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ARTICLE

# Phenology of hatching, emergence, and end-of-season body size in young-of-year coho salmon in thermally contrasting streams draining the Copper River Delta, Alaska

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**Abstract:** Phenology can be linked to individual fitness, particularly in strongly seasonal environments where the timing of events has important consequences for growth, condition, and survival. We studied the phenology of coho salmon (*Oncorhynchus kisutch*) hatching and emergence in streams with contrasting thermal variability but in close geographic proximity. Following emergence, we tracked body sizes of cohorts of young-of-year fish until the end of the growing season. Hatch and emergence occurred at the same time among streams with marked variability in thermal regimes. We demonstrate that this can be explained in part by the thermal units accumulated during embryo development. At the end of the first growing season, there were some differences in body size, but overall fish size was similar among streams despite strong differences in thermal regimes. Collectively, these results provide novel insights into the interactions between environmental variability and the early life-history stages of coho salmon, furthering our understanding of the consequences of phenology on growth and survival for individuals within the critical first summer of life.

**Résumé :** La phénologie peut être reliée à l'aptitude individuelle, particulièrement dans les milieux de forte saisonnalité où le moment d'évènements a d'importantes conséquences sur la croissance, l'embonpoint et la survie. Nous avons étudié la phénologie de l'éclosion et de l'émergence de saumons cohos (*Oncorhynchus kisutch*) dans des cours d'eau caractérisés par différentes variabilités thermiques, mais situés à faible distance les uns des autres. Après l'émergence, nous avons surveillé les tailles du corps de cohortes de jeunes de l'année jusqu'à la fin de la saison de croissance. L'éclosion et l'émergence se sont produites en même dans des cours d'eau présentant une variabilité des régimes thermiques marquée. Nous démontrons que cela peut s'expliquer en partie par les unités thermiques accumulées durant le développement des embryons. Si, à la fin de la première saison de croissance, il y avait certaines différences sur le plan de la taille du corps, la taille des poissons était toutefois globalement semblable d'un cours d'eau à l'autre malgré des régimes thermiques fort différents. Collectivement, ces résultats fournissent de nouveaux renseignements sur les interactions entre la variabilité des conditions ambiantes et les premières étapes du cycle biologique des saumons cohos, améliorant ainsi la compréhension des conséquences de la phénologie sur la croissance et la survie des individus durant l'étape critique qu'est le premier été de leur vie. [Traduit par la Rédaction]

## Introduction

The phenology of transitions in an individual's life cycle can have important consequences for growth and survival, particularly in strongly seasonal environments (Einum and Fleming 2000; Love et al. 2010; Johansson et al. 2015). Strongly seasonal environmental conditions impose varying constraints on different life stages, and a species' hatching or emergence phenology can evolve through natural selection to correspond with a suite of environmental conditions that maximize individual fitness (Stenseth and Mysterud 2002; Visser and Both 2005). Furthermore, because favorable environmental conditions for one life stage are not necessarily favorable for another (Schluter et al. 1991), it is important to evaluate connections between multiple stages in the life cycle for a comprehensive understanding of phenology.

Species such as salmon and trout are good subjects for the study of linked phenologies because their life cycles include multiple stages. The life cycle can involve both freshwater and marine environments with multiple transitions that must be timed to ensure growth opportunities for current and future life stages (Quinn 2005). Growth is important for the early life history of these species, as prior work indicates that larger-bodied individuals are more likely to survive through the winter in fresh waters (Quinn and Peterson 1996; Berg et al. 2009) and within the marine environment (Moss et al. 2005; Wainwright and Weitkamp 2013). In this study, we focused on the phenology of freshwater life stages of coho salmon (*Oncorhynchus kisutch*) from hatching through the first summer of life. Within this time frame, we empirically examined multiple linked phenologies, including hatch and emergence timings as well as the consequences of these phenologies on size near the end of the first growing season.

Water temperatures are a critical factor in all freshwater life stages of salmon and trout (Elliott 1994; Quinn 2005). We focused our study on a high-latitude (60°N) system characterized by strongly defined spatial and seasonal patterns in stream thermal regimes. In this system, coho salmon hatch and emerge in nearly adjacent streams that can have radically different thermal re-

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gimes. Adjacent streams with contrasting thermal regimes range from surface-water-dominated streams that have high seasonal thermal variability to groundwater-dominated streams that exhibit much lower thermal variability. In the streams we studied, adults return from the sea to spawn from early fall through early winter, with incubation occurring over the winter, hatching occurring in the late spring, and emergence occurring in the summer. We hypothesized that hatching and emergence of salmon fry would be influenced by prior thermal regimes, which have been demonstrated to influence embryo development and hatch timing in other settings (Fuhrman et al. 2018). Furthermore, we predicted that fish would attain larger sizes at the end of the growing season in the surface-water streams, as only these streams have temperatures favorable for growth (Brett 1971; Stewart and Ibarra 1991; Armstrong and Schindler 2013). We addressed the phenologies of the early stages in the salmon life cycle (hatching and emergence) and their consequences for individuals within the critical first summer of life (Elliott 1994; Fuiman and Werner 2002; Armstrong and Nislow 2006). Collectively, the results of this work provide a unique evaluation of linkages between phenologies of successive life stages in a species with a complex life cycle that plays out in a highly variable environment.

## Materials and methods

Our study streams were located on the west Copper River Delta, south-central Alaska, USA: 18 Mile Creek (60.45882°N, 145.29285°W), Blackhole Creek (60.44695°N, 145.23999°W), Hatchery Creek (60.59112°N, 145.63542°W), Salmon Creek (60.45485°N, 145.17139°W), and 25 Mile Creek (60.44176°N, 145.11794°W). Within each stream, a 200 m study reach was selected based on the presence of young-of-year coho salmon, accessibility to the site, and general similarities among sites including riparian vegetation, stream size, slope, and discharge. We assessed differences in thermal variability among streams with continuous year-round monitoring using water temperature data loggers (HOBO Pro, U-22 model, Onset Corp., Pocasset, Massachusetts, USA). All loggers were encased in a galvanized pipe (6.3 cm × 15.2 cm) for protection and attached by steel cables to anchors that were driven into the stream bed to withstand frequent storms and high flows. Four data loggers were deployed within the main-channel spawning habitat of each stream and recorded water temperature at hourly intervals from 1 September 2012 to 31 December 2013 in 18 Mile, Hatchery, Salmon, and 25 Mile creeks and from 1 April 2013 to 31 December 2013 in Blackhole Creek. Owing to hazardous weather conditions and the presence of brown bears (*Ursus arctos horribilis*) during the spawning season, it was impossible to conduct comprehensive spawning surveys.

Once emerged, coho salmon were collected twice each month from April to October in 2013 using baited minnow traps and dip nets. Fish were measured (fork length, mm) and released, except for a random subset of 10 fish per stream during each month. These 10 fish were euthanized with tricaine methanesulfonate (MS-222) and kept frozen for analysis of hatch and emergence dates using otoliths (Fuiman and Werner 2002). We analyzed a total of 122 otoliths to determine hatch and emergence dates among the study streams. Sagittal otoliths were mounted on a frosted glass slide with Crystalbond heated thermoplastic cement (SPI Supplies, West Chester, Pennsylvania, USA), wet polished with 0.3 μm grit paper, and buffed with aluminum oxide micropolish until daily ring increments were discernible. Otoliths were analyzed under a compound microscope (Leica DMLS, Buffalo Grove, Illinois, USA) using image analysis software (Image-Pro version 7.0, Media Cybernetics, Rockville, Maryland, USA). Ages were estimated by counting each complete daily increment, starting outside the primordia and counting outward in a straight trajectory to the last visible ring. Counts were conducted by two independent researchers to verify the count estimate. We used the daily increment technique, which is a well-recognized and widely used tool for estimating fish age (Panella 1971; Jones 1992; Fuiman and Werner 2002). Age validation (Beamish and McFarlane 1983; Campana 2001) was not possible owing to logistical difficulty and the inability to obtain permits to chemically tag wild fish or mark and recapture known-age fish. Once the ages were estimated, we subtracted the estimated age from the date of capture to determine hatch and emergence timing (Fuiman and Werner 2002).

In a separate analysis of emergence timing, we calculated a cumulative frequency distribution (CFD) of emergence timing for each stream, based on measurements of body lengths (fork length, mm) pooled across samples collected at regular intervals every 2 weeks throughout the spring, summer, and fall. For each stream, the estimated CFD reflected the cohort emergence dates or the proportion of fish having body lengths <35 mm, assessed during sampling events over the study period. We chose 35 mm to represent when fish had emerged based on the size of fish whose yolk sacs were fully absorbed during our field observations. One-way analysis of variance based on ranks and Dunn's pairwise comparisons were used to assess the significance of differences in dates of hatching and emergence and in fish size among streams. Differences in body size of juvenile salmon were determined by comparing mean lengths of all juvenile salmon measured in each stream in late October.

## Results

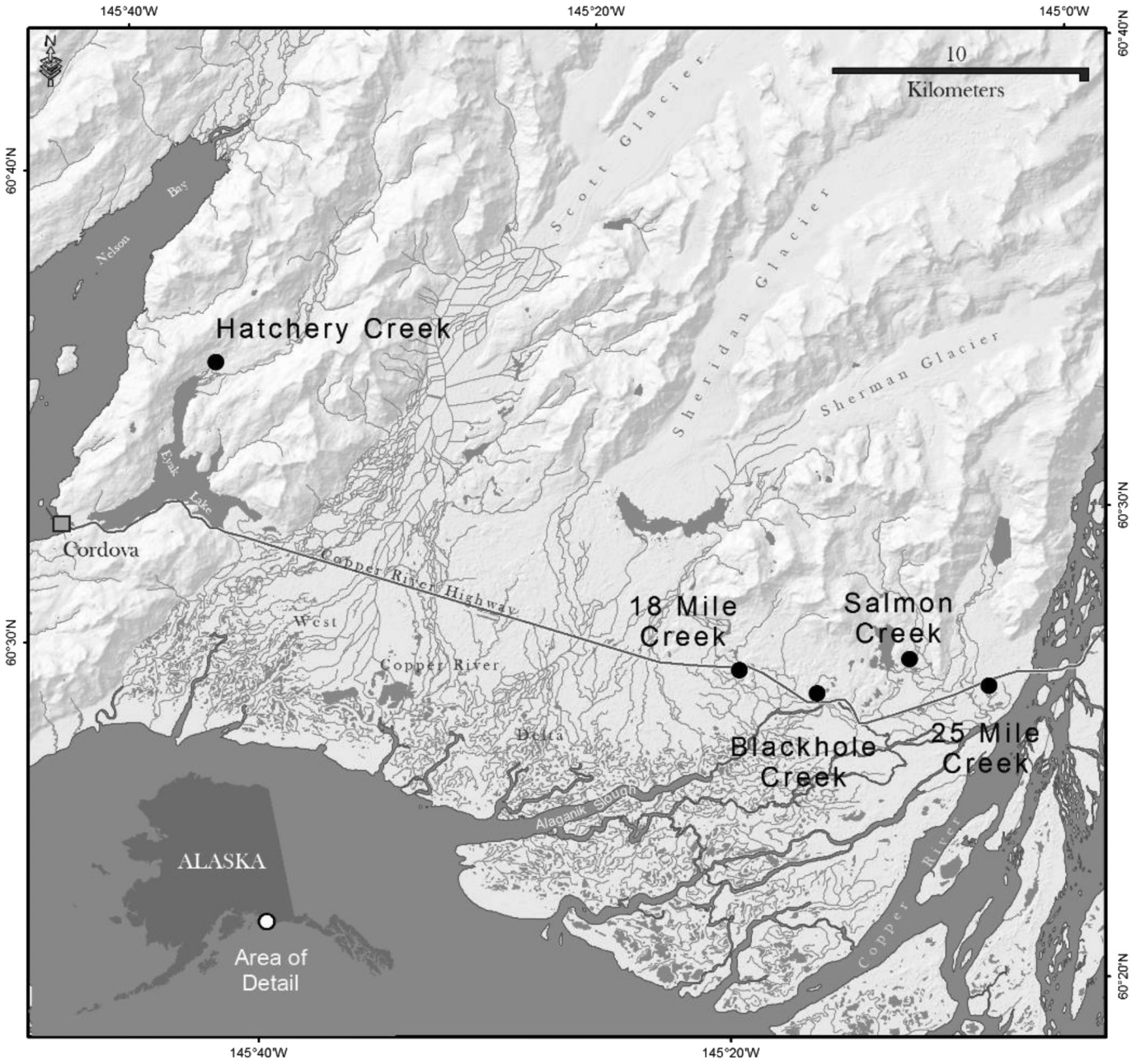
There were clear seasonal differences in thermal regimes among the five study streams (Figs. 1 and 2). 18 Mile and Blackhole creeks were dominated by surface water and showed higher annual thermal variation than the stable, groundwater-dominated thermal regimes of Hatchery, Salmon, and 25 Mile creeks. The thermal incubation environment was similar in 18 Mile and Blackhole creeks and showed relatively high thermal variation during embryo incubation. Hatchery Creek was different from all other creeks and showed an intermediate level of thermal variability. The thermal incubation environment was statistically similar in Salmon and 25 Mile creeks and showed the lowest thermal variation during embryo incubation.

Neither hatch dates ($p = 0.79$; Fig. 3) nor fry emergence dates ($p = 0.998$; Fig. 4) differed significantly among streams. The CFD of cohort emergence dates (Fig. 5) largely corroborated the otolith-determined emergence timing; in all but one stream, the cohort emergence dates fit within the 95% confidence interval of the otolith-determined emergence dates (Fig. 4). The exception was Hatchery Creek, in which size-determined (cohort) emergence dates were later than in all other streams. There were differences in the mean juvenile body lengths among streams whereby juveniles in 25 Mile and Salmon creeks were significantly larger than fish in Hatchery Creek ($p < 0.001$; Fig. 6).

## Discussion

We sought to understand linkages between thermal heterogeneity of surface-water and groundwater streams on the Copper River Delta, Alaska, and the phenology of coho salmon. There were important differences in the thermal incubation environment for embryos between the surface-water and groundwater streams. The thermal incubation environment was similar in 18 Mile and Blackhole creeks, which both showed relatively high thermal variation; in contrast, Salmon and 25 Mile creeks exhibited low thermal variation during winter incubation and throughout the rest of the year. We predicted that phenologies may vary among streams, as species inhabiting a wide range of winter thermal conditions may adopt variable tactics based in part on variable phenologies (Shuter et al. 2012). However, despite the observed thermal differences, we found relatively synchronized spring hatch timing and summer emergence timing among streams.

**Fig. 1.** Location of study streams on the Copper River Delta, Alaska. Surface-water streams: 18 Mile and Blackhole creeks. Groundwater streams: Hatchery, Salmon, and 25 Mile creeks. Map credit: K. Christiansen.




Across all streams, the timing of egg hatching ranged from mid-April to June, and fry emergence occurred from June to August.

Synchronous hatch and emergence phenology among streams may be driven by the timing of peak availability of food resources to young-of-year coho salmon (Einum and Fleming 2000; Letcher et al. 2004; Wipfli and Baxter 2010) as well as the need to attain sufficient size (Quinn and Peterson 1996) and condition (Berg et al. 2009) to survive the winter (Campbell 2017). Although we observed the same hatch and emergence timing among streams, with peak emergence in the summer (July), the distribution of emergence timing was wide and the full range of emergence timing in all streams spanned from late spring to late fall, which may be due to genetic or environmental differences among individuals within and among redds in each stream (Steel et al. 2012; Sear et al. 2014; Fuhrman et al. 2018).

In our system, earlier emergence of juveniles could give them more time to attain size and condition. In high-latitude environments, time may be considered as the product of photoperiod and number of days in the growing season, during which conditions are conducive to growth (e.g., food availability, physiologically favorable temperatures; Armstrong et al. 2016). Surprisingly, we found that many fish emerged well past the summer solstice, thus missing the longest days of the year and substantially shortening the length of time available to forage in the stream during the summer growing season (Villarreal et al. 1988; Veras et al. 2013; Kitagawa et al. 2015). This suggests other potential constraints on earlier emergence in this system, which could include lack of habitat owing to persistence of ice in main-channel and off-channel habitats (Brown et al. 2011) or low food availability in early spring (Wipfli 1997; Rine et al. 2016; Campbell 2017).

**Fig. 2.** Water temperatures (°C) collected from the main channel of the study streams on the Copper River Delta, Alaska, from 1 September 2012 to 31 December 2013. Surface-water (SW) streams: 18 Mile and Blackhole creeks. Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile creeks.

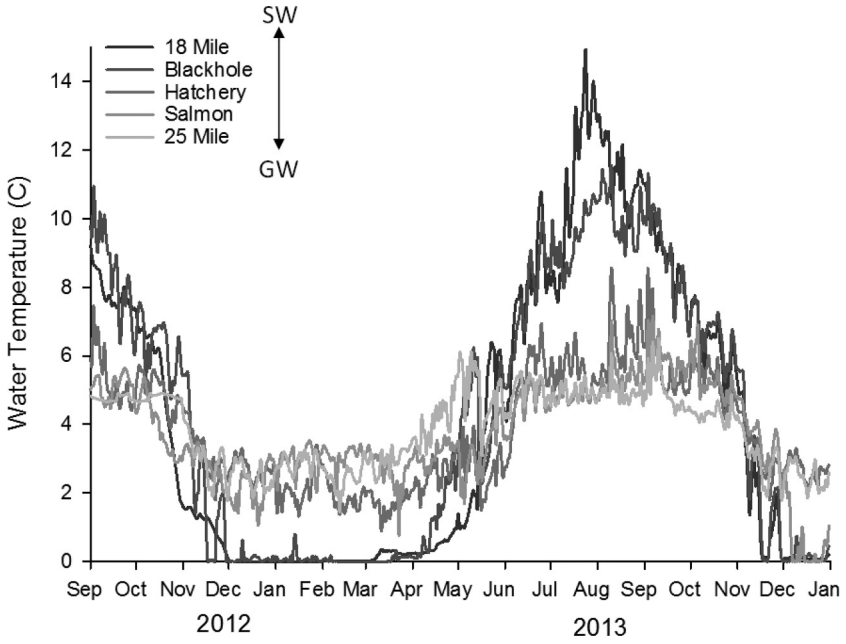



**Fig. 3.** Estimated time of hatching of coho salmon in the study streams on the Copper River Delta, Alaska. Surface-water (SW) streams: 18 Mile and Blackhole creeks. Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile creeks. Box and whisker plots show the median (middle line), first quartile (left of median line), third quartile (right of median line), and minimum and maximum data points (whiskers).

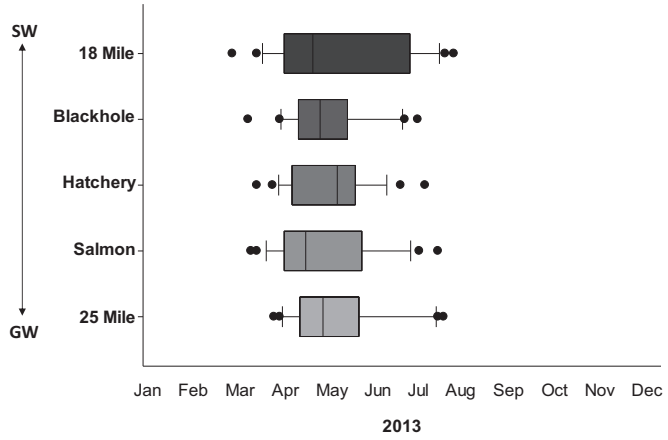
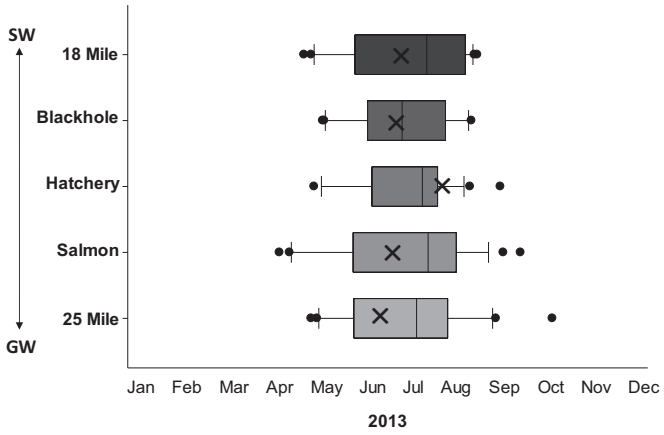



**Fig. 4.** Estimated time of emergence of coho salmon in the study streams on the Copper River Delta, Alaska. Surface-water (SW) streams: 18 Mile and Blackhole creeks. Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile creeks. Box and whisker plots show the median (middle line), first quartile (left of median line), third quartile (right of median line), and minimum and maximum data points (whiskers). "×" is the median emergence time in each stream based on a size cutoff (35 mm and below).




The observed synchronous timing of hatching and emergence for coho salmon is a pattern that has been more widely reported in other organisms (Liebhold et al. 2004). Synchrony of phenologies has also been shown to occur in parallel with the timing of food supplies, for example as in insect–host plant interactions (Dewar and Watt 1991; VanAsch and Visser 2006; Elzinga et al. 2007) or fledging of birds in concert with high densities of insect prey (Williams et al. 2015). The window for growth of emerging coho salmon is relatively short in Alaska, and it is reasonable to assume the capacity of individuals to grow within this brief window is at a premium (Armstrong et al. 2016).

We considered previous observations of spawn timing in conjunction with accumulated thermal unit (ATU) models (Murray and McPhail 1988) and found that previously reported ATUs required for hatching, or assumed spawn timings, do not fully describe the variability that we observed in hatch and emergence phenology. The ATU models of Murray and McPhail (1988) were based on laboratory studies, whereas embryo incubation conditions in the field may be much more variable. Accordingly, it seems reasonable to hypothesize that variability in incubation timing cannot be explained by ATU requirements alone. Furthermore, past work reveals plasticity in temperature (ATU) requirements for embryo incubation both among locations and among individuals (Alderdice and Velsen 1978; Farrell et al. 2008; Eliason et al. 2011; Steel et al. 2012).

**Fig. 5.** Estimated time of emergence of coho salmon in the study streams on the Copper River Delta, Alaska, using a size cutoff of <35 mm (cohort emergence dates) for emerging coho salmon. Surface-water (SW) streams: 18 Mile and Blackhole creeks. Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile creeks.

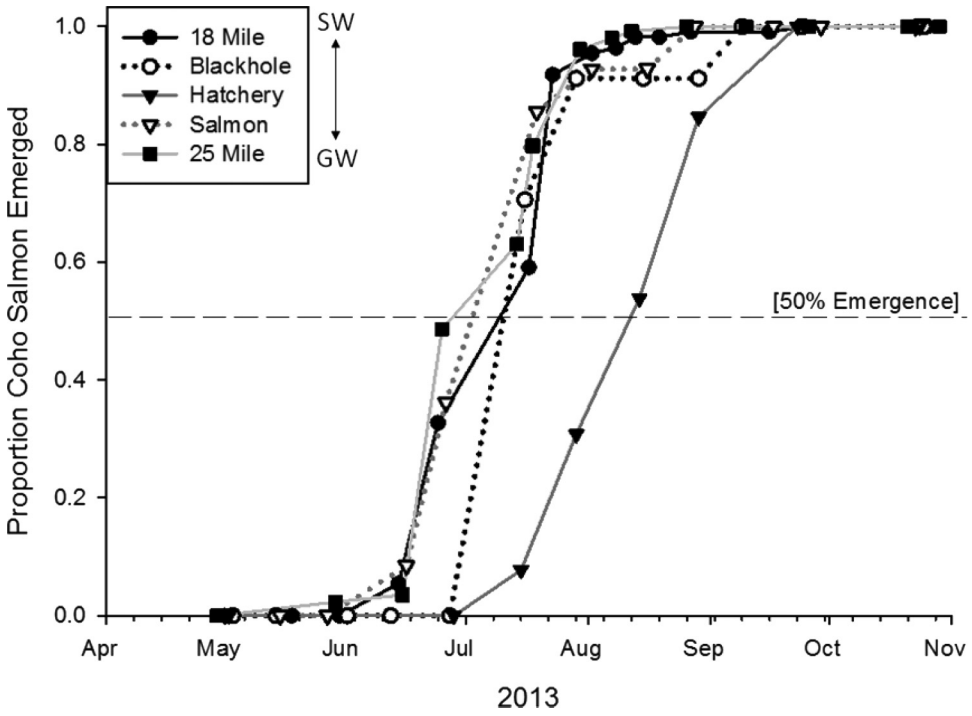
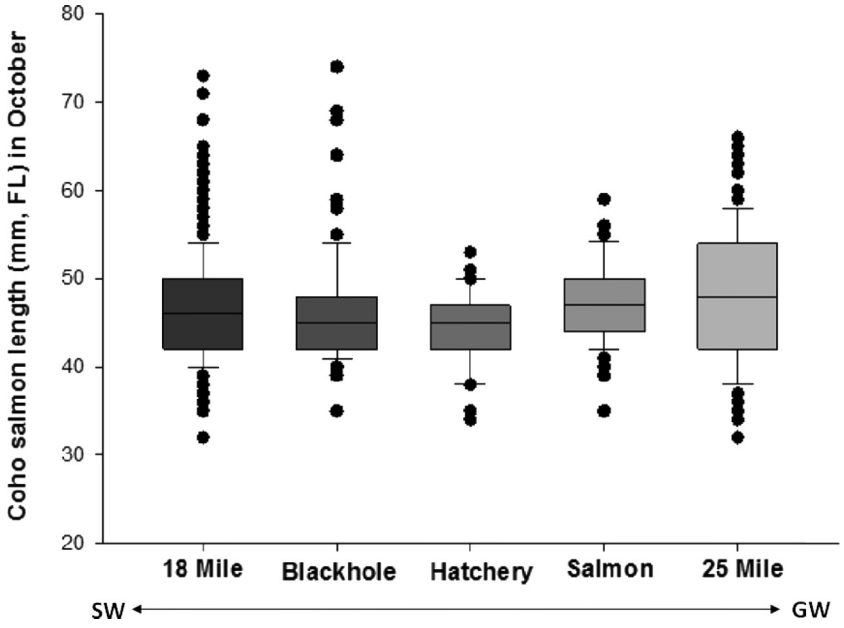



**Fig. 6.** Fork length (FL, mm) of coho salmon fry at the end of the growing season (October) in the study streams on the Copper River Delta, Alaska. Surface-water (SW) streams: 18 Mile and Blackhole creeks. Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile creeks. Box and whisker plots show the median (middle line), first quartile (bottom of box), third quartile (top of box), and minimum and maximum data points (whiskers).




Studies have found a link between temperature and spawning (Crozier et al. 2008; Eliason et al. 2011). Thus, variation in spawn timing can be of adaptive significance and may relate to optimal timing of fry emergence or improved fitness during other portions of the life cycle (Heggberget 1988; Jensen et al. 1991; Webb and McLay 1996; Rogers and Schindler 2008). There is some unpublished evidence of earlier spawning runs in the surface-water streams and later spawning runs in the groundwater streams of the Copper River Delta, Alaska (K. Hodges, US Forest Service, Chugach National Forest, personal communication). A difference in spawn timing such as this would allow for synchronized hatch timing owing to differences in incubation time and the rate of thermal unit accumulation. In an environment as heterogeneous and complex as the Copper River Delta, it is likely there are several interacting factors that determine salmon phenology. More detailed information on spawn timing and incubation (e.g., cap-

ping redds to track emergence) is needed to understand the full effects of temperature on that portion of the life cycle (Braun et al. 2013) in our study system.

At the end of the first summer growing season, we observed significant differences in the sizes of young-of-year fish among streams. The smallest fish were in Hatchery Creek and the largest fish were in Salmon and 25 Mile creeks. Hatchery Creek is farther away from the other streams and may have smaller fish at the end of the growing season owing to differences in geography, hydrology, trophic influences, or other unknown factors. In contrast, juveniles were largest at the end of the summer in the groundwater-dominated Salmon and 25 Mile creeks. Our results contradict our prediction that fish would attain larger sizes at the end of the growing season in the surface-water streams, as only these streams have temperatures favorable for growth (Brett 1971; Stewart and Ibarra 1991; Armstrong and Schindler 2013). Perhaps these groundwater sites provide an ideal thermal environment for growth or have more abundant prey for juveniles to feed on. Further investigation of these factors would be needed to more clearly elaborate how conditions in summer interact with the timing of emergence to drive size and condition of fish entering into winter (Campbell 2017). It is important to note that the absolute size difference at the end of the first growing season was relatively small (1–3 mm) among streams and perhaps these statistical differences are of little biological significance. Variation in body size is known to be attributed to a host of factors, including size-biased survival or movement, variability in food availability, bioenergetics, habitat quality, water temperature, and other potential biotic or abiotic factors in play during the summer growth season (Björnsson et al. 1989; Jensen et al. 1991; Sandercock 1991; Rosenfeld et al. 2005; Quinn 2005).

As the focus on climate vulnerability of salmon grows in the region (e.g., Leppi et al. 2014; Shanley and Albert 2014; Wobus et al. 2016; Sloat et al. 2017), there is a need to continue expanding our knowledge of this complex issue. Our results allowed us to evaluate linkages between multiple stages in the salmon life cycle and understand the consequences of phenology for individuals during the first summer of life. Climate change will continue to alter environmental conditions in streams within the region (Beamer et al. 2017), likely shifting the seasonal activities of organisms, with potential consequences to their fitness and life history trajectories (Power 2002; Visser and Both 2005; Kovach et al. 2015). For species such as coho salmon, which use multiple habitats for multiple life stages, the effects of climate-related variability may be particularly challenging to fully describe (Wainwright and Weitkamp 2013). Furthermore, the effects of climate-related changes are unlikely to be consistent across life stages and conflicting selection pressures are a distinct possibility (Schluter et al. 1991). The results of this research provide novel insights into the linkages between thermal variability and coho salmon phenology in a heterogeneous landscape. We hope this work inspires further studies, which are needed to fully describe the complexities embedded within the salmon life cycle.

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