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RESEARCH PAPER

Evaluating species-specific changes in hydrologic regimes: an iterative approach for salmonids in the Greater Yellowstone Area (USA)

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Abstract Despite the importance of hydrologic regimes to the phenology, demography, and abundance of fishes such as salmonids, there have been surprisingly few syntheses that holistically assess regional, species-specific trends in hydrologic regimes within a framework of climate change. Here, we consider hydrologic regimes within the Greater Yellowstone Area in the Rocky Mountains of western North America to evaluate changes in hydrologic metrics anticipated to affect salmonids, a group of fishes with high regional ecological and socioeconomic value. Our analyses assessed trends across different sites and time periods (1930–, 1950–, and 1970–2015) as means to evaluate spatial and temporal shifts. Consistent patterns emerged from our analyses indicating substantial shifts to (1) earlier peak discharge events; (2) reductions of summer minimum streamflows; (3) declines in the duration of river ice; and (4) decreases in total volume of water. We found accelerated trends in hydrologic change for the 1970–2015 period, with an average peak discharge 7.5 days earlier, 27.5% decline in summer minimum streamflows, and a 15.6% decline in the annual total volume of water (1 October–September 30) across sites. We did observe considerable variability in magnitude of change across sites, suggesting different levels of vulnerability to a changing climate. Our analyses provide an iterative means for assessing climate predictions and an important step in identifying the climate resilience of landscapes.

Keywords Climate change · Hydrologic regimes · Trout · Vulnerability

Introduction

Hydrologic regimes act as a template for biological processes and a filter for the composition of aquatic communities (Poff et al. 1997; Poff and Ward 1989). For riverine fishes, the timing and magnitude of discharge directly affect behavioral and life-history patterns (Mims and Olden 2012; Schlosser 1985) while also serving as a strong control on abundance and demographic rates (e.g., Gido and Propst 2012;

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Kiernan et al. 2012). Projected shifts in global and regional climatic conditions are anticipated to significantly alter air temperature, precipitation (IPCC 2014) and consequently, the hydrologic regimes of stream networks rendering a variety of consequences to species and populations (Kingsford 2011; Pittock et al. 2008). Shifts in climate coupled with concomitant rises in human demands for water consumption (McDonald et al. 2011; Vorosmarty et al. 2000) suggest considerable challenges in the future conservation and management of fishes.

For the Rocky Mountains in the western United States, recent changes in air temperatures (Pederson et al. 2010; Sepulveda et al. 2015) and precipitation (Mote 2003; Pederson et al. 2011) have led to well documented changes in snowmelt and runoff patterns. The predicted effects of future changes in climate (Westerling et al. 2011) include shifts to an earlier date of runoff, reduced and prolonged periods of baseflow conditions, and increases in the frequency and magnitude of winter floods (Goode et al. 2012; Leppi et al. 2012; Luce et al. 2013). Such predictions may have serious consequences for salmonids, a socioeconomically and ecologically important group of fishes in this region (Gresswell and Liss 1995; Wengeler et al. 2010) whose phenology, recruitment, growth, and survival are strongly tied with streamflow and stream temperature regimes (Bjornn 1971; Isaak et al. 2012; Kovach et al. 2016). For example, increases in winter flooding events can scour redds and wash out early life-stage juveniles (Goode et al. 2013), while decreases in summer base flow conditions can limit foraging opportunities (Uthe et al. in review). Furthermore, altered hydrologic regimes can have indirect consequences through differential responses across trophic levels and potential shifts to conditions more favorable to invasive species and pathogens (Rahel and Olden 2008). Holistically understanding how hydrologic regimes have and are likely to change is an important step in considering species and population vulnerability under a changing climate.

For montane regions, such challenges are likely to be varied as the realized effects of altered climatic patterns will be moderated by regional, topographic, and local controls (Aldous et al. 2011; McGlynn et al. 2004). For example, Thorne and Woo (2011) found considerable deviations in local hydrologic regimes within a single, montane basin. Understanding the hydrologic resilience of montane regions and the portfolio of such resilience is critical for successful conservation and planning of water resources.

Numerous studies have examined large-scale patterns of hydrologic shifts related to altered temperature and precipitation regimes over the past century (Hamlet and Lettenmaier 2007; Stewart et al. 2004). However, few have examined within-region variability of hydrologic trends particularly as they relate to specific groups of organisms (sensu Poff and Allan 1995), making it difficult to understand fisheries-relevant changes in hydrology at a scale relevant to managers.

Quantifying changes in hydrology is particularly relevant for freshwater salmonids given the widespread distribution of this group worldwide (Budy et al. 2013; Halverson 2010) and ecological and recreational importance of this group of fishes (e.g., Almodovar and Nicola 2004; Simon and Townsend 2003). Here, we consider regional and temporal trends in hydrologic regimes that are likely to affect salmonids within the Greater Yellowstone Area (GYA) in the Rocky Mountains of western North America. Salmonids such as Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* represent a critical food resource for dozens of avian and terrestrial species within the GYA (e.g., grizzly bear, *Ursus arctus*; Stapp and Hayward 2002). Salmonids also represent a substantial economic resource in the region—revenue from angling in Yellowstone National Park alone is valued at well over $50 million per year (Kerkvliet and Nowell 2000).

A concern for salmonids in the GYA stems from the increasing seasonal air temperatures over the past century (Supplemental Fig. 1; Sepulveda et al. 2015) and the linkages between warming climate and shifting hydrologic regimes (Clow 2010; Mote 2003). Within this framework, it remains critical to understand the how trends in hydrology are changing through time, particularly given the periodic shifts in climate (Hamlet et al. 2005) and the need for contemporary measures of change that aligns with current management and conservation strategies. Our specific objectives were to evaluate (1) temporal trends in discharge metrics relevant to salmonids and specifically identify which metrics have demonstrated the greatest changes; (2) the variability in long-term trends among metrics and across locations; and (3) how period of record complicates interpretations of change and variability. The growing concerns of climatic change on salmonid populations (Comte et al.

2013; Isaak et al. 2012; Jonsson and Jonsson 2009; Kovach et al. 2016) signifies the importance of our results in enhancing our understanding of the effects of climate change.

Materials and methods

Study area

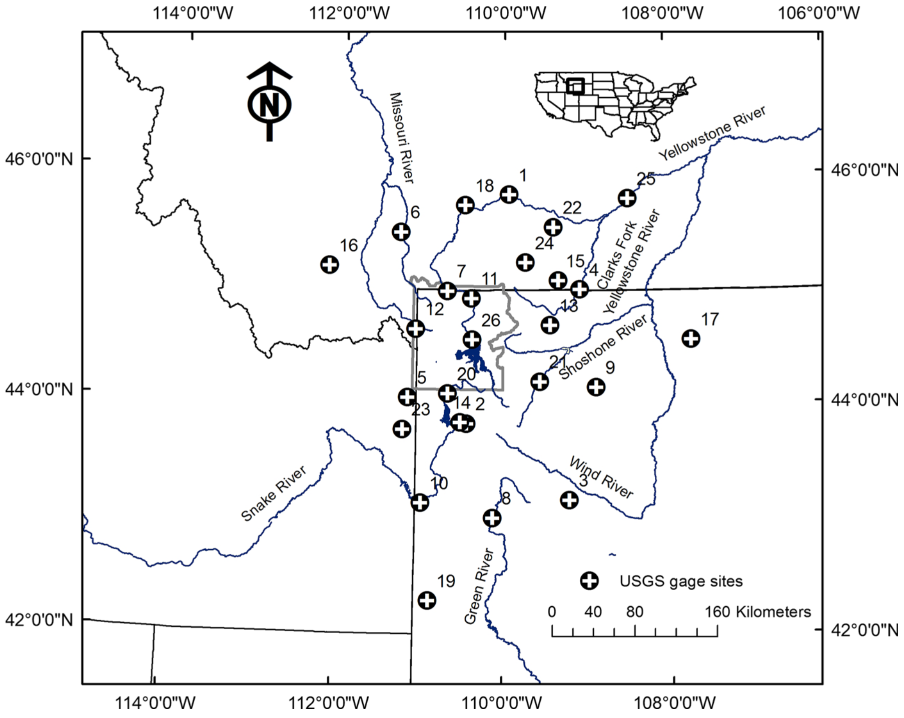
Our study included existing stream gaging stations within the GYA, a region that is a major headwater source of water for the Colorado, Missouri, and Snake Rivers and large portions of the western United States (Fig. 1). The GYA encompasses a vast expanse of over 20 million acres and spreads over portions of Montana, Wyoming, Idaho, and Utah, USA. The GYA covers large portions of public land including Yellowstone and Grand Teton national parks, and is considered one of the last great intact ecosystems within the mid-latitudes of North America (Noss et al. 2002). The region has considerable topographic complexity spanning elevations from 800 m to over 3300 m and vegetation types vary from low-elevation, arid grassland and shrub communities to high-elevation, alpine tundra. The range of elevations within the GYA results in considerable variability in climate throughout the year and across the region (Sepulveda et al. 2015; Tercek et al. 2012), but is generally characterized by cold, winter months and warm to hot summer months.

We considered all existing stream gage locations with the GYA and surrounding landscapes where continuous stream gage records were available. We limited our analyses to those sites without major impoundments and/or water withdrawals upstream of the gage. We then constrained our analyses to those sites with datasets spanning back to at least 1970 (see below).

Streamflow metrics

We summarized streamflow data from each gage station to evaluate trends in four metrics relevant to salmonids that are considered likely consequences of climate change for this region. First, we calculated the date of peak discharge ($\mathrm{Date}_{\mathrm{peakQ}}$), here converted to year–day, given the strong linkages between native cutthroat trout and non-native rainbow trout (*O. mykiss*) spawning patterns (Muhlfeld et al. 2009). The earlier peak discharge events are expected as a result of shifts in warming during the spring months, which has been documented for much of the region (Sepulveda et al. 2015; Stewart et al. 2005).

Fig. 1 A map of the study area with circled crosses indicating the location of sites within the Greater Yellowstone Area, USA. *Inset* map and *box* outlines location within the Rocky Mountains and numbers refer to Site ID for cross referencing site names in Table 1



Earlier spring freshets coupled with warming summer temperatures are expected to increase the magnitude and duration of summer, low discharge periods (Rood et al. 2008). A concern for salmonids is the strong negative effects of low stream flows on growth and survival (Kovach et al. 2016; Xu et al. 2010a), particularly as stream temperatures increase during the summer. Here, we quantified the minimum 7-day moving average of daily flows during the summer (June 21 to September 21; 7-day Min) as indication of the magnitude of drought.

Anticipated warming during the winter is expected to increase the frequency of rain-on-snow and high discharge events and thus limit recruitment for salmonids that spawn during the fall and winter by destroying spawning nests (i.e., redds) and eggs (Tonina et al. 2008; Weber et al. 2013). We evaluated temporal trends in winter high discharge events by summing the number of days above the 90th percentile (recent decade, 2001–2010) of winter flows (November–March; W_{90}) each year (Wenger et al. 2011b).

Next, we considered trends in ice cover. While climate change is likely to affect patterns of river ice (Prowse and Beltaos 2002), the majority of existing research related to ice cover and climate change has focused on lentic habitat (Rahel and Olden 2008), where the onset of ice establishment and break up have changed considerably (Winder and Schindler 2004). However, ice can be an important factor controlling native and invasive fish distributions in lotic habitats (Brown et al. 2011; Weber et al. 2013). At each gaging station, we quantified temporal trends as the number of days per year with ice ($\mathrm{Days}_{\mathrm{ice}}$).

In addition to these four metrics, we also considered annual trends in total volume for each water year (1 October–September 30; $\mathrm{Total}_{\mathrm{Q}}$). While total volume may not be directly tied to salmonid phenology or life-history stages, we considered trends in total volume as (1) a baseline measure of change in precipitation and runoff and (2) an indicator of potential conflict between fish and human water needs, given the agricultural and municipal demands for water in areas downstream of the GYA (e.g., Christensen et al. 2004). Changes in total volume will have indirect effects on fisheries as human demand for water in areas of decreasing trends are likely to increase the potential for water conflicts and stressful aquatic conditions.

Analyses

For metrics where data were available since 1930 (i.e., $\mathrm{Date}_{\mathrm{peakQ}}$, 7-day Min, W_{90}, and $\mathrm{Total}_{\mathrm{Q}}$), we delineated our dataset into three separate time periods to assess how trends are influenced by period of record. We considered sites with available data from 1930 to 2015, 1950 to 2015, and 1970 to 2015 for each of our analyses as these ranges of data span substantially different climatic periods (e.g., Pacific Decadal Oscillation; Graumlich et al. 2003). Analyses beginning in 1930 (hereafter 1930_{POR}) provide a means to evaluate contemporary patterns in the context of historical climate anomalies (i.e., the “Dust Bowl”; Donat et al. 2016). Next, we evaluated trends beginning in the 1950s (hereafter 1950_{POR}), given this was a period of relatively cool climate and a range consistent with numerous climate analyses—largely due to the initiation of data collection at many U.S Geological Survey (USGS) gaging stations (Leppi et al. 2012). In addition, we considered trend analyses beginning in 1970 (hereafter 1970_{POR}) as indications of recent hydrologic patterns, which matches the period of most rapid climatic change (Pederson et al. 2011) and is likely more tangible to present fish and water managers. Finally, our analyses considering the temporal trends of $\mathrm{Days}_{\mathrm{ice}}$ were constrained to the period of data availability (1988–2015).

We initially calculated Pearson correlation coefficients to quantify similarities in temporal patterns across sites and periods of record. To evaluate temporal trends, we demarcated the streamflow metrics into attributes describing anomalous and average conditions. Our anomalous metric included W_{90} while average conditions included 7-day Min, $\mathrm{Date}_{\mathrm{peakQ}}$, and $\mathrm{Days}_{\mathrm{ice}}$, and $\mathrm{Total}_{\mathrm{Q}}$. For W_{90} we used quantile regression (Cade and Noon 2003) to quantify temporal trends in the magnitude of rare winter floods using the 90th percentiles. Here, we conducted separate quantile regression analyses for each site with year-specific measures of W_{90} as the response year as the independent variable. For average conditions we used generalized linear models (GLM). For analyses of annual $\mathrm{Total}_{\mathrm{Q}}$, we standardized values at each sites (z-score) to allow for comparisons of trend estimates (i.e., beta estimates) across sites; all other estimates of trend were comparable across sites. For each metric, we conducted a separate linear regression analysis for each site to test for trends as a function of year and tested for violations of model assumptions and evidence of temporal autocorrelation

Table 1 Site ID (see Fig. 1), station identification (StationID), elevation, latitude, and longitude for U.S. Geological Survey stream gages (sites) in the Greater Yellowstone Area, USA

Site ID	Site	StationID	Elevation (m)	Drainage area (km^2)	Latitude	Longitude
1	Boulder River	06200000	1236	1360	45.834	−109.939
2	Buffalo Fork	13011900	2064	837	43.838	−110.441
3	Bull Lake Creek	06224000	1790	484	43.177	−109.203
4	Clarks Fork Yellowstone River	06207500	1215	2984	45.009	−109.065
5	Falls River	13046995	1762	837	44.062	−111.152
6	Gallatin River	06043500	1575	2121	45.497	−111.271
7	Gardner River	06191000	1714	513	44.990	−110.690
8	Green River	09188500	2276	1212	43.019	−110.119
9	Greybull River	06276500	1749	1764	44.159	−108.873
10	Greys River	13022500	1746	1160	43.143	−110.977
11	Lamar River	06188000	1831	1730	44.928	−110.394
12	Madison River	06037500	2027	1127	44.656	−111.068
13	North Fork Shoshone River	06279940	1701	1810	44.697	−109.430
14	Pacific Creek	13011500	2048	438	43.850	−110.518
15	Rock Creek	06209500	1951	272	45.086	−109.329
16	Ruby River	06019500	1645	1383	45.192	−112.143
17	Shell Creek	06278300	1332	60	44.566	−107.712
18	Shields River	06195600	1347	2191	45.738	−110.479
19	Smiths Fork	10032000	2027	427	42.293	−110.872
20	Snake River	13010065	2073	1259	44.098	−110.668
21	South Fork Shoshone River	06280300	1890	769	44.208	−109.555
22	Stillwater River	06205000	1203	2528	45.551	−109.388
23	Teton River	13052200	1814	873	43.782	−111.209
24	West Rosebud Creek	06204050	1992	138	45.243	−109.731
25	Yellowstone River-Billings	06214500	939	30,580	45.800	−108.468
26	Yellowstone River–Yellowstone Lake	06186500	2355	2577	44.567	−110.380

of the residuals. All analyses were conducted in R (MASS and quantreg packages; R Development Core Team 2012). Given the high interannual variability in streamflow patterns (Stewart et al. 2005) and the strong influence of hydrology on salmonids (Kovach et al. 2016), we used an alpha value of 0.10 to test for significance and minimize the chance of Type II errors (Table 1).

Results

Date of peak discharge (Date$_{\text{peakQ}}$)

Correlations in the annual date of peak discharge (Date$_{\text{peakQ}}$) across sites varied considerably by period of record with the highest correlations for the 1930$_{\text{POR}}$ (average $r = 0.64$, range 0.51–0.82) and the lowest from the 1970$_{\text{POR}}$ (average $r = 0.47$, range −0.39 to 0.94). Regardless of time period, parameter estimates of trends in Date$_{\text{peakQ}}$ were negative (i.e., earlier date of peak discharge) in all but five locations and time periods (Table 2).

The magnitude and significance of trends of Date$_{\text{peakQ}}$ varied by time period and location but we found no evidence of change for 1930$_{\text{POR}}$ (average slope $= -0.057$, SD $= 0.021$). For gage sites with data common to all three periods of record, we found increasingly negative slopes (average 1930$_{\text{POR}} = -0.058$, 1950$_{\text{POR}} = -0.123$, and 1970$_{\text{POR}} = -0.173$) but also increased variability across sites (SD 1930$_{\text{POR}} = 0.021$, 1950$_{\text{POR}} = 0.031$, and 1970$_{\text{POR}} = 0.069$). When all available sites per period of record were included, we found increasingly negative slope estimates for the

Table 2 Slope estimates (SE) from linear regression models of the changes in date of peak discharge (negative = earlier in the year) and quantile regression (90th percentile) for the number of days exceeding the 90th percentile of winter flows across sites (Site ID; Table 1; Fig. 1) and three time periods in the Greater Yellowstone Area, USA ("-" indicates missing values resulted in omission from analyses)

Period	Site (ID)	Date peak discharge		Days exceeding 90th percentile of winter flows	
		Slope (SE)	*P*	Slope (SE)	*P*
1930–2015	Clarks Fork Yellowstone R. (4)	−0.086 (0.053)	0.106	0.370 (0.452)	0.414
	Gallatin R. (6)	−0.036 (0.054)	0.514	−0.500 (0.400)	0.215
	Green R. (8)	−0.073 (0.063)	0.253	0.000 (0.198)	1.000
	Yellowstone R.-Billings (26)	−0.057 (0.047)	0.230	0.396 (0.303)	0.194
	Yellowstone R.-Yellow. Lake (27)	−0.040 (0.042)	0.343	0.952 (0.433)	0.031
1950–2015	Boulder R. (1)	−0.065 (0.078)	0.406	–	–
	Clarks Fork Yellowstone R. (4)	−0.164 (0.077)	0.037	0.500 (0.673)	0.461
	Gallatin R. (6)	−0.118 (0.077)	0.130	−0.800 (0.371)	0.035
	Green R. (8)	−0.138 (0.091)	0.135	0.000 (0.320)	1.000
	Greys R. (10)	−0.025 (0.075)	0.735	0.857 (0.910)	0.350
	Pacific Creek (14)	−0.224 (0.078)	0.006	−0.353 (0.692)	0.612
	Smiths Fork (19)	−0.062 (0.089)	0.491	0.196 (0.709)	0.783
	Stillwater R. (22)	0.017 (0.075)	0.822	0.560 (0.549)	0.312
	Yellowstone R.-Billings (25)	−0.080 (0.072)	0.266	−0.111 (0.424)	0.794
	Yellowstone R.-Yellow. Lake (26)	−0.115 (0.060)	0.061	0.250 (0.706)	0.725
1970–2015	Boulder R. (1)	−0.127 (0.136)	0.355	–	–
	Buffalo Fork R. (2)	−0.309 (0.144)	0.038	1.250 (0.753)	0.104
	Bull Lake Creek (3)	−0.141 (0.163)	0.391	0.250 (0.483)	0.607
	Clarks Fork Yellowstone R. (4)	−0.251 (0.141)	0.081	0.650 (1.124)	0.566
	Gallatin R. (6)	−0.141 (0.155)	0.368	–	–
	Green R. (8)	−0.077 (0.167)	0.648	−0.154 (0.473)	0.746
	Greys R. (10)	−0.117 (0.116)	0.321	0.273 (1.292)	0.834
	Pacific Creek (14)	−0.405 (0.146)	0.008	−0.342 (1.034)	0.743
	Ruby R. (16)	−0.236 (0.151)	0.125	–	–
	Smiths Fork (19)	0.006 (0.118)	0.957	0.923 (0.416)	0.032
	South Fork Shoshone R. (21)	−0.272 (0.136)	0.052	−0.276 (0.915)	0.765
	Stillwater R. (22)	−0.192 (0.129)	0.146	0.903 (0.957)	0.351
	Teton R. (23)	0.003 (0.201)	0.989	−1.550 (0.942)	0.107
	West Rosebud Creek (24)	<0.0001 (0.112)	0.998	0.265 (0.323)	0.417
	Yellowstone R.-Billings (25)	−0.175 (0.126)	0.172	−0.208 (0.864)	0.811
	Yellowstone R.-Yellow. Lake (26)	−0.225 (0.102)	0.032	−1.000 (0.735)	0.181

1950_{POR} (average slope = −0.098; SD = 0.066) and the 1970_{POR} (average slope = −0.166; SD = 0.117). For the 1970_{POR}, slope estimates from regression models suggest that contemporary peak discharge (2015) occurs on average 7.5 days earlier than in 1970; the variability in response across sites is evident in the Greys River (5.2 days earlier in 2015 than 1970) and Pacific Creek (18.3 days earlier in 2015 than 1970), which are both tributaries to the Snake River in WY.

Summer discharge

Interannual differences in 7-day Min discharge were moderately correlated across sites and this pattern was generally consistent from the 1930_{POR} (average = 0.67; range 0.46–0.89) to the 1950_{POR} (average = 0.65; range −0.06 to 0.94) and the 1970_{POR} (average = 0.61; range 0.18–0.90). Trends in 7-day Min at gage sites common to all three periods of record

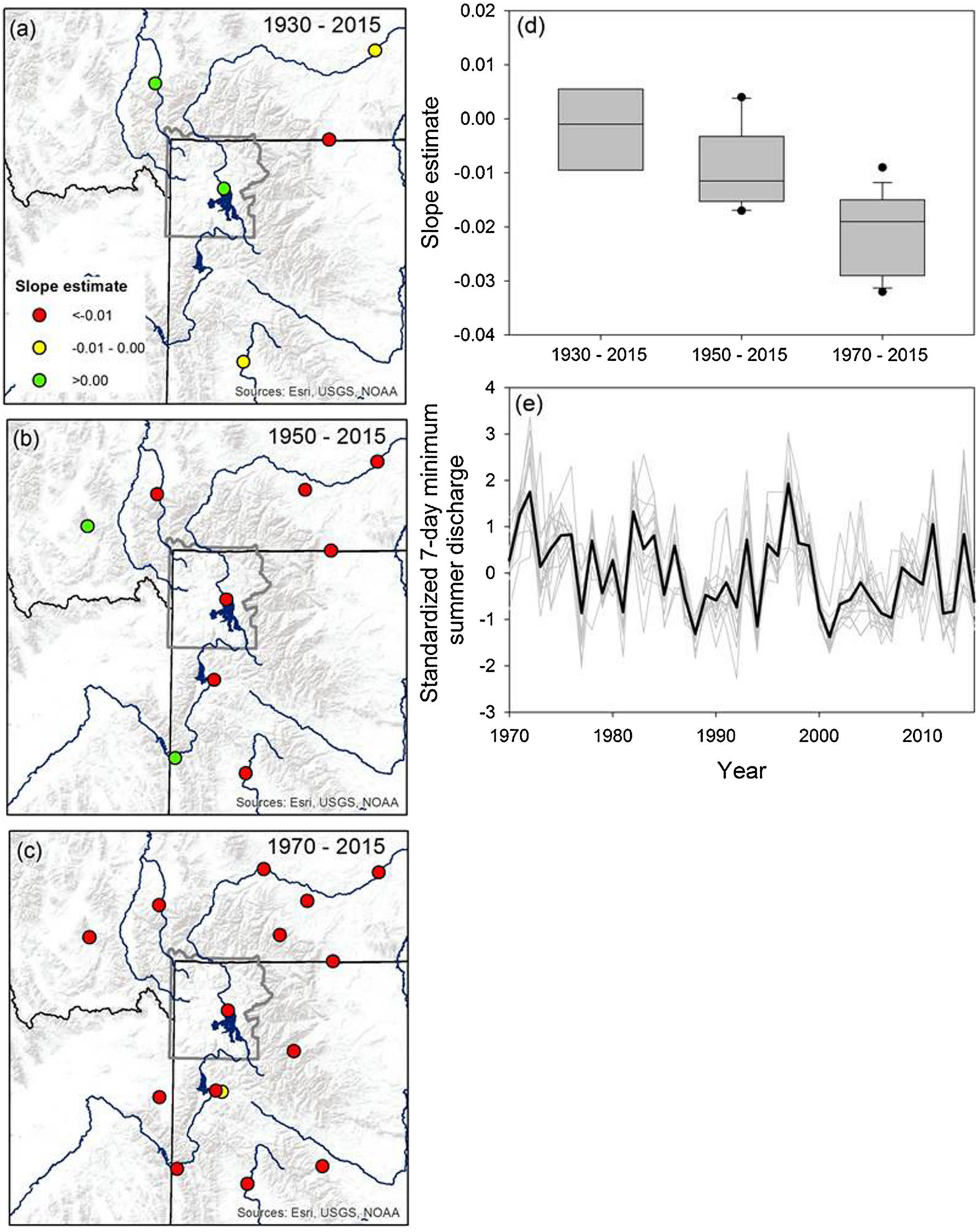


Fig. 2 Slope estimates of summer 7-day minimum streamflow (standardized; 7-day Min) for 1930–2015 (**a**), 1950–2015 (**b**), 1970–2015 (**c**), a *boxplot* of the regression slopes for each time period (*boxes* represent the 25th and 75th percentiles, whiskers show the 5th and 95th percentiles, points are outliers (**d**), and individual (*grey lines*) and mean (*black line*) summer 7-day minimum streamflow (standardized) at stream gages in the Greater Yellowstone Area, USA

indicated a shift to significant declining trends at all sites for the 1950_{POR} and steeper (i.e., more rapid declines), more negative trends (all significant) for the 1970_{POR} (Supplemental Table 1).

The pattern of steeper, more negative trends in minimum summer discharge (7-day Min) from the 1930_{POR} to the more contemporary 1970_{POR}, indicating more pronounced declines in low summer baseflows, was consistent with results when considering all sites. Across all sites, we observed no consistent pattern in trends of 7-day Min for the 1930_{POR} (Fig. 2a, d). The number of sites with significant declines in 7-day Min varied from 70% during the 1950_{POR} to 50% for the 1970_{POR} (Fig. 2b, c). The decrease in the proportion of sites demonstrating significant declines in 7-day Min is likely a result of reduced statistical power and high interannual variability (Fig. 2d). Despite this variability, average 7-day Min trends during the 1970_{POR} indicated substantial declines in 7-day Min across the region (slope −0.0209, SD = 0.0087, Fig. 2d). We also found increasingly negative estimates of trends through time suggesting that low summer baseflows are more rapidly declining in magnitude during the past half century (i.e., 1970_{POR}; Fig. 2e). Across sites, estimates from our regression models indicate contemporary (2015) summer baseflows have decreased on average by 27.5% (SD = 10.5%) since 1970.

Peak winter events

In general, correlations in annual W_{90} between sites were low ($r < 0.55$) regardless of the period of record (not shown). We observed little evidence of increasing numbers of anomalously high discharge events during the winter months (W_{90}; Table 3). No consistent patterns emerged when considering gage sites common to all three time periods of record and only three sites demonstrated significant increasing trends in high discharge events during the winter (regardless of time periods) suggesting that changes in W_{90} have not been common in the GYA. Further, we observed no consistent patterns of increasing or decreasing trends in W_{90} across sites or periods of record.

Days with ice

Ice data were available from 1988 at 17 sites in the GYA. We found little evidence of correlations in the interannual differences of Days_{ice} across sites (average $r = 0.15$; range −0.49 to 0.75). From 1988 through 2015, we found negative trends in the number of days with ice at the majority (88%) of the sites, but only significant trends at five of the sites (Table 3). The strongest relationships were found at the lowest elevation sites (Fig. 3a, b), but significant negative trends were found at elevations as high as 2048 m

Table 3 Slope estimates, SE, and P values from linear regression analyses describing trends in the number of days of ice at stream gages (1988–2015) across different sites in the Greater Yellowstone Area, USA

Site	Slope	SE	*P*
Boulder River (1)	−0.642	0.677	0.352
Buffalo Fork River (2)	−0.523	0.235	0.036
Clarks Fork Yellowstone River (4)	−1.931	0.595	0.003
Gallatin River (6)	−0.285	0.347	0.419
Gardner River (7)	−0.142	0.205	0.495
Greys River (10)	−0.514	0.572	0.377
Lamar River (11)	−1.070	0.294	0.001
Madison River (12)	0.199	0.186	0.296
Pacific Creek (14)	−0.865	0.345	0.019
Ruby River (16)	−0.480	0.324	0.151
Shields River (18)	−0.279	0.412	0.505
Smiths Fork (19)	−0.808	0.659	0.232
Snake River (20)	0.807	0.489	0.111
Teton River (23)	−0.412	0.422	0.338
W Rosebud Creek (24)	0.056	0.071	0.439
Yellowstone River-Billings (25)	−1.084	0.290	0.001
Yellowstone River–Yellowstone Lake (26)	−0.712	0.779	0.371

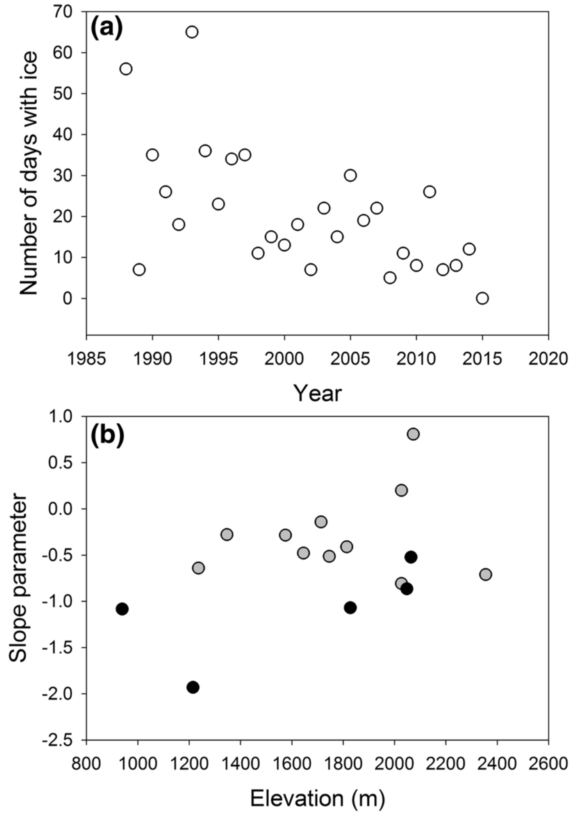


Fig. 3 The number of days of ice on the Yellowstone River near Billings, MT (**a**) and the significant (*black*) and non-significant (*grey*) slope coefficients from linear regression analyses by elevation of USGS stream gage (**b**) in the Greater Yellowstone Area, USA

(Pacific Creek). Overall, trend estimates were marginally correlated with elevation ($r = 0.40$; Fig. 3b).

Total volume

We found high correlations in interannual differences in Total_{Q} across sites, regardless of period of record (average r for the 1930_{POR}, 1950_{POR}, $1970_{\text{POR}} = 0.80$, 0.72, and 0.75, respectively). When considering sites common across all three periods of record, we found increasingly negative slope estimates since the 1930_{POR} (Supplemental Table 2). This patterns is consistent with trend results for all sites where the greatest declines in total volume (Total_{Q}) have occurred in the most recent period (1970–2015; Fig. 4a–c). Specifically, trends of Total_{Q} for datasets from 1930 indicated no clear pattern with two sites demonstrating significant, positive trends (Supplemental Table 2; Fig. 4a). A transition, however, is evident when considering Total_{Q} trends (all sites) from the 1950_{POR} where 90% of the sites

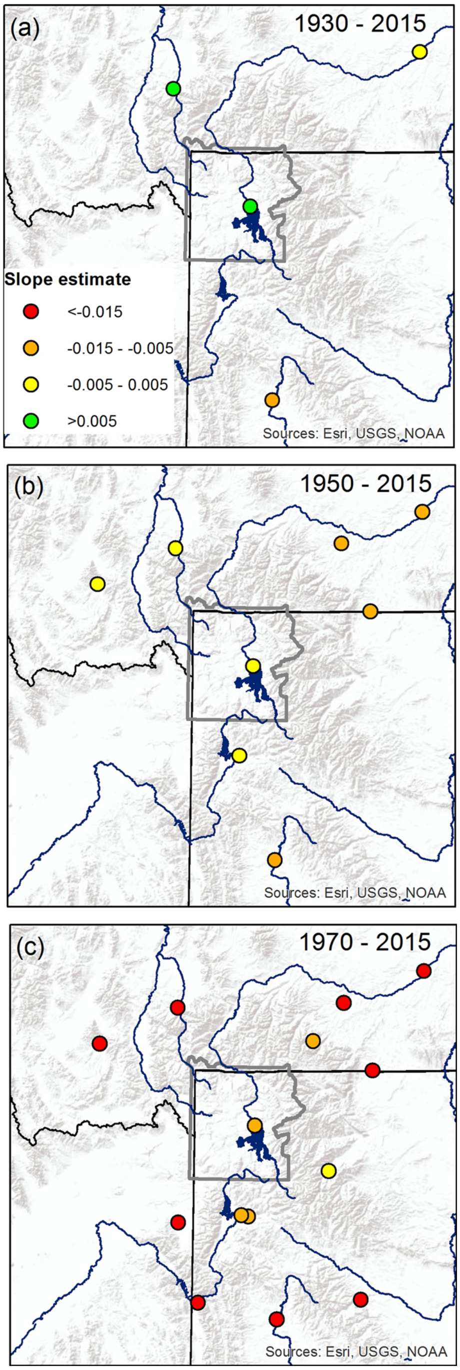


Fig. 4 Slope estimates from linear regression analyses evaluating trends in total streamflow volume (standardized) across three different time periods in the Greater Yellowstone Area, USA

demonstrate negative trend estimates (average slope = −0.0066; SD = 0.005; Fig. 4b). Despite considerably greater spatial coverage, all sites in the 1970_{POR} had negative estimates and steeper overall slopes (average slope = −0.0134, SD = 0.008) than previous periods indicating more pronounced declines during this period. Three sites in the 1970_{POR} indicated significant negative declines (Supplemental Table 2) and the overall pattern is consistent with our summer baseflow results. The steeper declines in $Total_Q$ slopes from the regression models correspond to an average of 15.6% (SD = 7.8%) decrease in water volume across sites with the smallest decrease at the SF Shoshone River, WY (0.5%) and greatest decline at the Ruby River, MT (26.9%).

Discussion

The importance of hydrologic regimes for riverine fishes such as salmonids is well documented (Kovach et al. 2016; Lytle and Poff 2004). Concomitantly, agricultural and municipal water demand remains a multinational concern for millions of people and changes in hydrologic patterns, including a declining trend in water supply documented herein, are certain to increase the tension between resource conservation for aquatic ecosystems and anthropogenic uses (Bates et al. 2008; Christensen et al. 2004).

As climatic conditions (e.g., air temperature, precipitation patterns) change, it will become increasingly important to iteratively evaluate shifts in hydrologic regimes as a means to refine conservation and management platforms for individual species and improve our assessments of vulnerability (e.g., Williams et al. 2009). Here, we focused specifically on those attributes considered to be important for salmonids and limit our discussion to implications of patterns of hydrologic trends to this regionally important group of fishes but acknowledge the implications extend beyond salmonids. We also limit our discussion to how these patterns act in isolation to affect salmonids, even though hydrological metrics likely interact within and among years to have additive and emergent effects on salmonids. However, we acknowledge that we do not consider the specific climate mechanisms for such change, which is covered more elegantly elsewhere (e.g., Hamlet and Lettenmaier 1999; Woodhouse et al. 2016).

Temporal trends in hydrologic attributes

For those metrics displaying temporal trends (see below), we consistently found evidence of accelerating change during the most recent period (1970_{POR}) when contrasted to the 1950_{POR}, indicating that the rate of change has increased in recent decades. The lack of clear trends in hydrologic metrics during the 1930_{POR} stems from the anomalous warm decade of the 1930s, which was symptomatically similar to the early 2000s in the GYA (Al-Chokhachy et al. 2013). These two warmer decades acted as book ends to the 80-years period of record, rendering hump-shaped temporal patterns (sensu Woodhouse et al. 2016; Supplemental Fig. 2).

Hydrologic trends and salmonid vulnerability in the GYA

A variety of changes to hydrologic regimes are anticipated for the Rocky Mountains as global and regional climate patterns shift (Bartlein et al. 1997; Gray and McCabe 2010). Our results suggest considerable variability in the response of fish-specific metrics in the GYA, especially over recent periods. We observed the most pronounced changes in the GYA via declines in the time of peak discharge ($Date_{peakQ}$), summer baseflows (7-day Min), and ice cover ($Days_{ice}$).

Trends in earlier peak discharge in the GYA are consistent with regional assessments (Barnett et al. 2005; McCabe and Clark 2005), but more concerning are the increasingly rapid declines (i.e., earlier peak discharge events) during recent decades that we documented. Shifts in earlier peak discharge are likely to have different effects on salmonids in this region. Native Yellowstone and westslope (*O.c. lewisi*) cutthroat trout typically spawn on the descending limb of the hydrograph, while non-native rainbow trout typically spawn on the ascending limb (Henderson et al. 2000; Muhlfeld et al. 2009). Data linking interannual variability in peak discharges with species phenological data is lacking in the GYA, though climate-induced shifts in reproductive timing are well documented in salmonids (Kovach et al. 2015a; Otero et al. 2014; Warren et al. 2012). There remains some uncertainty, however, in whether a shifted hydrograph may break down temporal segregation and further promote hybridization between cutthroat species and rainbow trout (Muhlfeld et al. 2014).

Earlier peak discharges are likely to have negative consequences for recruitment of fall spawning salmonids, which includes numerous genera, all considered sensitive to climatic shifts (Elliott and Bell 2011; Jonsson and Jonsson 2009; Wenger et al. 2011a). In the GYA, fall-spawning salmonids include species such as native mountain whitefish (*Prosopium williamsoni)* and non-native brown trout (*Salmo trutta)* and brook trout (*Salvelinus fontinalis*), all important sport fishes. High spring discharge events can reduce survival for newly emerged young-of-the year fish (Lobon-Cervia 2004; Warren et al. 2009). However, it is unclear how changes in the degree days associated with climate warming may alter the timing of emerging fry and moderate the vulnerability at this life stage.

A predicted consequence of earlier peak discharge in snow-melt dominated streams is lower summer baseflow (Ficklin et al. 2013; Stewart et al. 2004), a pattern substantiated in our analyses across the GYA. Our results are consistent with patterns found for August discharge in the Western United States (Leppi et al. 2012), but our results indicate more rapid declines in minimum flows since 1970. Indeed, numerous stream gages in the GYA documented record low baseflows during 2016, including the iconic Lamar River in Yellowstone National Park.

The effects of such declines are likely to manifest at multiple levels in salmonid populations. Strong ties between water volume and salmonid biomass (James et al. 2010; Regier and Meisner 1990) suggest continued water volume declines could result in overall reductions of salmonid biomass in the GYA. Salmonid declines are likely to be driven by density-dependent mechanisms as competition for space and optimal foraging locations increases (Huntsman and Petty 2014; Jenkins et al. 1999). Reduced summer streamflows are also likely to impact growth, and consequently survival, as macroinvertebrate drift, which is mediated by streamflow and is a main forage base/source for salmonids, declines (Harvey et al. 2006; Kennedy et al. 2008; Xu et al. 2010b). The negative effects of reduced summer streamflows are likely to be exacerbated as stream temperatures warm and metabolic demands increase (Al-Chokhachy et al. 2013).

Winter flooding is an important attribute limiting populations of fall-spawning salmonids (Kovach et al. 2015b). High discharge events during the winter can scour deposited eggs thus limiting recruitment (Cattaneo et al. 2002; Daufresne and Renault 2006; Seegrist and Gard 1972) and ultimately the distribution of fall-spawning salmonids (Wenger et al. 2011b). However, we found little evidence of changes in the frequency of winter floods in our analyses. Our results are contrary to findings from the Pacific Northwest (USA), where winter flooding has increased substantially during the past century (Hamlet and Lettenmaier 2007; Surfleet and Tullos 2013). Such differences are likely due to the relatively high elevation of the GYA (McCabe et al. 2006) and the declines of low-elevation snowpacks (Mote 2003), and highlight the need for region-specific climate vulnerability assessments. We acknowledge, however, that increases in the frequency of winter flooding may be possible in the future as elevational bands of rain versus snow increase with further warming (i.e., shifts from snow to rain; Barnett et al. 2005).

Temperature warming during the late autumn through spring (e.g., Westerling et al. 2006) has been attributed as a factor driving reductions in the duration of river ice across the globe (Bieniek et al. 2011; Magnuson et al. 2000). Here, we found variable patterns of ice loss over the past three decades, likely due to the physiographic complexity and local climate variability of the GYA (Sepulveda et al. 2015). Documented effects of river ice on fish behavior (Jakober et al. 1998; Whalen et al. 1999) and demographic and vital rates (Huusko et al. 2007; Linnansaari and Cunjak 2010) in other regions prompt concern for salmonids in the GYA. In many instances, ice cover facilitates higher salmonid growth and survival than ice-free conditions (Watz et al. 2016). Further, ice is considered a likely impediment to non-native species invasions that are ill-adapted to harsh temperatures and conditions (Rahel and Olden 2008). However, the direct and indirect effects of changes in ice conditions have been given little consideration in climate vulnerability assessments (e.g., Williams et al. 2009). Given that the processes of ice formation can be complex (Brown et al. 2011) and the observed trends in the reduced duration of river ice, there is a pressing need for further research on the implications for aquatic ecosystems in the GYA.

The economic importance of water for agricultural irrigation (Xu et al. 2014) and the ecological and economical value of salmonid populations suggests declining trends in total volume represent a rising concern for the GYA. As climate warms and evapotranspiration rates continue to rise (Walter et al. 2004) the demand for water is likely to increase, exacerbating the stress on aquatic ecosystems. While some states have established water rights for fisheries, these rights are relatively new (e.g., 1967 in Montana, USA; Murphy Water Rights) and must defer to any historical agricultural rights (Xu et al. 2014). Continued decreases to total volume and summer flows are likely to lead to difficult choices among aquatic conservation, the fishing industry, and agriculture (McShane et al. 2011).

Spatial variability across sites

Despite consistent trends for metrics where we observed change, variability in the magnitude of change across sites is apparent within the GYA. Spatial variation is not unexpected given the different landscape and local climatic controls on hydrology, which can yield variable hydrologic regimes at relatively small spatial scales (Tenant et al. 2015). Importantly, this variation also illustrates the challenges of extrapolating hydrologic information to ungaged watersheds and brings to question the accuracy of using relatively sparse stream gage data (e.g., Figure 1), with salmonid population data that typically occur at finer spatial resolutions (e.g., May et al. 2007). The challenge of extrapolating inference from gage sites is demonstrated in a post hoc analysis of the relationships between Euclidean distance (i.e., proximate gages) and differences in watershed area between sites and the correlations of annual volume ($\mathrm{Total_Q}$; Fig. 5a, b) and minimum summer discharge (7-day Min; Fig. 5c, d) at these same sites. Both

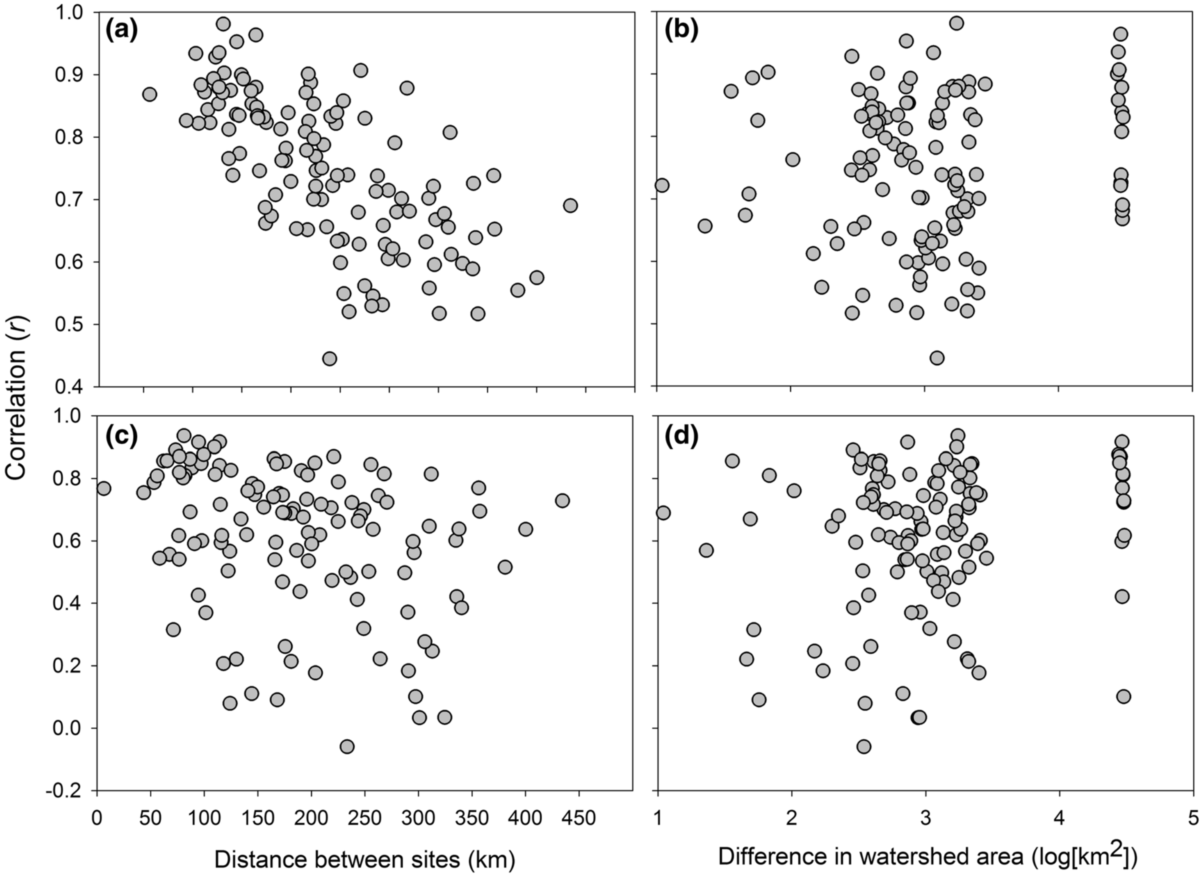


Fig. 5 The relationships between Euclidean distance and differences in watershed area ($\log_{10}$) between sites and correlations of annual total water volume ($\mathrm{Total_Q}$; **a**, **b**, respectively) and minimum summer discharge (7-day Min; **c**, **d**, respectively) between sites for the 1970–2015 period of record in the Greater Yellowstone Area, USA

metrics demonstrated strong temporal trends during the 1970_{POR}. While correlations of $Total_Q$ are generally high between sites and decline with distance, no apparent patterns exists for metrics such as 7-day Min (Fig. 5a) or other metrics (not shown). Ultimately, these results suggest the use of simple metrics (e.g., watershed area; Fig. 5b, d) to extrapolate hydrologic patterns from ungaged locations, even regionally, are unlikely to provide accurate representation of in situ hydrologic conditions in areas such as the GYA.

A challenge for salmonids stems from the fact that much of the existing hydrologic data is from relatively large, lower elevation streams (75% of gage sites in our sites occur at elevations < 2019 m), yet large portions of the existing stream networks that occupy salmonids in the GYA occur at elevations exceeding 2000 m. The limited amount of hydrologic data in these smaller watersheds, which are the ultimate sources of stream networks, is particularly problematic given the likelihood that higher-elevation habitats are anticipated to offer the greatest refugia for salmonids under future climate regimes (Hari et al. 2006; Isaak et al. 2015). Undoubtedly, collection of hydrologic data can be time consuming and costly at relatively fine spatial scales, yet improving our understanding of climate-resilient landscapes at a scale that matches species of interest and management will be critical (Beniston et al. 1997).

Conclusions

Stream hydrology is a critical attribute of aquatic ecosystems (Poff and Allan 1995), and historical trends in hydrology offer a prelude to likely regional shifts in regimes and species-specific vulnerability under a changing climate. Our results provide an iterative means for testing predictions and assessing vulnerability and suggest potential for hydrologic-related negative impacts to salmonids, which have accelerated since the 1930s. However, it is unclear if the predicted impacts have already manifested at the population level. Currently, there is a paucity of empirical results linking salmonid populations with interannual hydrologic and climate data (Kovach et al. 2016), which is surprising given the importance of salmonids to the economy and ecosystem function in the GYA. Recent observation of upstream range expansion of native and introduced cool-water fishes (e.g., smallmouth bass, *Micropterus dolomieu*) into historically cold-water sections of the Yellowstone River outside of Yellowstone National Park underscore the pressing need to assess the responses of salmonids to changing hydrologic shifts (sensu Lawrence et al. 2014).

Concomitantly, the observed hydrologic changes are highly correlated (Supplemental Fig. 3; Luce and Holden 2009), suggesting the need to isolate the implications of shifts of individual metrics and the potential synergistic effects on populations. Despite the complexities of these analyses (Bassar et al. 2016), efforts to merge climate and population-level data are an important step in identifying the climate resilience of landscapes and populations as a means to effectively prioritize conservation approaches.

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