration of near-freezing water temperatures (defined here as ≤ 0.5 °C) at these sites. For example, at Stump Lake Outlet Creek, periods of near-freezing water temperatures were rare during 2015–2016, the warmest winter in the study period (Fig. 3c); however, near-freezing water temperatures were the dominant condition for five months during the next year, the coldest interval of the study period (Fig. 3d).

In contrast, water temperature was least variable at sites where groundwater was upwelling from glacial outwash plains. At these sites, including 25-Mile Creek, the maximum daily mean water temperatures within the shallow streambed were 3–6 °C, even during the warmest days of summer, and interannual variability between warm and cool study years was low (Figs. 3e and 3f).

Although sites with groundwater upwelling are often considered “cold,” resulting from a human bias toward focusing on summer thermal regimes, these sites were usually the warmest places on the landscape in winter, particularly within the shallow streambed where salmon eggs incubate. Sites with upwelling groundwater were less likely to freeze and some sites did not freeze at all during the entire study period. At Hatchery Creek and 25-Mile Creek, for example, mean water temperatures within the shallow streambed exceeded 4 °C in December/January/February and the annual range in water temperature was less than 5 °C.

3.2. Modeled emergence varied by site thermal regime and spawning year

The mean water temperature during the incubation period between the simulated spawning date and the date of modeled emergence ranged from 1 °C to 13 °C across all sites, species, and study years, even when we modeled for a single mean spawning date for each site and species combination. This range of observed mean water temperatures during incubation translated into a more than 200-day range in duration of incubation across the study sites, from less than 90 days-to-emergence for sockeye salmon embryos developing during the warmest study year at the site with the warmest summer temperatures (Stump Lake Outlet Creek), to more than 300 days-to-emergence for coho salmon embryos incubating at the coldest site, a groundwater-fed stream near the terminus of a glacier (Upper Ibeck Side Channel, discussed in Adelfio et al. 2019).

3.3. Emergence timing windows

We modeled a broad range of emergence timing for all species (Fig. 4). Based on the mean spawning timing, mean modeled emergence timing was earliest for chum salmon (25 January) and latest for coho salmon (12 May). Sockeye salmon had the widest window for emergence timing based on mean spawning timing (21 October–22 June, 244 days). Even-year pink salmon were predicted to have the narrowest window for emergence, assuming mean spawning timing (149 days,

23 November–21 April). Odd-year pink salmon were predicted to have an emergence window nearly 3 months longer (228 days, 12 November–28 June) than even-year pink salmon using the exact same water temperature data and spawning dates, demonstrating the influence of population differences captured in the model coefficients.

3.4. Spawning timing effects on the emergence window

Broadening the window of spawning timing usually resulted in “expansion” (*sensu* Beer and Steel 2018, described in introduction) of the emergence-timing window (Fig. 5a). For example, on average (all sites and study years), spawning 15 days before the mean spawning timing resulted in a 24-days-earlier emergence for coho salmon and a 32-days-earlier emergence for sockeye salmon. Interactions between spawning timing, stream thermal regime, and species-specific model coefficients were the most important factors controlling the magnitude of expansion effects.

For summer-spawning salmon in streams with seasonally variable thermal regimes (warm in summer, near-freezing in winter), a relatively large proportion of the total accumulated thermal units (ATU) needed for development were acquired shortly after spawning. Thus, time of spawning was a particularly important driver of emergence timing, and a one-day change in spawning timing could change modeled emergence timing by 2–5 days. Chum and pink salmon in Prince William Sound streams provide the most extreme example: a one-day change in spawning changed modeled emergence timing by as much as 10–20 days (Fig. 5b). Spawning 7 days earlier in 10–12 °C water generated as many ATU (70–84) as the embryo gained during the entire winter, shifting emergence by many months. Similarly, when our model projected emergence in the autumn or winter based on the likely mean spawning timing, spawning 7 days later reduced the accumulation of thermal units around the time of spawning and delayed emergence by many months, into the spring.

For autumn-spawning coho salmon and for any species spawning in groundwater-influenced streams with less seasonal variation in temperature, the water temperature around the time of spawning was similar to the water temperature experienced throughout the incubation period, and expansion effects were muted. If the water temperature was warmer around the time of emergence than at the time of spawning, compression effects were observed. Our models predicted compression of the emergence window at certain sites across most spawning-timing scenarios for pink, chum, sockeye, and coho salmon.

Compression effects were particularly evident for coho salmon with modeled spawning dates 15–30 days after the mean spawning date (Fig. 5a). For example, compression effects were seen at East Fork 18-Mile Creek, where spawning scenarios 30 days after the mean spawning date reduced the total duration of the incubation period by 3 days. We have observed coho salmon spawning at this site in early November, 30 days after the mean spawning timing. Our modeling predicted that the offspring of these spawners would emerge 27 days after those of coho salmon that spawned 30 days earlier,

“compressing” the window of emergence relative to the window of spawning, assuming the same egg-development rate for early- and late-spawning individuals (see Discussion).

At sites with little seasonal variation in water temperature owing to upwelling groundwater, neither expansion nor compression effects were predicted. For example, the hypothetical offspring of a coho salmon modeled to spawn 30 days before mean spawning timing at groundwater-fed 25-Mile Creek would emerge 30 days earlier than the mean emergence timing. The spawning window and the emergence window were nearly the same duration at sites with low-amplitude seasonal stream-temperature variations, regardless of the spawning scenario or the species tested.

The model coefficients used for each species were clearly important in determining the magnitude of the expansion and compression effects. Evidence for this can be seen by comparing the expansion effects for the even-year and odd-year pink salmon scenarios (Figs. 5a and 5b). The magnitude of expansion effects was two- to three-fold greater for odd-year pink salmon compared to even-year pink salmon and the only difference between these model runs was the coefficients (*a*, *b*, and *c* in eq. 1).

3.5. Variability in emergence timing

An analysis of components of variance for predicted coho salmon emergence dates demonstrated that differences between streams explain the most (38%) variance in emergence day, assuming hypothetically for modeling purposes that all salmon are spawned on the mean spawning day at each site (Fig. 6). Interannual variation in temperature (spawn year) and larger-scale geographic variability (region) explained 32% and 17% of the variance in this mean spawning-timing scenario. Differences between surface and streambed temperature and sensors explained relatively little variance, even when combined (12.8%).

As the modeled spawning window increased from ± 7 - to ± 15 - to ± 30 days, spawning timing accounted for an increasing fraction of variance (7%, 18%, and 43%, respectively) in the emergence-window predictions (Fig. 6). A ± 15 -day range in spawning timing around the mean spawning date had almost as large an influence on emergence timing as interannual variation in temperature, despite capturing historically normal winter conditions and exceptionally warm winters that might be typical of the climate expected in the 2050s. Model residuals were near zero in all scenarios, suggesting that the variables tested explain nearly all the variability in predicted day of emergence.

3.6. Interactions between spawning timing and thermal regime varied by species

Together, stream and spawning timing explained between 68% and 99% of the variability in modeled day of emergence for coho, even-year pink, odd-year pink, and sockeye salmon, assuming a fixed ± 30 -day spawning window for each species. Results were similar when the model included all sites (Fig. 7a) and when the model was limited to the 10 sites where all three species were present (Fig. 7b).

Fig. 5. (A) Departure in modeled emergence date from the mean for each of the seven spawning date scenarios (−30, −15, −7, mean, +7, +15, +30 days) by species. Each point represents a single emergence date modeled for each combination of species, site, spawning year, data logger, and spawning-timing scenario. At the gray dashed line at zero days, the change in spawning timing equals the change in the emergence timing (e.g., spawning 15 days earlier resulted in 15 days earlier emergence). Positive values denote “expansion” of the emergence window and negative values “compression” of the emergence window relative to the spawning window. (B) Linear regressions (black lines) relating the site average range in annual air temperature to the daily average expansion or compression effect for the −7, mean, and +7 day spawning scenarios (gray points).

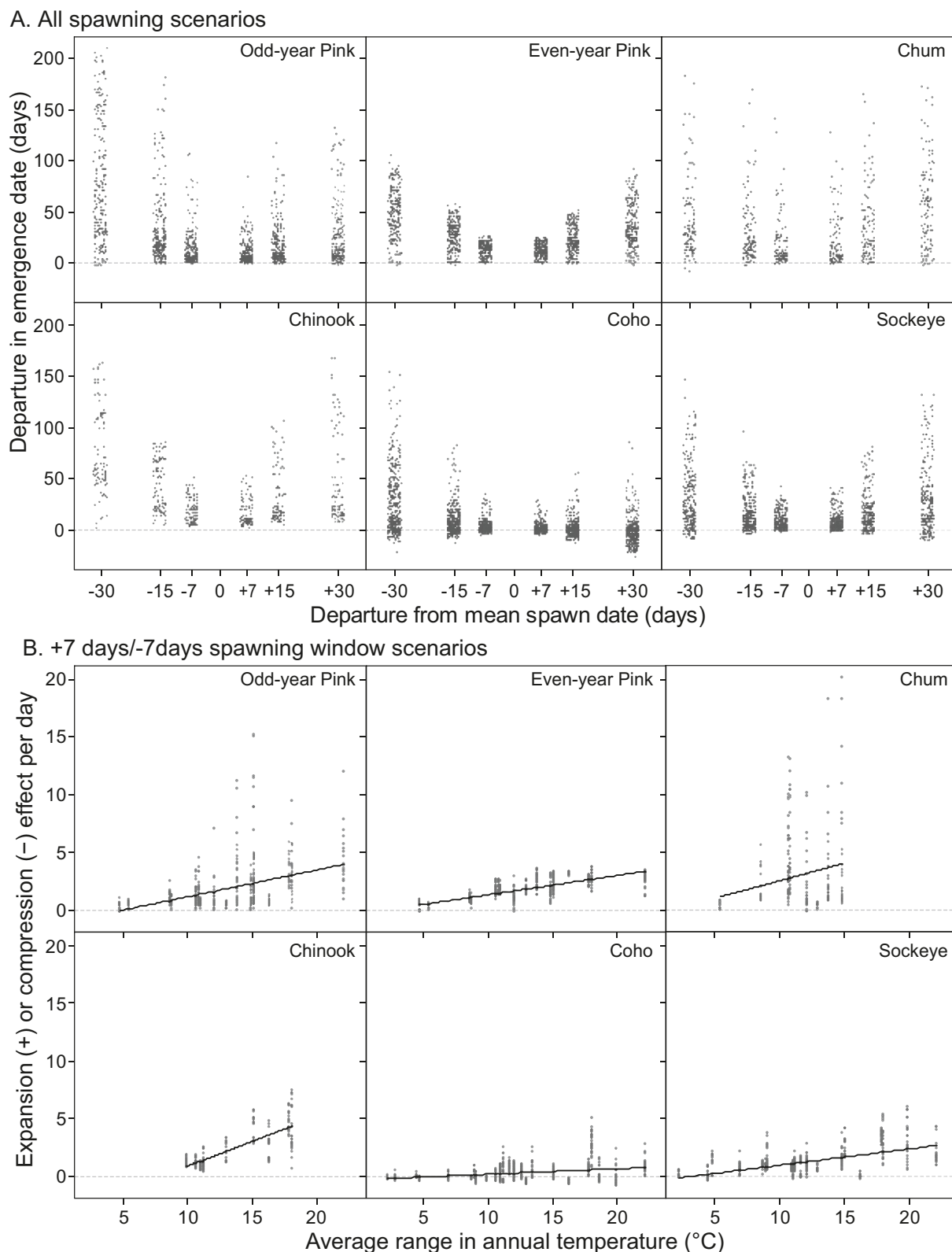
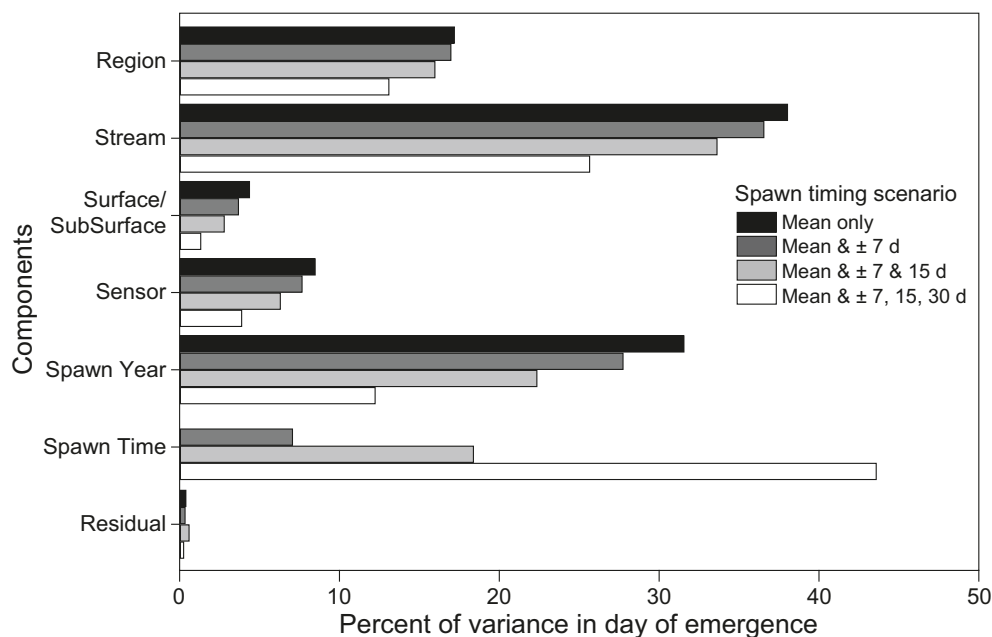


Fig. 6. Results of analysis of components of variance for coho salmon, the most widely distributed salmon species at our study sites (present at 28 of our 33 sites). Bar length is the percentage of variance explained by each of the six model variables: geographic region, stream, surface or streambed water temperature, temperature sensor location, spawning year, and spawning timing (estimated mean spawning date and $\pm 7, 15$, or 30 days), as described in Table 2. Bar color denotes the spawning-timing scenario.



Spawning timing was a particularly powerful driver for variability in predicted pink salmon day of emergence and the magnitude of the effect was nearly identical for the models run with even-year (76%) and odd-year (68%) spawning coefficients. In contrast, the stream thermal regime and the region were important explainers for variability in day of emergence of sockeye salmon (59%) and coho salmon (40%).

4. Discussion

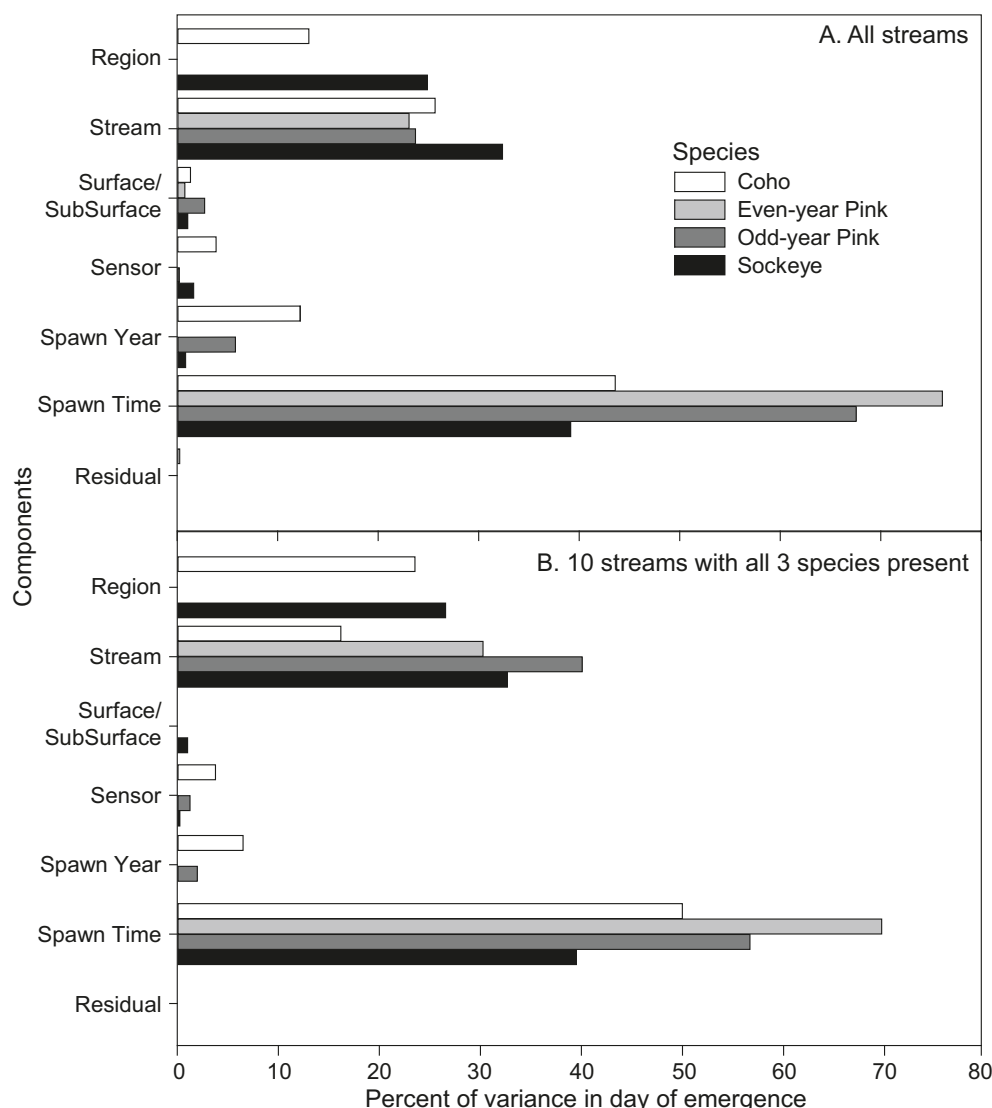
Incubation modeling revealed that interactions between spawning timing and seasonal variation in stream temperature can generate variability in emergence timing for Pacific salmon. Modeled emergence dates were especially sensitive to spawning date, producing broad windows of emergence timing in our results. However, we caution that the modeled emergence dates were not validated with field observations, the model coefficients were not calibrated to local salmon populations, and we relied on field-based estimates for spawning timing, so the accuracy of the modeled emergence times is uncertain. That said, this modeling exercise was helpful toward our objective of gaining insight into the impact of spawning timing variability across thermal regimes, species, and study years. The modeling predicted three basic emergence-timing responses to three spawning/thermal-regime scenarios: (1) summer spawning at sites with large annual temperature ranges; (2) late-autumn spawning at sites with large annual temperature ranges; and (3) spawning at sites with strong groundwater influence and a stable thermal regime, regardless of season. Between these

three scenarios, we suspect salmon populations may exhibit different adaptive responses in spawning behavior in reaction to both interannual climate variations and directional climate change.

When the water was warmer at the time of spawning than the time of emergence, a one-day change in the spawning window “expanded” (*sensu* Beer and Steel 2018) the emergence window by more than one day. Combining all sites and all years, we found that a 1-day change in the spawning timing window increased the emergence timing window by 1.5–2.7 days, depending on species (coho 1.5, sockeye 1.9, even-year pink 2.2, odd-year pink 2.5, chum 2.6, and Chinook 2.7). Sparks et al. (2019) predicted this same pattern at 25 sockeye salmon spawning sites in the Bristol Bay region of Alaska, where variability in egg-hatch timing was 2.5–4.5 times greater than variability in spawning timing and juvenile emergence occurred between December of the spawning year and August of the following year.

Expansion effects were greatest for summer-spawning salmon in streams with a large annual range in water temperature, where even a narrow window of spawning resulted in a broad window of emergence. For example, in the most extreme expansion scenarios, a one-week change in spawning timing at chum and pink salmon spawning sites in Prince William Sound could generate as many ATU (70–84 ATU for 10–12 °C water) as the developing embryos acquired during the entire winter, shifting modeled emergence timing by many months. Because most thermal energy was acquired early in egg development, time of spawning was a larger driver of emergence timing than interannual variability in

Fig. 7. Comparison of the components of variation using a constant ± 30 -day spawning window for (A) all streams known to provide habitat for coho ($n = 28$), pink ($n = 17$), and sockeye salmon ($n = 19$); and (B) the 10 streams in which all three of these species were present. Analysis is restricted to these species because they had the best spatial distribution at our sites, occupying all three geographic subregions. Bar color denotes the salmon species.



autumn, winter, and spring water temperature. Thus, we suspect that locally adapted spawning-timing behavior is a powerful driver of emergence timing for salmon that spawn in the summer in streams with a large annual range in water temperature. At the population level, expansion effects may broaden the emergence window, reducing the risk of phenological mismatches after emergence, even during periods with anomalous temperatures.

In contrast, compression effects were greatest for late-autumn spawning scenarios when the water was cooler around the time of spawning than the time of emergence. Warmer water temperatures late in the incubation period meant that the embryos from these “late spawners” were predicted to develop more quickly than those from “early spawners.” Lengthening the window of spawning by one day resulted in a less than one-day change in emergence, “compressing” the overall emergence-timing window. The

model predicted the greatest compression effects for late-spawning coho salmon, the latest-spawning salmon in our study area. Brannon (1987) documented compression of the emergence window for spring-spawning steelhead (anadromous *O. mykiss*). Sparks et al. (2019) observed compression of the emergence window for sockeye salmon embryos in a glacier-fed system, where most development was predicted to occur in the spring as the water warmed.

Compression may be an important mechanism to ensure that juvenile salmon emerge when seasonal food resources are abundant, near the beginning of the peak growing season. Compression of emergence may also be important in streams with powerful spring meltwater freshets, where juveniles are safest in the gravel until flows subside and the water begins to warm. However, when winter water temperatures rise and snowpack diminishes, the compression effect may be reduced and the offspring of late-spawning salmon

populations may emerge many months earlier in response (Adelfio et al. 2019).

When water temperature was the same at the time of spawning as at the time of emergence, the duration of the spawning-timing window equaled that of the emergence-timing window. This situation was predicted to occur over a narrow range of days for salmon populations with a spawning window that crossed the “expansion-compression threshold date” (Beer and Steel 2018). Further, the model predicted this situation to occur over a broad range of days in streams fed by groundwater, where seasonal fluctuations in water temperature were muted such that a one-day change in the spawning window resulted in a one-day change in the emergence window (no expansion or compression effects). Brannon (1987) and Sparks et al. (2019) observed similar patterns at sites with upwelling groundwater.

Brannon (1987) documented wider ranges in spawning timing for sockeye salmon spawning in upwelling groundwater as compared to nearby sites fed by precipitation. In the absence of expansion effects in thermally stable groundwater systems, an increase in the duration of the spawning-timing window may be the primary mechanism to generate variability in emergence timing, particularly for populations that incubate in groundwater-dominated areas but then quickly migrate to larger waterbodies with greater seasonal and inter-annual variability in temperature, such as lakes or the ocean, for rearing.

Broad windows of emergence timing may be beneficial for population viability in the face of both year-to-year climate variations and water-temperature increases expected to come with anthropogenic climate change. An analysis of components of variance predicted that stream thermal regime and spawning timing explain most of the variability in modeled emergence timing. Importantly, the combined effects of these two factors were substantially larger than the effects of spawning year, even though the study period included years with both climatologically normal air temperature (1981–2010) and record-breaking warmth (+2–3 °C annual anomaly) anticipated to be normal by the 2050s (Walsh et al. 2017).

Even for coho salmon, the species with the smallest average expansion effect, a ± 15 -day window of spawning timing had nearly as large of an effect on emergence timing as interannual variation in temperature. For pink, sockeye, and coho salmon, a ± 30 -day window of spawning timing explained most of the variation in emergence timing. Spawning windows exceeding this duration have been observed for all these species at some of the study sites and elsewhere across their native range (e.g., Helle 1966; Tallman and Healey 1991; Lang et al. 2006; DeFries 2020), suggesting that as long as water temperature remains within physiological tolerances, the existing variability in spawning and emergence phenology may be able to accommodate projected changes in water temperature in some streams. Further, small shifts in spawning timing in response to thermal constraints on spawning adult salmon or their embryos may drive large shifts in emergence, a potential mechanism for adaptation in response to warming water temperatures.

Accelerated egg development and earlier emergence for Pacific salmon are hypothesized impacts associated with pro-

jected changes in climate (Leppi et al. 2014; Wobus et al. 2015). Earlier emergence can affect juvenile growth, triggering life-long cascading effects on behavior and fitness (Holtby 1988; Jonsson and Jonsson 2018). If asynchronies develop between emergence timing and suitable environmental conditions, a counteracting change in spawning timing is thought to be the most likely adaptive response by a population over time (Crozier et al. 2008). Our analysis supports the plausibility of this idea by demonstrating how even a small change in spawning timing can result in a relatively large change in emergence timing owing to interactions between spawning timing and stream thermal regime.

Genetic variation in egg-development rate is an additional mechanism by which a spawning population may synchronize with the thermal regime of the natal environment (Hendry et al. 1998; Whitney et al. 2014; Fuhrman et al. 2017). Among coho salmon spawning in the Copper River Delta sub-region, preliminary genomic analysis has suggested patterns of adaptive genetic variation consistent with stream type (stable groundwater-dominated vs. more variable precipitation-dominated streams) (Thompson et al. 2023). Existing genetic adaptations will likely be important for some populations as the climate warms. For example, embryos from sockeye salmon populations that historically experienced relatively warm water temperatures had higher tolerance for even warmer water temperatures under projected future climate change scenarios than embryos from salmon populations sourced from colder environments (Whitney et al. 2013).

Incorporating locally adapted variation into our development models would have greatly improved our confidence in our emergence-timing model predictions, but we lacked population-specific egg-development coefficients for salmon populations in our study area. In the absence of better information, we used coefficients developed from empirical studies of populations from British Columbia and Washington that were incubated at warmer (and stable) water temperatures. Discrepancies between modeled egg development and actual rates are likely (Fuhrman et al. 2017). For this reason, we suspect that our modeled emergence dates may differ from those in nature, and we recommend deriving population-specific coefficients to hindcast emergence dates.

Sparks et al. (2017) tested coefficients from the same empirical studies that we used (Beacham and Murray 1990) and found that predicted egg hatch was 9–29 days earlier than observed egg hatch for sockeye salmon in the Bristol Bay Region of Alaska (about 650 km from our study area). The greatest departures from the Beacham and Murray (1990) models were observed at the coldest incubation temperatures. If these coefficients tend to predict a more rapid development rate than the actual rate in the colder water temperatures of Alaska in general, our modeling may have over-estimated expansion effects and under-estimated compression effects.

Our likely mean spawning-timing estimates were an additional potential source of inaccuracy in our emergence simulations. Many of the study sites were remote and lacked records of mean spawning timing and duration of the spawning window. We relied on regional averages based on qualitative observations to estimate mean spawning timing at some sites. Owing to the magnitude of expansion and com-

pression effects we predicted, even small inaccuracies in our spawning-timing estimates could have imparted relatively large discrepancies in modeled versus actual dates of emergence, in turn affecting our assessment of the relative size of the emergence-timing window compared to the spawning-timing window. More rigorous tracking of spawning timing would be helpful to better understand potential responses to climate change.

We did not account for thermal tolerances of embryos in our modeling exercise. For populations spawning in streams with warm ($\geq 13^\circ\text{C}$) summer maximum water temperatures, oxygen constraints may decrease embryo viability, restricting spawning timing to later in the year when water temperatures are cooler (McCullough 1999; Martin et al. 2017). We did not assess maternal effects of warm water temperatures that have been shown to affect the fitness of offspring (Braun et al. 2013); therefore, at some of the study sites with a large range in annual temperature, the early spawning scenarios, -30 days and -15 days (tested in our models across all thermal regimes), may have been unrealistic, particularly during the two record warm years observed during the study period. Locally adapted spawning-timing behavior that delays spawning until after summer warmth has passed may be particularly important in these streams as compared to streams with a small annual range in water temperature, such as groundwater-fed and glacial melt-fed streams, particularly as the climate warms.

Our modeling exercise did not incorporate population- and family-level differences known to affect egg-development rates. Egg characteristics may differ between early- and late-returning spawning runs (Ramstad et al. 2003). Genetic variation within populations and families may expand the emergence window for coho salmon by as much as 1–3 weeks (Konecki et al. 1995). Heritable differences between eggs from different families can significantly influence the impacts of daily and seasonal variation in water temperature on the rate of egg development (Hebert et al. 1998). Even at the same mean temperature, thermal variation changed emergence timing for Chinook salmon by about a week, with different responses by different families (Steel et al. 2012).

Although the impacts of within-population genetic variation on duration of incubation appear modest in magnitude compared to the expansion effects modeled in our study, trait differences between individuals within a population are an important component of that population's adaptive capacity. Those trait differences (both genetic and phenotypic) are fostered by having locally adapted salmon utilizing diverse habitats, including habitats with diverse thermal regimes within and between watersheds (Brennan et al. 2019). Expansion and compression effects may be an underappreciated factor driving some of the variation in traits observed between different stream thermal regimes and across spawning timing (early vs. late run). An improved collective understanding of interactions between stream thermal regimes, the spawning-timing effects described in this paper, and the genetic and behavioral adaptations observed both within and across populations will be important to better assess the adaptive capacity of salmon in the face of rapidly warming natal environments.

For Pacific salmon, rising stream temperatures will continue to be an important driver for the timing of life-history events. Changes in timing of spawning and emergence can be expected, but the magnitude of change is likely to vary across stream thermal regimes. Our results highlight how interactions between stream thermal regime and spawning timing may explain much of the observed variability in emergence timing at the landscape scale. Managers can maximize adaptive capacity by managing salmon stocks to maintain life-history diversity within and among populations and by restoring access to, and the quality of, spawning habitat across a range of thermal regimes, not only the "coldest" groundwater sites.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Luca A. Adelfo <https://orcid.org/0009-0007-4674-5736>

Author contributions

Conceptualization: LAA, SMW, NJM

Data curation: LAA, SMW

Formal analysis: LAA, SMW

Funding acquisition: GHR
Investigation: LAA, SMW, NJM
Methodology: LAA, SMW
Project administration: GHR
Supervision: SMW, GHR
Visualization: LAA, SMW
Writing – original draft: LAA
Writing – review & editing: SMW, NJM, GHR

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2023-0238>.

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