FEATURE

Premature Mortality Observations among Alaska's Pacific Salmon During Record Heat and Drought in 2019

Vanessa R. von Biela | U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK, 99508. E-mail: vvonbiela@usgs.gov

Christopher J. Sergeant | University of Montana, Flathead Lake Biological Station, Polson, MT | University of Alaska Fairbanks, Fairbanks, AK

Michael P. Carey | U.S. Geological Survey, Alaska Science Center, Anchorage, AK

Zachary Liller | Alaska Department of Fish and Game, Anchorage, AK

Charles Russell | Alaska Department of Fish and Game, Cordova, AK

Stephanie Quinn-Davidson | Tanana Chiefs Conference, Yukon River Inter-Tribal Fish Commission, Fairbanks, AK | Alaska Venture Fund, Anchorage, AK

Peter S. Rand | Prince William Sound Science Center, Cordova, AK

Peter A.H. Westley | University of Alaska Fairbanks, Fairbanks, AK

Christian E. Zimmerman | U.S. Geological Survey, Alaska Science Center, Anchorage, AK

Chinook Salmon *Oncorhynchus tshawytscha* make their way up Ship Creek in Alaska to spawn. Photo Credit: Ryan Hagerty, U.S. Fish and Wildlife Service.

DOI: 10.1002/fsh.10705

Widespread mortality of Pacific salmon *Oncorhynchus* spp. returning to spawn in Alaska coincided with record-breaking air temperatures and prolonged drought in summer 2019. Extreme environmental conditions are expected to happen more frequently with rapid climate change and challenge the notion that Alaska could indefinitely provide abundant, cool freshwater habitat for Pacific salmon. A total of 110 geographically widespread opportunistic observations of premature mortality (carcasses) were collected from a variety of sources. Premature mortalities were documented for Pink Salmon *Oncorhynchus gorbuscha*, Sockeye Salmon *O. nerka*, Chum Salmon *O. keta*, Chinook Salmon *O. tshawytscha*, and Coho Salmon *O. kisutch*. Additionally, observations of Pink Salmon returning to spawn in Prince William Sound streams in 2019, obtained from systematic aerial surveys conducted annually, revealed low migration success in 87% of rain-driven streams (n = 30), 52% of snow-driven streams (n = 65), and only 18% of glacier-driven streams (n = 11). Salmon mortality observations were consistent with death due to heat stress resulting from high water temperatures or drought caused hypoxia and stranding. Developing a better understanding of how broad-scale climate patterns manifest at the stream scale can help us determine whether a major shift in Pacific salmon productivity is underway and inform fisheries management plans to better mitigate future risks.

INTRODUCTION

Air temperatures have warmed more rapidly at northern latitudes compared to other areas of the globe, resulting in reduced snow and ice across northern landscapes (Post et al. 2019). The consequences of these climate conditions include warming of freshwater habitats and shifts in the hydrograph in some locations (Hinzman et al. 2005; O'Reilly et al. 2015; Beamer et al. 2017; Littell et al. 2018; Pitman et al. 2020). For decades, biologists predicted that warming and drying of northern freshwaters will eventually lead to declines in coldwater fishes, including salmonids (i.e., family Salmonidae) throughout their distribution (Houghton et al. 1990; Russo et al. 2014; Schoen et al. 2017). In the summer of 2019, these concerns became tangible in Alaska when record high temperature and persistent drought conditions (ACRC 2020) coincided with observations of Pacific salmon *Oncorhynchus* spp. premature mortality in the northern portion of their range (Figure 1). The annual average air temperature was 3.4°C warmer in 2019 than the long-term average (1925–2000; National Oceanic and Atmospheric Administration: www.ncdc.noaa.gov/cag). Drought conditions lasted 79 weeks (July 2018 – January 2020; National Integrated Drought Information System: www.drought.gov) and were caused by warm air temperatures that melted snowpack earlier in the year and, in the southern half of Alaska, below normal snowpack and below normal summer rains (Fisher et al. 2019a; ACRC 2020).

Declines in multiple salmon populations throughout more southerly parts of their range in the Pacific Northwest have been associated in part with premature mortality caused by poor environmental conditions along migration corridors and on spawning grounds (Goniea et al. 2006; Strange 2012; Hinch et al. 2021). Premature mortality is the death of upstream-migrating adult Pacific salmon before spawning and encompasses the terms en route mortality along migration corridors and prespawn mortality on spawning grounds (Bowerman et al. 2016; Keefer et al. 2017; Hinch et al. 2021). Warm water temperatures, low dissolved oxygen, or low water levels can cause high rates of premature mortality, in some cases exceeding 90% of total returning adults (Strange 2012; Sergeant et al. 2017; Tillotson and Quinn 2017; Hinch et al. 2021). In Alaska, observations and studies that associated poor freshwater conditions and premature mortality do exist prior to 2019, but are more localized (Murphy 1985; Sergeant et al. 2017; Tillotson and Quinn 2017), and are presumably due to Alaska's cooler conditions and more abundant freshwaters compared to the southern portion of their range.

Our goal was to evaluate whether observed Pacific salmon premature mortalities in 2019 were due to atmospheric conditions. The first objective was to assemble opportunistic observations of Pacific salmon premature mortalities during 2019 to describe the geographic extent and species affected. If mortalities were in response to atmospheric conditions, we anticipated widespread geographic observations of multiple affected species. The second objective was to better understand how the impact of the anomalous conditions were mediated by local habitat conditions such as the source of streamflow in rivers (i.e., rain, snow, or glacier). Available data for this objective were categorical observations of migration success acquired during routine escapement surveys of Pink Salmon *Oncorhynchus gorbuscha* returning to 134 streams in Prince William Sound (PWS) conducted by the Alaska Department of Fish and Game (Morella et al. 2021). We expected that migration success would be lowest in rain-driven systems, which tend to dry quickly during drought conditions, and highest in glacier-driven systems, which tend to provide greater amounts of stored water from snow and glaciers (Sergeant et al. 2020).

PREMATURE MORTALITY OBSERVATIONS

Methods for Premature Mortality Observations

An observation was defined as one or more Pacific salmon carcasses along a migration route or an unspawned carcass (i.e., a carcass containing gametes) on a spawning ground. Carcasses along migration routes were either trapped on riverbanks, sandbars, and dried streambeds or floating in the water. Most observers (87%, n = 110) did not explicitly note gamete retention to classify a carcass as a premature mortality. Rather, carcass observations were presumed to reflect premature mortalities based on location and time of year. For example, a carcass found along a migration route and well downstream of a spawning habitat was considered a premature mortality. The associated data release (von Biela and Stanek 2021) specified which observations included confirmation of gamete retention from internal examination of some carcasses and which did not. Each observation was specific to a location, time period, and species such that a single observer generated multiple observations in the database when more than one species was noted.

Observations from four sources were included in the database: (1) the Local Environmental Observer Network (LEONetwork.org), initiated by the Alaska Native Tribal Health Consortium, which provides local observers with a platform to share information that helps describe the connections between climate, environment, and public health; (2) reports to the Alaska Department of Fish and Game's Arctic-Yukon-Kuskokwim Region by community members or staff; (3) social media reports and traditional media articles; and (4) directed emails from the lead author to selected individuals to assess whether a lack of observations from particular geographic areas

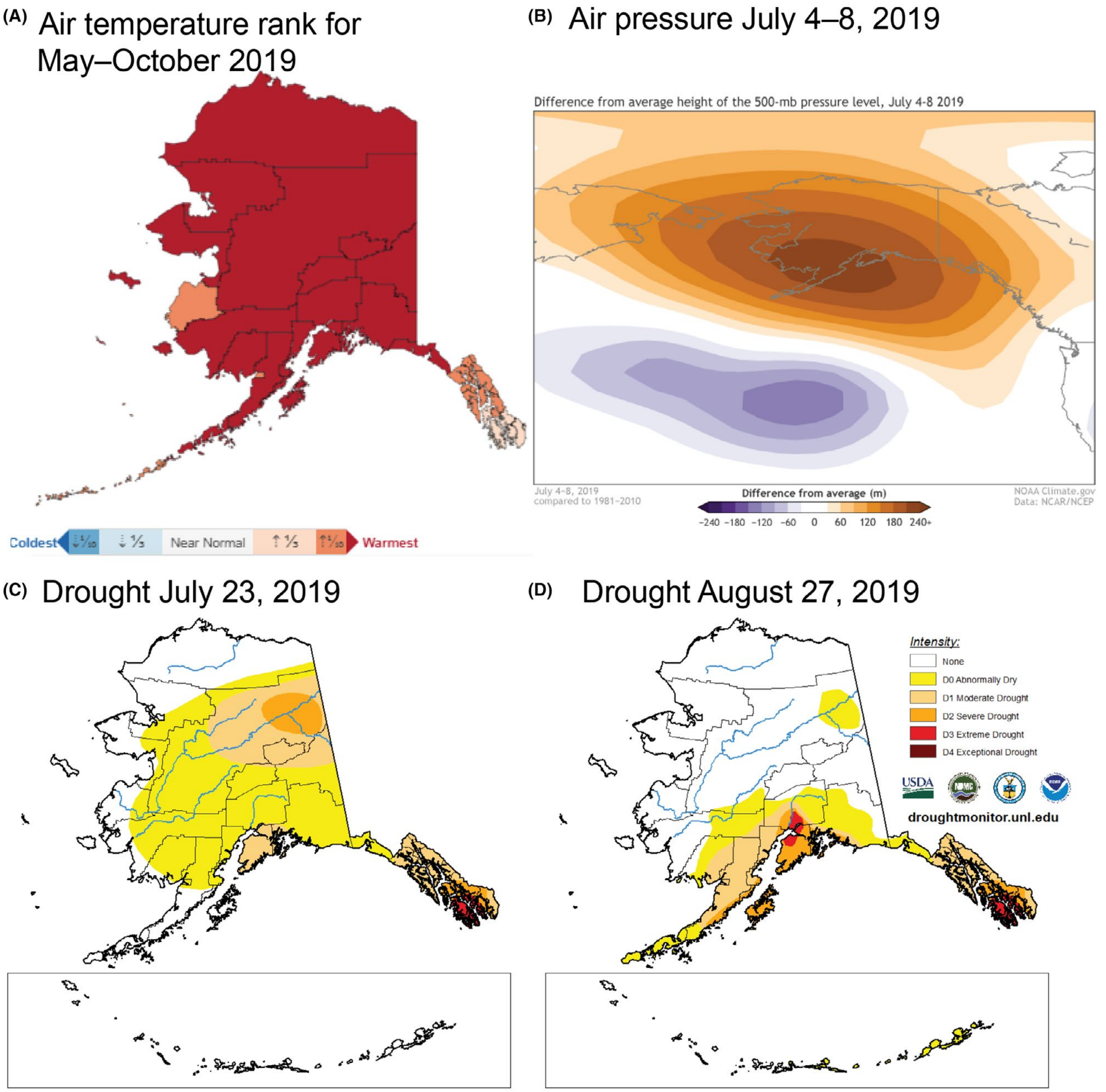

Figure 1. Maps depicting **(A)** 6-month air temperature rank for the Pacific salmon spawning period (May–October) in all boroughs (i.e., counties) in Alaska. **(B)** The high-pressure system associated with peak air temperatures in July 2019. **(C)** Drought extent for a representative week in July 2019. **(D)** Drought extent for a representative week in August 2019. For A, red indicates the warmest 6-month period on record for each borough (record length varies from 81 to 95 years). For C and D, colored shading represents drought severity, with yellow being the least severe and red the most severe. Sources: Panel A was generated using the National Oceanic and Atmospheric Administration (NOAA) National Center for Environmental Information Climate at a Glance Mapping Tool (https://bit.ly/3ILtqwq), Panel B is a NOAA Climate.gov image based on the National Center for Atmospheric Research/National Centers for Environmental Prediction Reanalysis data provided by the NOAA Earth System Reearch Laboratory Physical Sciences Division, and Panels C and D are from the U.S. Drought Monitor (https://bit.ly/3239zaZ).

were a true reflection of geographic scope or simply a reflection of biases or limitations inherent in the first three sources.

While the level of detail varied among observations, all observations included identification of carcasses to at least genus, month, and a location (e.g., specific river, lake, or beach). Other observation details were sometimes collected and included: additional location detail (descriptive narrative or latitude and longitude), number of carcasses observed (estimated by order of magnitude or counted), water temperature, observer name, and a website link to the report. If latitude and longitude were not provided with an observation, they were assigned by the first author based on the narrative location description provided. Observations were grouped into one of eight geographic regions identified by colloquial names that typically refer to the large river(s) or marine waterbodies where rivers and streams flow (Figure 2). All mortality observations in the database were made in rivers, streams, and estuaries.

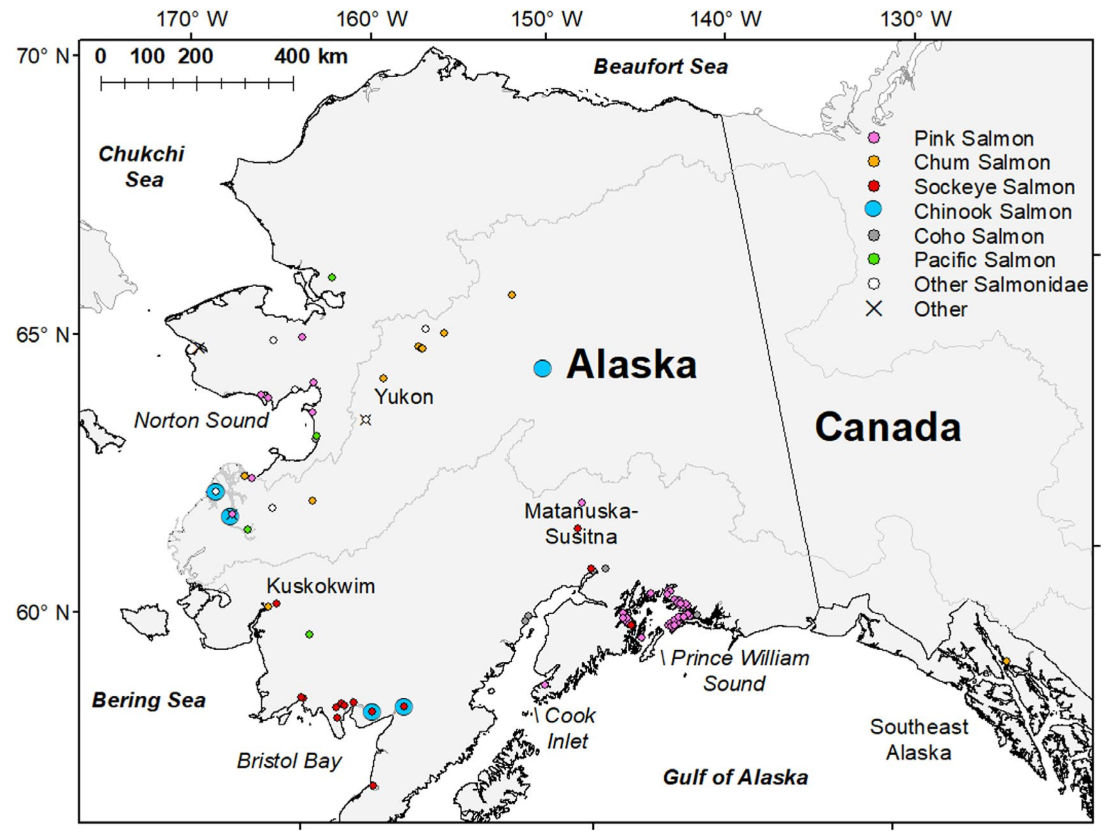

Figure 2. Premature mortality observations of Pacific salmon carcasses in Alaska during the summer and fall of 2019. Symbol color and shape denotes Pacific salmon species or alternative taxonomic groupings specified in the legend. Symbols denoting Chinook Salmon mortalities are slightly larger so that they remain visible, since these observations often occurred at locations with carcasses of another Pacific salmon species. Region names referenced in the text are shown on the map and are colloquial. Three regions are named for their large river(s): Yukon (outlined in light gray to separate it from Norton Sound to the north and Kuskokwim to the south), Kuskokwim, and Matanuska-Susitna. Four regions are named for marine waterbodies that their rivers and streams flow into: Norton Sound, Bristol Bay, Cook Inlet, and Prince William Sound, respectively. One region, the southernmost portion of Alaska, is named Southeast Alaska.

Estimates of carcass abundance reported here were used only for descriptive purposes. Carcass detection and counts of Pacific salmon are known to underestimate actual mortality (Patterson et al. 2007). Not only is it difficult for observers to get accurate counts of visible carcasses, but carcasses sink and cannot be seen in large, deep, and turbid river systems (Patterson et al. 2007) that characterize much of Alaska, and can also be removed by bears and other wildlife. Carcass count estimates were grouped into three categories: (1) abundant when ≥1,000 carcasses were reported, (2) moderate when ≥100 and <1,000 carcasses were reported, and (3) low when <100 carcasses were reported. We categorized the infrequent observations without a carcass count as a low count.

Results for Premature Mortality Observations

We collected a total of 110 observations of Pacific salmon premature mortalities in 2019 (Figure 2). Only four observations (3.6%) were identified as "Pacific salmon" rather than a specific species. Of the remaining observations, 60 (54.6%) were for Pink Salmon, 20 (18.2%) for Chum Salmon *O. keta*, 15 (13.6%) for Sockeye Salmon *O. nerka*, 6 (5.5%) for Coho Salmon *O. kisutch*, and 5 (4.5%) for Chinook Salmon *O. tshawytscha*. Observations of mortality occurred across many regions in Alaska, including Norton Sound, Yukon, Kuskokwim, Bristol Bay, Matanuska-Susitna, Cook Inlet, and PWS (Figure 2). Only a single observation of premature mortality was identified in Southeast Alaska, despite an effort by the authors to specifically seek out additional observations.

Most observations (89%) included an estimated carcass count. The number of carcasses for a single observation ranged from 1 to 35,000. Overall, 53 (48.2%) observations estimated abundant carcasses (≥1,000). Most observations with abundant carcasses were of Pink Salmon from PWS (47 observations) and involved drought so severe that low water or the absence of water prevented individuals from reaching spawning grounds (Figures 3, 4). The remaining instances with abundant carcasses involved Sockeye Salmon from Bristol Bay (three observations), Sockeye Salmon from Matanuska-Susitna (one observation from Larson Creek), Chum Salmon from the Yukon (Figure 5; one observation from the Koyukuk River; Westley 2020), and Coho Salmon from PWS (Figure 6). Observers often included additional details they deemed important about the biophysical settings associated with carcasses, including warm water temperature, low water level, low dissolved oxygen, and high fish density.

The remaining observations were split among moderate (≥100 and <1,000; 24.5%) and low carcass numbers (<100;

Figure 3. Image of a Pink Salmon premature mortality observation consisting of a large number of carcasses in Hogan Creek (Hogan Bay), Knight Island, Prince William Sound, Alaska, in early September 2019 during a field study conducted by the Prince William Sound Science Center. Photo credit: Brad von Wichman, Babkin Charters.

27.3%). Observations with moderate numbers of carcasses included Chum Salmon (29.6%) from Yukon, Bristol Bay, or PWS; Sockeye Salmon (29.6%) primarily from Bristol Bay; Pink Salmon (25.9%) primarily from PWS and Norton Sound; and Coho Salmon (14.8%) from Cook Inlet streams. Observations with low numbers included Chum Salmon (36.7%) primarily from the Yukon, Pink Salmon (20%) from Yukon and Norton Sound, Chinook Salmon (16.7%) from Yukon and Bristol Bay, Pacific salmon not identified to species (13.3%), Sockeye Salmon (10%) from Bristol Bay and Norton Sound, and one observation of Coho Salmon in Norton Sound (3.3%). A set of 11 observations of unusual mortality for species other than Pacific salmon were also included in the database.

RELATING MIGRATION SUCCESS TO STREAMFLOW SOURCE IN PRINCE WILLIAM SOUND

Methods for Relating Migration Success to Streamflow Source in Prince William Sound

In PWS, observations from a set of 134 salmon spawning index streams annually monitored by the Alaska Department of Fish and Game (ADFG; Morella et al. 2021) provided an opportunity to better understand how migration success corresponds to primary watershed runoff sources (i.e., rain, snow, or glacier ice). Index streams are surveyed systematically and have been used in the management of PWS Pink Salmon since the 1960s to monitor escapement across the ~1,000 streams that produce Pink Salmon. Aerial surveys occur approximately weekly during the spawning migration

Figure 4. Image of a Pink Salmon premature mortality observation in St. Matthews Creek, Prince William Sound, Alaska, 2019. This image was taken in a tidally influenced area following a high tide event that allowed Pink Salmon to enter the lower river, but did not provide enough time or water for spawning or further upstream migration. This picture is representative of observations in several Prince William Sound streams during 2019. Photo credit: Charles Russell.

Figure 5. Image of representative male (top) and female (bottom) summer Chum Salmon carcasses from an observation that included more than 1,000 carcasses in July 2019 on the Koyukuk River, Yukon watershed, Alaska (Westley 2020). Testes and eggs were determined to be underdeveloped, which confirmed that mortalities were premature and en route and was consistent with observation location on a migration corridor and not a spawning ground. Several carcasses had signs of fungal growth consistent with bacterial *columnaris* infection. Photo credit: Stephanie Quinn-Davidson.

Figure 6. Image of a Coho Salmon premature mortality observation in Ibeck Creek, Cordova Prince William Sound, Alaska, 2019. Photo credit: Jeremy Botz, Alaska Department of Fish and Game.

months of July and August. A single biologist (C. Russell, ADFG) categorized migration success in each index stream as high, medium, or low during routine aerial overflights to index salmon abundance in 2019. Categories were based on comparisons of Pink Salmon counts associated with three locations for each stream: marine bay staging waters, the stream mouth, and the spawning area. Streams with high migration success were those where abundance in marine bay staging waters was similar to that in the stream mouth and spawning area. Streams with medium migration success had noticeably fewer individuals reach the spawning area compared to the abundance in marine bay staging waters, while those categorized with low migration success had far fewer Pink Salmon reach the spawning area. This analysis complemented direct mortality observations by using aerial survey information to characterize migration success, not only carcass observations included in the observation database.

We used a Fisher's exact test to test the hypothesis that migration success in individual streams during drought was associated with the primary runoff source in the watershed. From the original set of 134 surveyed salmon spawning index streams, we identified primary runoff sources for 106 streams by matching latitude–longitude survey positions to watershed polygons of an existing streamflow classification for the Gulf of Alaska coast (Sergeant et al. 2020). Index streams with drainage areas <5 km^2 could not be classified and were removed from the analysis (n = 28). Rain source streams have hydrographs with maximum discharge in fall or winter; snow source streams have maximum discharge in spring or summer with a secondary maximum in fall; and glacier source streams have maximum discharge in summer without a secondary maximum in fall. Specific snow source classifications are based on differences in timing and amplitude of discharge maximums. Snow-II and Snow-IV source streams differ from Snow-I and Snow-III source streams in having larger watersheds and higher maximum discharges due to greater glacier areas (2–4% vs. 0–1%).

Because glaciers are an important and dynamic driver of streamflow patterns in PWS (Sergeant et al. 2020), we used logistic regression analysis to predict the probability of either reduced or high migration success. To represent a binary migration success outcome, we grouped low and medium migration success into a "reduced" migration success category with a binary response of 1 and assigned high migration success a binary response of 0. Responses were compared to the proportion of glacier(s) present in each watershed (*glm* function in R statistical software [Vienna] with binomial error). Glacier ice spatial extent (area) in each watershed was estimated using the Randolph Glacier Inventory, version 3.2 (Pfeffer et al. 2014).

Results for Relating Migration Success to Streamflow Source in Prince William Sound

Migration success of Pink Salmon returning to PWS streams was significantly associated with a stream's primary runoff source (Fisher's exact test; P = 0.0005). Low migration success was observed in 87% of Rain-I streams (n = 30), 75% of Snow-I streams (n = 8), 41% of Snow-II streams (n = 41), 89% of Snow-III Streams (n = 9), and 43% of Snow-IV streams (n = 7). In contrast, most Pink Salmon runs returning to Glacier-I streams had high migration success (82% of streams; n = 11; Figure 7). The proportional glacier coverage in a watershed was a significant predictor of binary migration success (high vs. reduced; P < 0.001). The inflection point of the logistic regression, where the probability of reduced migration success = 0.5, occurred at 18% glacier coverage (Figure 8). Across the 28 watersheds with some proportion of glacier ice coverage, 64% of Pink Salmon runs to streams with <18% coverage (n = 14) were observed to have reduced migration success, while only 21% of Pink Salmon runs returning to streams with >18% coverage (n = 14) had reduced migration success. Most (97%) Pink Salmon runs returning to streams with no glacier

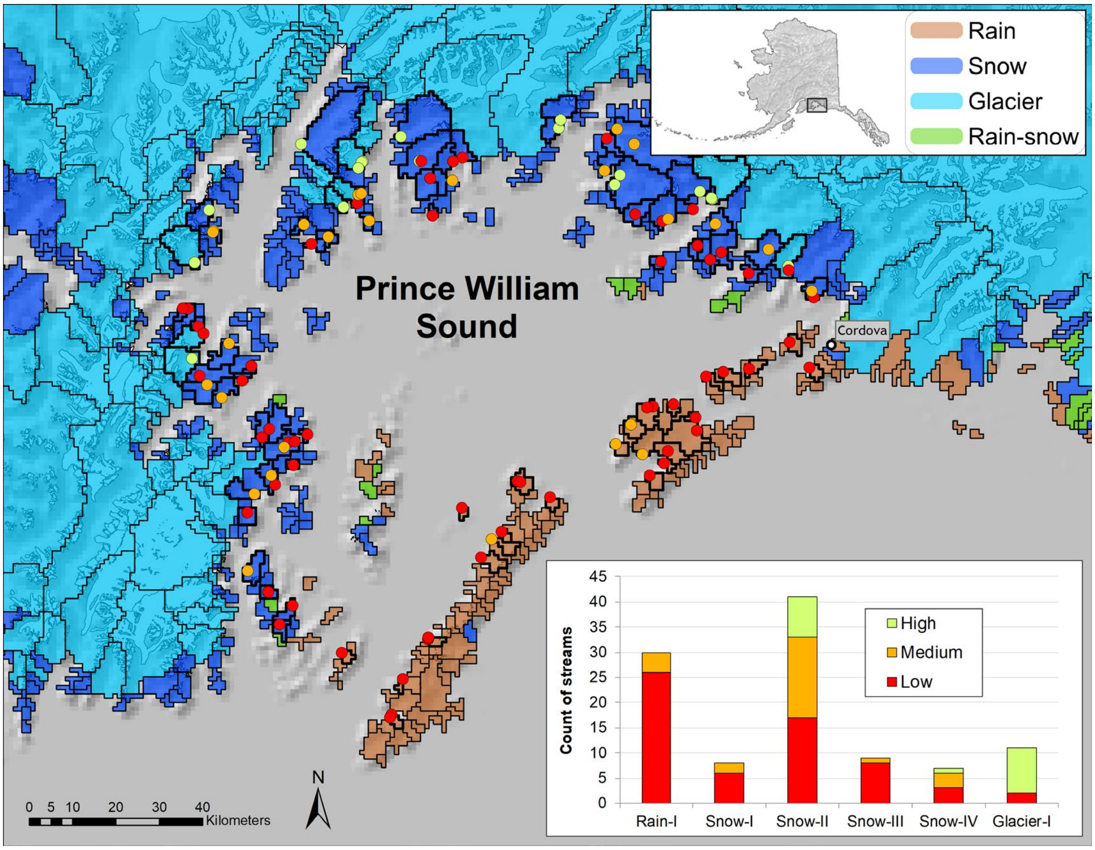

Figure 7. Observed summer 2019 migration success of Pink Salmon returning to streams in Prince William Sound (PWS), regularly surveyed for spawning salmon by the Alaska Department of Fish and Game. Colored circles indicate migration success, where green = high, orange = medium, and red = low. Polygons with black outlines represent individual watersheds with coastal outlets draining into PWS (thin line = not surveyed; thick line = surveyed). Polygon colors correspond to the primary runoff source. Bar chart represents counts of streams by streamflow class (as defined by Sergeant et al. 2020) that correspond with the three migration success categories.

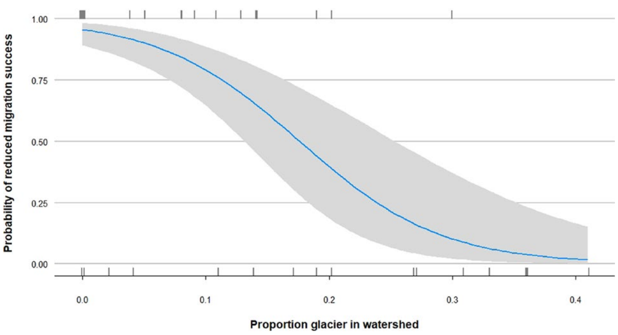

Figure 8. Probability of reduced spawning success (high vs. low or medium) for Pink Salmon returning to different Prince William Sound streams relative to the glacier proportion in a watershed. Gray shading represents a 95% confidence band. Gray tick marks at top and bottom of the horizontal axis indicates actual observations.

ice coverage (i.e., 0%) in the watershed experienced reduced migration success.

DISCUSSION

The first-documented widespread Pacific salmon mortality event in Alaska was related to a convergence of persistent climate extremes consistent with long-term climate warming: high temperatures, high pressure ridges, and drought. Opportunities for a cooling marine influence were reduced because marine waters were abnormally warm, as evidenced by the northeastern Pacific marine heatwave of 2019 and low September sea ice extent (ACRC 2020; Amaya et al. 2020). Mortality observations extended from Norton Sound in northwest Alaska through PWS in south-central Alaska (~1 million km^2), and included all five Pacific salmon species present. This geographic extent aligns with the area of record-breaking air temperatures and drought (Figure 1). The notable exception was Southeast Alaska, which experienced warm temperatures and drought, but had just one mortality observation. Conditions may have been more manageable for Pacific salmon returning to Southeast Alaska streams because the warm air temperature anomalies were more moderate and summer rainfall totals were higher on an absolute basis compared to other regions of Alaska (ACRC 2020).

In PWS, migration success of Pink Salmon runs was reduced (low and medium migration success categories) in nearly every rain- and snow-driven stream (Figure 7). Low water and dry stream channels associated with drought conditions seemed to be the primary barrier to migrating Pink Salmon. Drought also impacted some glacially influenced streams, including most streams with less than 18% glacial coverage in their watersheds. Reduced migration success was pervasive in rain-driven streams, common in snow-driven

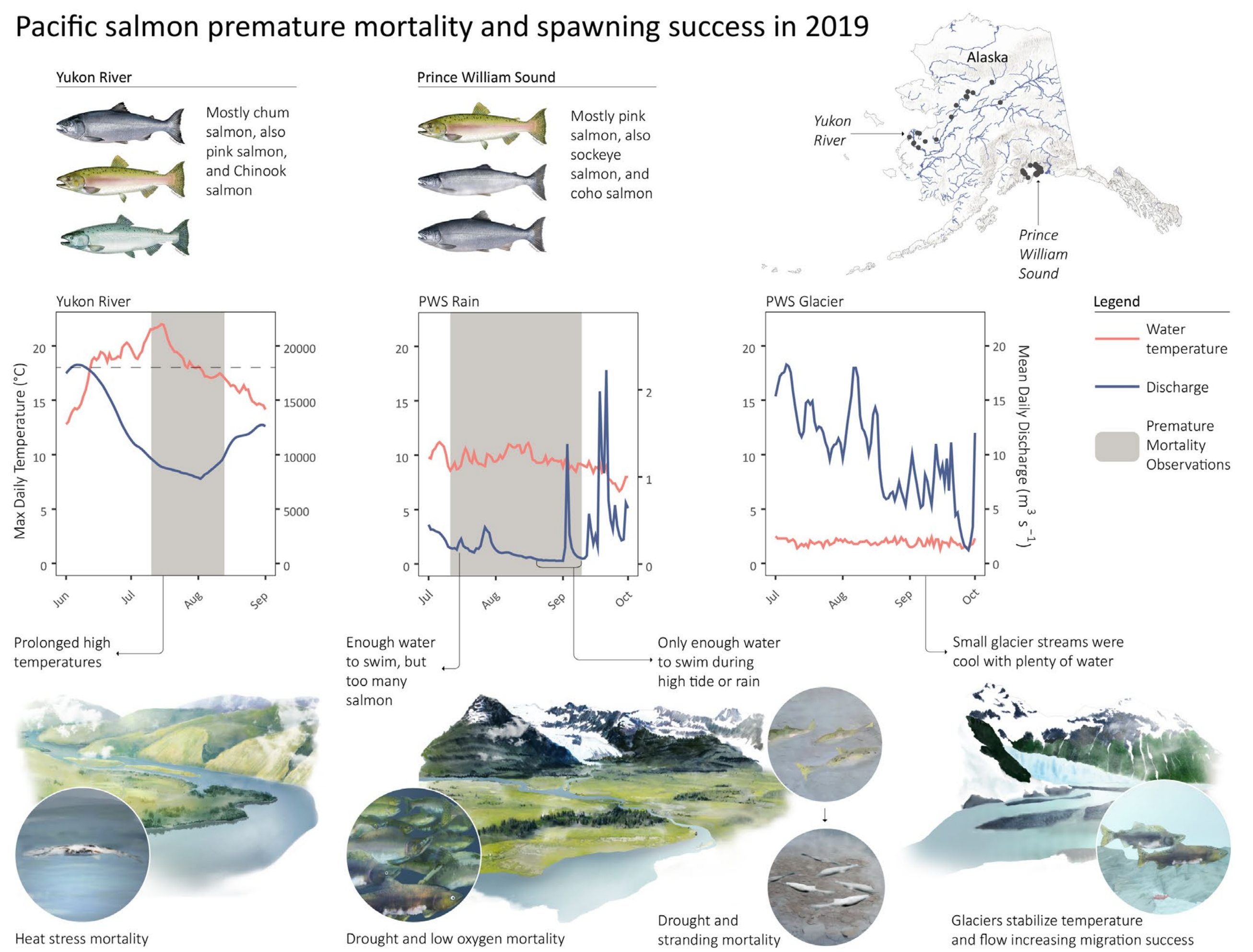

Figure 9. A conceptual model contrasting different conditions associated with Pacific salmon premature mortality in Alaska during record heat and drought in 2019, with conditions associated with typical levels of spawning success. Map (top right) shows selected mortality observations in Yukon and Prince William Sound (PWS) regions from Figure 2. Pictures of Pacific salmon species included in mortality observations from the Yukon region (top left) and PWS region (top center). Plot panels show maximum (max) daily water temperature (red line) and mean daily discharge (blue line; axes have different scales), contrasting physical conditions in three different streams during spawning migration (gray shading is mortality observation timing; no observations in right panel). Illustrations along the bottom depict Pacific salmon spawning outcomes under three different conditions. Left panel shows how prolonged, high water temperatures causes heat stress mortality of Pacific salmon when the upper thermal limit reached the Yukon River (water temperatures from Alaska Department of Fish and Game and discharge data from U.S. Geological Survey [USGS] gage station 15565447, Pilot Station; dashed line is 18°C water temperature threshold associated with heat stress from von Biela et al. 2020). Center panel shows representative PWS rain-driven stream where thousands of Pink Salmon carcasses were observed (water temperature and discharge data from USGS gage station 15215900, Glacier River, Cordova, glaciers actually outside this watershed). Also depicted are two ways in which drought causes hypoxia mortalities: (1) low and declining discharge reduced dissolved oxygen and increased crowding; (2) near zero discharge in August and early September inhibited upstream migration; thus, Pink Salmon entering intertidal regions on high tides or during an early September rain event were stranded at low tide or when the rain ended. Right panel shows representative PWS glacier-driven stream where Pink Salmon achieved high migration and spawning success in 2019 (water temperature and discharge from USGS gage station 15236900, Wolverine Creek, Whittier; gage located well above spawning areas, where water temperatures were not as cold). Figure design and illustration by Cecil Howell.

streams, and rare in glacier-driven streams. Our results support the perspective that understanding the local stream- or population-scale response to broad-scale climate forcing requires consideration of physical watershed characteristics as well as population-specific traits such as escapement abundance and run timing.

The propensity for spawning Pacific salmon to be influenced by water temperature and streamflow is well known (Rand et al. 2006; Quinn 2018; Dahlke et al. 2020). A recent meta-analysis revealed that across nearly 700 fish species, spawning adults had a narrower thermal tolerance with a cooler maximum temperature limit as compared to juveniles and nonspawning adults (Dahlke et al. 2020). The most likely cause for temperature sensitivity in spawning adults appears to be a reduced cardiorespiratory (aerobic) capacity associated with the energetic demands of gamete production (Dahlke et al. 2020). Cardiorespiratory capacity has been specifically identified as a limitation for spawning Pacific salmon in warm temperatures (Eliason et al. 2011) and is thought to explain the high rates of mortality with warm water temperatures in Fraser River Sockeye Salmon, as well as disproportionate negative effects on females, because they must produce energy-dense eggs (Quinn 2018; Hinch et al. 2021). Particularly difficult years for spawning salmon are occasionally apparent and provide examples where extreme atmospheric conditions resulted in particularly high mortality. For example, Pacific salmon spawning migrations in the U.S. Pacific Northwest during 2015 faced a similar set of environmental anomalies as Alaska in 2019, including record-breaking warm temperatures, low streamflows associated with drought, and the 2014–2016 Pacific marine heatwave (Crozier et al. 2020). This resulted in almost complete premature mortality among Snake River Sockeye Salmon and unusually high premature mortality among Snake River Chinook Salmon (Crozier et al. 2020).

Observations reported here are part of an emerging picture that biological tipping points are being reached for Alaska's Pacific salmon, where warming switches from beneficial to detrimental in some locations, years, and life stages. In western Alaska, evidence of heat stress was detected in about half of spawning Yukon River Chinook Salmon sampled during 2016 and 2017, when migration water temperatures exceed 18°C (von Biela et al. 2020). Jones et al. (2020), in a south-central Alaska study, also documented the negative effects of water temperatures above 18°C on annual measures of Chinook Salmon production. Unfortunately, protracted periods (weeks to a month) of summer water temperatures above 18°C are anticipated to be more common in south-central Alaska (e.g., Matanuska-Susitna and Cook Inlet regions) over the next 50 years (Shaftel et al. 2020). The opportunistic observations we collected reinforce concerns raised in these studies and identify additional Pacific salmon populations where detrimental effects from warming may also be emerging.

Premature Mortality Observations

The large number of premature mortality observations, involvement of multiple Pacific salmon species, and wide geographic distribution of the observations are consistent with a response to large-scale atmospheric conditions in 2019. While carcass detections grossly underestimate the true levels of premature mortality, Patterson et. al. (2007) noted that anecdotal carcass reports provide some of the earliest indicators of en route losses as mortality observations often occur in runs where negative discrepancies between en route escapement projections and final spawner escapement estimates are later identified. In fact, other data from 2019 also indicated unusually high levels of premature mortality in the Yukon region where carcasses were observed. High en route mortality for Yukon Chinook salmon was consistent with a large and negative discrepancy between the prediction of Canadian-bound fish estimated from the lower river monitoring station in Pilot Station, Alaska, and estimates at the Canadian border, which resulted in a Canadian fishery closure (JTC 2020). Similarly, summer Chum Salmon abundance in the Koyukuk River portion of the Yukon was well below average at both the Gisasa River and Henshaw Creek weirs, which were located upriver from areas where many carcasses were observed (Brenner et al. 2020).

Several factors preclude us from drawing conclusions about the number of premature mortality observations associated with each species, since observations were opportunistic and did not come from a designed study. For example, carcass detection was likely higher for more abundant species, clearer streams, shallower streams, warmer streams, and more frequented locations (Patterson et al. 2007). Indeed, all of these observation biases are present for observations of Pink Salmon, the most frequently reported species. Pink Salmon are far more abundant than the other species in Alaska (Brenner et al. 2020); there was a high degree of survey effort by the ADFG, and most PWS streams surveyed were clear and shallow since peak drought conditions occurred during the time spawning surveys were conducted.

Relating Migration Success to Streamflow Source in Prince William Sound

Conditions in the PWS region prior to and during the 2019 Pink Salmon spawning migration were unusual, and migration success varied widely (Figure 7). While April snowpack conditions were normal at higher elevations, snow melted early at lower elevations (Fisher et al. 2019a). For example, there was no snow in the Lowe River and Valdez in April, when normally snow depth would be 0.82 m and 0.71 m, respectively (Fisher et al. 2019a). Air temperature anomalies were warm in March and April, which melted snow at lower elevations, and warm from June through August, along with low precipitation (Fisher et al. 2019b).

Most regions of PWS include examples of Pink Salmon runs with high, medium, and low migration success, with high and low migration success streams often occurring in adjacent watersheds. Southern PWS's large islands (Montague, Hinchinbrook, and Hawkins) were the exception, with Pink Salmon migration success universally reduced to low and medium levels. Different streamflow sources among watersheds reliably predicted Pink Salmon migration success. Pink Salmon runs to rain- and snow-driven streams were vulnerable to the drought, with rain-driven systems being most vulnerable. Glacier-driven streams were generally buffered from the drought because glacier melt water provided a more reliable source of streamflow. Southern PWS's large islands have minimal glacier coverage and nearly all their watersheds are rain-driven, which explains why migration success was universally reduced there. Our results align with predicted climate change impacts, particularly increasing temperatures and drought severity in Arctic and subarctic watersheds that reduce the snowpack available for enhancing streamflow during summer and fall (Nilsson et al. 2015; Littell et al. 2018).

In PWS streams, Rain-I and Snow-II watersheds accounted for the largest number of streams with reduced migration success. Throughout the coastal Gulf of Alaska, these two watershed types account for 27% of the 4,140 watersheds that have been classified (Sergeant et al. 2020), suggesting that stream response to drought conditions could have been more widespread across southern Alaska. Snow-driven watersheds in this area are anticipated to continue shifting toward snow–rain transitional hydrographs through the end of the 21st century (Littell et al. 2018). Based on the results presented here, that streamflow transition would also confer a higher likelihood of reduced salmon migration success during summer drought conditions. While our analysis indicated that watersheds with glacier coverage greater than 18% appear to be somewhat buffered from low summer flows, modeling in southern coastal Alaska predicts the magnitude of summer flow will decrease as glacier volumes continue to diminish (Beamer et al. 2017; Pitman et al. 2020). In current times, short-term glacier melt can also be so rapid that it causes anomalously high flows that impede migration (Valentin et al. 2018). Indeed, high flows in PWS's glacierized Copper River appeared to impede the migration of radio-tagged Sockeye Salmon near Wood Canyon in 2019 and resulted in a high rate (>50%) of en route mortality for the component of the run migrating during mid-season (P. S. Rand, unpublished data).

In glaciated southern coastal Alaska (Cook Inlet through Southeast Alaska), two primary mechanisms have been described in which drought leads to adult salmon mortality despite generally cool (<15°C) freshwater temperatures: (1) exposure to lethally low dissolved oxygen levels due to reduced reaeration rates from lower water turbulence at low discharges and increased respiration due to high salmon density (Sergeant et al. 2017; Tillotson and Quinn 2017), and (2) stranding in channels that dry up as the tide ebbs (Murphy 1985; P. S. Rand, personal observations).

Prior to 2019, observations of drought-related mortality occurred in just a few streams during a particular year and tended to involve a few thousand carcasses or fewer (C. Russell, personal observations). Two exceptions were 1991 and 2004, when drought and related mortalities were widespread within PWS (ADFG records reviewed by Russell). However, 2019 conditions differed from those in 1991 and 2004 because marine water temperatures were also warm and reached at least 18°C in July (R. Campbell, Prince William Sound Science Center; unpublished data from central PWS). Some Pink Salmon appeared to respond to warm marine water temperatures by entering cooler streams (<13°C; P.S. Rand, unpublished data collected above the high tide line in PWS streams) earlier than normal (e.g., July instead of August). The intensity of die-offs in some PWS Pink Salmon streams may also be exacerbated by high rates of straying of hatchery-origin fish into natural streams, which, by increasing fish density and dissolved oxygen demand prior to spawning, can lead to density-dependent hypoxia. Hogan Creek, where a significant die-off event was observed, is comprised mostly of hatchery-origin Pink Salmon (>50% during 2013–2015; Knudsen et al. 2021), and had markedly higher fish densities, leading to a greater risk of premature mortality among natural-origin fish than would otherwise be the case.

Synthesis

Our three plots of water temperature and discharge (Figure 9) show the wide range of freshwater temperatures and flows under warm air temperature and drought conditions that occurred in Alaska during 2019, and also led us to identify three main causes of premature mortality when examined in conjunction with observations of carcasses: heat stress due to high water temperatures, hypoxia due to drought, and stranding due to drought. This did not occur in PWS's glacier-driven streams, where glacier runoff continued to provide a cold and stable water source. Elsewhere in Alaska, it is likely that glacial runoff, as well as cool groundwater sources, provided similar successful outcomes for migrating and spawning of Pacific salmon.

The strongest support for high water temperature as a cause of premature mortality came from the Yukon region salmon carcass observations in conjunction with available temperature and discharge data (Figure 9; ADFG temperature data and U.S. Geological survey [USGS] discharge data at station 15565447 from Pilot Station, Alaska). Other studies have also identified a heat stress response in several species of Pacific salmon in water near 18°C and mortalities in water ranging from 21°C to 25°C (McCullough 1999; Strange 2010; Donnelly et al. 2020; von Biela et al. 2020). For Yukon River Chinook Salmon, von Biela et al. (2020) reported heat stress during 2016 and 2017, when water temperatures were less extreme than in 2019 (von Biela et al. 2020). In 2019, the Yukon River had a maximum daily water temperature >18°C for 44 consecutive days (June 13 – July 26) and >21°C for 9 consecutive days (July 9–17). Pacific salmon mortality observation dates were well correlated with dates when water temperatures associated with mortality were reached (>21°C). Mortality observations in the Yukon region were first reported on July 10, just 1 d after the first daily maximum water temperature was >21°C, while the latest mortality observations were made in early August, just after maximum daily water temperatures fell to <18°C. Other factors may have also contributed to mortalities, including hypoxia, reduced streamflow from drought, and pathogens.

The strongest support for drought as a cause of premature mortality was in PWS Pink Salmon carcass observations in conjunction with aerial survey estimates of migration success and stream discharge information. Stream discharge levels dropped through July, but high densities of Pink Salmon still had enough water to move into streams. This combination of less water and many salmon likely caused hypoxic conditions that led to mortality observations in July (Figure 9). By August, water levels were often too low for upstream movement, and arriving Pink Salmon appeared to congregate in cooler (<13°C) and deeper PWS marine waters, where they were occasionally visible during aerial surveys in areas of cold water upwelling. This pattern persisted for several weeks and delayed the typical timing of upstream migration. By the middle of August, Pink Salmon attempted to migrate upstream during diurnal high tides, only to be either stranded in dewatered channels near stream mouths or trapped in tide pools during subsequent low tides (Figures 4, 9). Eventually, a rain event in early September provided a narrow window of opportunity for Pink Salmon to migrate upstream, and some were able to successfully complete their migration to spawning areas. The subsequent drop in water levels after the rain ended was associated with new mortality observations (Figure 9).

In contrast, high migration success was generally associated with runs into small glacier-driven PWS streams that were buffered or responded differently to the atmospheric effects of warm temperatures and drought. A water monitoring station just below Wolverine Glacier in western PWS demonstrated that glacier melt continued to provide cold, stable water temperatures near 2°C and discharges well above zero (Figure 9; data from USGS gage station 15236900 on Wolverine Creek near Whitter, Alaska; upstream of spawning grounds).

Despite the drought, return of PWS Pink Salmon from the 2019 brood in 2021 was above average for wild stocks (ADFG preliminary data for 2021 season). Both adaptive management decisions and biological compensatory responses potentially facilitated PWS Pink Salmon recruitment success despite an uncertain 2021 forecast (Brenner et al. 2021). After detecting premature mortality early in the 2019 fishing season, managers limited harvest at critical times to provide more opportunity for fish to successfully migrate and spawn during drought conditions (Russell, unpublished data). This provides an example of how proactive management can adapt to benefit fish populations experiencing unusual environmental conditions. However, major drivers of salmon population dynamics, like compensatory processes (e.g., density dependence and competitive interactions) and favorable ocean conditions, almost certainly contributed to improved recruitment and led to a relatively strong return in 2021. Among other species with premature mortality observations, generations times are longer and outcomes from the 2019 brood are not yet known.

Extreme heat and drought events are often viewed as windows into the future (Russo et al. 2014; Crozier et al. 2020). Observations from 2019 may prove to be one early warning of widespread shifts in Alaska's Pacific salmon production, given some recent studies on future water temperature and salmon production. First, watersheds with near optimal water temperatures over the past several decades are projected to warm beyond lethal limits of Pacific salmon within the next 50 years (Shaftel et al. 2020). Second, there is already evidence of declining population productivity with increasing water temperature in southcentral Alaska's warmest watersheds (Jones et al. 2020). Third, there is some evidence that warming will increase Pacific salmon production in rivers and streams that have been historically below thermal preferences (e.g., Schoen et al. 2017; Jones et al. 2020). Fourth, there is evidence that an increasing number of Pacific salmon will encounter challenging environmental conditions in marine as well as freshwater habitats as climate warming proceeds. Marine conditions are known to influence Pacific salmon production with warmer oceans previously linked to higher production in Alaska (Mueter et al. 2002), but more recent evidence hinting that extremely warm ocean conditions are problematic (Carey et al. 2021). More frequent extreme warm ocean conditions are anticipated (e.g., Pacific marine heatwaves in 2014–2016 and 2019; Amaya et al. 2020). This is particularly concerning because it would likely lower productivity more than if stressful conditions were limited to either marine or freshwaters.

Federal and state agencies, tribal organizations, nonprofit organizations, and citizen scientists are already working to maintain and increase the capacity to monitor water temperature, streamflow, and fish populations across Alaska's expansive and remote landscape. Mortality observations can continue to be reported via the LEO Network (LEONetwork.org). These efforts are an important step to better detect and prepare for long-term fisheries change and inform habitat conservation efforts at local and regional scales. However, systematic sampling of en route and prespawn mortality is extremely limited in Alaska and not easily implemented in most of Alaska's remote salmon spawning habitat that lack road access. Instead, researchers may need to validate new biomarkers or models that predict premature mortality from environmental conditions with the goal of developing alternative tools for monitoring premature mortality. Increased opportunities for data sharing and organized repositories (e.g., waterdata.usgs.gov and the anticipated AKTEMP water temperature repository from the Alaska Center for Conservation Science) can improve the utility of all these data sources, and will help fishery scientists and managers determine whether a major shift in Pacific salmon productivity is underway. A shift in the abundance of Pacific salmon would be a significant disruption for communities that depend on salmon to sustain their culture, food security, and local economy.

ACKNOWLEDGMENTS

We thank the dozens of citizens and scientists who generously shared their observations of unusual fish mortality across Alaska during 2019. Please see the associated data release for acknowledgments of each observer associated with their specific observations. We also thank Michael Brubaker, Erica Lujan, and the Alaska Native Tribal Health Consortium for their efforts in developing and maintaining the LEO Network. Erik Schoen, Bill Templin, Jack Erickson, and Matthew Nemeth provided helpful reviews of the initial version of this article. Nate Mantua, Matthew Keefer, and an anonymous reviewer provided constructive comments that improved the article during journal review. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

ORCID

Vanessa R. von Biela https://orcid.org/0000-0002-7139-5981
Christopher J. Sergeant https://orcid.org/0000-0002-3363-3213
Michael P. Carey https://orcid.org/0000-0002-3327-8995
Peter S. Rand https://orcid.org/0000-0003-0166-2201
Peter A.H. Westley https://orcid.org/0000-0003-4190-7314
Christian E. Zimmerman https://orcid.org/0000-0002-3646-0688

REFERENCES

ACRC (Alaska Climate Research Center). 2020. 2019 Alaska climate review. The Alaska Climate Research Center, Fairbanks.

Amaya, D. J., A. J. Miller, S. P. Xie, and Y. Kosaka. 2020. Physical drivers of the summer 2019 north Pacific marine heatwave. Nature Communications 11:1–9.

Beamer, J. P., D. F. Hill, D. McGrath, A. Arendt, and C. Kienholz. 2017. Hydrologic impacts of changes in climate and glacier extent in the Gulf of Alaska watershed. Water Resources Research 53:7502–7520.

von Biela, V. R., L. Bowen, S. D. McCormick, M. P. Carey, D. S. Donnelly, S. Waters, A. M. Regish, S. M. Laske, R. J. Brown, S. Larson, S. Zuray, and C. E. Zimmerman. 2020. Evidence of prevalent heat stress in Yukon River Chinook Salmon. Canadian Journal of Fisheries and Aquatic Sciences 77:1878–1892.

von Biela, V. R., and A. Stanek. 2021. Observations documenting premature mortality among Alaska's Pacific salmon in 2019. U.S. Geological Survey data releaseAvailable: https://bit.ly/3AcnDfr (January 2022).

Bowerman, T., M. L. Keefer, and C. C. Caudill. 2016. Pacific salmon prespawn mortality: patterns, methods, and study design considerations. Fisheries 41:738–749.

Brenner, R. E., S. J. Larsen, A. R. Munro, and A. M. Carroll, editors. 2020. Run forecasts and harvest projections for 2020 Alaska Salmon Fisheries and Review of the 2019 season. Alaska Department of Fish and Game, Divisions of Sport Fish and Commerical Fisheries, Special Publication 20–06, Anchorage.

Brenner, R. E., S. L. Larsen, A. R. Munro, and A. M. Carroll, editors. 2021. Run forecasts and harvest projections for 2021 Alaska salmon fisheries and review of the 2020 season. Alaska Department of Fish and Game, Divisions of Sport Fish and Commerical Fisheries, Special Publication 21-07, Anchorage.

Carey, M. P., V. R. von Biela, A. Dunker, K. D. Keith, M. Schelske, C. Lean, and C. E. Zimmerman. 2021. Egg retention of high-latitude Sockeye Salmon (*Oncorhynchus nerka*) in the Pilgrim River, Alaska, during the Pacific marine heatwave of 2014–2016. Polar Biology 44:1643–1654.

Crozier, L. G., J. E. Siegel, L. E. Wiesebron, E. M. Trujillo, B. J. Burke, B. P. Sandford, and D. L. Widener. 2020. Snake River Sockeye and Chinook Salmon in a changing climate: implications for upstream migration survival during recent extreme and future climates. PLOS One 15:9:e0238886.

Dahlke, F. T., S. Wohlrab, M. Butzin, and H.-O. Pörtner. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. Science 369:65–70.

Donnelly, D. S., V. R. Von Biela, S. D. McCormick, S. M. Laske, M. P. Carey, S. Waters, L. Bowen, R. J. Brown, S. Larson, and C. E. Zimmerman. 2020. A manipulative thermal challenge protocol for adult salmonids in remote field settings. Conservation Physiology 8:coaa074.

Eliason, E. J., T. D. Clark, M. J. Hague, L. M. Hanson, Z. S. Gallagher, K. M. Jeffries, M. K. Gale, D. A. Patterson, S. G. Hinch, and A. P. Farrell. 2011. Differences in thermal tolerance among Sockeye Salmon populations. Science 332:109–112.

Fisher, D., T. DeMarco, and D. Kenney. 2019a. Alaska Snow Survey Report May 1, 2019. U.S. Department of Agriculture, Natural Resources Conservation Service, Palmer, Alaska.

Fisher, D., T. DeMarco, and D. Kenney. 2019b. Alaska Snow Survey Report April 1, 2019. U.S. Department of Agriculture, Natural Resources Conservation Service, Palmer, Alaska.

Goniea, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook Salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135:408–419.

Hinch, S. G., N. N. Bett, E. J. Eliason, A. P. Farrell, S. J. Cooke, and D. A. Patterson. 2021. Exceptionally high mortality of adult female salmon: a large-scale pattern and a conservation concern. Canadian Journal of Fisheries and Aquatic Sciences 78:639–654

Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, G. J. Jia, T. Jorgenson, D. L. Kane, D. R. Klein, G. Kofinas, A. H. Lynch, A. H. Lloyd, A. D. McGuire, F. E. Nelson, W. C. Oechel, T. E. Osterkamp, C. H. Racine, V. E. Romanovsky, R. S. Stone, D. A. Stow, M. Sturm, C. E. Tweedie, G. L. Vourlitis, M. D. Walker, D. A. Walker, P. J. Webber, J. M. Welker, K. S. Winker, and K. Yoshikawa. 2005. Evidence and implications of recent climate change in Northern Alaska and other Arctic regions. Climatic Change 72:251–298.

Houghton, P. J., G. Jenkins, and J. Ephraums, editors. 1990. Climate change: the IPCC scientific assessment. Cambridge University Press, New York.

Jones, L. A., E. R. Schoen, R. Shaftel, C. J. Cunningham, S. Mauger, D. J. Rinella, and A. St. Saviour. 2020. Watershed-scale climate influences productivity of Chinook Salmon populations across southcentral Alaska. Global Change Biology 26:4919–4936.

Keefer, M. L., M. A. Jepson, G. P. Naughton, T. J. Blubaugh, T. S. Clabough, and C. C. Caudill. 2017. Condition-dependent en route migration mortality of adult Chinook Salmon in the Willamette river main stem. North American Journal of Fisheries Management 37:370–379.

Littell, J. S., S. A. McAfee, and G. D. Hayward. 2018. Alaska snowpack response to climate change: statewide snowfall equivalent and snowpack water scenarios. Water 10:(5):668.

McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of Salmonids, with special reference to Chinook Salmon. U.S. Environmental Protection Agency Region 10 Water Resources Assessment Report No. 910-R-99-010, Seattle.

Morella, J., C. W. Russell, J. Botz, and S. B. Haught. 2021. 2019 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report No. 21-19, Anchorage.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Murphy, M. L. 1985. Die-offs of pre-spawn adult Pink Salmon and Chum Salmon in southeastern Alaska. North American Journal of Fisheries Management 5:302–308.

Nilsson, C., L. E. Polvi, and L. Lind. 2015. Extreme events in streams and rivers in arctic and subarctic regions in an uncertain future. Freshwater Biology 60:2535–2546.

O'Reilly, C. M., S. Sharma, D. K. Gray, S. E. Hampton, J. S. Read, R. J. Rowley, P. Schneider, J. D. Lenters, P. B. McIntyre, B. M. Kraemer, G. A. Weyhenmeyer, D. Straile, B. Dong, R. Adrian, M. G. Allan, O. Anneville, L. Arvola, J. Austin, J. L. Bailey, J. S. Baron, J. D. Brookes, E. de Eyto, M. T. Dokulil, D. P. Hamilton, K. Havens, A. L. Hetherington, S. N. Higgins, S. Hook, L. R. Izmesteva, K. D. Joehnk, K. Kangur, P. Kasprzak, M. Kumagai, E. Kuusisto, G. Leshkevich, D. M. Livingstone, S. MacIntyre, L. May, J. M. Melack, D. C. Mueller-Navarra, M. Naumenko, P. Noges, T. Noges, R. P. North, P.-D. Plisnier, A. Rigosi, A. Rimmer, M. Rogora, L. G. Rudstam, J. A. Rusak, N. Salmaso, N. R. Samal, D. E. Schindler, S. G. Schladow, M. Schmid, S. R. Schmidt, E. Silow, M. E. Soylu, K. Teubner, P. Verburg, A. Voutilainen, A. Watkinson, C. E. Williamson, and G. Zhang. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42:10,773–10,781.

Patterson, D. A., K. M. Skibo, D. P. Barnes, J. A. Hills, and J. S. MacDonald. 2007. The influence of water temperature on time to surface for adult Sockeye Salmon carcasses and the limitations in estimating salmon carcasses in the Fraser River, British Columbia. North American Journal of Fisheries Management 27:878–884.

Pfeffer, W. T., A. A. Arendt, A. Bliss, T. Bolch, J. G. Cogley, A. S. Gardner, J. O. Hagen, R. Hock, G. Kaser, C. Kienholz, E. S. Miles, G. Moholdt, N. Mölg, F. Paul, V. Radić, P. Rastner, B. H. Raup, J. Rich, M. J. Sharp, L. M. Andreassen, S. Bajracharya, N. E. Barrand, M. J. Beedle, E. Berthier, R. Bhambri, I. Brown, D. O. Burgess, E. W. Burgess, F. Cawkwell, T. Chinn, L. Copland, N. J. Cullen, B. Davies, H. De Angelis, A. G. Fountain, H. Frey, B. A. Giffen, N. F. Glasser, S. D. Gurney, W. Hagg, D. K. Hall, U. K. Haritashya, G. Hartmann, S. Herreid, I. Howat, H. Jiskoot, T. E. Khromova, A. Klein, J. Kohler, M. König, D. Kriegel, S. Kutuzov, I. Lavrentiev, R. Le Bris, X. Li, W. F. Manley, C. Mayer, B. Menounos, A. Mercer, P. Mool, A. Negrete, G. Nosenko, C. Nuth, A. Osmonov, R. Pettersson, A. Racoviteanu, R. Ranzi, M. A. Sarikaya, C. Schneider, O. Sigurdsson, P. Sirguey, C. R. Stokes, R. Wheate, G. J. Wolken, L. Z. Wu, and F. R. Wyatt. 2014. The Randolph glacier inventory: a globally complete inventory of glaciers. Journal of Glaciology 60:537–552.

Pitman, K. J., J. W. Moore, M. R. Sloat, A. H. Beaudreau, A. L. Bidlack, R. E. Brenner, E. W. Hood, G. R. Pess, N. J. Mantua, A. M. Milner, V. Radić, G. H. Reeves, D. E. Schindler, and D. C. Whited. 2020. Glacier retreat and Pacific salmon. BioScience 70:220–236.

Post, E., R. B. Alley, T. R. Christensen, M. Macias-fauria, B. C. Forbes, M. N. Gooseff, A. Iler, J. T. Kerby, K. L. Laidre, M. E. Mann, J. Olofsson, J. C. Stroeve, F. Ulmer, R. A. Virginia, and M. Wang. 2019. The polar regions in a 2°C warmer world. Science Advances 5:eaaw9883.

Quinn, T. P. 2018. The behavior and ecology of Pacific salmon and trout, second edition. University of Washington Press, Seattle.

Rand, P. S., S. G. Hinch, J. Morrison, M. G. G. Foreman, M. J. MacNutt, J. S. Macdonald, M. C. Healey, A. P. Farrell, and D. A. Higgs. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River Sockeye Salmon. Transactions of the American Fisheries Society 135:655–667.

Russo, S., A. Dosio, R. G. Graversen, J. Sillmann, H. Carrao, M. B. Dunbar, A. Singleton, P. Montagna, P. Barbola, and J. V. Vogt. 2014. Magnitude of extreme heat waves in present climate and their projection in a warming world. Journal of Geophysical Research: Atmospheres. 119:12,500–12,512.

Schoen, E. R., M. S. Wipfli, E. J. Trammell, D. J. Rinella, A. L. Floyd, J. Grunblatt, M. D. McCarthy, B. E. Meyer, J. M. Morton, J. E. Powell, A. Prakash, M. N. Reimer, S. L. Stuefer, H. Toniolo, B. M. Wells, and F. D. W. Witmer. 2017. Future of Pacific salmon in the face of environmental change: lessons from one of the world's remaining productive Salmon regions. Fisheries 42:538–553.

Sergeant, C. J., J. R. Bellmore, C. McConnell, and J. W. Moore. 2017. High salmon density and low discharge create periodic hypoxia in coastal rivers. Ecosphere 8:e01846.

Sergeant, C. J., J. A. Falke, R. A. Bellmore, J. R. Bellmore, and R. L. Crumley. 2020. A classification of streamflow patterns across the coastal Gulf of Alaska. Water Resources Research 56:1–17.

Shaftel, R., S. Mauger, J. Falke, D. Rinella, J. Davis, and L. Jones. 2020. Thermal diversity of salmon streams in the Matanuska-Susitna Basin, Alaska. Journal of the American Water Resources Association 56:630–646.

Strange, J. S. 2010. Upper thermal limits to migration in adult Chinook Salmon: evidence from the Klamath River Basin. Transactions of the American Fisheries Society 139:1091–1108.

Strange, J. S. 2012. Migration strategies of adult Chinook Salmon runs in response to diverse environmental conditions in the Klamath River Basin. Transactions of the American Fisheries Society 141:1622–1636.

Tillotson, M. D., and T. P. Quinn. 2017. Climate and conspecific density trigger pre-spawning mortality in Sockeye Salmon (*Oncorhynchus nerka*). Fisheries Research 188:138–148. Elsevier B.V.

Valentin, M. M., T. S. Hogue, and L. E. Hay. 2018. Hydrologic regime changes in a high-latitude glacierized watershed under future climate conditions. Water 77:1878–1892.

Westley, P. A. H. 2020. Documentation of en route mortality of summer Chum Salmon in the Koyukuk River, Alaska and its potential linkage to the heatwave of 2019. Ecology and Evolution 10:10296–10304. AFS