

Wind-driven upwelling in lakes destabilizes thermal regimes of downstream rivers

Peter J. Lisi^{*,†} and Daniel E. Schindler

School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington

Abstract

Natural lakes are generally assumed to stabilize thermal regimes of downstream rivers. This conceptual model does not account for the potential destabilizing effects that wind has on the surface temperatures of thermally stratified lakes and, therefore, on thermal regimes of outflowing rivers. We examined the thermal variation in streams and rivers from 24 watersheds without lakes and 15 draining lakes that varied in surface area (0.3–101 km²) and thus, their potential exposure to wind. Rivers draining large lakes (> 10 km² surface area) had summer thermal regimes with 1.8 times more variation (expressed as the coefficient of variation) than both rivers draining smaller lakes and watersheds lacking lakes. Statistical decomposition of thermal regimes revealed that ~ 3% (range: 1–5%) of the thermal variability in rivers below large lakes was from diel-scale variation, compared to 31% (14–48%) in streams lacking lakes and 24% (6–34%) in those draining smaller lakes. Instead, rivers downstream of large lakes had distinct summer thermal regimes characterized by abrupt cooling events involving drops in temperature of 5–10°C that lasted 1–3 d. These events were generally synchronous across space and not observed in watersheds without lakes or in watersheds draining small lakes. Cooling events in rivers were coordinated with high velocity winds that passed thresholds for upwelling of cool hypolimnetic water to lake outlets. Wind driven upwelling may be a common source of thermal variation in rivers draining large stratified lakes and reservoirs, making them more thermally variable than previously appreciated. The ecological responses to this thermal instability remain unexplored.

A central challenge for river ecologists is to understand how the thermal regimes of rivers are controlled by atmospheric, hydrologic, and geomorphic processes at multiple spatial scales (Caissie 2006). Temperature is fundamental for organizing ecological processes in ecosystems (Brown et al. 2004), directly modifying a variety of biological processes such as reproduction, metabolism, and behavior in ectothermic aquatic animals (Poole and Berman 2001), and ecosystem processes such as nutrient cycling and primary production (Allan and Castillo 2007). Thermal variation, like many physical attributes of rivers, is often hierarchically controlled by the geomorphic template that filters climate signals through various physical features along the river continuum (Vannote et al. 1980; Frissell et al. 1986; Benda et al. 2004). Vannote et al. (1980) provided a conceptual model to describe how thermal variation in rivers was regulated by their watershed size (Fig. 1—solid line; also see Ward and Stanford 1983; Caissie 2006). Short, narrow, and often

shaded headwater streams draining small watersheds should display less thermal variation relative to larger downstream rivers. As rivers grow in size, they typically become relatively shallow and wide, exchanging energy rapidly with ambient air temperature fluctuations and solar irradiation. Large higher order rivers are expected to show less diel variation as they are buffered by more thermal mass (Ross 1963). Still, empirical data are lacking that describe the various physical mechanisms producing thermal variation through discontinuous river features, such as in river systems that drain through lakes (Jones 2010). This knowledge gap is likely widened because rivers and lake systems are often studied separately despite their physical connections.

Lakes are common features of river networks in some geographic regions, (e.g., glaciated and permafrost regions) with substantial influence on the structure and function of rivers that drain them (Malmqvist and Rundle 2002; Jones 2010). Lakes can influence downstream morphology (Arp et al. 2007), water chemistry (Kling et al. 2000), primary productivity (Stockner et al. 2000), invertebrate communities (Robinson and Minshall 1990), and fish communities (Degerman and Sers 1994) of rivers that drain them. Many of these ecological dynamics at lake outlets are determined by seasonal

*Correspondence: peter.j.lisi@gmail.com

[†]Present address: Center for Limnology, University of Wisconsin, Madison, Wisconsin

variation in water temperature that are controlled by lake circulation, stratification, and mixing (Wetzel 2001; Jones 2010). Conventional wisdom suggests that longer water residence times in lakes relative to free-flowing rivers allows source water from lake inflows to warm at the surface during summer months in lakes that thermally stratify (Wetzel 2001; Marcarelli and Wurtsbaugh 2007). Lakes typically warm and cool more slowly than streams due to longer residence times and greater thermal mass of water. Therefore, streams downstream of lakes outlets are generally thought to be more buffered from variation in air temperature and solar radiation, reducing annual and daily amplitude of stream water temperature fluctuations relative to comparable streams with no upstream lakes (Wetzel 2001; Jones 2010). However, there are few empirical examples showing how river thermal regimes are influenced by upstream lakes (Dorava and Milner 2000; Mellina et al. 2003; Laval et al. 2008; Fellman et al. 2014). Further, how the size of a lake influences the thermal variability of lake outlets and associated downstream rivers remains virtually undescribed.

Most lakes vertically stratify during summer months causing isolation of cooler hypolimnetic water from entering surface discharge at lake outlets (Wetzel 2001). However, high velocity winds can push warm surface waters in the direction of the wind and produce a pronounced tilt in the thermocline along the fetch axis of the lake (Wedderburn 1912; Wetzel 2001). At the point the wind subsides, the thermocline will move back toward equilibrium, forming an internal seiche—an oscillation in the tilt of the thermocline lasting for hours to several days depending on the length of the lake basin and the density difference between surface water and the hypolimnion (Monismith 1986; Wetzel 2001). After particularly large winds, the initial oscillation of the thermocline may even allow deep cool water to reach the surface of lake via “upwelling.” If such upwelling occurs at river outlets, cold water would be transported to downstream rivers. Upwelling is known to generate abrupt temperature declines by as much as 10°C at lake outlets in as little as an hour and remain cool for several hours to days (Stevens and Lawrence 1997; Laval et al. 2008). Although the mechanisms behind upwelling and internal seiches in lakes are well understood, their effects on water temperature at lake outlets are not incorporated into models of thermal regimes of river networks (Caissie 2006).

Here, we studied the thermal regimes of streams and rivers in southwest Alaska to evaluate how lakes affect the variability in thermal regimes of their outlets. We hypothesized that large lakes are particularly susceptible to wind-driven upwelling of hypolimnetic water, thereby destabilizing the thermal regimes of downstream rivers. We expect that rivers draining large lakes express more thermal variation than rivers without upstream lakes (Fig. 1, dashed line). To test this conceptual model, we examined the variation of thermal regimes among a series of streams and rivers with and

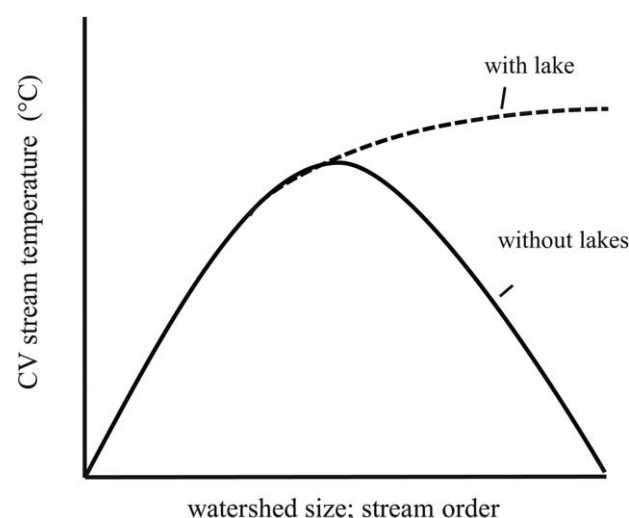


Fig. 1. Conceptual diagram showing the proposed relationship between stream temperature variability and watershed size or stream order. Solid line indicates the conventional relationship (Vannote et al. 1980; Ward and Stanford 1983; Caissie 2006), which does not include the effects of upstream lakes. Dashed line is the proposed alternative relationship for watersheds containing large lakes that are the water source for downstream rivers. Increased variability at large watershed sizes would result from wind-driven upwelling in source lakes.

without lakes. Specifically, we tested whether temperature changes in streams are linked with wind driven events that cause the surface and thermocline of the lakes to upwell across the region.

Methods

Study site

This study was conducted in southwestern Alaska in three neighboring basins of the Wood, upper Nushagak, and Togiak rivers, which all drain south into Bristol Bay (Fig. 2). These river basins and the surrounding region consist of several large, deep, oligotrophic lakes which are fed by numerous tributaries and connected by short rivers. Each of these rivers has distinct geomorphic features and drains lakes among which there is also substantial variation in their bathymetry, orientation, and surface area. Lakes within these drainages annually stratify within weeks after the lake surface is free of ice in the spring, typically the last week of May to the first week in June (Schindler et al. 2005). We monitored summer water temperatures in the mouth of tributary streams and larger main stem rivers of 24 watersheds lacking lakes and 15 watersheds draining lakes with surface areas that ranged from 0.3 km² to 202 km² and watershed areas from 1.1 km² to 1043 km² (Fig. 2). For the largest lake (Lake Nerka) we only considered half of the total lake area (101 km²), because of the distinct articulation between the upper and lower basins and the outflowing river leaves the lake near the end of the south arm. Location, physical

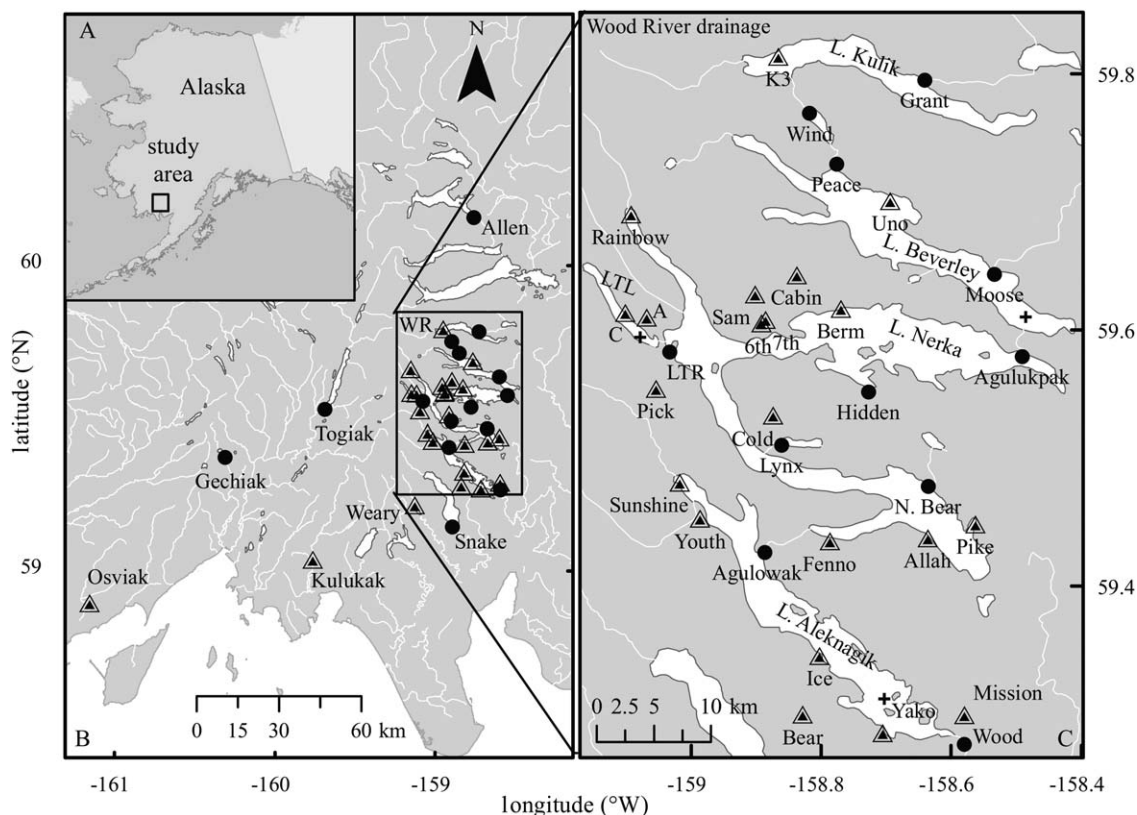


Fig. 2. (A) Map of study region in Alaska and (B) locations of data water temperature loggers in the Togiak and Upper Nushugak drainage. (C) Enlarged version of the Wood River (WR) drainage. Position of water temperature loggers on streams draining lakes (circles), streams without lakes (triangles), and position of water temperature arrays (plus sign) on Little Togiak Lake (LTL), Lake Beverley, and Lake Aleknagik.

characteristics, and thermal attributes for each stream have been included in Table 1.

The majority of stream thermal regimes were monitored with iButton® temperature recorders (Maxim Integrated Products) programmed to log at hourly intervals (0.125°C to 0.5°C resolution) between early June and early September. Temperature loggers were placed above the streambed by attaching them to steel rebar and tied to features along the river bank or fixed to the river bottom. In the Nushugak drainage, we used publicly available river temperature data from USGS stage gage located on the Allen River below Lake Chikuminuk (<http://waterdata.usgs.gov>, Sta. 15301500). In the Togiak drainage, we used hourly stage gage loggers maintained by the US Fish and Wildlife Service in the Togiak National Wildlife Refuge. Vertical temperature profiles of the lakes were monitored continuously with iButton® temperature recorders and Hobo ProV2 (Onset Computer Corp.) suspended from the lake surface at 1 m, 3 m, 10 m, 15 m, and 30 m on Lake Beverley, Lake Nerka, Lake Aleknagik, and Little Togiak Lake in ~ 50 m of water near the lake end (Fig. 2). All loggers were cross-calibrated before the start and at the end of the study and crossed checked with ambient readings in the field. Vertical temperature profiles using a sonde

(Yellow Springs Instruments, YSI, model 600LS) every ten days from 10 June to 10 September on Lake Aleknagik, Lake Nerka, and Little Togiak Lake and opportunistically on Lake Beverley. Local weather was monitored by measuring wind speed and direction and rainfall. Meteorological measurements were made at a weather station on a small island on Lake Nerka with a Hobo micro weather station (Onset Computer Corp.) and compared with a nearby coastal airport weather station in Dillingham Alaska (National Oceanic and Atmospheric Administration weather Sta. PADL) at the base of the Wood River.

Data analyses

We used the coefficient of variation (CV; standard deviation relative to the mean) to compare how stream thermal variation corresponded with its watershed area in watersheds with and without lakes at both hourly and daily averaged time steps from 30 June 2012 to 09 September 2012. Using least squares regression, we tested the hypothesis that the variation in summer water temperature is associated with watershed area, but that the strength and sign of this relationship is different in watersheds with and without lakes. The conventional expectation would be that larger lakes buffer diel thermal variation (Wetzel 2001; Jones 2010).

Table 1. Locations of stream temperature loggers, the upstream watershed area (km²) upstream lake area (km²) and summer time thermal characteristics expressed as the average summer temperature, the CV (standard deviation $\times$ mean⁻¹) at the daily time step and the CV the hourly time step.

Stream	Latitude	Longitude	Watershed area (km ²)	Lake area (km ²)	Average temp. (°C)	Daily CV	Hourly CV
Agulowak	59.409	-158.910	1043	101.0	9.29	0.18	0.19
Agulukpak	59.576	-158.532	580	90.2	9.32	0.26	0.27
Snake	59.148	-158.889	274	79.9	10.07	0.20	0.22
Allen	60.160	-158.747	896	94.6	6.13	0.25	0.26
Togiak	59.530	-159.710	518	38.8	8.46	0.22	0.24
Wind	59.754	-158.890	427	47.0	10.46	0.17	0.16
Wood	59.270	-158.581	632	87.8	9.53	0.19	0.19
LTR	59.560	-159.080	81	8.1	10.06	0.16	0.17
Gechiak	59.370	-160.350	86	4.8	12.19	0.12	0.13
Grant	59.787	-158.714	124	7.7	10.48	0.10	0.14
Lynx	59.494	-158.896	26	1.6	13.06	0.08	0.10
Peace	59.754	-158.890	38	1.8	10.72	0.15	0.15
Hidden	59.540	-158.767	8.3	0.3	10.56	0.08	0.14
N. Bear	59.470	-158.664	11	1.5	11.29	0.12	0.16
Moose	59.639	-158.584	93	3.6	10.86	0.13	0.16
Allah	59.430	-158.659	10	—	5.90	0.16	0.19
K3	59.797	-158.946	19	—	5.77	0.13	0.16
Cold Trib.	59.500	-158.901	18	—	5.63	0.10	0.15
Sam	59.589	-158.895	10	—	7.28	0.15	0.19
Sixth	59.577	-158.923	1.3	—	6.50	0.08	0.12
Seventh	59.580	-158.914	2.0	—	6.88	0.10	0.15
Ice	59.332	-158.814	94	—	9.03	0.10	0.17
Rainbow	59.665	-159.157	66	—	4.78	0.13	0.16
Uno	59.691	-158.755	18	—	5.53	0.10	0.16
Fenno	59.422	-158.811	38	—	8.23	0.11	0.14
Cabin	59.596	-158.847	4.9	—	5.62	0.16	0.21
Berm	59.599	-158.814	2.2	—	5.86	0.10	0.19
A	59.577	-159.131	1.1	—	3.52	0.10	0.13
C	59.582	-159.154	1.9	—	3.83	0.12	0.15
Mission	59.275	-158.600	3.5	—	4.58	0.10	0.14
Yako	59.275	-158.708	14	—	6.22	0.08	0.16
Pick	59.550	-159.064	20	—	5.82	0.11	0.25
Pike	59.443	-158.588	56	—	9.67	0.11	0.18
Bear	59.296	-158.778	14	—	6.53	0.09	0.16
Youth	59.432	-159.014	79	—	7.02	0.15	0.24
Sunshine	59.459	-159.049	160	—	6.75	0.16	0.19
Kulukak	59.040	-159.780	1010	—	8.90	0.13	0.16
Osviak	58.880	-161.190	639	—	9.89	0.15	0.17
Weary	59.220	-159.130	412	—	8.66	0.13	0.18

However, we propose that thermal variation expressed at daily time scales is higher in rivers draining large, deep lakes reflecting the episodic disturbances of wind events on thermal structure in lakes.

We used time-series decomposition to quantify how diel cyclic variation contributed to the total variation in the thermal regime compared to longer modes of variation. By

“diel cyclic variation,” we are referring to the daily cycle in temperature that is expressed in hourly scale data. We separated these high frequency diel signals from the complete temperature time-series using seasonal and trend decomposition based on the Loess procedure (STL, Cleveland et al. 1990). STL is an iterative nonparametric filtering procedure that decomposes time-series into three main components: a

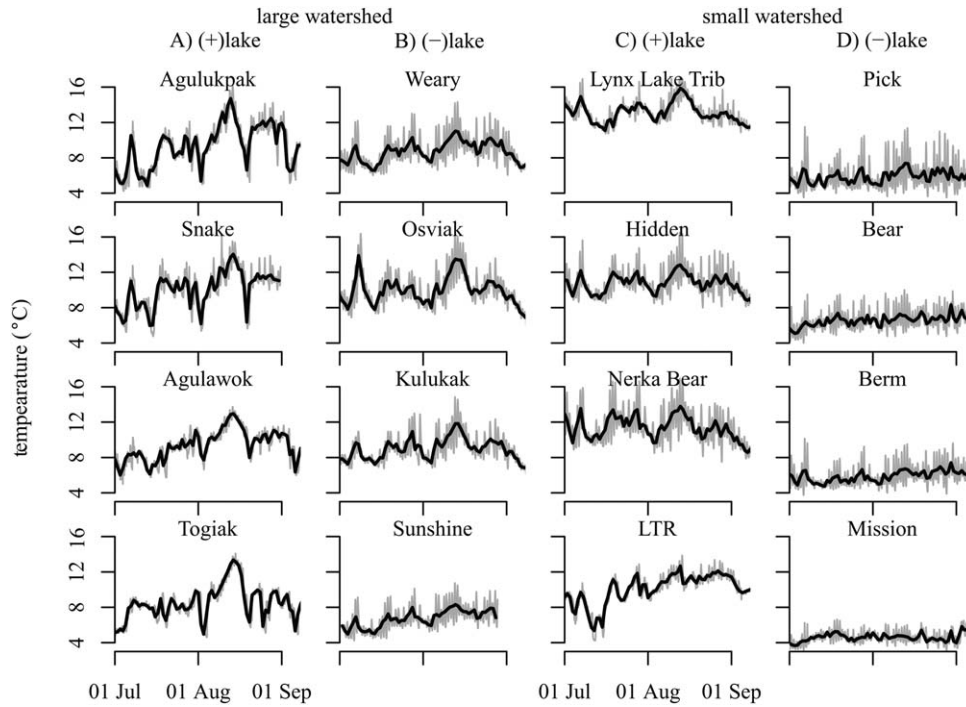


Fig. 3. Examples of the variation in water temperature regimes from 16 of 39 study streams and rivers. Solid line indicates the daily average temperature, while gray points indicate hourly temperatures. (A) rivers draining large lakes (watershed area 270–1070 km²); (B) rivers from large lake-less basins (93–1010 km²); (C) streams draining medium and small lakes with watershed areas (8.5–85 km²), and (D) streams and headwater tributaries lacking lakes (1.1–20 km²).

low frequency trend (super-daily), diel cyclic variation (sub-daily), and a remainder component. We then calculated the proportion of variance of the original time series (r^2) explained by the trend, diel, and remainder components. The compiled component variances from all 24 streams were then regressed against watershed area and lake area to test the hypothesis that less diel variation is observed in streams draining larger watersheds, and that the variance in rivers draining large lakes is dominated by low-frequency “trend” variation over finer-scale diel variation that dominates in small streams or rivers without upstream lakes. Time series decomposition was conducted with the STL function in R (R Development Core Team 2011).

As a final analysis, we examined three river thermal regimes below large lakes to understand if their unique regimes are linked to wind-driven upwelling events and thus, providing a mechanism to explain the unique variation observed in thermal regimes in downstream rivers. Potential upwelling events during stratification are traditionally described using the parameter W , the Wedderburn number (Monismith 1986; Stevens and Lawrence 1997; Laval et al. 2008). W is a dimensionless number defined as:

$$W = \frac{g' h_1^2}{u_*^2 L}$$

Here, h_1 is the surface layer depth, u_* is the shear velocity induced by wind, L is the length of the basin or lake fetch,

the reduced gravity is $g' = g(\rho_1 - \rho_2) \rho_2^{-1}$ due to difference in water density of warmer surface and cooler lower layers (Thompson and Imberger 1980). Wind speed (m s^{-1}) was filtered with a simple moving average with a temporal window spanning one quarter of the internal seiche period; equations for the seiche period (T_1) and shear wind velocity (u_*) are described by Stevens and Lawrence (1997). W does not take into account the geometry or bathymetry of the lake or wind direction. For values of $W < 1$, there is a high probability that the thermocline will tilt sufficiently to allow upwelling of hypolimnetic or metalimnetic water to the surface of the lake. The Wedderburn number provides a scale for the magnitude of seicheing expected from surface winds rather than an exact estimate of thermocline displacement (Shintani et al. 2010). We calculated W for Little Togiak Lake, Lake Aleknagik, and Lake Beverley during periods when we expected upwelling to occur given our continuous record of the lakes' surface and hypolimnetic temperatures. All three lakes of the study lakes generally parallel one another with the dominant fetch running Northwest–Southeast and the outlet on the southeast end of the lakes (Fig. 2).

Results

Stream and river temperatures varied substantially among sites and through time, ranging between 2.8°C and 18.1°C from 30 June 2012 to 09 September 2012 (Fig. 3). Visually,

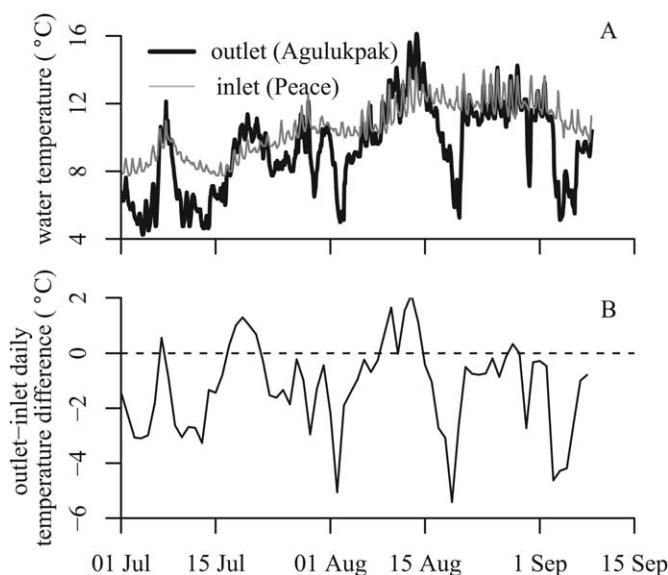


Fig. 4. (A) Hourly water temperatures of the outlet (Agulukpak River—dark line) and the main inlet (Peace River—thin gray line) of Lake Beverley. (B) Temperature difference between outlet at the Agulukpak River and inlet of the Peace River. Note that the Peace River also drains a smaller upstream lake.

temperature regimes of larger outlet rivers displayed 5–7 distinct temperature excursions that dropped 5°C to 10°C within 8–20 h. Often these thermal divergences occurred synchronously among the larger rivers draining larger lakes (Fig. 3A) but were not observed in streams draining smaller lakes or streams without lakes (Fig. 3B–D, a representative subset of study streams). The Agulukpak River, the outlet below Lake Beverley, showed average daily temperature excursions that were ~ 5°C to 6°C cooler compared to the daily average at the main lake inlet in the Peace River, a warm river also fed by a smaller upstream lake (Fig. 4). Small headwater streams that lacked lakes had the coolest average summer temperatures that were also generally stable through time. Among watersheds lacking lakes, average summer stream temperatures was positively correlated with watershed size (least squares with $\log_{10}$ watershed area, $r^2 = 0.52$, $p < 0.01$, Fig. 5). In comparison, watersheds containing lakes showed the opposite pattern. Streams draining small lakes displayed some of the warmest average temperatures. Streams and rivers draining lakes were cooler with increasing watershed size (least squares regression with $\log_{10}$ watershed area, $r^2 = 0.46$, $p < 0.01$, Fig. 5).

Do lakes stabilize thermal regimes of streams and rivers?

Stream thermal variation at the hourly scale (calculated as the CV) varied by $3 \times (0.09\text{--}0.27)$ among streams, ranging from the lowest CV below the outlet of Lynx lake (lake area = 1.6 km²) and highest CV below a larger lake outlet at the Agulukpak River (Lake Beverley area = 90.1 km²). Rivers draining large lakes (> 10 km² surface area) had summer

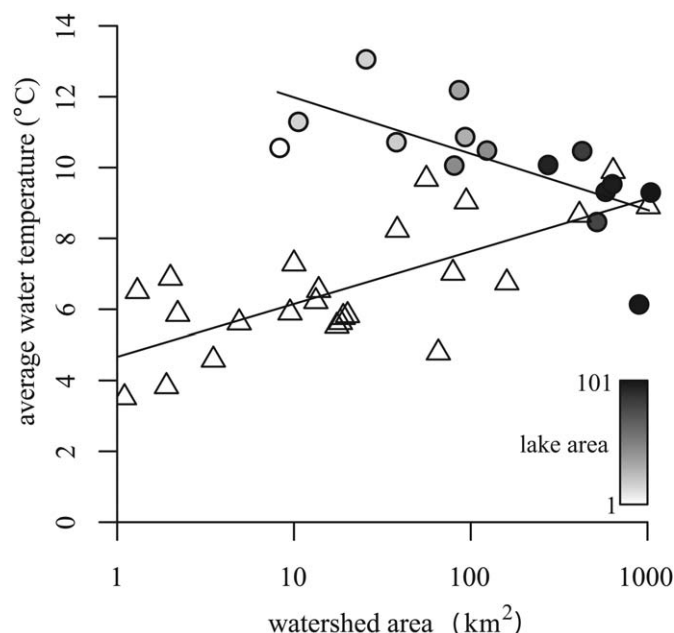


Fig. 5. Average summer temperature as a function of watershed size for streams and rivers draining lakes as open circles and shaded as a function of their lake area (least squares regression with $\log_{10}$ watershed area, $r^2 = 0.46$, $p < 0.01$). Streams lacking lakes are the open triangles ($r^2 = 0.52$, $p < 0.01$, least squares with $\log_{10}$ watershed area).

thermal regimes with $1.8 \times$ more variation relative to the mean than both rivers draining smaller lakes and those lacking lakes. Among lake-less watersheds, we found no significant association between watershed area and CV of water temperature (least squares with $\log_{10}$ watershed area, $r^2 = 0.01$, $p > 0.2$, Fig. 6A). In comparison, CV was positively associated with increasing watershed area in watersheds containing lakes (least squares with $\log_{10}$ watershed area, $r^2 = 0.59$, $p < 0.01$, Fig. 6A). In addition, lake area (km²) was correlated with CV (least squares, $r^2 = 0.58$, $p < 0.01$, $y = 0.0009x + 0.14$), against the conventional wisdom that large lakes provide stable stream temperatures to their outlets.

We also quantified temperature variation expressed at daily average time intervals. If diel-scale variation is important, the CV calculated at the daily time scale should be less than the CV calculated at the hourly scale. For lake-less watersheds, the seasonal CV calculated at the daily scale was on average ~ 30% lower compared to the seasonal CV at the hourly scale (Fig. 6B). We found some support for a linear positive association between log watershed area and CV for lake-less watersheds at the daily scale ($r^2 = 0.17$, $p < 0.05$). Smaller streams draining lakes had ~ 17% less variation relative to the mean at the daily scale, indicating that some diel variation contributed to overall summer thermal variability. In comparison, watersheds draining large lakes only had a 3% reduction in their CV at the daily scale, suggesting that diel fluctuations were not important in large lakes and likely buffered by upstream thermal mass (Fig. 6A vs. B). Again, we

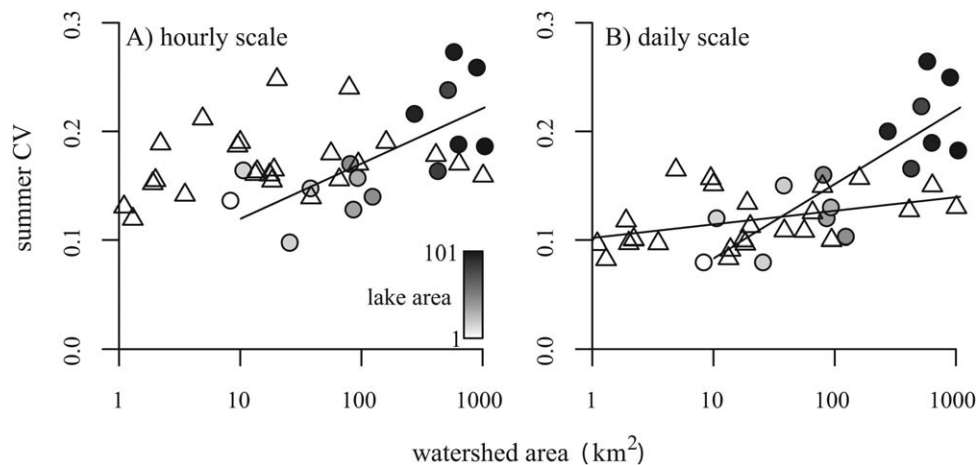


Fig. 6. Summer thermal variation relative to the mean (as CV) of 39 streams as a function of watershed area (km^2) at (A) hourly time intervals and (B) summer CV at daily average time intervals. Streams and rivers draining lakes as open circles and shaded as a function of their size. Streams lacking lakes are the open triangles.

found a positive linear relationship between log watershed area and summer CV at the daily scale (least squares with $\log_{10}$ watershed area: $r^2 = 0.63$, $p < 0.001$, Fig. 6B).

Decomposition of thermal regimes with STL was effective at separating diel cycles from the original temperature time series (e.g., Fig. 7A). This analysis revealed that diel scale variation explained only 3% (0.01–5%) of the total variation in rivers below large lakes, confirming that large lakes buffered diel temperature variation (Fig. 7B). Instead, the trend component, that included episodic but large temperature excursions, explained $\sim 94\%$ (90–96%) of total thermal variation in rivers below large lakes (Fig. 7B). By comparison, diel scale variation contributed on average 35% (57–14%) of the total thermal variability in streams without lakes (Fig. 7B) and 16% (2–33%) to those draining smaller lakes with surface areas less than 10 km^2 . The trend component explained $\sim 54\%$ (35–80%) of the variation for lake-less watersheds (Fig. 7C). Only 8% (2–16%) of the variation was explained by the remainder component for all streams and rivers, with more residual variation associated with headwater tributaries.

Does lake upwelling destabilize temperatures in rivers below large lakes?

We explored the mechanisms that might explain why rivers below large lakes are the most thermally variable environments compared to other drainages even though diel variation appeared to be buffered by upstream lakes. Here, we examined thermal variation in the Agulupak, Little Togiak, and the Wood River, where lake thermal arrays could be used to detect periods of lake upwelling and, therefore, cooling pulses to downstream rivers that characterized the thermal regimes below larger lakes. We observed several wind events over the course of the summer (Fig. 8A), with primarily west to northwesterly winds over the lake surface ($> 4 \text{ m s}^{-1}$, Fig. 8B) that were followed by large temperature

swings throughout the water column of each lake (Fig. 8C-E). For example, on 18 August, heavy winds resulted in an internal seiche with a period of 3.6 d on Lake Beverley, with temperatures at 30 m of water oscillating between 4°C and 10°C . Similarly, we observed Lake Aleknagik with a 3.4 d seiche period and Little Togiak a 1.2 d seiche period. On occasion, the Wedderburn number was less than one for all three lakes, indicating that wind events created conditions where upwelling should occur (Fig. 8C-E note figure's $\log_{10}W$ scale). All three lakes had upwelling conditions ($W < 1$) in early July when the epilimnion in each lake was relatively shallow (7–8 m) and density differences were less distinct between the surface and hypolimnion.

Temperature conditions at the river outlets were often linked with surface conditions in the lake during upwelling. Abrupt drops in temperature occurred for the Agulupak River on 29 July, 02 August, 18 August, and 03 September and these events were associated with periods where $W < 1$ in Lake Beverley (Fig. 8C). The Wood River did not always indicate upwelling even on a few occasions when W was < 1 for upstream Lake Aleknagik (e.g., 18 August, Fig. 8D). In comparison, Little Togiak Lake (lake area = 8.9 km^2), a much smaller lake than Beverley or Aleknagik, showed stable river temperatures, supported by conditions where upwelling was unlikely to occur in August and September (Fig. 8E).

Discussion

We observed that rivers draining large lakes are more thermally variable than rivers and streams without upstream lakes. Day to day thermal dynamics in rivers appeared to be associated with episodic upwelling of cool hypolimnetic water in large upstream lakes, which episodically destabilize river thermal regimes. We speculate that upwelling may be a common source of thermal variation during stratification in

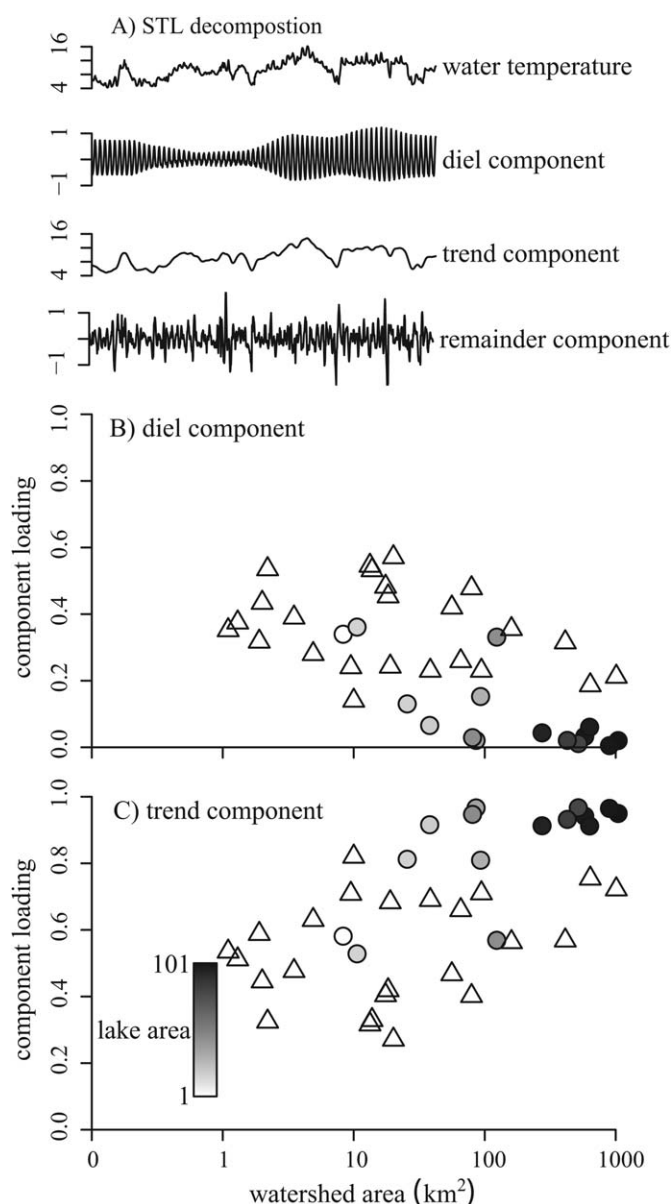


Fig. 7. (A) Example of seasonal trend decomposition of a temperature time series into the diel, trend, and remainder components. (B) “diel,” and (C) “trend” component contribution to stream thermal regimes. Streams and rivers draining lakes as open circles and shaded as a function of their size. Streams lacking lakes are the open triangles.

temperate river drainages that contain large lakes as part of the river system. Given the magnitude and frequency of such thermal variation associated with upwelling events we postulate that this variation imposes novel but undescribed perturbations to lotic habitats downstream of large lakes.

Our results contribute to evolving conceptual models describing how geomorphic characteristics of river basins translate into variation in water temperatures across landscapes. This study confirms much of what is described by Vannote et al. (1980) for watersheds lacking large lakes.

Headwater streams draining small watersheds displayed less thermal variation than intermediate sized streams. Large higher order rivers did appear to show less diel variation relative to intermediate sized streams, likely as they are buffered by more thermal mass (Ross 1963). However, our results provide an interesting contrast when considering the potential effects of lakes on stream temperature regimes. We found that large lakes are prone to instabilities in their thermal stratification where upwelling of hypolimnetic water can have effects on the thermal regimes of rivers that drain them (Fig. 1).

We were limited in the extent to which we were able to quantify the association between watershed size and thermal variation in this landscape. The river drainages we sampled are many times smaller than the watersheds that river ecologists would consider “large” (e.g., Columbia, Amazon). Yet, watersheds that we considered large contained lakes that were 10–101 km² which represent approximately the upper 0.01% of world lakes. Consequently, this also illustrates that upwelling events are probably an uncommon phenomenon in many river drainages that contain only small lakes that are much less than 1 km² (Downing et al. 2006). Many of these temperature recorders were positioned within 2–3 km of the lake outlet and the lake effect of upwelling is likely dissipated further downstream (Jones 2010), but was not quantified here.

Here, we considered lake size as general descriptor of the sensitivity of lake thermal structure to wind action and, therefore, the tendency of a lake to upwell deep water to the river outlet. Other physical features that describe a lake’s morphology such as lake depth, articulation, bathymetry, watershed topography, orientation relative to prevailing wind direction, and outlet position may also produce additional constraints on the potential for a lake to upwell deep water to the outlet. Although some of our study lakes varied in terms of the orientation and outlet position, all the large lakes > 10 km² appeared to be susceptible to wind and some degree of upwelling. We also did not observe repeat upwelling when the lake thermocline seichid; rather, upwelling occurred only during the initial tilt of the thermocline during the maximum wind speeds. It is possible that upwelling may have occurred on the first deflection of the thermocline if the outlet was positioned in the direction of the wind or during the initial tilt of the thermocline in the opposite direction of the wind after the wind subsides.

Wind is known as a potential factor controlling stream temperatures but often the mechanisms are unclear. Stream surfaces are positioned low in river valleys and, therefore, protected from wind by riparian vegetation or high channel stream banks (Poole and Berman 2001; Caissie 2006). Therefore, wind is thought to contribute less to the thermal variability in streams relative to other drivers such as air temperature, irradiance, and precipitation. Cooler air temperatures, lower light conditions, and precipitation

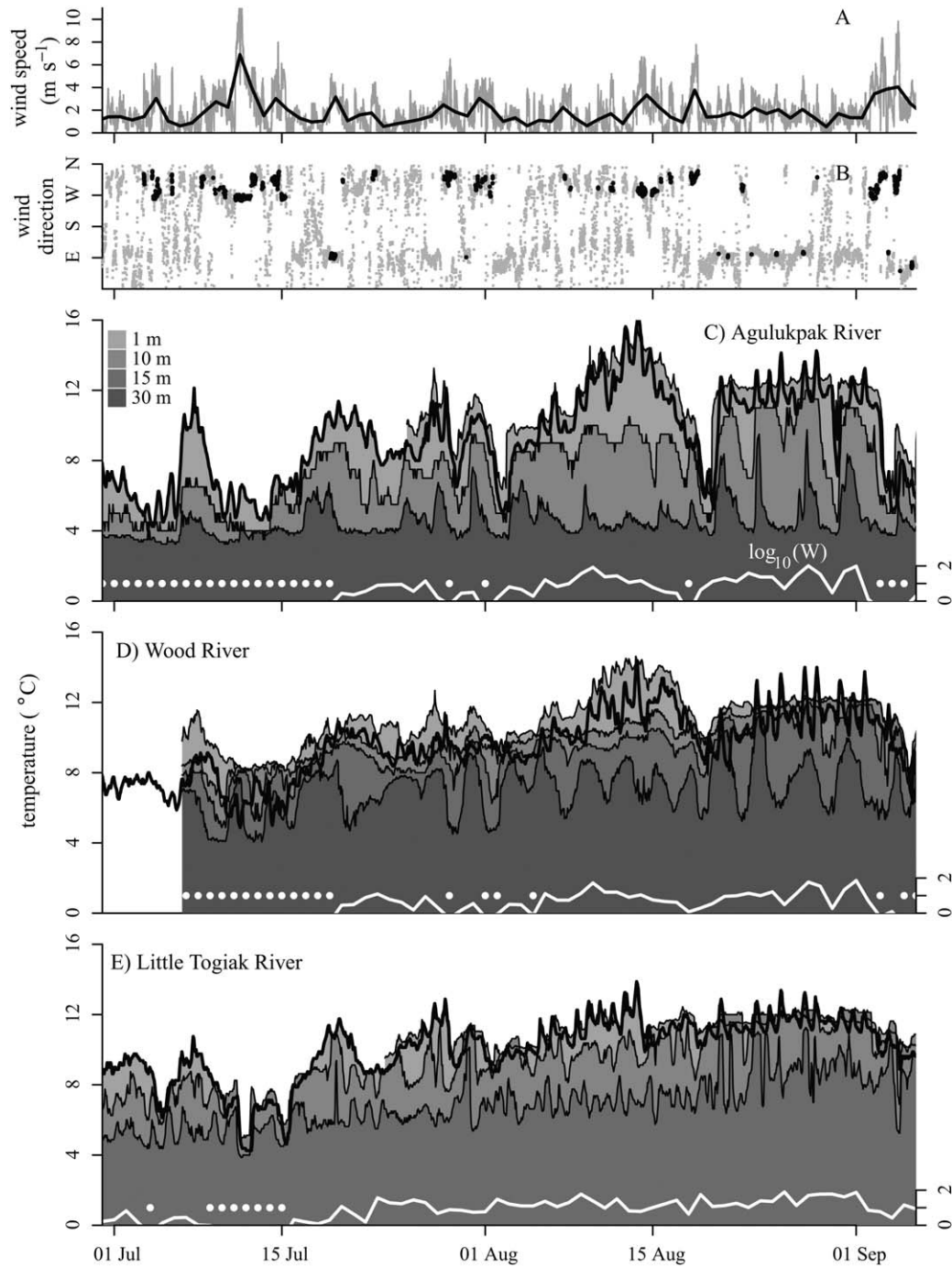


Fig. 8. (A) Hourly wind speed m s^{-1} (gray line) and the daily average (black line). (B) Hourly direction of winds $> 4 \text{ m s}^{-1}$ (dark points) and $< 4 \text{ m s}^{-1}$ (gray points). (C-E) River thermal regimes of the (C) Agulupak River, (D) Wood River, and (E) Little Togiak River as the dark solid line and each of their upstream lake temperatures from vertical arrays in each lake. Polygon color corresponds to water temperatures at different depths. White line indicates $\log_{10}(W)$ for each upstream lake, where upwelling may be possible during wind events when $W < 1$, as indicated with white dots above this line.

associated with low pressure weather likely cooled some of the streams in the Wood River basin but with only marginal effects on the surface temperature of lakes. Here, we found that upstream lakes integrate through diel scale thermal variation due to their large thermal mass compared to fluctuations found

in nearby shallow streams and rivers without lakes. In addition, our analyses suggest upwelling of hypolimnetic water to river outlets following wind events. Taken together, our analyses suggest that wind events cool rivers through upwelling rather than via radiative heat loss during inclement weather.

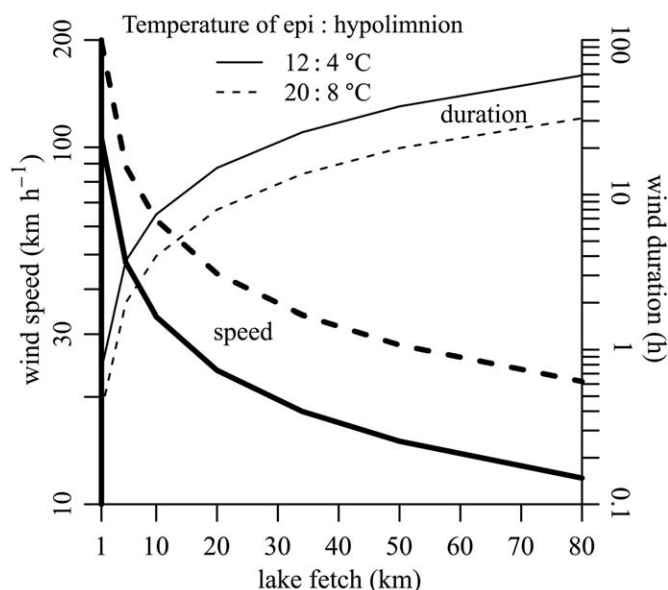


Fig. 9. Wind speed m s^{-1} and duration of wind expected by the Wedderburn number for upwelling to occur (e.g., $W = 1$) across a range in lake fetch (1–80 km). Epilimnetic to hypolimnetic temperatures of 12°C and 4°C, respectively, (solid lines) represent thermal conditions in this study region, while 20°C and 8°C represent conditions typical of warmer freshwater lakes in temperate climates (dashed lines).

To better describe potential upwelling events elsewhere over a range of lake sizes, we provide a conceptual figure of the wind speed (m s^{-1}) and wind duration (h) necessary to produce as determined by $W = 1$ (Fig. 9). For simplicity, we assumed that all lakes (fetch length 1 km to 80 km) have a 15-m-deep epilimnion that is 12°C and 4°C hypolimnion. For contrast with thermal conditions of lakes in warmer temperate climates, we compared wind speed and wind duration needed for upwelling in lakes characterized by epilimnetic and hypolimnetic temperatures of 20°C and 8°C, respectively. Notably, much stronger winds (100–200 km h^{-1}) are necessary for upwelling to occur on short one kilometer lakes compared to lakes with longer fetches. Wind speeds of 12–40 km h^{-1} are necessary to produce conditions where $W = 1$ on lakes with fetches > 20 km (Fig. 9). Stronger winds are necessary for upwelling to occur on warmer temperate lakes, where density differences between the epilimnion and hypolimnion are greater. However, the duration of the wind necessary for upwelling is a function of the seiche period, which is shorter on smaller lakes and also shorter where thermal density differences between the epilimnion and hypolimnion are greater. This theoretical model provides a simple conceptual tool for understanding under what conditions upwelling may occur over a range of lake sizes.

We speculate that lake upwelling may have important ecological consequences for lotic communities. At present, we know of no research that has assessed the ecological effects of abrupt changes in river temperatures associated

with abrupt wind-driven drops in river temperature. In addition to destabilizing river thermal regimes, lake upwelling could also provide rivers with a midsummer pulse of hypolimnetic water, rich in nutrients that may benefit primary producers downstream. Stratified lakes often have large differences in nutrients and dissolved oxygen above and below the thermocline. Nutrient-rich hypolimnetic water has the potential to support benthic production during upwelling or mixing events (MacIntyre and Flynn 1999). Alternatively, larger eutrophic lakes may develop periods of stressful or lethal oxygen conditions for fish and other aquatic animals because anoxic conditions can occur in the hypolimnion of stratified eutrophic lakes. For example, an upwelling event on a culturally eutrophic lake (Onondaga Lake, New York) produced surface oxygen concentrations < 1 mg L^{-1} at the lake end, where typically they are 10 mg L^{-1} , creating “rotten egg” smell from upwelling of H_2S and juvenile fish kills (Effler et al. 2004). At this point, we have a limited understanding of how upwelling dynamics of lakes influence the community ecology of downstream rivers, but presume they may be more important than is currently appreciated.

Across southwest Alaska the majority of rivers drainages contain lakes that are large enough to be susceptible to upwelling given their size, length, and outlet position near the end of the lake at the terminal moraine (e.g., lakes Iliamna, Becharof, Ugashik, Naknek, Nonvianuk, Kukaklek, and Ualik in addition to those lakes studied here). These river drainages, in addition to the study rivers, also support high quality spawning habitat for sockeye salmon (*Oncorhynchus nerka*) which support a lucrative commercial fishery, and recreational fisheries for rainbow trout (*Oncorhynchus mykiss*) and other resident freshwater fishes. In this study, the Agulukpak River alone annually supports over 100,000 spawning sockeye salmon in less than 1.3 km of river length (University of Washington, Alaska Salmon Program, unpubl. data). In addition, the Agulukpak River receives ~ 700–1500 angler days per year with each visitor paying several thousand dollars per week of fishing (Dye and Schwanke 2009). Local sport fishing guides acknowledge that large wind storms create unfavorable fishing conditions for rainbow trout for 1–3 d following a storm and they speculate that poor fishing conditions may be related to stressful conditions induced by rapid fluctuations in river temperatures. The physiological and ecological basis for these observations remains unresolved.

Conceptual models of thermal regimes in rivers often focus on describing changes to seasonal averages and lethal limits to specific organisms rather than the conditions that maintain natural thermal variability in streams and rivers. However, increasing evidence suggests that the temporal variation that is characteristic of natural thermal regimes is equally important to the health of fluvial ecosystems and aquatic ectothermic species (Olden and Naiman 2010; Steel et al. 2012; Vasseur et al. 2014). Our data reveal how lakes as

features within landscapes generate thermal variation in rivers through wind action and upwelling, but the effect may only be characteristic of rivers with larger lakes. Such variation highlights the unique complexity of river systems with natural lakes, with perhaps unappreciated ecological significance.

References

- Allan, D. M., and M. M. Castillo. 2007. Stream ecology: Structure and function of running waters, 2nd ed. Springer.
- Arp, C. D., J. C. Schmidt, M. A. Baker, and A. K. Myers. 2007. Stream geomorphology in a mountain lake district: Hydraulic geometry, sediment sources and sinks, and downstream lake effects. *Earth Surf. Process. Landforms* **32**: 525–543. doi:10.1002/esp.1421
- Benda, L., N. Poff, D. Miller, T. Dunne, and G. Reeves. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. *Bioscience* **54**: 413–427. doi:10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789. doi:10.1890/03-9000
- Caissie, D. 2006. The thermal regime of rivers: A review. *Freshw. Biol.* **51**: 1389–1406. doi:10.1111/j.1365-2427.2006.01597.x
- Cleveland, R. B., W. S. Cleveland, J. E. McRae, and I. Terpenning. 1990. STL: A seasonal-trend decomposition procedure based on loess. *J. Off. Stat.* **6**: 3–73.
- Degerman, E., and B. Sers. 1994. The effect of lakes on the stream fish fauna. *Ecol. Freshw. Fish* **3**: 116–122. doi:10.1111/j.1600-0633.1994.tb00113.x
- Dorava, J. M., and A. M. Milner. 2000. Role of lake regulation on glacier-fed rivers in enhancing salmon productivity: The Cook Inlet watershed, south-central Alaska, USA. *Hydrol. Process.* **14**: 3149–3159. doi:10.1002/1099-1085(200011/12)14:16/17<3149::AID-HYP139>3.0.CO;2-Y
- Downing, J. A., and others. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* **51**: 2388–2397. doi:10.4319/lo.2006.51.5.2388
- Dye, J. E., and C. J. Schwanke. 2009. Report to the Alaska Board of Fisheries for the recreational fisheries of Bristol Bay, 2007, 2008, and 2009. Alaska Department of Fish and Game. Special Publication No. 09-14.
- Effler, S. W., B. A. Wagner, and S. M. O'Donnell. 2004. An upwelling event at Onondaga Lake, NY: Characterization, impact and recurrence. *Hydrobiologia* **511**: 185–199. doi:10.1023/B:HYDR.0000014040.88372.82
- Fellman, J. B., S. Nagorski, S. Pyare, A. W. Vermilyea, D. Scott, and E. Hood. 2014. Stream temperature response to variable glacier coverage in coastal watersheds of Southeast Alaska. *Hydrol. Process.* **28**: 2062–2073. doi:10.1002/hyp.9742
- Frissell, C., W. Liss, C. Warren, and M. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environ. Manage.* **10**: 199–214. doi:10.1007/BF01867358
- Jones, N. E. 2010. Incorporating lakes within the river discontinuum: Longitudinal changes in ecological characteristics in stream–lake networks. *Can. J. Fish. Aquat. Sci.* **67**: 1350–1362. doi:10.1139/F10-142
- Kling, G. W., G. W. Kipphut, M. M. Miller, and W. J. O'Brien. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. *Freshw. Biol.* **43**: 477–497. doi:10.1046/j.1365-2427.2000.00515.x
- Laval, B. E., and others. 2008. Wind-driven summertime upwelling in a fjord-type lake and its impact on downstream river conditions: Quesnel Lake and river, British Columbia, Canada. *J. Great Lakes Res.* **34**: 189–203. doi:10.3394/0380-1330(2008)34[189:WSUIAF]2.0.CO;2
- MacIntyre, S., and K. Flynn. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. *Limnol. Oceanogr.* **44**: 512–529. doi:10.4319/lo.1999.44.3.0512
- Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. *Environ. Conserv.* **29**: 134–153. doi:10.1017/S0376892902000097
- Marcarelli, A. M., and W. A. Wurtsbaugh. 2007. Effects of upstream lakes and nutrient limitation on periphytic biomass and nitrogen fixation in oligotrophic, subalpine streams. *Freshw. Biol.* **52**: 2211–2225. doi:10.1111/j.1365-2427.2007.01851.x
- Mellina, E., R. D. Moore, S. G. Hinch, J. S. Macdonald, and G. Pearson. 2003. Stream temperature responses to clear-cut logging in British Columbia: The moderating influences of groundwater and headwater lakes. *Can. J. Aquat. Fish. Sci.* **59**: 1886–1900. doi:10.1139/f02-158
- Monismith, S. 1986. An experimental study of the upwelling response of stratified reservoirs to surface shear stress. *J. Fluid Mech.* **171**: 407–439. doi:10.1017/S0022112086001507
- Olden, J. D., and R. J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater ecosystem integrity. *Freshw. Biol.* **55**: 86–107. doi:10.1111/j.1365-2427.2009.02179.x
- Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. *Environ. Manage.* **27**: 787–802. doi:10.1007/s002670010188
- R Development Core Team. 2011. R: A language and environment for statistical computing. R foundation for statistical computing, version 3.1.1. Vienna, Austria.
- Robinson, C. T., and G. W. Minshall. 1990. Longitudinal development of macroinvertebrate communities below oligotrophic lake outlets. *Great Basin Nat.* **50**: 303–311.
- Ross, H. H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* **59**: 235–242.
- Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey. 2005. Effects of changing climate on zooplankton

- and juvenile sockeye growth in southwestern Alaska. *Ecology* **86**: 198–209. doi:[10.1890/03-0408](https://doi.org/10.1890/03-0408)
- Shintani, T., A. de la Fuente, Y. Niño, and J. Imberger. 2010. Generalizations of the Wedderburn number: Parameterizing upwelling in stratified lakes. *Limnol. Oceanogr.* **55**: 1377–1389. doi:[10.4319/lo.2010.55.3.1377](https://doi.org/10.4319/lo.2010.55.3.1377)
- Steel, E., A. Tillotson, and D. Larsen. 2012. Beyond the mean: The role of variability in predicting ecological effects of stream temperature on salmon. *Ecosphere* **3**: 1–11. doi:[10.1890/ES12-00255.1](https://doi.org/10.1890/ES12-00255.1)
- Stevens, C. L., and G. A. Lawrence. 1997. Estimation of wind-forced internal seiche amplitudes in lakes and reservoirs, with data from British Columbia, Canada. *Aquat. Sci.* **59**: 115–134. doi:[10.1007/BF02523176](https://doi.org/10.1007/BF02523176)
- Stockner, J. G., E. Rydin, and P. Hyenstrand. 2000. Cultural oligotrophication: Causes and consequences for fisheries resources. *Fisheries* **25**: 7–14. doi:[10.1577/1548-8446\(2000\)025<0007:CO>2.0.CO;2](https://doi.org/10.1577/1548-8446(2000)025<0007:CO>2.0.CO;2)
- Thompson, R.O.R.Y., and J. Imberger. 1980. Response of a numerical model of a stratified lake to wind stress. *Proc. Int. Symp. Stratif. Flows* **2**: 562–570.
- Vannote, R. L., W. G. Minshall, K. W. Cummings, J. R. Sedel, and C. E. Cushing. 1980. The River Continuum Concept. *Can. J. Aquat. Fish. Sci.* **37**: 130–137. doi:[10.1139/f80-017](https://doi.org/10.1139/f80-017)
- Vasseur, D. A., and others. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B Biol. Sci.* **281**: 1–8. doi:[10.1098/rspb.2013.2612](https://doi.org/10.1098/rspb.2013.2612)
- Ward, J. V., and J. A. Stanford. 1983. Serial discontinuity concept of lotic ecosystems, p. 29–42. In T. D. Fontain III and S. M. Bartell [eds.], *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers.
- Wedderburn, E. M. 1912. Temperature observations in Loch Earn; with further contribution to the hydrodynamical theory of temperature oscillations. *Trans. R. Soc. Edinburgh* **48**: 629–695. doi:[10.1017/S0080456800015842](https://doi.org/10.1017/S0080456800015842)
- Wetzel, R. G. 2001. *Limnology: Lake and river ecosystems*, 3rd ed. Academic Press.

Acknowledgments

This work is a contributed effort from the Western Alaska Landscape Conservation Cooperative (WALCC) and the University of Washington - Alaska Salmon Program. We are grateful for the field and data provided through collaborations with Michael Swaim and Patrick Walsh with the US Fish and Wildlife at the Togiak Wildlife Refuge, and Ben Jones with US Geological Survey. We also thank the Wood-Tikchik State Park for enabling our field research.

Financial support was provided by the WALCC and the Gordon and Betty Moore Foundation, the National Science Foundation, the Harriet Bullitt Professorship, and the Alaska salmon processing industry. The first author was supported by the National Science Foundation Graduate Research Fellowship grant number DGE-0718124.

Submitted 6 June 2014

Revised 6 October 2014

Accepted 2 October 2014

Associate editor: Alexander D. Huryn