High salmon density and low discharge create periodic hypoxia in coastal rivers

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Abstract. Dissolved oxygen (DO) is essential to the survival of almost all aquatic organisms. Here, we examine the possibility that abundant Pacific salmon (*Oncorhynchus* spp.) and low streamflow combine to create hypoxic events in coastal rivers. Using high-frequency DO time series from two similar watersheds in southeastern Alaska, we summarize DO regimes and the frequency of hypoxia in relationship to salmon density and stream discharge. We also employ a simulation model that links salmon oxygen respiration to DO dynamics and predicts combinations of salmon abundance, discharge, and water temperature that may result in hypoxia. In the Indian River, where DO was monitored hourly during the ice-free season from 2010 to 2015, DO levels decreased when salmon were present. In 2013, a year with extremely high spawning salmon densities, DO dropped to 1.7 mg/L and 16% saturation, well below lethal limits. In Sawmill Creek, where DO was monitored every six minutes across an upstream–downstream gradient during the 2015 spawning season, DO remained fully saturated upstream of spawning reaches, but declined markedly downstream to 2.9 mg/L and 26% saturation during spawning. Modeled DO dynamics in the Indian River closely tracked field observations. Model sensitivity analysis illustrates that low summertime river discharge is a precursor to salmon-induced oxygen depletion in our study systems. Our results provide compelling evidence that dense salmon populations and low discharge can trigger hypoxia, even in rivers with relatively cold thermal regimes. Although climate change modeling for southeastern Alaska predicts an increase in annual precipitation, snowfall in the winter and rainfall in the summer are likely to decrease, which would in turn decrease summertime discharge in rain- and snow-fed streams and potentially increase the frequency of hypoxia. Our model template can be adapted by resource managers and watershed stakeholders to create real-time predictive models of DO trends for individual streams. While preserving thermally suitable stream habitat for cold-water taxa facing climate change has become a land management priority, managers should also consider that some protected watersheds may still be at risk of increasingly frequent hypoxia due to human impacts such as water diversion and artificially abundant salmon populations caused by hatchery straying.

Key words: Alaska; bioenergetics; dissolved oxygen; ecosystem engineer; hatcheries; hypoxia; Pacific salmon; strays; subsidy–stress gradient; thermal regime.

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INTRODUCTION

Dissolved oxygen (DO) is essential to the survival of almost all aquatic organisms. Reports of oxygen depletion events (hypoxia) in nearshore marine environments have increased exponentially since the mid-20th century (Diaz and Rosenberg 2008, Vaquer-Sunyer and Duarte 2008). Freshwaters are also vulnerable to hypoxia (Mallin et al. 2006), and these events have contributed to documented fish kills across the globe (La and Cooke 2011). Natural events such as deep water entrainment at fjord sills (Arneborg et al. 2004) and prolonged ice cover in lakes (Wetzel 2001) often lead to hypoxia, but human-induced changes to aquatic systems such as nutrient overloading and flow regime modification commonly contribute to oxygen depletion, as well (USEPA 2007). There is also the growing appreciation that other aquatic species can strongly influence DO levels; for example, large beds of invasive plants can decrease DO levels in lowland rivers (Caraco and Cole 2002). Here, we examine the possibility that abundant Pacific salmon (*Oncorhynchus* spp.) and low streamflow can combine to create hypoxic events in coastal rivers.

Large sections of coastline along British Columbia and Alaska encompass watersheds with some of the most abundant populations of Pacific salmon in the world. As mature semelparous salmon return from the sea to spawn and subsequently die in their natal rivers, they require cool water that is high in oxygen, low in excess nutrients, and relatively free of pollution. These oligotrophic waters receive an influx of salmon-derived nutrients that subsidize terrestrial and aquatic food webs (Gende et al. 2002). While these subsidies are generally viewed as a benefit to stream food webs, the ecological consequences of spawning salmon can vary depending on the habitat characteristics of individual watersheds and reaches (Janetski et al. 2009, Holtgrieve et al. 2010*b*, Campbell et al. 2011, Bellmore et al. 2014, Benjamin et al. 2016).

In small watersheds (<30 km²), dense spawning salmon can significantly modify the physical and chemical characteristics of rivers through processes such as respiration, nest building, and carcass decomposition (Montgomery et al. 1996, Peterson and Foote 2000, Moore et al. 2004, Holtgrieve and Schindler 2011, Levi et al. 2013, Fellman et al. 2015). Salmon nest building, for instance, has been shown to increase air–water gas exchange (Holtgrieve and Schindler 2011) and reduce the abundance of benthic organisms (Moore and Schindler 2008, Collins et al. 2011, Campbell et al. 2012). It is also possible that the metabolic demands of high densities of salmon spawners could reduce DO to levels that are harmful or lethal to salmon themselves and other sensitive aquatic life.

For over sixty years, biologists in southeastern Alaska have observed salmon die-offs in small watersheds (Murphy 1985, Chaloner et al. 2004). Most recently, Tillotson and Quinn (2017) demonstrated that high pre-spawn mortality rates of sockeye salmon (*Oncorhynchus nerka*) in a small southwestern Alaska creek were strongly correlated with low DO levels caused by dense salmon populations, warm water, and low discharge. To date, most studies touching on this issue provide point estimates or ranges of DO measurements within an individual year. Relatively little is known about how often low DO events occur, how long they persist, and importantly, how often salmon contribute to hypoxic events in concert with other environmental conditions.

Dissolved oxygen regimes vary not only with fluctuations in salmon density and water temperature, but also with discharge, which is a function of watershed size and water source (Hauer and Lamberti 2007). Even during times of high salmon abundance, water quality in medium (30–200 km²) to large watersheds (>200 km²) with high annual average discharge (>10 m³/s) is likely to be controlled by abiotic factors such as bedrock geology or glacial coverage. Thus, small watersheds with relatively low discharge should be more vulnerable to observable DO depletion due to dense salmon aggregations than larger watersheds. Even in regions with high precipitation rates, these smaller watersheds can experience extremely low flows between rainfall events. Interacting human impacts such as artificially high abundance of straying hatchery salmon (salmon intended to return to a hatchery that instead migrate to other streams; Brenner et al. 2012, Piston and Heinl 2012) and water diversion in these watersheds would likely intensify DO depletion by decreasing available water volume in stream channels and increasing salmon density. But, across the geographic range of salmon, little long-term data exist describing the

inter-annual patterns of DO regimes and seasonal magnitude and duration of hypoxia events.

The Northern Pacific Coastal Temperate Rainforest (NPCTR), defined by O'Neel et al. (2015) as, "the perhumid and subpolar region extending from the Skeena River watershed in British Columbia, to Kodiak Island, Alaska (total area = 448,550 km^2)," encompasses thousands of small to large watersheds that are ideal for examining the impact of dense salmon populations on DO regimes. Watersheds in the NPCTR range from small rain- and snow-fed streams to large glacially influenced rivers. Within the sub-region of southeastern Alaska alone, there are nearly 3000 coastal watersheds with drainage areas >1.2 km^2 that empty directly into saltwater (D'Amore et al. 2016). Although climate change modeling in this region predicts an overall increase in future annual precipitation, snowfall in the winter and rainfall in the summer are likely to decrease (Shanley and Albert 2014, Shanley et al. 2015), especially during warm phases of the Pacific Decadal Oscillation (PDO; Neal et al. 2002), which would in turn decrease summertime discharge in rain- and snowfed streams and potentially increase the magnitude, duration, and frequency of hypoxia events.

We present high-frequency time series of DO from two similar watersheds dominated by rainfall and snowmelt in southeastern Alaska to summarize the inter- and intra-annual DO regimes and frequency of riverine hypoxia in relationship to spawning salmon density and stream discharge. In addition, we use an existing bioenergetics model of salmon respiration (Trudel et al. 2004, Holtgrieve and Schindler 2011) linked to an oxygen reaeration model to assess the extent to which observed decreases in DO can be attributed to spawning salmon. We extend this model to explore combinations of salmon abundance, discharge, and water temperature that may result in hypoxic conditions. Using this combination of field observation and modeling, we provide compelling evidence that dense salmon populations and low discharge can trigger hypoxia, even in rivers with relatively cold thermal regimes.

METHODS

Study sites

Coastal southeastern Alaska is dominated by steep topography, a wet maritime climate,

glacially formed valleys, and temperate rainforest lowlands (Gallant et al. 1995). The Indian River and Sawmill Creek (Fig. 1) were chosen as complementary datasets for exploring potential mechanisms leading to low riverine DO in similar watersheds: The Indian River dataset provides water quality data at high temporal resolution over multiple years (2010–2015), while the Sawmill Creek dataset provides high temporal resolution across an upstream–downstream longitudinal gradient over one season (2015).

The Indian River watershed is located in Sitka, Alaska (Fig. 1), and has moderate human development from the mouth upstream to approximately river km 2.4. Annual precipitation in this area averages 217 cm (Western Regional Climate Center Data: http://www.wrcc.dri.edu/summary/Climsmak.html). The lowest 0.8 km flows through Sitka National Historical Park. In this lower floodplain reach, approximately half or less of substrates are finer than 64 mm, which is somewhat coarser than other streams in southeastern Alaska (Paustian and Hardy 1995). Several entities hold legal water rights to the river, including the National Park Service, Alaska Department of Fish and Game (ADFG), Sheldon Jackson Salmon Hatchery, and City and Borough of Sitka (CBS). While the CBS has infrequently diverted up to 0.11 m^3/s of river discharge for emergency drinking water, the only year-round water diversion occurs at river km 1.3 for use at the Sheldon Jackson Salmon Hatchery. From 1 December 2012 to 11 October 2016, diversion rates averaged 0.20 m^3/s and reached a maximum of 0.45 m^3/s (T. Schwarz, Alaska Department of Natural Resources, *personal communication*, 10 November 2016). This diversion is upstream from the water quality monitoring site in this study (river km 0.8). The majority of the upper Indian River watershed remains undeveloped and within the Tongass National Forest. Pink salmon (*Oncorhynchus gorbuscha*) comprise >95% of annual salmon spawning activity in the river (Stark et al. 2012), with the remainder consisting of chum (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). From 2013 to 2015, 0–62% of sampled pink salmon carcasses were strays from the nearby Sheldon Jackson Salmon Hatchery (S. Gende, National Park Service, *unpublished data*), which has released approximately 700,000–3,000,000 pink salmon fry every year since 2008 (Stopha 2015). During the years of our study,
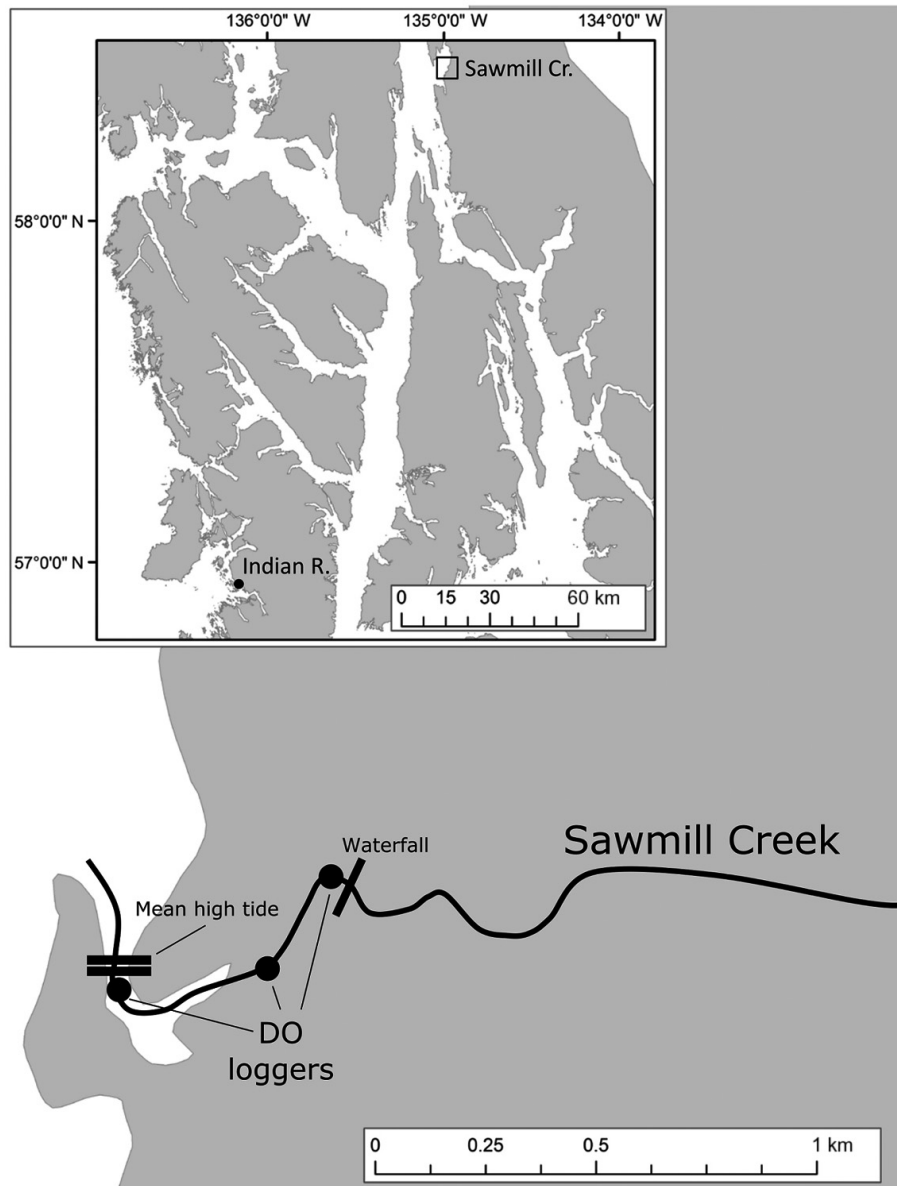
Fig. 1. Map of study area and Sawmill Creek dissolved oxygen (DO) logger locations in relation to anadromous barrier (waterfall) and mean high tide.

peak aerial counts of spawning pink salmon summed over the intertidal delta, river mouth, and main river channel ranged from 80,000 to 295,000 during August (Stopha 2015; ADFG, *unpublished data*).

Sawmill Creek drains a steep and undeveloped watershed located 45 km north of Juneau, Alaska (Fig. 1). Annual precipitation at the Juneau International Airport, the nearest long-term climate station, averages 147 cm (Western Regional Climate Center Data: http://www.wrcc.dri.edu/summary/Climsmak.html). Approximately 600 m above the mean high tide line, a 15-m waterfall blocks upstream anadromous migration and creates a plunge pool with constantly saturated DO levels. Extreme low tides expose an additional 700 m of intertidal spawning area used for spawning by pink salmon. From June to August 2015,

chum and pink salmon were the predominant spawners in Sawmill Creek (see *Results*). During the study period, hatchery strays comprised 51% of total chum salmon returning to spawn (i.e., escapement; C. McConnell, *unpublished data*).

While the Indian River has a longer channel than Sawmill Creek, both study systems are similar in other general watershed characteristics (Table 1). Both rivers have specific conductance and discharge characteristics representative of southeastern Alaska watersheds fed primarily by rain and snow runoff. From 2010 to 2015, specific conductance in the Indian River was inversely proportional to relative river stage (i.e., river height or elevation) and ranged from 10 to 80 μS/cm during the ice-free season (Sergeant and Johnson 2016). The relative river stages of the Indian River and Sawmill Creek increase quickly in response to precipitation (See Neal et al. 2004 and Fig. 2 for Indian River; Fig. 3 for Sawmill Creek).

Water quality and discharge measurements

In the Indian River, from 2010 to 2015, DO concentration (mg/L), DO saturation (%), and water temperature (°C) were measured hourly at river km 0.8 from approximately mid-April to early November using a YSI 6920-V2 multiparameter sonde equipped with YSI 6150 optical DO sensor and YSI 6560 conductivity/temperature probe (YSI Incorporated, Yellow Springs, Ohio, USA). Sensors were checked, cleaned, and calibrated approximately monthly to confirm and sustain measurement accuracy. Data quality was assessed according to consistently applied long-term monitoring protocols (See Standard Operating Procedures 1–3 in Sergeant et al. 2013). Data collected using methods deviating from monitoring protocol standards (e.g., incorrect sensor calibration procedures) or data collected during periods when instruments were damaged or malfunctioning were removed from all analyses. Relative river stage (m) was recorded at the same location every

15–60 min during the study period using either a Druck 1830 (GE Druck, Boston, Massachusetts, USA) or In-Situ Level TROLL 500 vented pressure sensor (In-Situ, Fort Collins, Colorado, USA) housed within a small metal shelter mounted to the top of a bedrock-bolted steel pipe. From December 2013 to July 2014, seven wading discharge measurements ranging from 0.14 to 3.56 m^3/s were collected using a SonTek Flow-Tracker Handheld Acoustic Doppler Velocimeter (SonTek, San Diego, California, USA) to develop a stream stage–discharge relationship for DO modeling purposes described in the *DO modeling* subsection below.

In Sawmill Creek, from 1 June to 21 August 2015, DO concentration (mg/L), saturation (%), and water temperature (°C) were measured every six minutes at three stations (river km 0.6, 0.4, and 0.0) using miniDOT loggers manufactured by Precision Measurement Engineering (Precision Measurement Engineering, Vista, California, USA). To decrease the potential for sensor biofouling, each logger was shaded from sunlight by being mounted inside a section of polyvinyl chloride (PVC) pipe. Surveyors cleared any particulate matter build-up in the pipe approximately every two days during the study period. Relative river stage (m) was recorded during spawning salmon surveys by visually inspecting a staff plate installed in the channel at river km 0.5. Precipitation data were derived from the Federal Aviation Administration weather station at Juneau International Airport.

We defined hypoxic conditions as periods when DO concentrations were <7 mg/L and/or saturation <70% for water temperatures ranging from 5° to 15°C. Above these DO levels, freshwater fish species are unlikely to exhibit negative physiological effects caused by low DO (Davis 1975). Below these levels, biologists have observed decreased swimming performance and delayed upstream migration in sockeye (*O. nerka*), Chinook (*O. tshawytscha*), and coho

Table 1. Watershed characteristics for each study site.

Watershed	Watershed area (km^2)	Length (km)	Max. elevation (m)	Glacier (%)	Wetland (%)	Forest (%)
Indian R.	31	19.8	1158	1	18	55
Sawmill Cr.	23	7.0	1525	<0.5	2	50

Notes: Indian River characteristics were calculated for the watershed area above the fixed water quality sampling site at river km 0.8, while Sawmill Creek characteristics were described for the entire watershed. Data were derived from the National Hydrography Dataset and National Land Cover Database (http://viewer.nationalmap.gov/viewer/nhd.html).
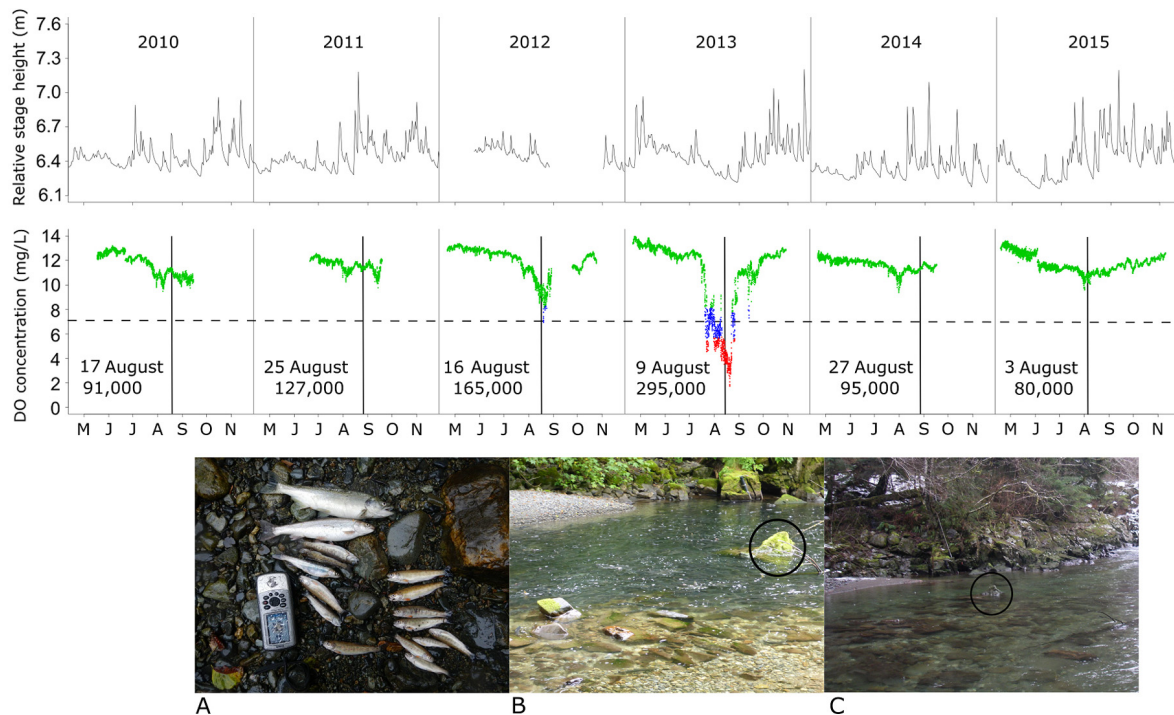
Fig. 2. Inter-annual patterns of Indian River dissolved oxygen (DO) concentration and saturation in comparison with relative river stage and salmon presence. In the lower panel, colored points represent DO saturation levels (green > 70%, blue 50–70%, and red < 50%). The horizontal dashed line represents a DO concentration of 7 mg/L, our threshold for defining hypoxic stream conditions for spawning Pacific salmon. Vertical lines represent the date of peak daily salmon counts collected via aerial survey. Peak counts are included below each peak count date. Photo (A) portrays juvenile cutthroat trout and Dolly Varden mortalities observed during an informal streamside survey conducted on 30 August 2013 (Photo courtesy of S. Gende/National Park Service), shortly after DO concentration at the Indian River study site reached a minimum of 1.7 mg/L at 16% saturation (average stage = 6.20 m). Open mouth and flared opercula in several individuals are typical signs of asphyxiation. Photo (B) was taken on 15 August 2013 and shows the high density of salmon present in the pool, where DO was measured for this study. For comparison, Photo (C) was taken on 19 November 2014 at the same location approximately three months after the peak spawning migration of pink salmon. The same rock is circled in photos (B) and (C) for spatial reference.

salmon (Davis 1975, Spence et al. 1996). Dissolved oxygen levels below 5 mg/L are likely to distress most freshwater species in cold-water systems (Davis 1975). Additionally, the Alaska Department of Environmental Conservation (ADEC) freshwater water quality regulations state that, "DO must be greater than 7 mg/L in waters used by anadromous or resident fish. In no case may DO be less than 5 mg/L..." (ADEC 2017).

Spawning salmon counts

In the Indian River, a relative index of spawning pink salmon abundance was reported each year of our study as a peak daily count derived from aerial surveys conducted by ADFG. Peak daily counts included the sum of pink salmon observed in the intertidal delta, river mouth, and main river channel. In Sawmill Creek, on-the-ground visual surveys conducted from the base of the waterfall downstream to the mean high tide line counted all visible chum salmon during periods when water clarity permitted. No spawning chum salmon were observed below mean high tide line. Due to their high density, pink salmon were counted along a 50-m index reach when water clarity and observer capacity allowed. The index reach was an active spawning area and provided surveyors with a
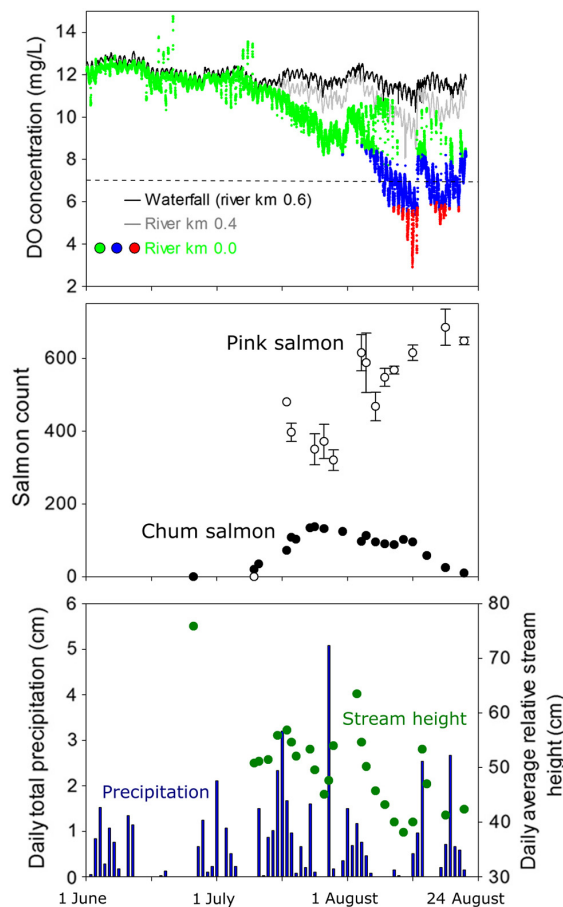
Fig. 3. Intra-annual patterns of Sawmill Creek dissolved oxygen (DO) concentration and saturation at three stream locations in comparison with stream height and salmon abundance. In the upper panel, colored points represent DO saturation levels at river km 0.0 (green > 70%, blue 50–70%, and red < 50%). Dissolved oxygen saturation levels at river km 0.4 (gray line) and river km 0.6 (black line) remained above 70% at all times during the study period. The horizontal dashed line represents a DO concentration of 7 mg/L, our threshold for defining hypoxic stream conditions for spawning Pacific salmon. In the middle panel, error bars represent ±1 SD (see *Methods* for differences in visual count methodology between species).

high bank and forested shoreline for optimum visibility. For pink salmon only, two surveyors counted spawners independently and averaged the two counts for the final index section abundance.

DO modeling

The effect of salmon on DO dynamics was simulated using a two-process model coupling atmospheric oxygen reaeration with salmon respiration of oxygen. The rate of change in DO as a function of both of these processes was given by:

$$\frac{d[O_2]}{dt} = (k([O_{2sat}] - [O_2])) - R_{sal}$$

where $[O_2]$ is DO concentration (mg/L), $[O_{2sat}]$ is the DO saturation concentration (DO concentration at atmospheric equilibrium), k is the rate of reaeration with the atmosphere (1/h), and R_{sal} is the instantaneous respiration rate of the salmon population (mg $O_2 \cdot L^{-1} \cdot h^{-1}$). The concentration of DO at complete saturation varies with water temperature and was calculated with the equation in Benson and Krause (1980). The rate of oxygen reaeration with the atmosphere was calculated using the energy dissipation model (Owens et al. 1964):

$$k_{20°C} = \left[\frac{50.8 \times v^{0.67} \times d^{-0.85}}{d} \right]$$

where $k_{20°C}$ is the oxygen reaeration rate when water temperature is 20°C, v is water velocity (cm/s), and d is average water depth (cm). The reaeration rate at ambient water temperature (T) is calculated as follows (Elmore and West 1961):

$$k_{T°C} = k_{20°C} \times 1.024^{(T-20)}.$$

Salmon respiration was calculated using a bioenergetics model (Trudel et al. 2004, Holtgrieve and Schindler 2011) that relates oxygen consumption to individual salmon mass (W; g), swim speed (U; cm/s), and water temperature (T; °C) as:

$$R_{sal} = N_{sal}(\alpha W^\beta \times e^{\varphi T} \times e^{\nu U})$$

where R_{sal} is the amount of oxygen respired by spawning salmon (mg $O_2 \cdot L^{-1} \cdot h^{-1}$); N_{sal} is the number of spawning salmon per liter of water (salmon/L = salmon/m² × 1/depth (m) × m³/1000 L); α is the standard metabolic rate of 1 g fish at 0°C (0.060); and β, φ, and ν are coefficients describing the metabolic costs of mass, temperature, and swim speed, respectively (0.791, 0.086, and 0.0234; values that have been previously used for chum, pink, and sockeye salmon; Beauchamp et al. 1989, Trudel et al. 2004).

All of the components that combine to generate overall ecosystem metabolism (gross primary production and all oxygen-consuming reactions in the ecosystem; Holtgrieve et al. 2010*a*) were not included in our model. Ecosystem metabolism can strongly influence DO dynamics in some rivers (Holtgrieve et al. 2010*a*), particularly diel dynamics; however, we hypothesized that a simpler model, one that only included atmospheric reaeration and salmon respiration, could reproduce observed seasonal patterns in DO in the oligotrophic rivers of southeastern Alaska (Kline et al. 1997, Sterling et al. 2000). In addition, because our goal was to understand the effect of live spawning salmon on DO dynamics, we did not include oxygen respiration associated with decaying salmon carcasses.

Model parameterization and simulation

We used the model to simulate hourly DO dynamics in the Indian River before, during, and after salmon spawning in years 2010–2015. We parameterized the model with hourly water temperature, discharge data, and salmon spawning counts. Discharge was calculated from relative river stage using a stage–discharge relationship established from 2014 wading discharge measurements (Sergeant and Schwarz 2017). The model converted discharge into its components of depth (d) and velocity (v) using the Manning equation (Gordon et al. 2004) parameterized with empirical channel morphology data collected in 2016 (bankfull width and depth, bank angle, channel gradient; C. Sergeant, *unpublished data*). While the stage–discharge relationship may have shifted as a result of high flow events modifying the channels in either study system, relative river stage remained an effective indicator of comparatively low vs. high discharge. To determine the sensitivity of modeled DO predictions to a shifting stage–discharge relationship for the Indian River, we altered discharge values ±20% and re-calculated modeled DO to examine model residuals between the primary and shifted stage–discharge relationships.

Spawning counts conducted by ADFG (see *Spawning salmon counts* sub-section above) were used to construct time series of salmon abundance within the spawning reach (Appendix S1). Estimates were converted to spawners/m² by dividing by the wetted area of the spawning reach (wetted length × average wetted width from Manning equation). Thus, spawning density can increase due to both salmon entering the spawning reach, as well as reductions in wetted area associated with lower discharges. In the respiration component of the model, we assumed an approximate individual pink salmon mass of 2 kg and a swim speed of 50 cm/s (approximately 1 body length/s). Once parameterized, model simulations were compared against empirical DO data for the Indian River.

Sensitivity analysis

To evaluate conditions that may result in hypoxia, we conducted a global sensitivity analysis. We ran the model approximately 15,000 times with different values of salmon abundance, stream discharge, and water temperature to produce approximately 15,000 independent estimates of DO. The ranges of values used in this analysis were as follows: (1) salmon abundance, 0–100 spawners/m; (2) stream discharge, 0.01–20 m³/s; and (3) water temperature, 0–20°C. These ranges fully incorporated the conditions observed in the Indian River, as well as conditions outside the observed range. These model runs were used to produce response surfaces that visually illustrate threshold values of temperature and discharge that may produce hypoxia at low (10 spawners/m), medium (40 spawners/m), and high (70 spawners/m) salmon densities. We report linear spawning densities (spawners/m), rather than areal densities (spawners/m²), because linear densities are not influenced by discharge. Reductions in modeled discharge, however, concurrently influence modeled DO due to decreasing atmospheric reaeration rates as well as increasing areal estimates of salmon respiration (higher respiration per unit area).

Results

Indian River

During the 2010–2015 ice-free seasons in the Indian River, DO regimes were highly variable but displayed periods of sharp decreases during July, August, and September when river stage was low and spawning pink salmon were present (Fig. 2). Across all measurements, hourly point measurements of DO concentration ranged from 1.7 to 14.0 mg/L and DO saturation ranged

from 16% to 112% (Fig. 2). Hourly water temperature ranged from 2.2° to 12.6°C. Hypoxic conditions, which we defined as DO concentrations <7 mg/L and saturation <70% (Davis 1975), were observed over a five-day period in 2012 (28 August–1 September) and a 37-d period in 2013 (29 July–4 September). Brief periods (several hours to approximately one day) of DO conditions greater than our thresholds for hypoxia were included in these event summaries when they were bounded by periods of hypoxia. During the five-day 2012 event, DO levels were reduced below hypoxic thresholds for only 18% of hourly measurements. Dissolved oxygen concentrations ranged from 7.0 to 9.7 mg/L, DO saturations ranged from 60% to 84%, and the peak salmon density occurred approximately 12 d before hypoxia developed (16 August; Fig. 2). During the 37-d 2013 hypoxic period, DO levels were reduced below hypoxic thresholds for 91% of hourly measurements. Dissolved oxygen concentrations ranged from 1.7 to 10.1 mg/L, DO saturations ranged from 16% to 86%, and peak salmon density occurred in the middle of the event (9 August; Fig. 2).

Each year, peak daily salmon estimates in the Indian River occurred between 3 and 27 August and ranged from approximately 80,000 individuals in 2015 to 295,000 in 2013 (Fig. 2). Average August river stage from 2010 to 2015 ranged from 6.26 to 6.54 m with an August minimum single measurement of 6.19 m and maximum of 8.18 m. During the minimum DO measurement of 1.7 mg/L on 29 August 2013, river stage was 6.21 m (Fig. 2). A 15-min streamside survey conducted <24 h after the minimum DO measurement discovered juvenile cutthroat trout and Dolly Varden mortalities exhibiting signs of asphyxiation such as flared opercula (Fig. 2, Photo A; S. Gende, National Park Service, *unpublished data*). Concurrently, in the same stream reach, 88% of haphazardly surveyed body cavities of 100 dead female pink salmon had most of their ripe eggs intact, suggesting a large prespawn mortality event (S. Gende, National Park Service, *unpublished data*).

Sawmill Creek

From 1 June to 21 August 2015, DO loggers placed in three locations in Sawmill Creek revealed high longitudinal variability in DO regimes in relation to relative stream stage, seawater inundation due to tidal fluctuations, and spawning salmon (Fig. 3). Across all measurements, DO concentrations ranged from 2.9 to 14.8 mg/L and DO saturations ranged from 26% to 124% (Fig. 3). Water temperature ranged from 6.1° to 15.6°C. The two uppermost DO loggers did not record any hypoxic conditions during the study period, but DO trends progressively decreased moving downstream (Fig. 3). In the waterfall plunge pool at river km 0.6 and at river km 0.4, DO concentration ranged from 8.0 to 13.1 mg/L and DO saturation ranged from 70% to 103%. At river km 0.0 (mean high tide line), DO concentration ranged from 2.9 to 14.7 mg/L and DO saturation ranged from 25% to 124%. At this lowest DO logger, high tides occasionally inundated the site with seawater and created temporary DO spikes (Fig. 3).

Two hypoxic events occurred at river km 0.0. The first event occurred for approximately 1.5 h overnight on 25 and 26 July during a spike in pink salmon abundance, while the second event lasted for at least 22 d from 30 July to 21 August, when DO loggers were retrieved (Fig. 3). During the second event, DO concentration ranged from 2.9 to 11.3 mg/L, DO saturation ranged from 26% to 98%, and peak salmon density occurred in the middle of the event (17 August; Fig. 3). Brief periods of increased DO during this event corresponded with isolated precipitation and tidal seawater inundation (Fig. 3).

Peak daily salmon counts occurred on 20 July for chum salmon ($n = 137$) and 17 August for pink salmon ($n = 685$ for index reach; Fig. 3). During the monitoring period, relative river stage ranged from 38 to 76 cm. The minimum DO measurement of 2.9 mg/L was recorded on 9 August when river stage was between 38 and 40 cm (nearly the lowest observed) and temperature was 10.4°C (Fig. 3).

DO modeling

The magnitude and pattern of the oxygen reaeration–salmon respiration DO model generally matched field-observed DO trends, and the two time series were highly correlated across all study years (Spearman's rank correlation coefficient 0.73–0.97, all $P < 0.001$; Fig. 4; Appendix S2). Model residuals ranged from −2.11 to 5.87 mg/L and were largest during the peak spawning
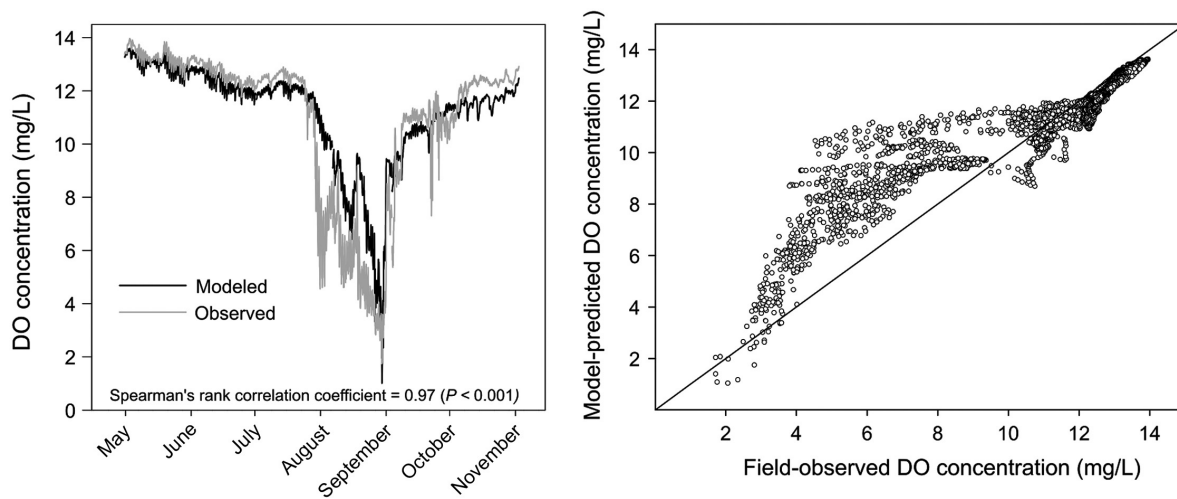
Fig. 4. Dissolved oxygen (DO) model vs. field DO measurements. Left panel compares modeled (black line) DO time series to field observations (gray line) during 2013. Right panel is a scatter plot of modeled vs. field DO measurements; black line represents 1:1 values.

months of August and September (Fig. 4; Appendix S2). The model tended to over-predict DO values from approximately 4 to 10 mg/L, which occurred during sharp transitions from high to low oxygen events. Model results most closely matched field-observed DO from 2–4 mg/ L to 10–14 mg/L (Fig. 4; Appendix S2). In general, shifting discharge values by ±20% within the model had a minimal impact on predicted DO values. Across all modeled years except 2013, there was no notable difference in DO predictions across the range of tested discharge values, but some divergence was present in 2013 once DO levels dropped below 9.0 mg/L. During that year, residuals between modeled DO using the stage–discharge relationship and modeled DO using ±20% discharge ranged from −1.2 to 1.6 mg/L (Appendix S3).

Modeled sensitivity analyses revealed that the presence of spawning salmon, even in high densities, does not necessarily result in hypoxia or low DO (Fig. 5). When river discharge was relatively high, and/or water temperature low, salmon respiration did not appear to strongly influence on DO levels. Rather, hypoxia was only predicted when high salmon densities coincided with lower discharges and higher water temperatures. Specific combinations of discharge and temperature that induce hypoxia depend on the density of salmon in the stream. At low salmon

densities for the Indian River (10 spawners/m), the thresholds of discharge (<0.01 m^3/s) and water temperature (>12°C) necessary to trigger hypoxia are limited and unlikely to occur (Fig. 5). A typical annual low discharge measurement in the Indian River ranges from 0.4 to 0.6 m^3/s (Neal et al. 2004, Sergeant and Schwarz 2017), and the maximum water temperature from the 2010 to 2016 monitoring seasons was 12.6°C. At medium salmon densities (40 spawners/m), salmon respiration was predicted to create hypoxia across a broader range of discharge (<0.2 m^3/s) and water temperature (>6°C; Fig. 5). At high salmon spawning densities (70 spawners/m), the range of discharge (<0.7 m^3/s) and water temperature (>6°C) that resulted in hypoxia were much greater (Fig. 5) and are well within the range of conditions that occur annually in the Indian River.

Discussion

We provide compelling evidence that spawning salmon can create hypoxia, even in low-productivity streams with relatively cold thermal regimes. Our combination of field observations and modeling illustrates that low summertime river discharge is a precursor to salmon-induced hypoxia. In the rainfall- and snowmelt-dominated watersheds of southeastern Alaska,
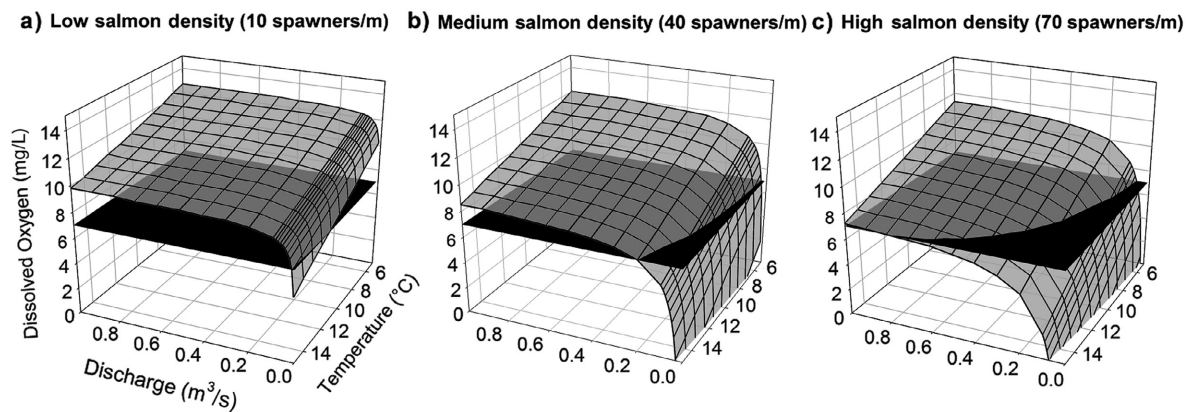
a) Low salmon density (10 spawners/m) b) Medium salmon density (40 spawners/m) c) High salmon density (70 spawners/m)

Fig. 5. Three-dimensional model representation of Indian River dissolved oxygen dynamics (mg/L) based on varying discharge (m³/s) and water temperature (°C) across three pink salmon spawning densities (spawners/m). The flat black plane represents our defined hypoxic level of 7 mg/L.

we expect increases in the future frequency and magnitude of hypoxic events due to decreasing winter precipitation falling as snow, decreasing summer precipitation during warm PDO phases, and warming air temperatures (Neal et al. 2002, Shanley and Albert 2014, Shanley et al. 2015). Hypoxic events may also be intensified by human-mediated actions that further increase spawning densities such as straying hatchery salmon and water diversion. By combining high-frequency water quality monitoring data with a mechanistic model, accurate predictions of DO can be made using relatively simple datasets that include salmon counts and watershed habitat characteristics.

The results from our study systems illustrate that low discharge can be the primary physical driver of three phenomena that combine to deplete DO: (1) Reduced water turbulence decreases oxygen reaeration with the atmosphere, (2) reduced water volume for spawning salmon increases areal respiration rates, and (3) increased water temperature decreases DO saturation concentration and increases salmon respiration. Thus, similar numbers of spawning salmon may have very different effects on DO in different water years depending on flow and thermal regime variation.

Our model effectively predicted DO trends and magnitude in comparison with field measurements despite excluding primary production and overall ecosystem respiration (Fig. 4;

Appendix S2). We hypothesize that under-predicted values in the spring resulted from excluding photosynthesis by primary producers, while over-predicted values in the fall may have been caused by excluding additional components of ecosystem respiration beyond live salmon respiration, particularly oxygen use by decomposing salmon carcasses. During periods of low discharge, the importance of decomposition increases as carcass retention is likely very high in slow-flowing habitat features such as deep pools. Although the model was coded specifically for the Indian River, its low gradient floodplain channel is typical of many pink and chum salmon streams in the NPCTR (Paustian 1992). Thus, we expect DO response surfaces (Fig. 5) to be broadly representative of the conditions that can produce hypoxia in small- to medium-sized watersheds with runoff dominated by rainfall and snowmelt. The mechanisms of hypoxia we describe were parallel to recent similar research conducted in a small southwestern Alaska stream (Tillotson and Quinn 2017). Our model may not perform as well in small- to medium-sized watersheds in the NPCTR with high percentages of wetland coverage (>30%) and more complicated groundwater dynamics or lake systems contributing significant flow to downstream channels (e.g., see Peterson Creek in Fellman et al. 2015).

In addition to the DO dynamics we describe here, past field observations of depleted DO

conditions in southeastern Alaska streams were also caused by two additional mechanisms: (1) inundated intertidal stream channels becoming overcrowded with stranded salmon and hypoxic after tidal marine waters retreat and (2) elevated surface water temperatures originating from upper watershed lakes reducing oxygen solubility downstream (Murphy 1985). Lakes and dendritic intertidal channels were not present in either of our study systems. Our data from Sawmill Creek demonstrate that DO in tidally influenced channels with simple morphology can also be recharged during seawater inundation (Fig. 3). In similar systems, hypoxic events may result in intertidal spawners being the most successful spawning cohort during a given year. However, the success of fertilized eggs within the intertidal zone may be limited by high salinity (Bailey 1964).

Beyond natural drivers of DO depletion, human impacts such as hatchery straying and water diversion may increase the probability of hypoxia. Comprehensive data on salmon straying rates and mechanisms for straying behavior are sparse, but pink and chum salmon appear to have the highest propensity for straying among all Pacific salmon species (Quinn 2005). In Prince William Sound, Alaska, 77% of surveyed streams contained hatchery pink salmon from three or more hatcheries, and hatchery strays comprised 0–98% of pink salmon escapement within individual streams (Brenner et al. 2012). In the Indian River from 2013 to 2015, 0–62% of sampled pink salmon carcasses were hatchery strays (S. Gende, National Park Service, *unpublished data*). In Sawmill Creek during 2015, hatchery chum salmon strays comprised 51% of total number of spawning chum (C. McConnell, *unpublished data*), although they were a small percentage of total salmon escapement in comparison with wild pink salmon (Fig. 3). An earlier Sawmill Creek study conducted in 2009 and 2010 found that 78% and 44% of sampled chum salmon carcasses, respectively, were hatchery strays (Piston and Heinl 2012). Even though stray rates tend to decrease as the distance from hatchery release sites increases (Brenner et al. 2012, Piston and Heinl 2012), continuing hatchery production levels and widely distributed juvenile salmon release sites in southern Alaska will likely keep the potential for continued straying to many coastal river systems

high (Stopha 2015). While hypoxia-induced mortality before successful spawning would potentially create a density-dependent decline in the productivity of wild salmon populations (Quinn et al. 2007, Tillotson and Quinn 2017), hatchery populations, which only require small numbers of spawners to maintain production goals, do not receive this population feedback and have the potential to continue supplying large numbers of strays to streams in years immediately following die-off events. Thus, resident fishes in streams that are repeatedly populated with high densities of straying salmon may experience long-term declines in productivity, but data are currently lacking to strongly support this possibility.

In some systems, water diversions may combine with hatchery strays to cumulatively deplete DO levels. The Sheldon Jackson Salmon Hatchery, which operates approximately 1 km from the mouth of the Indian River, diverts water from the Indian River to maintain operations. Data are limited, but from October 1998 to September 2000, daily diversion discharge ranged from 0.11 to 1.16 m^3/s, and during August 1999 and 2000, it ranged from 0.42 to 0.85 m^3/s (USGS gage 15087730, http://waterdata.usgs.gov/nwis). During August in years 2013–2016, the mean diversion rate was 0.25 m^3/s, while the maximum was 0.45 m^3/s (T. Schwarz, Alaska Department of Natural Resources, *personal communication* 10 November 2016). During these periods, an unknown amount of water was returned to the Indian River approximately 0.4 river km below our DO monitoring location. Our model demonstrates that during high salmon density periods (70 spawners/m), a discharge reduction from 0.6 to 0.3 m^3/s at 12°C can equate to a DO drop of 1.0 mg/L (Fig. 5), so it is likely that both strays from the hatchery and water diversion cumulatively contribute to seasonal DO depletion. Based on the evidence presented here, it appears that hypoxia in nearby streams could be an underappreciated risk stemming from hatchery operations.

Management applications

While the combinations of discharge, water temperature, and salmon density that trigger hypoxia will differ based on individual watershed variation in stream channel morphology and flow regime drivers, our model could easily

be parameterized to specific streams to create real-time predictive models of DO trends based on current observed salmon density and short-term predictions of discharge. In watersheds impacted by flow diversion and hatchery stray salmon, local stakeholders could collaboratively examine the effect of future management actions on DO levels using an intuitive model visualization tool (we have developed an online example at https://goo.gl/WY3seH). For other watersheds with historical salmon density and habitat data, this model could also explore the past frequency of hypoxic events in comparison with future events and create watershed-scale predictions of hypoxia risk across the study region. Our general modeling approach could be built upon to be applicable in other systems, such as those with large-scale migrations of spawning suckers (Childress et al. 2014).

In addition to hatchery operations, mining and hydropower are two common land uses that also divert water. Many small-scale hydropower operations are planned for southeastern Alaska communities in response to rising costs of diesel power generation (Cherry et al. 2010, Ray 2011). Future and current hydropower projects should consider electrical generation methods that minimize flow diversion from spawning salmon reaches and mitigate for warm surface waters created by reservoirs (Olden and Naiman 2010). As these land uses progress in the NPCTR, careful consideration of best practices can assist in balancing community needs with the health of freshwater ecosystems.

These local drivers of hypoxia will likely combine with regional-climate trends to decrease discharge magnitude for some streams; thus, the prevalence of hypoxic events may increase in the future. Given this likelihood, it will be critical to understand how these events impact the future productivity of individual salmon populations. We are unaware of any studies evaluating the potential influence of hypoxia on the productivity of anadromous and resident stream fishes. A first step to achieving this goal is to assess trends across a greater number of streams and variety of watershed types to determine the extent to which hypoxia risk and impact are system dependent. Future modeling and mechanistic interpretation of DO trends within individual watersheds would benefit from more rigorous estimates of salmon density and collecting longitudinal DO time series across multiple years from above and below anadromous migration barriers. Understanding the level of threat to freshwater ecosystem integrity presented by hypoxia in the NPCTR and the appropriate management responses will involve continued commitments to long-term ecosystem monitoring, applied research, and cooperative adaptive management of aquatic resources among stakeholders.

In general, our data demonstrate the importance of collecting and maintaining long-term water quality data for rivers that go beyond water temperature and across varying gradients of human impact. These time series data, in combination with continued research on hatchery to wild salmon proportions on spawning grounds and rates of pre-spawn mortality (Quinn et al. 2007, Tillotson and Quinn 2017), will allow ecologists and managers to collaboratively develop and apply models that explore the potential for hypoxia-driven mortality to influence anadromous and resident stream fish population productivity. While preserving thermally suitable stream habitat for cold-water taxa facing climate change has become an important land management priority (e.g., see Isaak et al. 2016), managers should also consider that some protected watersheds may still be at risk of increasingly frequent hypoxia due to cumulative human impacts such as water diversion and artificially abundant salmon populations caused by hatchery straying.

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summaries of southeastern Alaska watershed size and annual average discharge originally used in Shanley and Albert (2014). J. Nichols (ADFG) and E. Tucker (United States Forest Service) provided valuable input and stream habitat data for the salmon respiration model. We thank M. Bower, R. Brenner, B. Carter, S. Gende, J. Hard, J. Hughes, E. Ward, L. Welling, and one anonymous reviewer for preliminary manuscript reviews. Two anonymous referees provided thoughtful peer reviews.

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