Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2018-0003.R2
Manuscript Type:	Article
Date Submitted by the Author:	09-Apr-2018
Complete List of Authors:	Campbell, Emily; Oregon State University, Fisheries and Wildlife Dunham, Jason; U.S. Geological Survey Reeves, Gordon; USDA Forest Service Wondzell, Steve; U.S. Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Lab
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	phenology, SALMON < Organisms, life cycle, TEMPERATURE < General

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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

Emily Y. Campbell¹, Jason B. Dunham², Gordon H. Reeves³ and Steve M. Wondzell³

¹Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon; embug50@gmail.com

²U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon; jdunham@usgs.gov

³U.S. Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Lab, Corvallis, Oregon; greeves@fs.fed.us, swondzell@fs.fed.us

Abstract

Phenology can be linked to individual fitness, particularly in strongly seasonal environments where the timing of events have important consequences for growth, condition, and survival. We studied the phenology of Coho Salmon 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 timing 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, however overall fish size among streams were similar 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.

Key Words: phenology, salmon, life cycle, temperature

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 as 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 freshwaters (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 timeframe 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 regimes. 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 winter, hatching 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. 2017). Further 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 et al. 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, 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, these are: 18 Mile Creek (N60.45882°W145.29285°), Blackhole Creek

(N60.44695°W145.23999°), Hatchery Creek (N60.59112°W145.63542°), Salmon Creek (N60.45485°W145.17139°), and 25 Mile Creek (N60.44176°W145.11794°). Within each stream, a 200m study reach was selected based on the presence of young-of-year Coho Salmon, accessibility to the site; and general similarities between 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 September 1, 2012 to December 31, 2013 in 18 Mile, Hatchery, Salmon, and 25 Mile Creeks; and from April 1, 2013 to December 31, 2013 in Blackhole Creek. Due to hazardous weather conditions and 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 sub-set 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 Crystal Bond® heated thermoplastic cement (SPI Supplies, West Chester, Pennsylvania, USA) and wet-polished with 0.3µm grit paper and buffed with

aluminum oxide micro-polish 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 readers to clarify the count estimate. We used the daily increment technique, which is a well-recognized and widely used tool for fish age estimates (Panella 1971; Jones 1992; Fuiman and Werner 2002). Age validation (Beamish and McFarlane 1983; Campana 2001) was not possible due 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 (CDF) of emergence timing for each stream, based on measurements of body lengths (fork length, mm) pooled across samples collected at regular intervals every two weeks throughout the spring, summer, and fall. For each stream, the estimated CDF reflected the cohort emergence dates or the proportion of fish having body lengths <35mm, assessed during sampling events over the study period. We chose 35mm 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 (ANOVA) based on ranks and Dunn's pair-wise comparisons were used to assess the significance of differences in dates of hatching, emergence, and 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 (Figures 1 & 2). 18 Mile and Blackhole Creeks were dominated by surface-water and showed higher annual thermal variation relative to 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 ($p=0.79$; Figure 3), nor the fry emergence dates ($p=0.998$; Figure 4) differed significantly among streams. The cumulative frequency distribution of cohort emergence dates (Figure 5) largely corroborated the otolith-determined emergence timing; in all but one stream, the cohort emergence dates fit within the 95% CI of the otolith-determined emergence dates (Figure 4). The exception was Hatchery Creek in which size-determined (cohort) emergence dates occurred later than 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 ($p<0.001$; Figure 6).

Discussion

We sought to understand linkages between thermal heterogeneity of surface-water and groundwater streams on the Copper River Delta, AK and the phenology of Coho Salmon. There were important differences in the thermal incubation environment for embryos among the

surface-water and groundwater streams. The thermal incubation environment was similar in 18 Mile and Blackhole Creeks where both creeks 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 a relatively synchronized spring hatch timing and summer emergence timing among streams. 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 a peak emergence time 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. 2017).

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 available to earlier emerging individuals due 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).

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 1987) 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 (1987) 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. Further, 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).

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 improve fitness during other portions of the life cycle (Heggberget 1988; Jensen et al. 1991; Web et al. 1996; Rodgers and Schindler 2008). There is some un-published evidence of earlier spawning runs in the surface-water streams and later spawning runs in the groundwater streams of the Copper River Delta, AK (K. Hodges U.S. Forest Service, Chugach National Forest, personal communication). A difference in spawn timing such as this would allow for a synchronized hatch timing due 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., capping 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 further away from the other streams and may have smaller fish at the end of the growing season due 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 et al. 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 (1-3mm) 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 et al. 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 (Kovach et al. 2015; Power 2002; Visser and Both 2005). 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). 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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Acknowledgements:

We thank C. Salazar, K. Kirkby, A. Morin, L. Adelfio, L. Hotca, C. Malstrom, K. Hodges, D. Kuntzsch, S. Meade, M. Sloat, C. Zimmerman, M. Heck, S. Johnson, C. Marshall, the Fisheries and Wildlife Department at Oregon State University, and the entire Cordova Ranger District of the Chugach National Forest. Thanks to K. Christiansen for providing the study map. This research was permitted by Oregon State University ACUP #4364. We are grateful to our funding sources: The National Fish and Wildlife Foundation, the U.S. Department of Agriculture Forest Service PNW Research Station, and the Environmental Protection Agency Science to Achieve Results (STAR) Fellowship. Use of trade or firm names is for descriptive purposes only and does not constitute endorsement of any product or service by the U.S. Government.

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List of Figures:

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

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

Figure 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 and 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 the minimum and maximum data points (whiskers).

Figure 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 and 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 the minimum and maximum data points (whiskers). “×” is the median emergence time in each stream based on a size cut-off (35mm and below).

Figure 5. Estimated time of emergence time of Coho Salmon in the study streams on the Copper River Delta, Alaska using a size cut-off of <35 mm (cohort emergence dates) for emerging Coho Salmon. Surface-water (SW) streams: 18 Mile and Blackhole Creeks and Groundwater (GW) streams: Hatchery, Salmon, and 25 Mile Creeks.

Figure 6. Length (mm) (fork) 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 and 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 the minimum and maximum data points (whiskers).

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Figure 4.

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Figure 5.

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Figure 6.

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