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Landcover and geomorphology influence streamwater temperature sensitivity in salmon bearing watersheds in Southeast Alaska

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Abstract

Climate warming is projected to increase the regional air temperature in Southeast Alaska and alter precipitation patterns and storage, with potentially important implications for the region's aquatic ecosystems. The climate-landcover relationships influencing stream temperature have not been comprehensively evaluated in Southeast Alaskan watersheds, many of which provide spawning and rearing habitat for five species of Pacific salmon. Thus, improving our understanding of current streamwater thermal regimes is critical to assess how stream temperatures across the region may be altered by ongoing climate change. We evaluated seasonal streamwater thermal regimes in forty-seven salmon-spawning watersheds in Southeast Alaska to assess the influence of watershed geomorphic and landscape characteristics on streamwater temperature and sensitivity to variation in air temperature. Stream temperatures were measured during the 2015 water year and analyzed for winter and summer seasons. Mean summer stream temperatures ranged from 4.0 °C–17.2 °C, while mean winter stream temperatures were less variable (0.5 °C–3.5 °C). Maximum weekly average temperatures ranged from 4.3 °C–21.5 °C. Regression and time-series analyses revealed that low gradient watersheds with higher lake coverage experienced warmer summer stream temperatures and were more sensitive to air temperature fluctuations compared to streams draining watersheds with high gradients. Winter mean stream temperatures were warmer in higher gradient watersheds with greater forest and lake coverage. These findings demonstrate that streamwater thermal regimes and sensitivity to air temperature are strongly moderated by watershed geomorphology and landcover, resulting in substantial thermal heterogeneity in streams across the complex terrain characterizing the coastal temperate rainforest of Southeast Alaska.

1. Introduction

Water temperature is a master hydrologic variable in freshwater ecosystems (Caissie 2006). It is a fundamental driver of physical and biological processes in lotic ecosystems (Webb *et al* 2008), strongly influencing habitat variables such as oxygen solubility and nutrient availability as well as the physiologic processes of aquatic organisms (Poole and Berman 2001). Cold-

water fishes such as Pacific salmon, are adapted to the thermal regimes to which they evolved (Caissie 2006). As a result, streamwater temperature influences spawn timing, incubation, growth, distribution, and abundance of cold water fish species across a range of spatial and temporal scales (Berman and Quinn 1991). As climate becomes warmer and more variable, biological communities in lotic ecosystems will have to adapt to changing thermal regimes. Thus, quantifying the

impacts of climate variability on streamwater thermal regimes is a fundamental concern among scientists and land managers (Isaak *et al* 2012, Schindler *et al* 2008).

Stream thermal regimes are controlled by the geomorphic and hydrological conditions of their watershed and interactions with localized climate, primarily air temperature (Poole and Berman 2001). The strong relationship between stream temperature and air temperature is well documented (Mohseni *et al* 1998), however this relationship can be modulated by localized watershed attributes. For example, runoff from snow (Lisi *et al* 2015) and glacier (Fellman *et al* 2014) melt can decrease streamwater sensitivity to air temperature fluctuations. Thus, quantifying the interaction between watershed landscape characteristics and air temperature can be a powerful tool for predicting stream temperatures at regional scales and understanding watershed sensitivity to variations in climate (Isaak and Hubert 2001).

Terrestrial and aquatic ecosystems in the Pacific coastal temperate rainforest in Alaska are rapidly being altered by climate change (O'Neel *et al* 2015), with unknown implications for keystone species such as Pacific salmon (Willson and Halupka 1995, Bryant 2009). In Southeast Alaska, regional climate models project that by 2100 mean annual air temperature may increase by 3.7 °C, annual precipitation may increase 15%, and annual snowfall may decline 40% (Shanley *et al* 2015, McAfee *et al* 2014). Warming winter air temperatures and a decrease in the proportion of precipitation falling as snow are expected to affect seasonal precipitation storage as snow and the timing of surface water runoff in Southeast Alaska (Shanley *et al* 2015), with potentially important implications for aquatic thermal regimes. Small increases in stream temperature and greater daily thermal variation during winter months may potentially alter salmon egg incubation rates and emergence timing (Bryant 2009, Steel *et al* 2012). Diminished end-of-winter snowpack will also impact streamwater thermal regimes in spring and summer by decreasing the snowmelt contribution to streamflow. This, in turn, both increases the sensitivity of streamwater to air temperature by reducing the thermal buffering effect of snowmelt (Lisi *et al* 2015) and reduces stream discharge during warm summer months (Shanley and Albert 2014). Taken together, these effects of diminished snow cover in Southeast Alaska may also alter salmon spawn timing as they seek to avoid peak stream temperatures or adapt to warmer thermal regimes (Kovach *et al* 2013, 2015).

Overall, there remains considerable uncertainty about how projected climate warming will influence streamwater thermal regimes in Southeast Alaska (Shanley *et al* 2015). The primary reasons for this uncertainty are twofold: (1) the influence of diverse geomorphic and landscape conditions on streamwater temperature in the region has not been comprehensively evaluated (Fellman *et al* 2014), and (2) hydrologic regimes are highly variable because of

inter-watershed differences in the proportion of streamflow derived from groundwater, rainfall runoff, snowmelt, and glacial melt (Edwards *et al* 2013).

To address these knowledge gaps, we quantified summer and winter streamwater thermal regimes in Southeast Alaska by establishing a regional stream temperature monitoring network to quantify spatial and temporal patterns in stream temperature. We used regression and multivariate time-series techniques to quantify the influence of landscape characteristics on thermal regimes and streamwater sensitivity to changes in air temperature in both summer and winter seasons. Our findings reveal considerable variability in seasonal thermal regimes in the region's salmon-bearing streams, and provide insight into how streamwater thermal regimes will respond to future climate change.

2. Methods

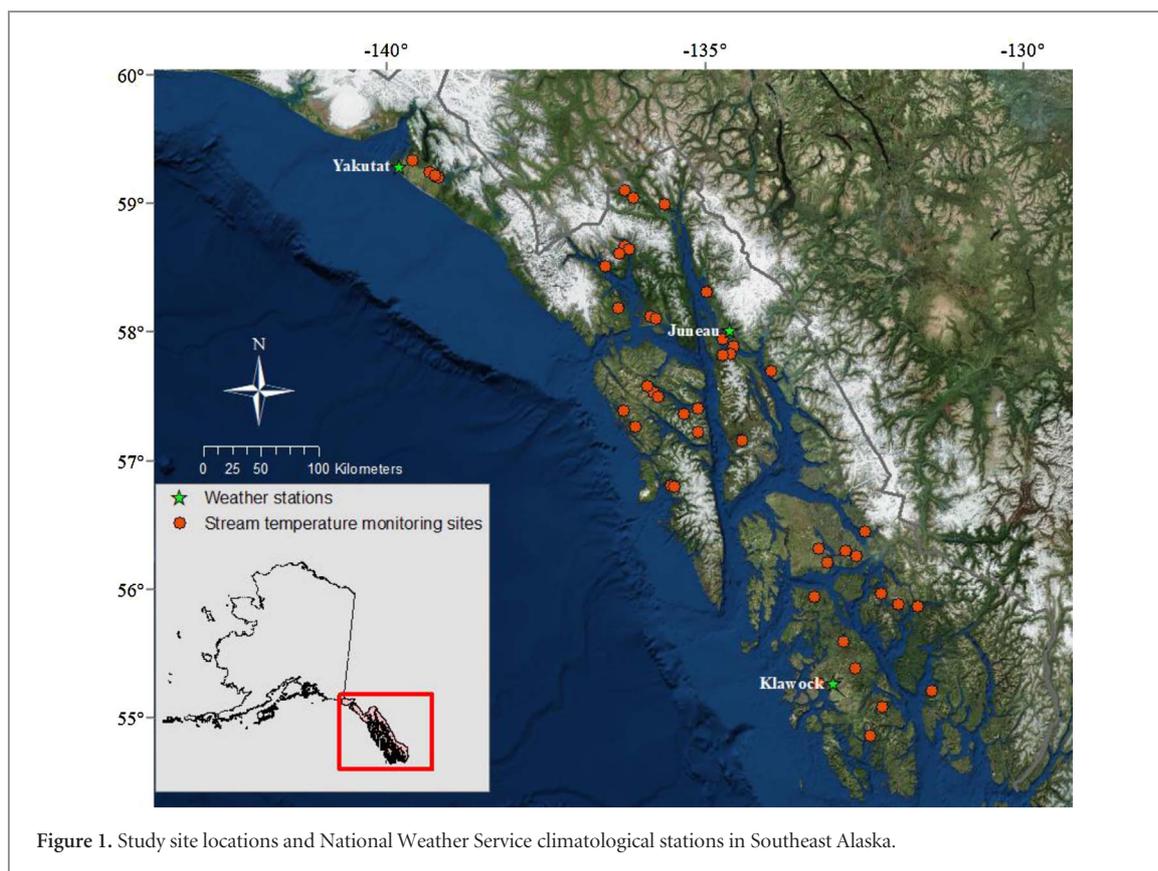
2.1. Study area

The ~81 000 km² study area encompasses the northern coastal temperate rainforest spanning the panhandle of Southeast Alaska (figure 1). The maritime climate, dominated by weather fronts from the Gulf of Alaska, interacts with topographical, latitudinal, and longitudinal gradients, leading to highly variable patterns in precipitation and air temperature that influence land-cover and vegetation community structure throughout the region (Shanley *et al* 2015). Average elevation across the study watersheds ranges from 50 m–1094 m.

2.2. Stream and air temperature monitoring

The study watersheds were located throughout Southeast Alaska (figure 1) and were selected based on the following characteristics: minimally impacted by infrastructure; catchment area ≤ 150 km²; no historical timber harvest in the riparian zone; salmon-bearing; and $\leq 10\%$ glacier coverage. Stream temperature data were collected in 35 watersheds during winter (December 2014–February 2015) and 43 watersheds during summer (June–August 2015) using two HOBO ProV2 temperature loggers per stream, with several exceptions (table S1 available at stacks.iop.org/ERL/13/064034/mmedia). Sensors were cross-calibrated prior to and following deployment. Raw stream temperature data were collected at 15–60 minute intervals and summarized to mean daily stream temperatures.

Alaska's highest average annual air temperatures and precipitation are found in Southeast Alaska (Shulski and Wendler 2007). During the study period, air temperatures measured at Yakutat, Juneau, and Klawock National Weather Service climatological stations (figure 1, www.wrcc.dri.edu) were anomalously warm in both summer and winter compared to long-term averages (Overland *et al* 2015, figure S1). The amounts of precipitation as snow were also anomalously low. Mean annual air temperatures ranged from 11.6 °C–13.5 °C and annual precipitation



from 1580–3490 mm at the three weather stations during the study period. From a regional perspective, strong correlations between summer (Pearson's $r = 0.56$ – 0.64) and winter (Pearson's $r = 0.77$ – 0.80) air temperatures among the stations suggest the climatological data from Juneau used in regional air sensitivity analyses are broadly representative of regional air temperature patterns.

2.3. Stream temperature metrics and predictive models

Four stream temperature metrics were computed for each watershed: maximum weekly average temperature (MWAT), mean summer (June–August) stream temperature (AVE-Tsum), winter (December–February) maximum daily stream temperature (MAX-Twin), and mean winter stream temperature (AVE-Twin). Empirical linkages between thermal metrics and watershed characteristics were evaluated with multiple linear regression (MLR) using R statistical software (R Development Core Team 2016). Model parameters (table S2) included the following characteristics: watershed area (log transformed km^2), mean watershed elevation (m), alpine area (%), lake coverage (%), mean watershed slope (degree), wetland area (%), forest coverage (%), and latitude (decimal degrees). Outliers identified using Cook's distance were removed from the analyses.

2.4. Time-series analysis

Dynamic factor analysis (DFA) was used to evaluate underlying regional trends in mean daily stream

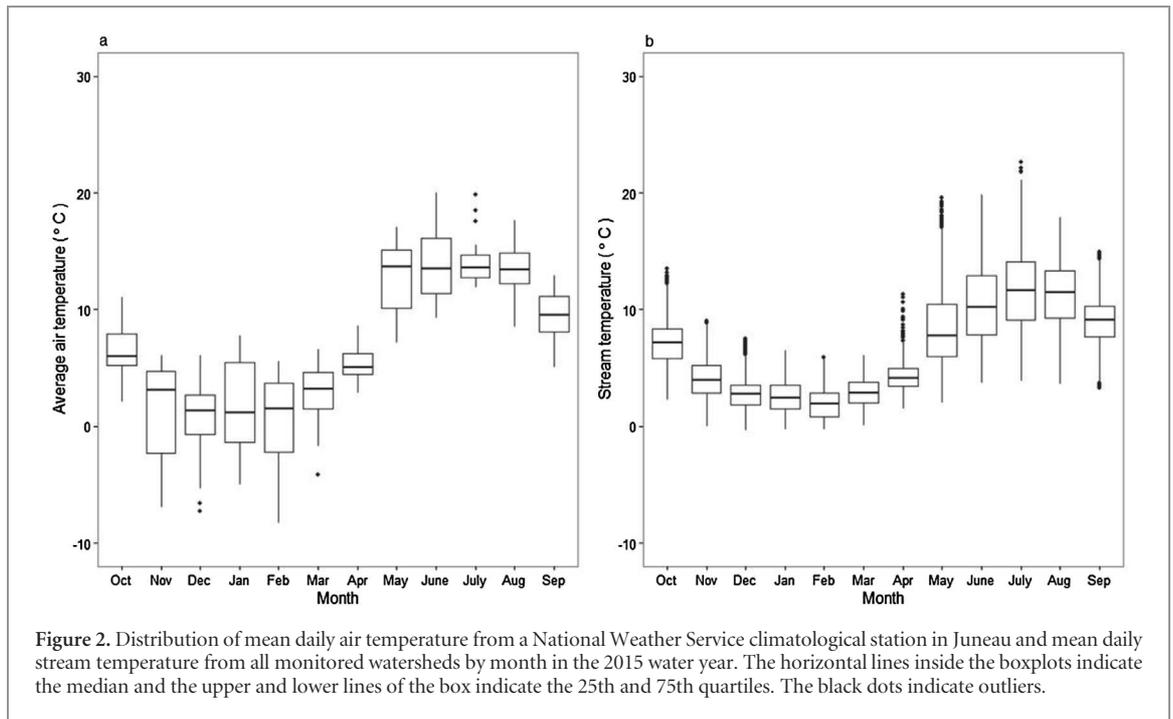
temperature during summer and winter seasons, following Lisi *et al* (2015). Using DFA, common trends among stream temperature time-series were estimated by treating the observed data as linear combinations of one or more unobservable common trends (Zuur *et al* 2003, 2007). Shared trends are the information common to each stream temperature time-series that are not explained by air temperature. Because DFA is an autoregressive state-space model, it accounts for temporal autocorrelation in the observed data (Zuur *et al* 2003, 2007).

The DFA model was used to evaluate spatial and temporal trends in stream temperatures as they responded to variation in air temperature. Using Template Model Builder (Kristensen *et al* 2016), linear multivariate autoregressive state-space models with Gaussian errors were fit to the data. Following Zuur *et al* (2003), the model form is written as follows:

$$y_t = Zx_t Dg_{t-1} \dots + Dg_{t-n} + v_t \quad (1)$$

$$x_t = x_{t-1} + w_t. \quad (2)$$

Here, the response variable y_t equals n observed stream temperature observations at time t , x_t is the common trend at time t with normally distributed error (w_t), which is multiplied by Z stream specific factor loadings. Covariate loadings $Dg_{t+}, Dg_{t-1}, \dots, Dg_{t-n}$ are parameterized by air temperature at time $t, t-1, \dots, t-n$, v_t equals random observation error with a multivariate normal distribution mean equal to zero and a



variance-covariance matrix R . Models exploring different daily air temperature time lags and error matrix structures were assessed using Akaike information criterion (Burnham and Anderson 2002). We fit separate models to each the winter and summer thermal regimes.

2.5. Landscape influence on stream sensitivity to air temperature

Thermal sensitivity of streamwater to air temperature was evaluated following methods in Lisi *et al* (2015). Stream specific air sensitivity ($\Delta^{\circ}\text{C } T_w / ^{\circ}\text{C } T_a$), a metric quantifying the average change in stream temperature per 1°C change in air temperature, was computed for both summer and winter seasons. Geomorphic controls on summer and winter air sensitivity were evaluated using multiple linear regression.

3. Results

3.1. Regional overview

Stream temperatures exhibited substantial variation across time and space during the 2015 water year. Mean daily air temperature and stream temperature displayed similar seasonal patterns and were remarkably similar at the monthly scale (figure 2), with the coldest temperatures occurring in February, followed by a gradual increase peaking in July. Near-freezing air temperature conditions were prevalent between December and February.

There was considerable variation in the magnitude of MWAT in the forty-three streams with complete summer records, ranging from 4.3°C – 21.5°C (figure 3(a)). The date of occurrence of MWAT ranged from 2 May–15 August (figure 3(b)); however, there

was considerable regional temporal coherence, with MWAT occurring between 4 July and 7 July in 70% of watersheds. AVE-Tsum ranged from 4.0°C – 17.2°C (figure 3(c)) and was strongly correlated with MWAT ($R^2_{\text{adj}} = 0.98$, $p < 0.001$). AVE-Twin exhibited less variation compared to summer, ranging from 0.5°C – 3.5°C (figure 3(d)). MAX-Twin ranged from 2.3°C – 5.9°C (data not shown).

3.2. Landscape controls on thermal regimes

Observed AVE-Tsum were positively correlated with lake, wetland, and forest coverage and negatively correlated with slope, elevation, alpine area, and latitude. Despite significant correlations, no single watershed characteristic explained a majority of the variation in AVE-Tsum ($R^2_{\text{adj}} = 0.07$ – 0.41 ; figure S2). Correlations between MWAT and watershed characteristics were similar in direction and magnitude to those for AVE-Tsum (figure S3). AVE-Twin were positively correlated with lake and forest cover and negatively correlated with latitude; however, watershed characteristics explained less of the variation in mean winter temperature compared to summer ($R^2 = 0.00$ – 0.22 ; figure S4).

The strongest MLR models for AVE-Tsum ($R^2_{\text{adj}} = 0.64$) and MWAT ($R^2_{\text{adj}} = 0.67$) showed positive correlations with watershed lake coverage and were negatively correlated with slope, forest cover, and latitude (table 1). Little predictive power was lost for MWAT and AVE-Tsum when excluding land-cover metrics and including only geomorphic variables derived from the digital elevation model ($R^2_{\text{adj}} = 0.62$ and 0.60 , respectively; data not shown).

The strongest MAX-Twin model, parameterized with elevation, lake coverage, and latitude, explained 57% of the variance (table 1; $R^2_{\text{adj}} = 0.57$). The

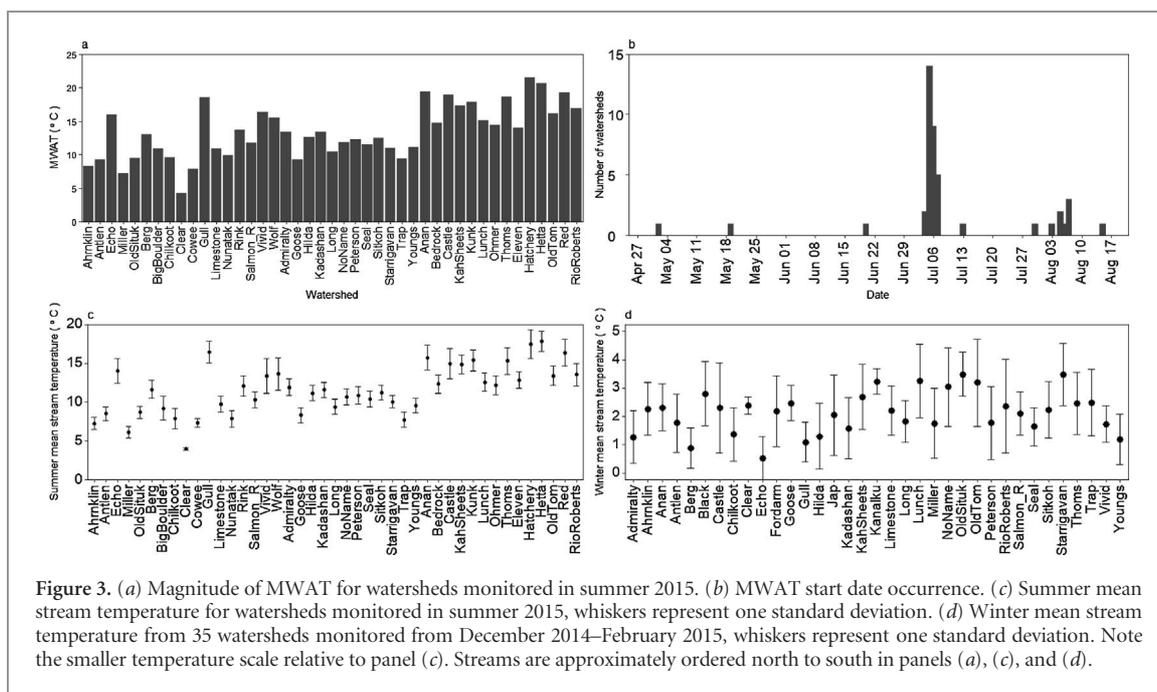


Figure 3. (a) Magnitude of MWAT for watersheds monitored in summer 2015. (b) MWAT start date occurrence. (c) Summer mean stream temperature for watersheds monitored in summer 2015, whiskers represent one standard deviation. (d) Winter mean stream temperature from 35 watersheds monitored from December 2014–February 2015, whiskers represent one standard deviation. Note the smaller temperature scale relative to panel (c). Streams are approximately ordered north to south in panels (a), (c), and (d).

Table 1. Multiple linear regression predictive models fitting stream temperature metrics with landcover and geomorphic variables during the summer and winter seasons of the 2015 water year.

| Season | Model metric | Model and coefficients | R ² _{adj} | SE | p-value |
|--------|--------------|--|-------------------------------|------|---------|
| Summer | MWAT | 148.15*** -0.24(slope)*** + 0.53 (%lake)** -0.05(%forest)* -2.22(lat)*** | 0.67 | 2.31 | <0.001 |
| | AVE-Tsum | 115.34*** -0.19(slope)*** + 0.44 (%lake)** -0.04(%forest)* -1.71(lat)*** | 0.64 | 1.91 | <0.001 |
| Winter | MAX-Twin | 43.52*** -0.002(elev)* -0.17 (%lake)* - 0.67(lat)* | 0.57 | 0.69 | <0.001 |
| | AVE-Twin | -0.30 + 0.035(slope). + 0.11 (%lake). +0.016(%forest)*** | 0.23 | 0.67 | <0.01 |

Significance: '.' = <0.10, '*' = <0.05, '**' = <.01, '***' = <0.001.

AVE-Twin model revealed positive correlations with slope, lake coverage, and forest cover, with lower predictive power than the MAX-Twin model (table 1; R²_{adj} = 0.23). The lower variance explained by winter stream temperature models relative to summer models is largely due to more homogenous stream temperatures across the landscape during the winter.

3.3. Landscape controls on stream specific air sensitivity

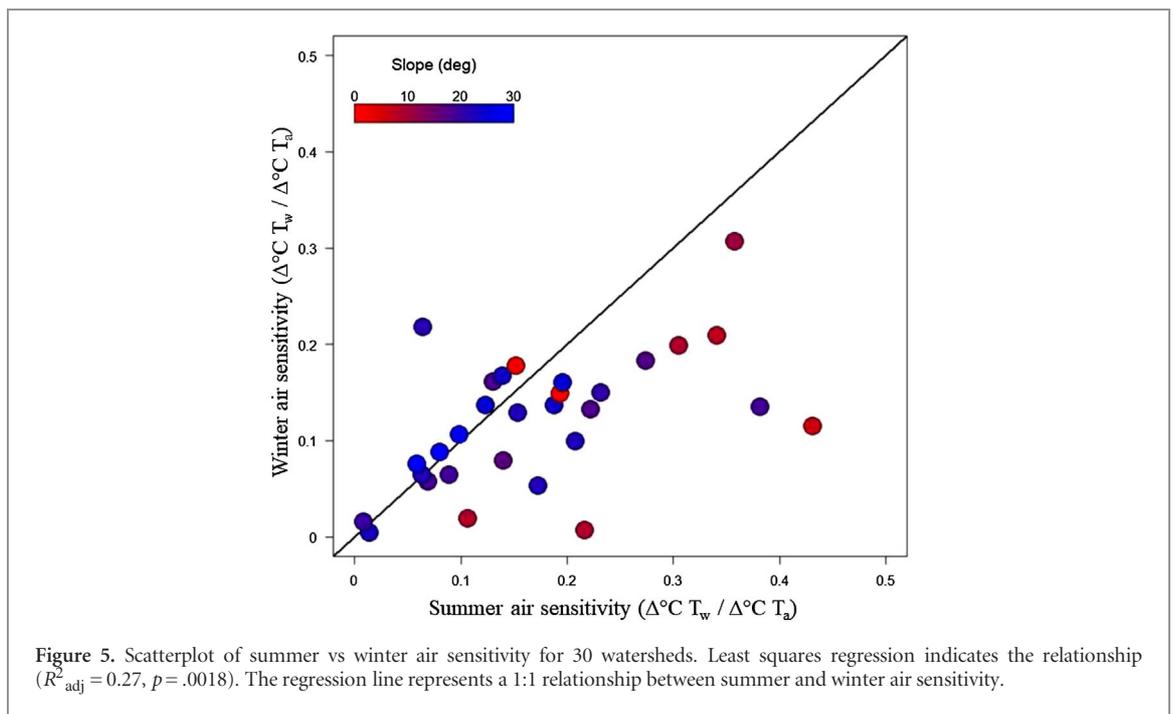
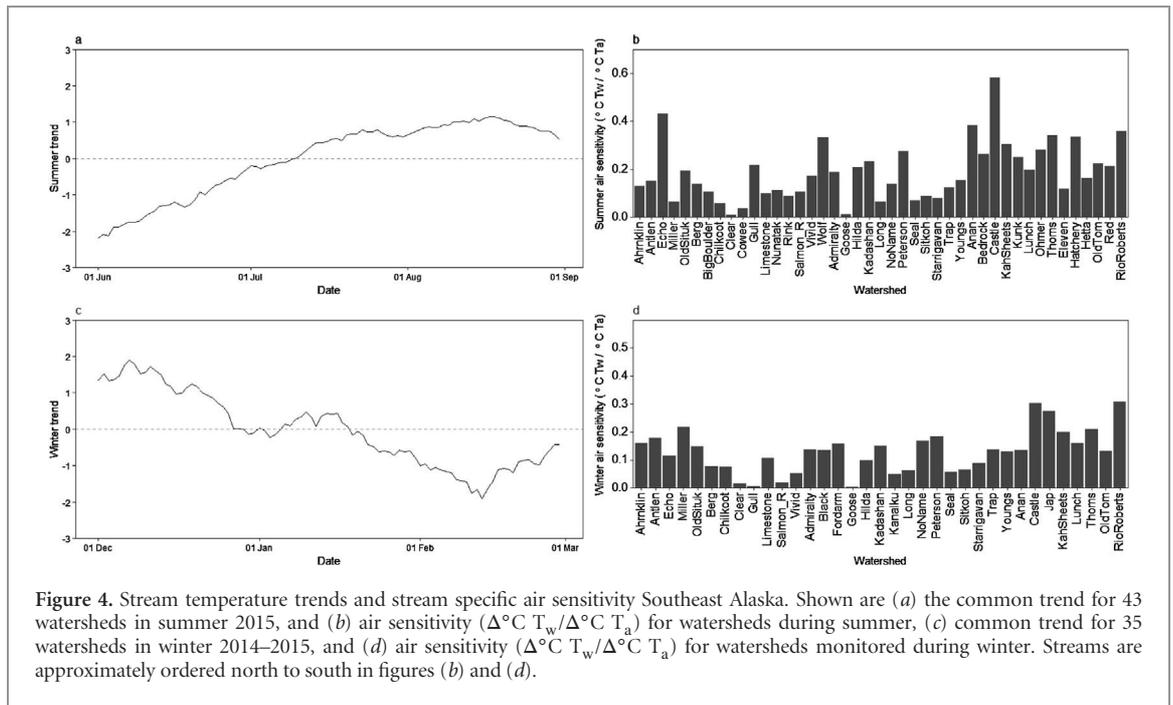
Common trends in stream temperatures shared among watersheds were modeled using DFA. These shared trends, independent of air temperature, showed a smooth increase from 1 June to a peak in mid-August, followed by a slow decline to 1 September (figure 4(a)). In winter, temperatures tended to drop from 1 December until mid-February, after which they tended to warm slowly until 1 March (figure 4(c)). The strongest summer and winter models included daily air temperature and air temperature at a lag of one day as covariates. Excellent model fits indicate the analysis captured variation in summer (figure S5) and winter (figure S6) stream temperatures, which allowed evaluation of seasonal air sensitivity. Summer air sensitivity was spatially variable and ranged from 0.01 °C–0.58 °C T_w/°C T_a (figure 4(b)). The best MLR model revealed that summer air sensitivity was negatively correlated

with watershed slope along a latitudinal gradient (table 2, R²_{adj} = 0.27). Winter air sensitivity was lower in magnitude compared to summer (0.01 °C–0.31 °C T_w/°C T_a, figure 4(d)), and was similarly negatively correlated with watershed slope and latitude, indicating low relief watersheds are more sensitive to air temperature relative to higher gradient watersheds and the influence of air temperature decreased with increasing latitude (R²_{adj} = 0.19, table 2). For individual watersheds, stream specific air sensitivity was relatively coherent between summer and winter (figure 5), consistent with the fact that watershed slope and latitude was inversely correlated with air sensitivity during both seasons.

4. Discussion

4.1. Regional patterns in streamwater thermal regimes and air sensitivity

Streamwater temperatures in salmon-bearing watersheds across Southeast Alaska exhibited considerable variation similar to recent regional studies in coastal Alaska, British Columbia (BC), and Pacific Northwest (PNW). AVE-Tsum and MWAT in Southeast Alaska ranged from 4.0 °C–17.2 °C (figure 3(c)) and 4.3 °C–21.5 °C (figure 3(a)) respectively. Observed



thermal regimes were somewhat cooler compared to streamwater thermal regimes in the PNW (Isaak *et al* 2012), BC (Moore 2006, Moore *et al* 2013), and southcentral Alaska (Mauger *et al* 2017), and generally similar in range to Prince William Sound (Adelfio 2016). Both average summer stream temperature and air sensitivity were similar to those observed in southwest Alaska (Lisi *et al* 2013, 2015). Winter average stream temperatures in Southeast Alaska ranged from 0.5°C – 3.5°C , and were colder than PNW (Isaak *et al* 2012) and BC (Moore 2006), though no studies report winter air sensitivity for comparison to this study. The colder summer and winter stream temperatures

in Southeast Alaska compared to PNW and BC result from decreased solar radiation and colder air temperatures associated with lower sun angles at higher latitudes. The lack of method standardization (i.e. different thermal metrics, watershed sizes, and season definitions) among regional studies makes comparisons challenging, and caution should be exercised when interpreting results among regions.

4.2. Seasonal thermal regimes and air sensitivity

Our findings reveal that watershed landscape characteristics in the coastal temperate rainforest of Southeast Alaska are an important control on underlying

Table 2. Multiple linear regression predictive models fitting stream specific air sensitivity with geomorphic variables during the summer and winter seasons of the 2015 water year.

| Season | Model metric | Model and coefficients | R^2_{adj} | SE | p -value |
|--------|-----------------|--|-------------|------|------------|
| Summer | Air sensitivity | 2.40 ^{**} -0.008(slope) ^{**} -0.035(lat) ^{**} | 0.27 | 0.1 | 0.001 |
| Winter | Air sensitivity | 1.86 ^{**} -0.003(slope) [*] -0.029(lat) ^{**} | 0.19 | 0.07 | 0.012 |

Significance: ^{*} = <0.05, ^{**} = <.01, ^{***} = <0.001.

physical processes that influence summer and winter streamwater thermal regimes and air sensitivity. Multiple linear regression models identified slope, lake coverage, forest coverage, and latitude as the watershed attributes most closely linked to stream temperature, while slope and latitude exerted the strongest influence on air sensitivity. The negative correlations between watershed slope and both summer stream temperature and air sensitivity are likely the products of multiple cooling mechanisms. In the case of air sensitivity, streams draining high gradient watersheds were less responsive to changes in air temperature than streams draining low gradient watersheds. The DFA model indicates stream temperature is most responsive to air temperature from the current and previous day, highlighting that the relationship between slope and water residence time is a particularly important control of thermal regimes. The duration of surface water's exposure to solar radiation and atmospheric energy flux is shorter in high gradient watersheds with greater streamflow velocities (Poole and Berman 2001). Finally, topographic shading associated with steep watersheds also suppresses stream temperature by reducing exposure to solar radiation (Webb and Zhang 1997).

Watershed slope is also strongly related to summer stream temperature because slope was highly correlated with watershed elevation (Pearson's $r=0.65$), which exerts a strong cooling influence on summer stream temperatures in coastal Alaska (Lisi *et al* 2013, Fellman *et al* 2014, Mauger *et al* 2017). The influence of elevation on stream temperature is primarily associated with snow accumulation at high elevations, which provides surface waters and groundwater aquifers with a source of cold water, and thus the impact of elevation on summer stream temperature is diminished in years with low winter snow accumulation (Hood and Berner 2009, Lisi *et al* 2015). Southeast Alaska experienced a low snow winter during the study period, and snowmelt inputs to streamwater were likely below normal. Therefore, the relationship between elevation and summer stream temperatures may have been weaker compared to higher snow years. As climate warms and snow accumulation decreases in Southeast Alaska (Shanley *et al* 2015), the strong cooling influences of physical mechanisms represented by slope that we documented during an anomalously warm year suggest slope may become an increasingly important predictor of summer stream temperatures in the future.

Our results indicate high gradient watersheds were also correlated with warmer AVE-Twin. Similar thermal response occurred in PWS, where relatively steep watersheds experienced higher frequency of days of above-freezing water temperatures (Adelfio 2016). Several factors, such as reduced snowmelt inputs from high elevation reaches of a watershed and the moderating influence of groundwater may contribute to the observed winter thermal response in streams (Hood and Berner 2009, Caissie 2006). The DFA model reveals high gradient watersheds also exhibited lower air sensitivity during winter. Winter stream temperature is most sensitive to the air temperature of the current and previous day, implying that, similar to summer, shorter water residence time is an important control of winter air sensitivity, possibly reducing the influence of air temperature on groundwater derived base flows.

Forest cover was correlated with cooler summer stream temperatures, likely through shading of surface water and shallow groundwater sources (Beschta *et al* 1987, Kurylyk *et al* 2015). Forest canopy also influences snow accumulation within a watershed and snowmelt contribution to streams. Low density forests accumulate more snow relative to high density forests (Varhola *et al* 2010). Forest canopy is considered high throughout the study area (Harris and Farr 1974), which in turn may compensate for lower snow accumulation by extending the ablation period through shading from solar radiation (Anderson *et al* 2014). In contrast to summer, forest cover had a slight association with warmer winter streamwater thermal regimes. Riparian vegetation reduces net energy loss from streams (Beschta *et al* 1987, Webb and Zhang 1997), particularly during base flows.

The warming influence of lakes reflected in the summer streamwater temperature models is consistent with previous findings in the region (Fellman *et al* 2014) and is likely a function of increased duration of exposure to solar radiation and air temperature heating the lake surface and subsequently the outlet streams (Mellina *et al* 2002). Lake coverage was also associated with warmer winter stream temperatures, likely due to increased water residence time. Moore (2006) similarly demonstrated the year-round warming influence of lakes in BC. Interestingly, lake coverage was not an important variable in summer or winter air sensitivity (table 2). The relationship between lake coverage and air sensitivity in Southeast Alaska's landscape is complex, with the location, elevation, size, and number of lakes within a watershed all affecting

the influence of lake coverage on air sensitivity (Jones 2010). In Southwest Alaska, stream temperature sensitivity was dampened in watersheds with higher (7%–29%) lake coverage (Lisi and Schindler 2015). Lake coverage was predominantly less than 5% in our study, possibly limiting buffering effects, and thus the importance of lakes as a control of seasonal air sensitivity. Future research on the role of lentic systems influence on year-round thermal regimes will be critical in understanding the potential impacts of climate change in Southeast Alaska.

Across a region as extensive as Southeast Alaska (>four-degree range in latitude), patterns in seasonal thermal regimes and air sensitivity can be expected to change with latitude. Latitude explains much of the variation in stream temperature and air sensitivity models. Similar to BC (Moore 2006), latitude likely represents macroclimate, serving as a proxy for variation in sun angle and thus solar radiation, and air temperature across the region. This can impact stream temperature directly and also indirectly through its influence on landcover variables (forest cover) and hydrologic processes (snow accumulation).

4.3. Implications for pacific salmon and land management

The complex landscape of Southeast Alaska's coastal temperate rainforest filters energy inputs into the system, inducing a thermal response in lotic systems that affect salmon populations at multiple scales and life history stages (Griffiths *et al* 2014). For example, basin scale geomorphic controls of summer thermal regimes influence spawn timing and location in Southwest Alaska (Lisi *et al* 2013). Ongoing shifts in streamwater thermal regimes are also eliciting phenotypical adaptations in Southeast Alaska's salmon fisheries (Kovach *et al* 2015). Long-term increases in stream temperature in Auke Creek, a low gradient watershed with high lake coverage, have resulted in shifts in the timing and duration of spawning (Kovach *et al* 2012, 2013). Such adaptations are occurring region-wide, with avoidance of peak stream temperatures and low stream discharge leading to temporal shifts of migratory patterns among salmon populations (Kovach *et al* 2015). Furthermore, complex interactions between stream temperature and biophysical processes may degrade water quality for salmon via dissolved oxygen depletion events (Fellman *et al* 2015, Sergeant *et al* 2017). These impacts to salmon are most apparent in streams fitting our study's geomorphic template for being warmer and having higher air temperature sensitivity.

With approximately 4000 anadromous streams within the coastal temperate rainforest of Southeast Alaska (Halupka *et al* 2003), it is important for managers to understand landscape influences on current and future streamwater thermal regimes. The geomorphic template presented here provides a framework for identifying thermally sensitive watersheds

and understanding streamwater thermal responses to climate variability. However, it is important to note that regional scale models do not capture thermal heterogeneity at the reach-scale where variable groundwater influence can moderate stream temperatures and reduce air sensitivity (Moore *et al* 2013, Callahan *et al* 2015). Furthermore, at the watershed scale, the relationships between explanatory and response variables are in constant flux, and nonstationarity will introduce uncertainty into predictive performance of models (Schindler and Hilborn 2015). Consequently linear models such as those developed here have the strongest predictive power during the temporal range in which they were developed (Arismendi *et al* 2014). Our models were developed using data collected during an anomalously warm year, thus interannual climatic variation should be considered when applying these models. Climate models for the region project warmer winters with increased precipitation, decreased precipitation as snow, and warmer summer air temperature (Shanley *et al* 2015), thus, the seasonal models developed in this study may be more applicable to future climatic conditions rather than under what have been normal climate conditions.

Acknowledgments

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