



Hypoxia vulnerability in the salmon watersheds of Southeast Alaska

Christopher J. Sergeant^{a,b,*}, J. Ryan Bellmore^c, Rebecca A. Bellmore^d, Jeffrey A. Falke^e, Franz J. Mueter^a, Peter A.H. Westley^f

^a College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Rd, Juneau, AK 99801, USA

^b Flathead Lake Biological Station, University of Montana, 32125 Bio Station Ln, Polson, MT 59860-6815, USA

^c U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 11175 Auke Lake Way, Juneau, AK 99801, USA

^d Southeast Alaska Watershed Coalition, 1107 W 8th St, Juneau, AK 99801, USA

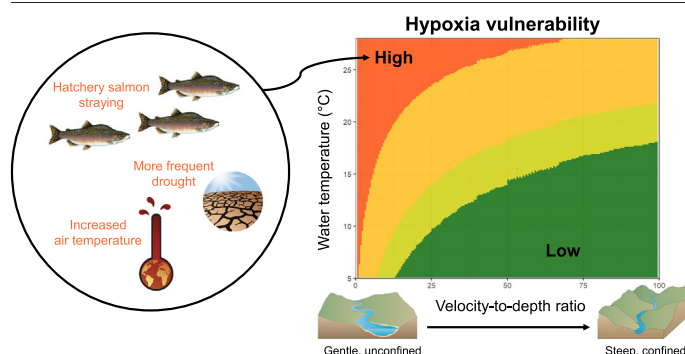
^e U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, 2140 Koyukuk Drive, Fairbanks, AK 99775-7020, USA

^f College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 2150 Koyukuk Drive, Fairbanks, AK 99775, USA

HIGHLIGHTS

- Freshwater hypoxia and implications for northern species remain poorly understood.
- Drought and artificially high fish densities can interact to cause hypoxia.
- Our hypoxia model combines channel hydraulics, water temperature, and fish density.
- Mapped spatial variability of watershed hypoxia vulnerability in 91,000 km² region
- Our repeatable methodology identifies watersheds at risk of hypoxia.

GRAPHICAL ABSTRACT



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ABSTRACT

The frequency of dissolved oxygen depletion events (hypoxia) in coastal aquatic ecosystems has risen dramatically since the late 20th century, yet the causes and consequences of hypoxia for some culturally and economically important species remain poorly understood. In rivers, oxygen depletion can be caused by high densities of spawning Pacific salmon (*Oncorhynchus* spp.) consuming oxygen faster than can be replaced by reaeration. This process may be exacerbated when salmon densities are artificially inflated, such as when hatchery-origin salmon stray into rivers instead of returning to hatcheries. In Southeast Alaska, hatchery salmon production has increased rapidly since the 1970s, with over 553 million chum salmon (*O. keta*) and 64 million pink salmon (*O. gorbuscha*) released in 2021 alone. Straying is pervasive in streams with outlets <25 km from nearshore marine hatchery release sites. Using a previously ground-truthed mechanistic model of dissolved oxygen dynamics, we examined how water temperature and low-flow channel hydraulics contribute to hypoxia vulnerability. We then applied the model to predict hypoxia vulnerability for watersheds within 25 km of hatchery salmon release points, where straying salmon spawner densities are expected to be higher and promote dissolved oxygen depletion. Our model predicted that low-gradient stream reaches, regardless of water temperature, are the most prone to hypoxia due to low reaeration rates. Our spatial analysis determined that nearly 17,000 km of anadromous-accessible stream reaches are vulnerable to high densities of hatchery-origin salmon based on 2021 release sites. To our knowledge, this study is the first to map the spatial variation of hypoxia vulnerability in anadromous watersheds, identify habitat conditions most likely to promote hypoxia, and provide a repeatable analytical approach to identify hypoxia-prone stream reaches that can be updated as empirical data sets improve.

* Corresponding author at: College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Rd, Juneau, AK 99801, USA.

E-mail addresses: christopher.sergeant@umontana.edu (C.J. Sergeant), james.r.bellmore@usda.gov (J.R. Bellmore), rebecca@sawcak.org (R.A. Bellmore), jeffrey.falke@alaska.edu (J.A. Falke), fmuetter@alaska.edu (F.J. Mueter), pwestley@alaska.edu (P.A.H. Westley).

1. Introduction

In coastal aquatic ecosystems world-wide, the frequency of dissolved oxygen depletion events (also called, ‘hypoxia’) has increased dramatically since the late 20th century (Vaquer-Sunyer and Duarte, 2008). Hypoxia can result from causes such as drought (Magoulick and Kobza, 2003), decomposition of organic material (Dahm et al., 2015; Whitworth et al., 2012), high water temperature (Rabalais et al., 2010), or respiration by dense populations of organisms such as aquatic plants (Caraco and Cole, 2002) and Pacific salmon (*Oncorhynchus* spp., hereafter referred to as ‘salmon’; Sergeant et al., 2017). As climate change and human competition for water increase the potential for drought and high water temperatures (Dudgeon et al., 2006), it is important to better understand the specific physical and biological conditions that expose groups of species to hypoxia. Bouts of hypoxia lasting hours to several days may lead to sublethal effects or large mortality events for aquatic organisms (La and Cooke, 2011). Therefore, improving our ability to predict hypoxia in various settings is important for conserving and managing the abundance and biodiversity of aquatic ecosystems. Here, we focus on culturally and economically important salmon populations in northern latitudes (Carothers et al., 2021; Johnson et al., 2019). Even though these fish remain generally abundant (Ruggerone et al., 2010), reports of hypoxia-related mortality from individual watersheds have become more frequent due to combinations of low streamflow, high water temperature, and dense spawning populations (Murphy, 1985; Sergeant et al., 2017; Tillotson and Quinn, 2017; von Biela et al., 2022).

Salmon migrate from the ocean upstream to their natal rivers or lakes for spawning. These migrations may end abruptly at the intertidal mouth of small streams or range thousands of km into large watersheds (Quinn, 2018). At any point during these migrations, several known mechanisms lead to *premature mortality*, defined as the in-river death of adult salmon migrating upstream or holding on the spawning grounds before depositing their gametes (Bowerman et al., 2016). In many rivers, especially in the southern range of salmon, prolonged and elevated water temperatures >18 °C can increase the rate of premature mortality by delaying spawning migration, rapidly depleting energy reserves, increasing disease risk, and exceeding cardiovascular limits for delivering oxygen to body tissues at pace with increasing metabolic demand (Hinch and Martins, 2011; Strange, 2012; Bowerman et al., 2018). In the northern range of salmon (~>52°N), there is less historical evidence of in-river heat stress, but notable exceptions have recently been documented in the Yukon River basin (von Biela et al., 2020; Westley, 2020) and Bristol Bay watersheds (Quinn et al., 2007). Hypoxia is a related mechanism of premature mortality. Observations of hypoxia-related mortality dating back to at least the 1940s suggest that spawning salmon can respire oxygen faster than it can be replaced by the atmosphere when spawning densities are high and reaeration rates are low, even when water temperatures are relatively cool (<12 °C; Murphy, 1985; Sergeant et al., 2017).

Water temperature, streamflow, channel hydraulics, and spawning density are key predictors of summer and autumn dissolved oxygen dynamics (Fellman et al., 2018; Sergeant et al., 2017). The capacity for water to hold oxygen molecules decreases as water temperature increases (Benson and Krause, 1980). Thus, sufficient oxygen reaeration via gas exchange at the air-water boundary may not occur when periods of drought increase water temperature and reduce stream velocity and turbulence, especially in low-gradient stream reaches (Garvey et al., 2007; Hall and Ulseth, 2020). Broad-scale climate patterns also play an important role in dissolved oxygen dynamics. Future snowpack reductions will likely exacerbate the severity of drought by supplying less meltwaters to rain- and snow-fed watersheds in the summer. Even though mean annual precipitation is predicted to increase up to 18 % in Southeast Alaska by the 2080s, mean annual precipitation falling as snow may decrease as much as 58 % (Shanley et al., 2015). The combination of reduced snowpack and warmer summer air temperatures is expected to generally increase water temperatures during salmon spawning windows (Shaftel et al., 2020; Winfree et al., 2018) except in watersheds where substantial glacier coverage (>30 %) remains

(Fellman et al., 2014). Based on this knowledge, we expect that hypoxic conditions harmful to salmon are most likely to occur in low-gradient streams with relatively warmer water (>~15 °C) that receive most of their flow from rain and are more prone to summer drought. In addition to these atmospheric and physical habitat controls, respiration by spawning salmon themselves can further reduce dissolved oxygen levels when stream reaeration rates are low. Oxygen consumption rates by individual salmon can range from 10s to 100s of mg O₂/kg/h depending on swimming speed and water temperature (Brett, 1972).

In southern coastal Alaska, where many salmon populations remain abundant, hypoxia-related mortalities can occur during periods of high wild-origin spawner abundance (Murphy, 1985; Tillotson and Quinn, 2017) or can be exacerbated by large numbers of hatchery-origin salmon that stray into natural spawning grounds instead of being harvested in fisheries or returning to hatcheries (Brenner et al., 2012; Josephson et al., 2021; Knudsen et al., 2021; Piston and Heintz, 2012; Sergeant et al., 2017). Hatchery salmon production in Southeast Alaska started during the 1970s, and total release numbers steadily increased leading up to the turn of the 21st century (Wilson, 2021). Since 2005, juvenile pink (*O. gorbuscha*) and chum (*O. keta*) salmon, which comprise most of Alaska's hatchery-raised salmon, have been released at 30 different nearshore marine sites across Southeast Alaska. Annual releases of juvenile chum salmon have ranged from approximately 0.2 to 87 million individuals per site, while juvenile pink salmon releases have ranged from approximately 0.1 to 97 million individuals per site (<https://mtalab.adfg.alaska.gov/CWT/Reports/>). In 2021 alone, over 553 million chum salmon were released from 21 sites across Southeast Alaska, while over 64 million pink salmon were released from three sites.

Hatchery-origin salmon mature in the ocean and migrate back toward their nearshore marine release sites. If not captured in a fishery, some individuals will enter rivers located near hatchery release sites and attempt to spawn naturally. Studies conducted in Southeast Alaska between 2008 and 2015 showed that the proportion of hatchery-origin conspecific spawners can be as high as 90 % in watersheds with coastal outlets <25 km from a release site, (Josephson et al., 2021; Piston and Heintz, 2012). From 2013 to 2015, 0.4–1.2 % of the total Southeast Alaska hatchery chum salmon returns were estimated to stray to 81 study streams (Josephson et al., 2021). Recent studies stress the potential effects of hatchery introgression on wild population fitness (reproductive success), but less attention is paid to the acute ecological impacts from hypoxia events, such as premature mortality of naturally spawning salmon and other resident stream fishes such as cutthroat trout (*O. clarkii*) and Dolly Varden (*Salvelinus malma*) (for example, as documented in Sergeant et al., 2017). These acute impacts may conflict with the Alaska salmon hatchery program's goal of protecting and maintaining the abundance of wild salmon stocks (Heard, 2012), but the empirical data necessary to quantify the ecological impacts and prevalence of hypoxia (e.g., stream density of hatchery- versus natural-origin spawners, continuous water temperature/streamflow/dissolved oxygen time series) are widely lacking. Considering these limitations, we present three related analyses that combine best available modeled and empirical datasets with a ground-truthed mechanistic model of dissolved oxygen dynamics to identify specific stream reaches and general habitat conditions where salmon-related hypoxia events are most probable:

- (1) The first analysis calculates summertime hypoxia vulnerability across Southeast Alaska for 62 stream reaches with hourly water temperature data. These streams represent culturally important salmon populations and a range of watershed types across the region, although they are not statistically representative of the variability present in the region. The metric for hypoxia vulnerability was defined as the estimated density of spawning salmon necessary to create hypoxic conditions—defined here as a dissolved oxygen level of 7 mg/L or less, following Sergeant et al. (2017)—in each stream reach based on channel hydraulics, hourly water temperatures, and salmon bioenergetics.
- (2) To explore a broader set of combinations of habitat characteristics than were present in the 62 monitored watersheds, we calculated and

visualized hypoxia vulnerability over a range of low-water velocity, depth, and temperature conditions to illustrate the mechanistic interplay between these factors and hypoxia vulnerability. A realistic range of values for each characteristic was based on data from the 62 stream reaches.

- (3) Lastly, for the tens of thousands of stream reaches in Southeast Alaska lacking water temperature data but at risk for high salmon spawning densities due to hatchery straying, we predicted and mapped hypoxia vulnerability for anadromous-accessible stream reaches in watersheds with outlets <25 km from 2021 hatchery release sites.

To our knowledge, this study is the first to map the spatial variation of hypoxia vulnerability in anadromous watersheds, identify habitat conditions most likely to promote hypoxia, and provide a repeatable analytical approach to identify hypoxia-prone stream reaches as empirical datasets improve.

2. Methods

2.1. Study area

The streams included in this study (Fig. 1) fall within Southeast Alaska, the southern boundary of which begins at the maritime zone known as Dixon Entrance (approximately 54.52°N, 131.65°W) and stretches northwesterly along the Alaska coastline to Icy Bay (approximately 59.96°N, 141.44°W). Based on climate normals calculated from 1991 to 2020 (<https://www.ncei.noaa.gov/access/us-climate-normals/>), average annual rainfall ranges from 64 cm in Skagway to 380 cm in Ketchikan. Much of this rainfall (63 %) occurs during salmon spawning and embryo incubation between September and February. Average annual air temperature across the region is approximately 6 °C, with an average June–August temperature of 13 °C (minimum and maximum average summer values range from approximately 9 °C to 18 °C). This region is part of the larger Northern Pacific Coastal Temperate Rainforest (O'Neil et al., 2015) and consists of four

ecologically distinct regions: Alexander Archipelago, Boundary Ranges, Chugach-St. Elias Mountains, and Gulf of Alaska Coast (Nowacki et al., 2003). The extensive ice coverage, steep terrain, and abundant vegetation creates a diversity of watersheds exposed to climate patterns ranging from wet and mild maritime to drier and colder continental climates. Twelve distinct categories of streamflow patterns in approximately 2600 coastal watersheds ranging from 5 to 54,770 km² reflect different combinations of rain, snow, and glacier runoff (Curran and Biles, 2021; Sergeant et al., 2020).

2.2. Water temperature and channel hydraulics data

The hypoxia vulnerability calculation described in the next sub-section (Eq. (2)) requires inputs for water temperature and channel hydraulics that include width, depth, and velocity. We describe how we aggregated those inputs here. The 62 water temperature monitoring sites used in this analysis represented a wide range of watershed and stream channel characteristics across Southeast Alaska (Table 1). Water temperature data were aggregated by “site-summer,” which we defined as a unique stream location having at least 90 % of hourly water temperature measurements during July 1–September 30 of a single year. This time frame overlaps with periods when spawning salmon densities, primarily pink and/or chum salmon, have the potential to be very high and contribute to hypoxic conditions via respiration. Individual stream locations across Southeast Alaska ($n = 62$) had from 1 to 12 site-summers available for analysis, totaling 275 site-summers of water temperature across the years 2008–2021 (Fig. 1).

Water temperature data were collected by many organizations across Southeast Alaska, including federal, state, Tribal, university, and non-profit groups. Most water temperature data were curated by the Southeast Alaska Freshwater Temperature Monitoring Network (<https://www.alaskawatershedcoalition.org/southeast-alaska-stream-temperature-monitoring-network/>). The network supplies data collectors with temperature loggers (Hobo Tidbit or Pro v2, Onset Computer Corporation, Bourne, Massachusetts), which have a precision of <0.2 °C and are validated against

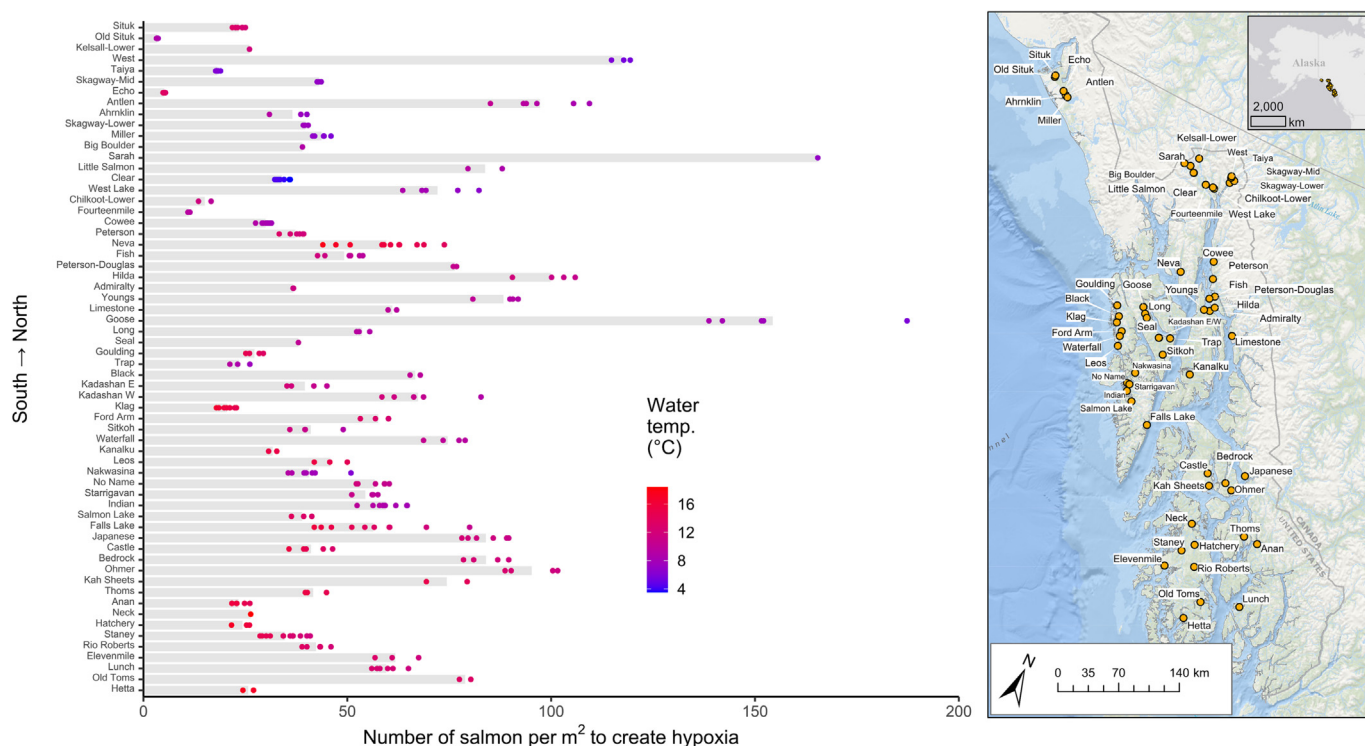


Fig. 1. Hypoxia vulnerability at each water temperature monitoring site in Southeast Alaska represented by the estimated number of pink salmon/m² to create hypoxia (7 mg/L). (A) Average hypoxia vulnerability across all monitored years for each site (gray bars). Sites are ordered from south to north. Individual points correspond to the average hypoxia vulnerability metric for a given site-summer and are color-coded by average summer water temperature. (B) Locations for all water temperature monitoring sites in Southeast Alaska ($n = 62$) used in this analysis. The map was created using the Ocean Basemap in ArcMap 10.8.2 (Esri, Redlands, California).

a NIST-certified thermometer at 0 °C and room temperature (~20 °C), following standardized protocols for Alaska (Mauger et al., 2015). Loggers are shaded within a PVC housing with holes through which water may rapidly flow. Housings are either attached to a stable bank structure with steel cable or anchored to the streambed. Temperature data are not representative of surface water if a logger is exposed to air, frozen, or buried in sediment. To identify potential non-surface water temperatures, data were automatically flagged for large diurnal variability, rapid hourly temperature changes, and extreme low and high temperatures. All data were subsequently visualized, and suspect data were manually removed after reviewing automated flags, field notes, and comparing to air temperature data, when available. Values were averaged at a site when two loggers were deployed within 15 m of each other and not influenced by different water sources. Other water temperature data were downloaded from publicly available sources following published monitoring protocols and quality control procedures such as the U.S. Geological Survey (<https://waterdata.usgs.gov/nwis>) and the U.S. National Park Service (Goodwin et al., 2021).

For each water temperature monitoring location and anadromous stream reaches without water temperature data, we used the NetMap synthetic stream network (Benda et al., 2016, 2007) for the Tongass National Forest (derived from a 20-m or finer resolution digital elevation model) to extract watershed attributes of interest (Clarke et al., 2008), including channel gradient (m/m), bankfull width/depth (m), bankfull velocity (m/s), bankfull discharge (m³/s), roughness (unitless Manning's *n*), upstream basin area (km²), mean basin elevation (m), and mean annual precipitation (m). For each water temperature monitoring site, attributes were averaged across all reaches surrounding the logger location from the first upstream tributary junction to the first downstream tributary junction. At two low-gradient sites (Taiya River and Clear Creek) NetMap reported channel gradients of 0 m/m, which we adjusted to 0.001 m/m to ensure the hydraulic simulations described provided a non-zero value for the low flow calculation. The 98-percent duration flow is defined as the level of discharge that is equaled or exceeded 98 % of the time over a given water year. We estimated 98-percent duration flow for the July–September time frame (*J* – *S98*) using a regionally calibrated regression (Wiley and Curran, 2003):

$$J - S98 = 2.532 \times 10^{-9} A^{1.142} P^{1.521} E^{1.674} \quad (1)$$

where *J* – *S98* is discharge (ft³/s), *A* is upstream drainage area (mi²), *P* is mean annual precipitation (in), and *E* is upstream mean basin elevation (ft). Discharge was converted to m³/s for subsequent calculations.

We computed the wetted channel depth (*d*) and velocity (*V*) associated with low flow conditions (98-percent duration flow) for each reach based on the estimated bankfull width, bankfull depth, bank angles (assumed 45°), channel gradient, and roughness (Manning's *n*) for a given site, using the Manning equation (Gordon et al., 2004). The final combination of reach-specific water temperature and low-flow channel velocity and depth were used to calculate hypoxia vulnerability.

Table 1

Minimum (Min), maximum (Max), and mean of watershed and stream channel characteristics across all water temperature monitoring sites (*n* = 62) in Southeast Alaska. Upstream basin area and mean basin elevation are calculated for the watershed upstream of the monitoring site.

	Min	Max	Mean
Upstream basin area (km ²)	0.2	751	70
Mean basin elevation (m)	26	1124	435
Mean annual precipitation (m)	1.0	5.6	2.7
Mean summer water temperature (°C)	3.5	18.4	10.9
Gradient (m/m)	0.001	0.111	0.032
Bankfull width (m)	4.4	43.3	18.7
Bankfull depth (m)	0.4	0.8	0.6
Bankfull velocity (m/s)	1.3	5.0	3.6

2.3. Calculating hypoxia vulnerability at water temperature monitoring sites

We defined the metric for hypoxia vulnerability as the density of pink salmon necessary to reduce dissolved oxygen in a given stream reach at ambient water temperature from full saturation (which ranges from 14.6 mg/L at 0 °C to 7.8 mg/L at 28 °C) to 7 mg/L, which is the threshold at which biologists have observed decreased swimming performance and delayed upstream migration of spawning salmon (Davis, 1975; Spence et al., 1996). State of Alaska freshwater water quality regulations also state that, “DO [dissolved oxygen] 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...” (Alaska Department of Environmental Conservation, 2020). Even at water temperatures as high as 28 °C, fully saturated dissolved oxygen levels are approximately 7.8 mg/L (Benson and Krause, 1980); therefore, until water temperatures in Southeast Alaska begin exceeding 28 °C, 7 mg/L always represents a reduction from full saturation due to biochemical oxygen demand. We chose pink salmon for this calculation because they tend to be the most numerically dominant natural spawners (Ruggerone et al., 2010) and are the most commonly documented species in mass mortality events (Murphy, 1985; Sergeant et al., 2017). There is evidence that pink salmon may have the highest respiration rates among Pacific salmon species, but comparative studies of metabolism across species and body sizes are limited (Abe et al., 2019). Our calculations could be modified to accommodate other salmon species, but this would not change the relative differences in hypoxia risk due to physical habitat characteristics across sites.

For each stream site, the number of pink salmon necessary to incite hypoxic conditions was calculated using water temperature, discharge, physical habitat characteristics, and pink salmon bioenergetics. The final metric equation was derived from a previously used model that successfully estimated dissolved oxygen in a snow-fed watershed based on atmospheric oxygen reaeration and salmon respiration (Sergeant et al., 2017; full derivation in Appendix A):

$$\frac{\text{salmon}}{L} = \frac{(50.8 \times V^{0.67} \times d^{-0.85})}{d} \times 1.024^{(T-20)} \times ([O_{2sat}] - 7 \frac{\text{mg}}{L}) \quad (2)$$

$$78.957 \times e^{0.086T}$$

where *salmon* is the number of pink salmon (individual mass = 2000 g), *V* is water velocity (cm/s), *d* is average water depth (cm), *T* is water temperature (°C), and *[O_{2sat}]* is the dissolved oxygen concentration at atmospheric equilibrium (mg/L). In the Indian River in Sitka, Alaska, USA—where this model was originally implemented—the correlation between observed and modeled dissolved oxygen concentrations ranged from 0.73 to 0.97 across 6 years of water quality monitoring, which included a hypoxic event (Spearman's rank correlation coefficient, all *P* < 0.001; Sergeant et al., 2017).

To create a fish density with units that are more intuitive to visualize in a stream channel, we converted $\frac{\text{salmon}}{L}$ to the final response variable, $\frac{\text{salmon}}{\text{m}^2}$, using:

$$\frac{\text{salmon}}{\text{m}^2} = \frac{\text{salmon}}{L} \times d \times \frac{1000 L}{\text{m}^3} \quad (3)$$

In Eq. (3), *d* is expressed in m instead of cm (as in Eq. (2)).

The hypoxia vulnerability metric was reported as the density of pink salmon (number of salmon/m²) needed to create hypoxic conditions (≤ 7 mg/L) averaged across all hourly water temperature measurements for a given site-summer. Therefore, lower values of the metric represent higher vulnerability to hypoxia. Hypoxia vulnerability metric values were compared against the average summer water temperatures and velocity-to-depth ratios for each site at the 98-percent duration flow for July–September, which encompasses the primary spawning timeframe in these systems. Velocity-to-depth ratios provide an indication of the general reaeration potential for a given stream reach. High values imply more turbulence and a higher potential for gas exchange at the air-water boundary.

High velocity-to-depth ratios generally represent a steeper stream channel within a confined floodplain, while low velocity-to-depth ratios represent lower gradient stream channels with unconfined, broader floodplains (Montgomery, 1999). Quantile regressions describing relationships between hypoxia vulnerability, velocity-to-depth ratio, and water temperature were conducted in R statistical software version 3.6.2 (R Core Team, 2019) using the “quantreg” package (Koenker, 2020).

2.4. Calculating hypoxia vulnerability for combinations of velocity, depth, and water temperature

The water temperature monitoring sites provided a range of potential velocity, depth, and water temperature values that represent relevant habitat conditions for spawning salmon across the study region. We used these ranges to calculate how the hypoxia vulnerability metric (Eq. (2)) varies across all realistic combinations of channel hydraulics and water temperature. For the analysis, we considered all combinations of low-flow velocity from 1 to 100 cm/s, low-flow depth from 1 to 25 cm, and water temperature from 5 to 28 °C.

2.5. Calculating hypoxia vulnerability in stream reaches near hatchery release sites

After overlaying coastal watershed polygons in the NetMap synthetic stream network (Benda et al., 2016, 2007) with 2021 hatchery chum and pink salmon release points ($n = 21$; <https://mtalab.adfg.alaska.gov/CWT/Reports/>), we used the Euclidean Distance tool in ArcMap 10.8.2 (Esri, Redlands, California) to identify all watersheds with coastal outlets <25-km over-water distance from release sites. Within those watersheds, we conservatively assumed that all reaches with downstream channel gradients <10 % were accessible to salmon (Pitman et al., 2021). Since this portion of our analysis moved beyond just the field-monitored sites, water temperature data were not available for these reaches. To solve for the hypoxia vulnerability metric in Eq. (2), we set $T = 10^{\circ}\text{C}$ and calculated V and d for low-water conditions using the same Manning equation approach described for the 62 sites where water temperature was monitored (see Section 2.2 *Water temperature and channel hydraulics data*). Since the relationship between water temperature and dissolved oxygen saturation concentration is nearly linear (Benson and Krause, 1980), the calculated hypoxia vulnerability metrics for all reaches will have the same relative differences using any realistic water temperature. This created a relative metric of hypoxia vulnerability within each ~100-m stream reach delineated by NetMap. To visualize hypoxia vulnerability at the watershed-scale, we color-coded watershed polygons by discrete ranges of the mean number of pink salmon/m² necessary to create hypoxic conditions across all reaches. This metric calculation isolates the importance of physical habitat factors in hypoxia risk and does not consider the potential for some streams to be more vulnerable to warm water temperatures. For data interpretation, it is also important to note that in this steep coastal region, some watershed polygons do not always represent one coastal stream outlet but rather multiple coastal stream outlets from small catchments where drainage areas are often <5 km².

3. Results

3.1. Hypoxia vulnerability at water temperature monitoring sites

Across all site-summers ($n = 275$), hourly water temperatures from July through September ranged from 1.9 °C to 26.2 °C. The mean site-summer water temperature across all hourly measurements at individual sites ($n = 62$) ranged from 3.5 °C to 18.4 °C (site-level SD ranged from 0.2 °C to 3.9 °C with CV from 5 % to 26 %). Water temperatures tended to be cooler at northern sites where a larger number of watersheds with relatively higher mean elevation and greater extent of glacier coverage provided a greater volume of cooling meltwaters (Fig. 1). Mean site-summer water temperature across the 31 northernmost-sites was 9.5 °C (SD =

1.3 °C), while the mean for the 31 southernmost-sites was 12.2 °C (SD = 1.7 °C). Velocity-to-depth ratios at 98-percent duration flows across individual sites ranged from 0.2 to 49.1 (mean = 19.7). The estimated number of pink salmon/m² to create hypoxia (i.e., the hypoxia vulnerability metric) increased with higher velocity-to-depth ratios and resulted in a wedge-shaped scatter due to the influence of water temperature (Fig. 2). The hypoxia vulnerability metric ranged from 3.2 to 187.3 salmon/m² across all site-summers (Figs. 1 and 2). While higher velocity-to-depth ratios generally represented decreased vulnerability to hypoxia at an individual stream site, increasing mean summer water temperature for a given ratio increased hypoxia vulnerability (i.e., lowered the value of the metric). For example, at Stanley Creek, which had a velocity-to-depth ratio of 17.1, the hypoxia vulnerability metric was 41 salmon/m² at a mean summer water temperature of 11.6 °C but 29 salmon/m² at 14.5 °C (Figs. 1 and 2). Across all site-summers, incidents of hypoxia vulnerability metrics above the 90th percentile range (quantile regression; $P = 0.0003$; Fig. 2) (i.e., low vulnerability) had a mean site-summer water temperature of 6.4 °C (SD = 1.7), while incidents of hypoxia metrics below the 10th percentile ($P = 0.0002$; Fig. 2) (i.e., high vulnerability) had a mean site-summer water temperature of 14.2 °C (SD = 3.4). These 90th and 10th percentile thresholds represented mean summer water temperatures where hypoxia vulnerability was especially low or high regardless of channel hydraulics.

3.2. Hypoxia vulnerability for combinations of velocity, depth, and water temperature

Modeling hypoxia vulnerability based on realistic combinations of low-flow velocity, depth, and water temperature provided insights into the non-linear, dynamic relationship among habitat conditions that create the greatest hypoxia vulnerability (Fig. 3). For example, across the lowest values of reaeration potential (represented by velocity-to-depth ratios ranging from approximately 0–10), conditions creating hypoxia at spawning densities of 0–10 salmon/m² become rapidly more limited in a non-linear fashion until water temperatures become >20 °C. In general, sites with high velocity-to-depth ratios appear unlikely to become hypoxic unless temperatures are high (Fig. 3). At very low stream velocities (1 cm/s), hypoxia vulnerability is high across all realistic water temperature and depth values due to a lack of reaeration. Whereas, at higher velocities (50–75 cm/s), hypoxia vulnerability becomes high primarily when water temperatures increase to >15 °C (Fig. 3).

3.3. Hypoxia vulnerability in stream reaches near hatchery release sites

We identified 157 watersheds with coastal outlets <25 km from 2021 hatchery release sites. This numerically represents 6 % of the approximately 2600 coastal watersheds >5 km² in Southeast Alaska (Sergeant et al., 2020) and encompasses 16,806 ~ 100-m reaches accessible to spawning anadromous salmon (Fig. 4). Velocity-to-depth ratios across all reaches ranged from 0.01 to 89.6 (mean = 11.3). This represents a broader diversity of channel hydraulics than the 62 water temperature monitoring sites described above (maximum ratio = 49.1).

Hypoxia vulnerability varied widely across watersheds and individual stream reaches. The mean hypoxia vulnerability metric ranged from 3.1 to 98.4 salmon/m² (mean = 40.5) across individual watersheds, while individual reaches ranged from 0.5 to 187.1 salmon/m² (mean = 37.4). Across all reaches, 16 % had values of the hypoxia vulnerability metric from 0.5 to 10 salmon/m², 46 % from 10 to 40 salmon/m², 24 % 40 to 70 salmon/m², and 13 % >70 salmon/m² (Fig. 5).

While Fig. 4 illustrates hypoxia vulnerability averaged across stream reaches at the watershed-scale, it does not convey the variability present at the stream reach-scale within watersheds, or the extent of anadromous stream reaches that contributed to the averages. A more detailed examination of the watersheds adjacent to the Gunnuck Creek (near Kake, Alaska) and Southeast Cove hatchery chum salmon release sites provides some insights into the types of stream reaches that influence the wide range of average hypoxia vulnerability metrics across watersheds in this area (Fig. 6).

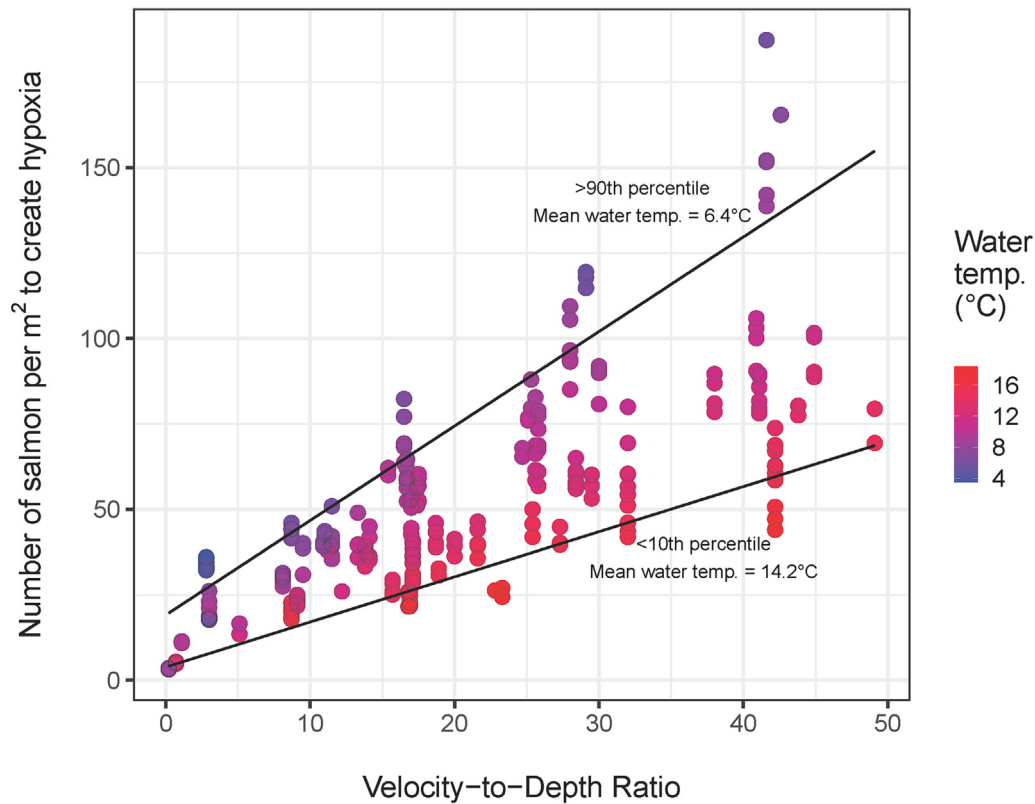


Fig. 2. Velocity-to-depth ratio vs. estimated number of pink salmon/m² to create hypoxia in Southeast Alaska streams. Points represent average hypoxia vulnerability across all hourly measurements for an individual site-summer and are color-coded by average summer water temperature. Black lines represent quantile regressions of sites in the 10th (high hypoxia vulnerability) and 90th percentile (low hypoxia vulnerability) of the number of pink salmon/m² to create hypoxia.

Hypoxia vulnerability tended to follow spatial patterns within each stream network: small tributaries and reaches near the coastal watershed outlets (where channel gradients are often low) tended to have the highest vulnerability to hypoxia while vulnerability in larger mainstem reaches with

higher velocity-to-depth ratios was comparatively low (Fig. 6). In some cases, the presence of potential anadromous barriers lower in a watershed's stream network led to average watershed-scale hypoxia vulnerability metrics based on a relatively small numbers of reaches. For example, the

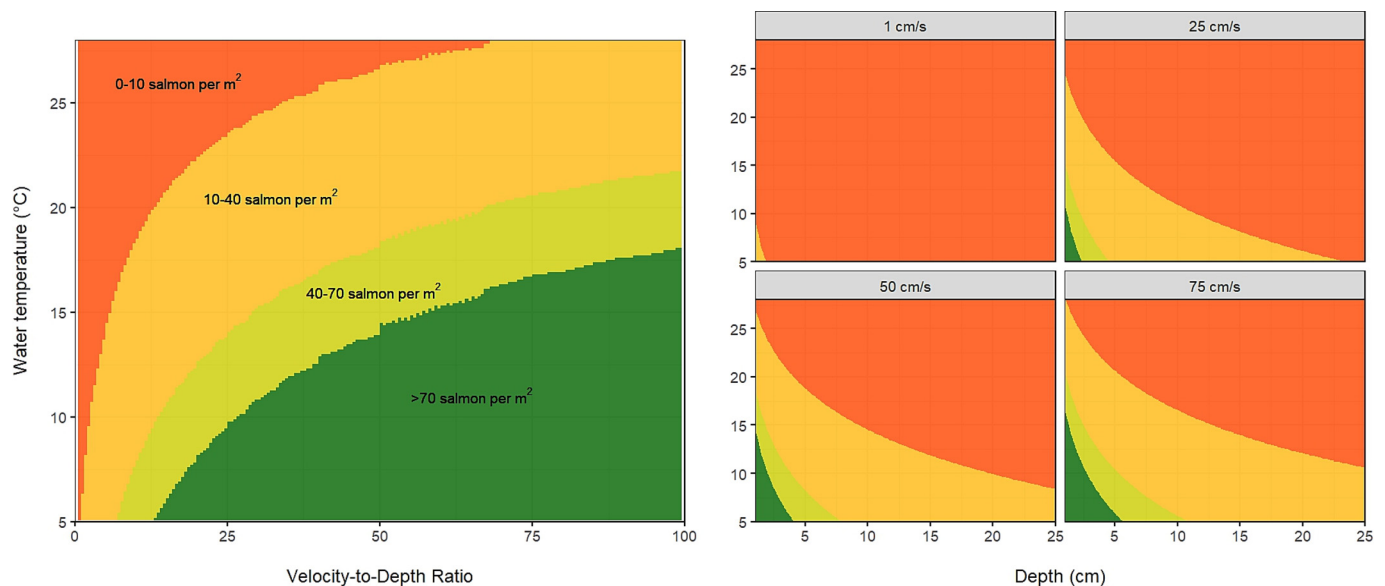


Fig. 3. Modeled contours of the estimated number of pink salmon/m² to create hypoxia in Southeast Alaska streams across all potential combinations of velocity, depth, and water temperature. (Left) estimated number of pink salmon/m² to create hypoxia based on velocity-to-depth ratio and water temperature. Cells with multiple values of the hypoxia vulnerability metric for each discrete value of velocity-to-depth ratio (e.g., $V = 5$ cm/s, $d = 1$ cm and $V = 50$ cm/s, $d = 10$ cm both have ratios = 5) were averaged. (Right) To avoid averaging within individual cells, the estimated number of pink salmon/m² to create hypoxia can also be modeled across the full range of depths and water temperatures but using discrete velocities (1, 25, 50, and 75 cm/s). Colors in both panels represent the same range of pink salmon/m² to create hypoxia.

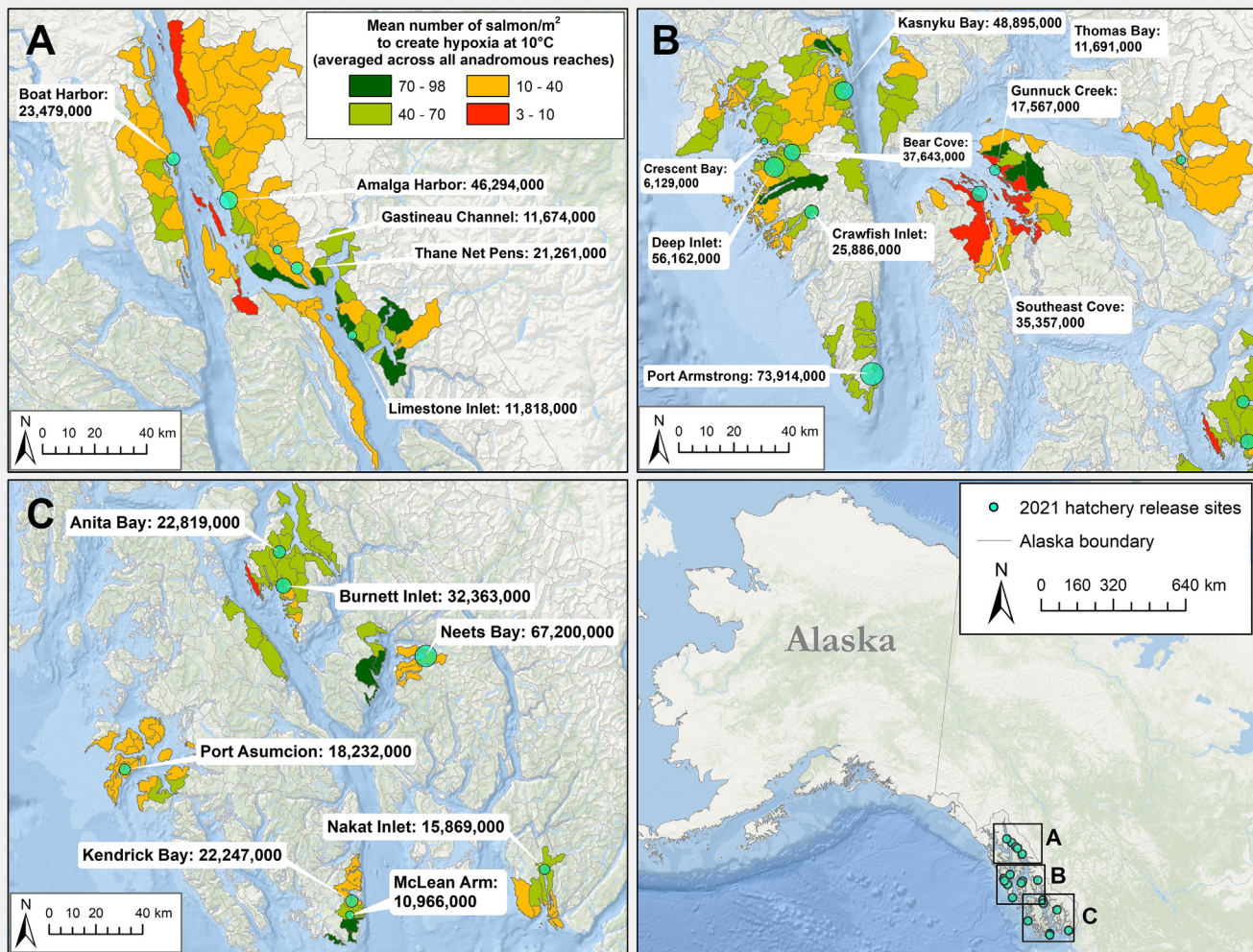


Fig. 4. Watersheds in the northern (A), central (B), and southern (C) portions of Southeast Alaska with coastal outlets <25 km from 2021 salmon hatchery release sites. Watersheds are color-coded by the hypoxia vulnerability metric calculated at 10 °C and averaged across all anadromous reaches within the watershed; see legend in (A). The labeled teal points represent 2021 hatchery release sites and are sized proportionally according to the total number of pink and chum salmon released (rounded to the nearest thousands). The map was created using the NetMap synthetic stream network and Ocean Basemap in ArcMap 10.8.2 (Esri, Redlands, California).

large watershed south of the Southeast Cove hatchery release site includes Kadake Creek (labeled in Fig. 6) and several smaller drainages that were not individually delineated by NetMap. In this example, <1600 m of anadromous reaches were used in the average hypoxia risk calculation for the entire watershed (Fig. 6). Although Kadake Creek has documented anadromous reaches above the sections included in this analysis (Harding and Coyle, 2011), most of these were excluded from this analysis because the downstream-most reach in the watershed had a channel gradient >12 % (this analytical artifact is discussed further in Section 4.4 Study limitations).

4. Discussion

Premature mortality in salmon populations due to hypoxia is a natural phenomenon, yet determining its mechanisms and the extent to which human activities increase vulnerability to mortality remains an active field of study with implications for salmon hatchery management and water diversion activities. We used a previously ground-truthed model based on first-principles calculations to describe dissolved oxygen dynamics and estimate hypoxia vulnerability for streams across Southeast Alaska using a repeatable analytical framework that simultaneously considers low-flow channel hydraulics, water temperature, and spawning salmon

bioenergetics. Using the framework in concert with contemporary hatchery salmon release sites, we demonstrated that thousands of stream km in the study region adjacent to release sites may be exposed to greater numbers of stray spawning salmon, which have the potential to reduce dissolved oxygen in watersheds. More broadly, our framework could be adapted in other regions where high fish densities combined with low reaeration precipitate hypoxia.

4.1. Channel hydraulics

Channel hydraulics play a critical role in the dissolved oxygen estimates produced by our model (Eq. (2)) by controlling reaeration rate. Similar to empirical studies, our estimates suggest that hypoxia can occur even when water temperatures are relatively cool (<15 °C) in locations with low velocity-to-depth ratios. For example, the Indian River, which is on the outer coast of central Southeast Alaska, had a maximum summer water temperature of 12.6 °C, a mean across all hourly summer measurements of 8.7 °C, and relatively moderate hypoxia vulnerability across nine site-summers (mean = 59.4 salmon/m² to create hypoxia). Yet, severe hypoxia events (as low as 1.7 mg/L and 16 % saturation) have been measured in the Indian River due to low reaeration rates during low water and unnaturally high fish densities caused by hatchery-origin pink salmon returning

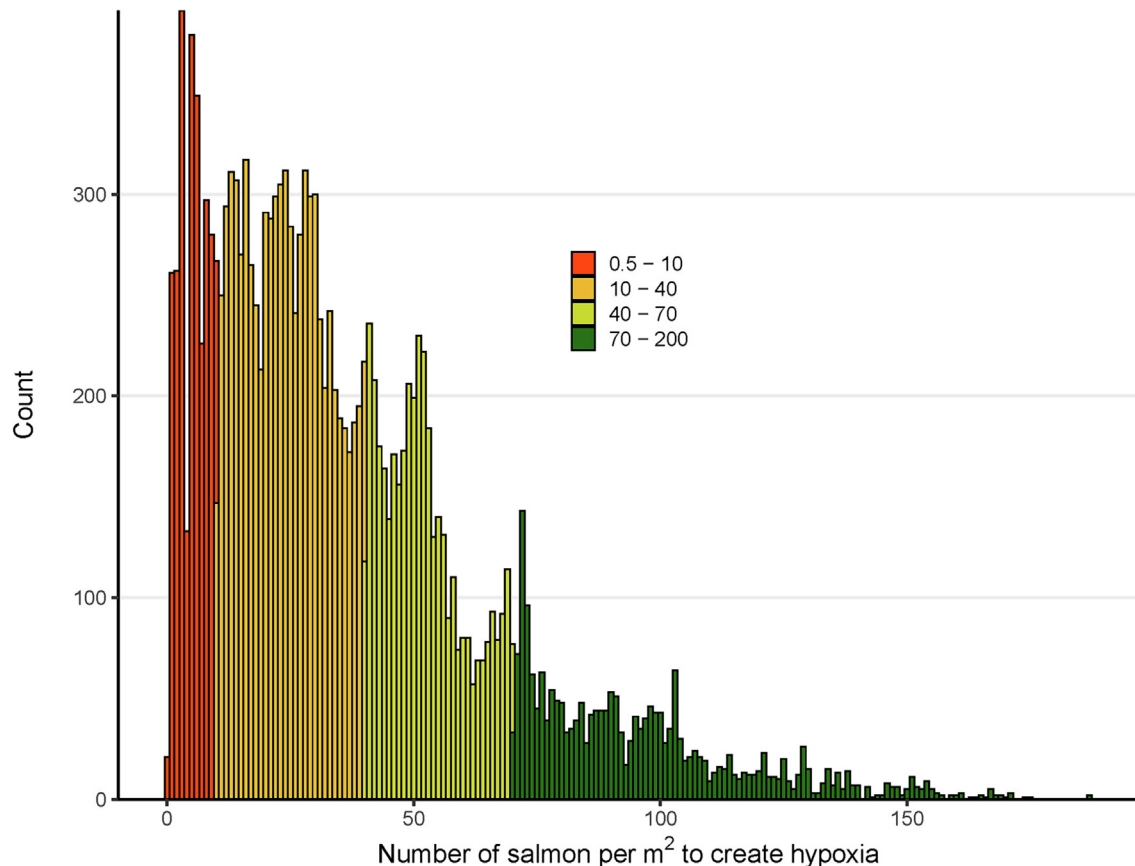


Fig. 5. Histogram of the hypoxia vulnerability metric for all anadromous-accessible stream reaches ($n = 16,806$) in Southeast Alaska watersheds with coastal outlets <25 km from 2021 pink and chum salmon hatchery release sites. Color scales for the metric match those in Figs. 3, 4, and 6.

to spawn in the river instead of the hatchery, which is located only 1 km from the river mouth (Sergeant et al., 2017).

Low-gradient reaches such as the estuarine and floodplain channels common to the outlets of small watersheds (<40 km²) in southern coastal Alaska (Paustian, 2010) are often locations where mass mortality events are documented. Such events may occur due to different combinations of low-water migration blockage, warm water, or low dissolved oxygen (Murphy, 1985; Sergeant et al., 2017; von Biela et al., 2022). In these coastal habitats, velocity-to-depth ratios—and therefore, reaeration rates—tend to be low, while water temperature may vary widely depending on the influence of intertidal marine waters. Our study suggests that these lower watershed reaches are among the most hypoxia-prone due to their channel hydraulics, and under the right conditions may represent seasonal migratory barriers that prevent or reduce access to spawning habitat in the upper reaches of watersheds.

4.2. Salmon-spawner densities estimated by the hypoxia vulnerability metric

Modeled spawner densities predicted to result in hypoxia varied widely across stream reaches. These estimates should be interpreted as the relative risk of hypoxia. In other words, a stream reach with a metric value of 5 fish/m² is much more vulnerable to hypoxia than a reach with a metric value of 70 fish/m², regardless of whether the potential spawning density at a specific site is realistic. Additionally, the salmon-spawner densities represented by the hypoxia vulnerability metric are most relevant at smaller spatial scales (one to several 100-m stream reaches) where individuals in the reach experience similar fish densities. For example, spawners clustered in a pool experience the spawner density in that pool. The lead author (CJS) has visually estimated that dense pink salmon spawning aggregations in the Indian River can reach 10–30 fish/m² in depths of 0.5–1 m. These densities contrast with studies that report salmon-spawner densities

averaged over the entire length of a surveyed stream channel, which is often several km in length. When averaged over a larger spatial scale, “high” salmon-spawner densities measured in previous studies of small Alaska streams are typically <3 fish/m² (e.g., Gende et al., 2001; Tillotson and Quinn, 2017; McConnell et al., 2018), which is lower than most of the range of our hypoxia vulnerability metric values.

4.3. Hatchery supplementation and other human influences

Human activities have the potential to exacerbate hypoxia risk, especially for streams with outlets located <25 km from hatchery release sites. Depending on the spatial arrangement of hatchery release sites and number of fish released at each site for a given year, the number of watersheds and stream reaches vulnerable to artificially increased spawning salmon density can be geographically extensive. Using the 2021 hatchery release sites, nearly 17,000 km of anadromous-accessible stream reaches met our distance criterion for increased straying potential, and this is likely a conservative estimate (see the Section 4.4 Study limitations section below). Any water diversion for human-use in these stream reaches—including hatcheries, mining operations, drinking water, or hydropower—would further increase hypoxia vulnerability by reducing stream discharge and increasing spawner density (e.g., Sergeant et al., 2017). In addition, while the effects of logging on streamflow patterns are complex and context-dependent, it is generally believed that extensive forest harvest within a catchment leads to reduced summertime baseflow (Gronsdahl et al., 2019). The potential severity of these human uses may be further compounded by climate change impacts in watersheds affected by reduced ice or snow runoff and increasing drought frequency (Cherry et al., 2017; Schoen et al., 2017; Vynne et al., 2021).

A clear question that arises from this study is whether hatchery-driven hypoxia events in streams like the Indian River are rare or common. In

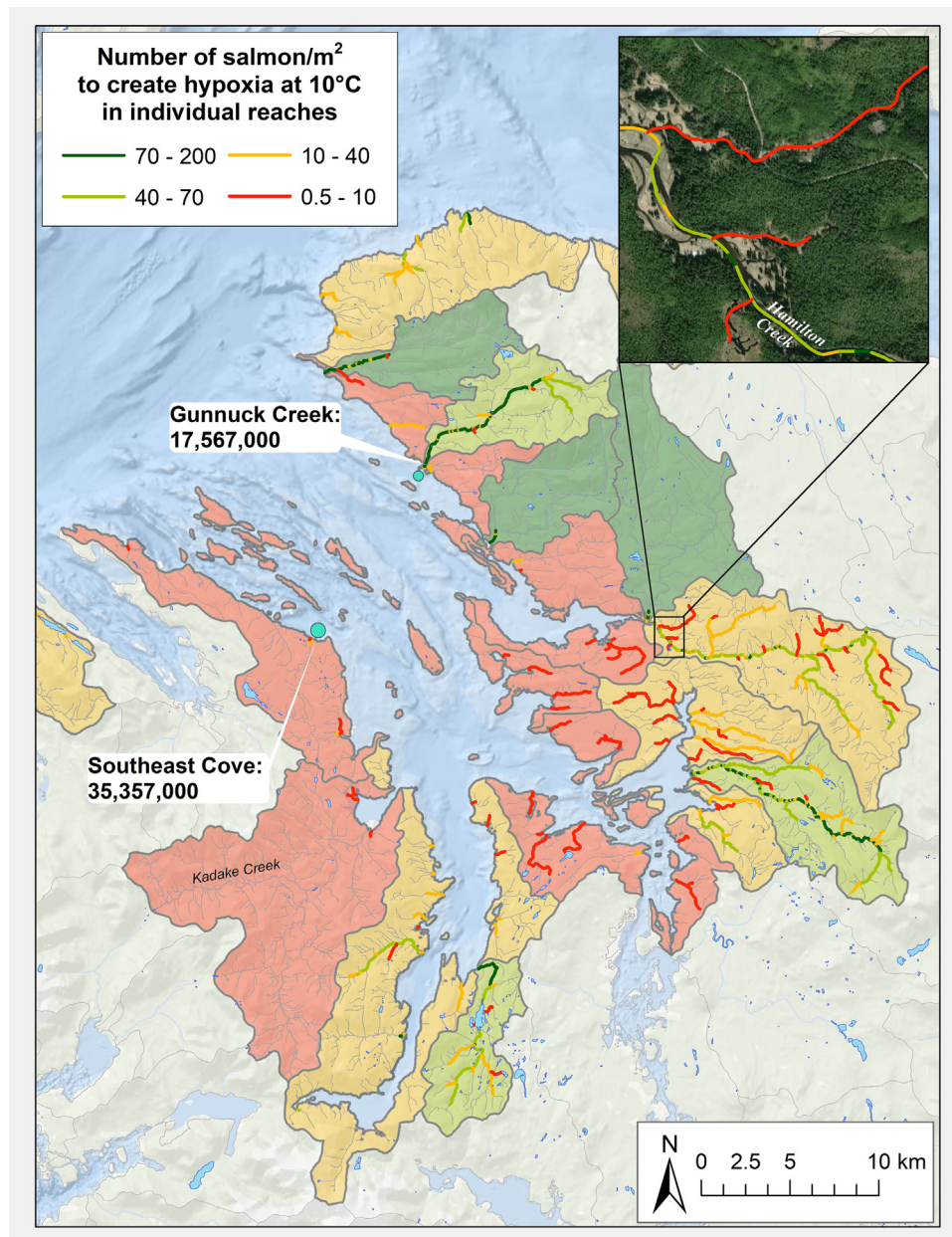


Fig. 6. Detailed view of a central Southeast Alaska area adjacent to Gunnuck Creek (near Kake, Alaska) and Southeast Cove hatchery release sites (teal points; labels represent 2021 total number of hatchery-released chum salmon rounded to the nearest thousands). See Fig. 4B for geographic location in Southeast Alaska. In this example, stream reaches are color-coded by the number of salmon/m² to create hypoxia. Watershed polygons from Fig. 4 follow the same color coding but are muted to better highlight stream reach-scale variability in the hypoxia vulnerability metric. The inset combines reach-scale hypoxia vulnerability in Hamilton Creek with satellite imagery to illustrate habitat variability within the watershed. Light gray stream lines within colored watersheds represent reaches upstream of reaches with >10 % channel gradient and therefore not considered anadromous reaches in this analysis. The map was created using the Ocean Basemap and default satellite imagery (18 April 2020) in ArcMap 10.8.2 (Esri, Redlands, California).

other words, how frequently do stray hatchery salmon crowd streams at sufficient densities to incite hypoxia that otherwise would not occur if only natural spawners were present? For a given stream and year, answering this question using our dissolved oxygen model would require a time series of areal spawner density for all species separated into hatchery- and natural-origin individuals, channel dimensions, discharge, and water temperature. We are not aware of any studies that provide these data. Instead, we briefly review previous research to support the notion that pink and chum salmon stray rates for individual streams can be very high across years and geographically wide-ranging.

A study from Prince William Sound using data collected from 1997 through 2010 demonstrated that hatchery-origin pink salmon can comprise up to 98 % of spawners and hatchery-origin chum salmon up to 63 % of

total spawner abundance in a single stream; in the same study, hatchery-origin chum salmon at two weirs comprised 93–100 % of sampled fish (Brenner et al., 2012). A follow-on study conducted from 2013 to 2015 in Prince William Sound estimated that annual proportions of hatchery-origin pink salmon in single streams were as high as 90 % and chum salmon as high as 97 % (Knudsen et al., 2021). In two Southeast Alaska studies conducted from 2008 to 2010 and 2013 to 2015, the maximum proportion of hatchery-origin chum salmon in a single stream were 88 % and 85 %, respectively (Josephson et al., 2021; Piston and Heintz, 2012). In 2018 and 2019, unexpectedly large chum salmon returns to a new hatchery release site in Southeast Alaska (Crawfish Inlet on the west coast of Baranof Island) led to concerns that the marine fishery could not keep pace with harvesting the majority of the estimated 3.5 million and 2.1 million returning fish,

respectively (Piston and Heintz, 2020). Many of these hatchery-origin fish were observed straying to the adjacent West Crawfish Inlet where their run timing overlapped with wild fish. In September of 2018 and 2019, sampling demonstrated that the main spawning stream in West Crawfish Inlet had 99 % and 94 % hatchery-origin spawners, respectively. In 2019, biologists conservatively estimated that over 10,000 chum salmon attempted to spawn in this stream (Piston and Heintz, 2020). In 2008 and 2009, before any nearby hatchery releases occurred, peak spawner count estimates in this same stream were only 4300 and 3500, respectively, with accompanying hatchery-origin proportions of 4 % and 0 % (Piston and Heintz, 2012).

4.4. Study limitations

While the dissolved oxygen model used here relies on established functional relationships and has been validated within the study region using empirical data (Sergeant et al., 2017), the accuracy of hypoxia vulnerability metrics may be limited in some reaches by the digital elevation models used to estimate habitat conditions and the lack of consideration for other components of ecosystem respiration that create or use oxygen. Some Southeast Alaska stream channel characteristics in NetMap are based on 2-m digital elevation models that use light detection and ranging (LiDAR) techniques, but most habitat data used here are based on a 20-m digital elevation model. Coarse elevation models may, for example, lead to incorrect estimates of gradient by averaging over sharp breaks in channel slopes (knickpoints) that could underestimate reaeration estimates. However, digital elevation models for Alaska are improving (<https://elevation.alaska.gov/>) and will be less likely to limit future studies. Bank angles and migration blockage thresholds are additional components of the analysis that remain widely unmeasured and uncertain in our study region.

In order to estimate low flow channel velocity and depth, all bank angles were assumed to be 45°. Increasing bank angle from 45° to 90° while maintaining the original bankfull width decreases velocity, while decreasing bank angle to <45° increases depth and velocity. In most instances, decreasing bank angles would result in a higher salmon density and increase hypoxia risk. For the analysis of stream reaches near hatchery release sites, we chose 10 % gradient as a conservative barrier threshold for migration that is similar to previous studies in the region (Romey, 2018; Pitman et al., 2021). There is no widely used channel gradient threshold at which upstream migration by anadromous salmon is blocked. In some places, this choice may exclude known anadromous waters from analysis. For example, Kadake Creek near Kake, Alaska (Fig. 6), is a known anadromous stream, but because the lowest stream reach channel gradient was estimated at >12 %, the upstream network was excluded from analysis. In future analyses, measurements of characteristics such as channel gradient barriers to migration and bank angles using field measurements or finer-scale digital elevation models would improve estimates and mapping of hypoxia vulnerability.

Since a goal of our study was to explore the role of spawning salmon respiration in dissolved oxygen dynamics, we did not consider other components of ecosystem respiration that create or remove oxygen such as photosynthesis, salmon carcass decomposition, or respiration by other aquatic organisms (Gende et al., 2002; Holtgrieve and Schindler, 2011). Additionally, we did not consider groundwater inputs that may either supply low dissolved oxygen water or provide micro-refugia during summer by providing cooler temperatures (Power et al., 1999). Groundwater and stream channel habitat complexity are known to play important roles in the thermal regimes of salmon watersheds, but data describing groundwater sources and thermal micro-refugia are often lacking (Mauger et al., 2017; Torgersen et al., 1999). Nevertheless, our relatively simple model analysis highlights opportunities for more nuanced modeling and empirical measurements that account for other factors that contribute to dissolved oxygen dynamics.

5. Conclusions: looking ahead to monitoring and managing dissolved oxygen in streams

While current concerns around the impacts of hatchery-origin salmon spawning with natural-origin salmon have focused primarily on genetic

consequences (Christie et al., 2014; Josephson et al., 2021; Shedd et al., 2022), our analysis supports the additional concern that hypoxic stream conditions brought about by artificially high spawner densities have the potential to create a suite of acute ecological impacts across a broad geography, including premature mortality of spawning salmon and other resident fishes (Murphy, 1985; Tillotson and Quinn, 2017; von Biela et al., 2022), mortality or reduced diversity of benthic macroinvertebrate communities (Davis, 1975), inhibited salmon embryo growth (Shumway et al., 1964), and sublethal physiological stress of numerous aquatic organisms (Davis, 1975). In wild salmon populations with no hatchery straying influence, hypoxia-induced mass mortality events during periods of high abundance may only temporarily decrease population productivity due to a density-dependent decrease in successful spawning. In contrast, hatchery salmon populations lack this density-dependent feedback on the spawning grounds and have much higher egg-to-smolt survival rates than natural populations (Bradford, 1995; MacKinlay et al., 2004). Where straying salmon continue to return to streams near hatchery release points in high abundance year-after-year, the acute ecological impacts to that stream ecosystem and productivity of wild salmon may occur with greater frequency and become more chronic than streams with only naturally spawning populations.

Small rain- and snow-fed watersheds, where meltwaters from snow and ice are limited or non-existent during the summer, are likely the most important places to conduct hypoxia monitoring (Bellmore et al., 2023; Sergeant, 2022). These watersheds will be most prone to drought during salmon spawning periods, which can inhibit upstream migration, create warmer waters that hold less oxygen, and promote higher fish densities (Sergeant et al., 2020; von Biela et al., 2020).

Looking ahead, this research calls attention to three key questions that can guide future ecological monitoring programs: 1) Where and in how many places do straying salmon increase the frequency and intensity of hypoxia events? 2) Do hypoxia events result in observable ecosystem responses such as decreased natural spawning productivity or decreased diversity of aquatic macroinvertebrates? 3) Are climate change and associated extreme events creating physical habitat and flow conditions that decrease the ability of streams to reaerate efficiently? Our repeatable analytical framework for identifying hypoxia vulnerability can be used to address these questions and refined with empirical habitat and salmon density data at the reach and watershed scales. We see an opportunity to integrate research on these emerging ecological questions with existing long-term monitoring programs in regions like Southeast Alaska, where the focus to-date is mainly on juvenile and adult salmon enumeration. Government agencies such as the Alaska Department of Fish and Game and National Oceanic and Atmospheric Administration have research infrastructure in place throughout Southeast Alaska that could be leveraged to support monitoring programs geared toward the key ecological questions posed above. Future monitoring programs could be designed to assess the prevalence and ecological impacts of hypoxia events intensified by high rates of salmon straying. In streams where hatchery-induced hypoxia vulnerability is high, fisheries managers can take actions such as constructing in-stream weirs to control the number of hatchery fish straying into the stream. Macaulay Hatchery in Juneau, Alaska currently operates two weirs to limit straying (<https://www.adfg.alaska.gov/index.cfm?adfg=fishingHatcheriesPlanning.annual>). Pressures on the salmon watersheds of southern coastal Alaska brought about by climate change and hatchery supplementation increase the urgency to determine the ecological impacts of freshwater hypoxia. Our research strives to illuminate the degree to which hatchery strays may induce hypoxia-related mortality and create conflict with salmon hatcheries' goal of protecting and maintaining the abundance of wild salmon stocks.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165247>.

CRediT authorship contribution statement

Christopher J. Sergeant: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **J. Ryan Bellmore:**

Conceptualization, Methodology, Formal analysis, Writing – original draft. **Rebecca A. Bellmore:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – review & editing. **Jeffrey A. Falke:** Conceptualization, Methodology, Formal analysis, Project administration, Writing – review & editing. **Franz J. Mueter:** Formal analysis, Writing – review & editing. **Peter A.H. Westley:** Writing – review & editing.

Data availability

The following data will be available as a single .zip file stored on ScienceBase at LINK: 1) Hourly hypoxia vulnerability calculations at water temperature monitoring sites; 2) Hourly hypoxia vulnerability calculations near hatchery release sites; 3) Habitat characteristics at water temperature monitoring sites; 4) R code for reproducing the hypoxia conditions analysis in Fig. 3.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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