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FORM AND FUNCTION

Increasing synchrony of high temperature and low flow in western North American streams: double trouble for coldwater biota?

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Abstract Flow and temperature are strongly linked environmental factors driving ecosystem processes in streams. Stream temperature maxima (T_{max_w}) and stream flow minima (Q_{min}) can create periods of stress for aquatic organisms. In mountainous areas, such as western North America, recent shifts toward an earlier spring peak flow and decreases in low flow during summer/fall have been reported. We hypothesized that an earlier peak flow could be shifting the timing of low flow and leading to a decrease in the interval between T_{max_w} and Q_{min}. We also examined if years with extreme low Q_{min} were associated with years of extreme high T_{max_w}. We tested these hypotheses using long-term data from 22 minimally human-influenced streams for the period 1950–2010. We found trends toward a shorter time lag between T_{max_w} and Q_{min} over time and a strong negative association between their magnitudes. Our findings show that aquatic biota may be increasingly experiencing narrower time windows to recover or adapt between these extreme events of low flow and high temperature. This study highlights the importance of evaluating multiple environmental drivers to better gage the effects of the recent climate variability in freshwaters.

Keywords Climate change · Freshwater ecosystems · Hydrology · Temperature · Hydroclimatology

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Introduction

Stream ecosystem structure and function are fundamentally shaped by temperature and flow (Magnuson et al., 1979; Vannote & Sweeney, 1980; Smakhtin, 2001). Both temperature and flow are key physical processes affecting the suitability of instream habitats (Montgomery, 1999; Smakhtin, 2001; Benda et al., 2004; Lytle & Poff, 2004) and distribution of populations (Shelford, 1931). An additional important

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influence of temperature and flow on aquatic biota is via changes in dissolved oxygen concentrations. Temperature also affects the performance of individuals by influencing development, metabolism, locomotory activity, and survival (Fry, 1947). Though temperature and flow are key factors in streams, they are often studied individually, limiting our understanding of their combined temporal dynamics.

Annual temperature maxima and flow minima are two hydro-climatic events whose synchrony could result in potential stress to stream biota. Periods of high temperature can limit growth and survival of coldwater species, as well as increasing the probability of other stress responses such as increasing the infection rate or virulence of fish pathogens (McCullough et al., 2009). The low flow period results in reduced extent of suitable habitats (May & Lee, 2004; Hakala & Hartman, 2004; Harvey et al., 2006). In many regions, the low flow period often occurs during the same season each year (Poff & Ward, 1989; Smakhtin, 2001) and in western North American streams it occurs in late summer and early fall (Mantua et al., 2010; Leppi et al., 2011). Maximum stream temperature in this region generally occurs earlier during midsummer (Johnson & Jones, 2000; Mantua et al., 2010). The year to year variability in timing for each of these two events has not been examined previously, nor has the potential for their synchrony. Times or locations where high temperatures and low flows occur as synchronous events may be particularly stressful to many species. These become especially relevant in light of climate change, which may impact stream temperature (Mantua et al., 2010; Van Vliet et al., 2011; Arismendi et al., 2012), increase frequency and duration of low flow, and decrease minimum stream flow (Lins & Slack, 1999; Svensson et al. 2005; Luce & Holden, 2009; Leppi et al., 2011). Climate predictions have also suggested that earlier timing of low flows could occur, leading to more synchronous timing of maximum temperatures and low flows. To evaluate this possibility, we need to understand how the recently warming climates have influenced the timing, magnitude, and synchrony of temperature maxima and flow minima. Long-term, historical data for both temperature and flow provide an opportunity to evaluate if such shifts are occurring (e.g., Arismendi et al., 2012).

Here, we evaluate seasonal temperature maxima and flow minima at minimally human-influenced streams across western North America to examine potential changes in their timing, magnitude, and synchrony with recent climate change. In this region, recent changes in climate have included declines in snowpack (Mote et al., 2005; Nolin & Daly, 2006), with corresponding shifts toward an earlier spring peak flow (Regonda et al., 2005; Barnett et al., 2008) and a decreased magnitude of low flow in summer/fall (Lins & Slack, 1999; Luce & Holden, 2009; Leppi et al., 2011). We hypothesize that if the stream flow peak during spring is occurring earlier (Regonda et al., 2005; Barnett et al., 2008), we might find a shift in the timing of low flow, which could decrease the interval between the annual stream temperature maxima and the annual flow minima, and increase the potential synchrony of these events (Fig. 1). Second, because of the relatedness of hydro-climatic events, we are interested in examining the association among the magnitude of stream temperature maxima, air temperature maxima, and stream flow minima (Fig. 1) and evaluating trends in the magnitude of these extreme annual events over time. Under this hypothesized scenario, increasing synchrony and magnitude of these temperature maxima and flow minima events could lead to intensified biotic effects. Overall, this study highlights the importance of considering timing and synchrony among environmental drivers to understand

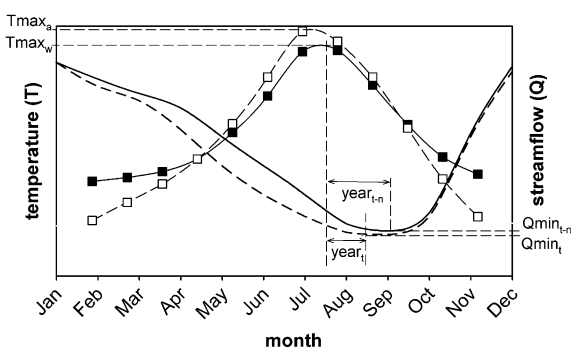


Fig. 1 Conceptual model of the hypothesized shift in timing of biologically relevant hydro-climatic variables affecting streams in Western North America between the years *t* and *t* − *n*. The figure represents the seasonal distribution for monthly mean values of stream flow for the year *t* − *n* (*solid line*), the hypothesized stream flow for the year *t* (*dotted line*), the stream temperature (*solid line* with *filled symbols*), and the air temperature (*dotted line* with *open symbols*). The lag between the annual stream temperature maxima (T_{max_w}) and the annual stream flow minima (Q_{min}) is shown for the year's *t* and *t* − *n*

the effects of climate change on freshwater ecosystems.

Materials and methods

Study sites and time series information

The study domain included watersheds in the six western states of the conterminous United States (California, Idaho, Montana, Nevada, Oregon, and Washington). This region is characterized by warm dry summers and cool wet winters with significant amount of precipitation falling as snow at higher elevations. We used historical data (1950–2010) of available daily mean stream temperature and flow collected from 22 gage stations located in watersheds of different sizes ranged from 14 to 14,295 km^2 (Table 1; Appendix 1 in Supplementary material). We searched for data from least-disturbed watersheds, based on a recent classification of human impacts (Falcone et al., 2010). All of the selected streams had no water regulation upstream the gage station. Air temperature information available from 1950 to 2005

Table 1 Characteristics of watersheds ($n = 22$) and time series examined in this study

Site characteristics									Time series length (# of years)		
Code	USGS ID	Site name	State	Lat N	Long W	BFI	Elevation (m)	Drainage area (km^2)	Air Temp	Stream flow	Stream Temp
Site 1	10309000	E_Fork Carson River	NV	38.845	−119.705	0.72	1,524	925	56	62	27
Site 2	10313400	Marys River	NV	41.550	−115.306	0.59	1,811	186	56	19	20
Site 3	10343500	Sagehen Creek	CA	39.432	−120.238	0.73	1,926	28	56	57	17
Site 4	11381500	Mill Creek	CA	40.055	−122.024	0.68	117	338	56	62	13
Site 5	11383500	Deer Creek	CA	40.014	−121.948	0.64	146	540	56	62	13
Site 6	12056500	N_Fork Skokomish River	WA	47.514	−123.330	0.56	232	147	56	62	17
Site 7	12115000	Cedar River	WA	47.370	−121.625	0.60	475	103	56	62	14
Site 8	12147500	N_Fork Tolt River	WA	47.712	−121.789	0.59	183	103	56	58	16
Site 9	12147600	S_Fork Tolt River	WA	47.707	−121.600	0.39	564	14	56	51	17
Site 10	1 2355500	N_Fork Flathead River	MT	48.496	−114.127	0.74	959	4,009	56	62	14
Site 11	13340000	Clearwater River	ID	46.478	−116.258	0.72	302	14,269	56	46	18
Site 12	13340600	N_Fork Clearwater River	ID	46.840	−115.621	0.75	506	3,355	56	44	39
Site 13	14091500	Metolius River	OR	44.626	−121.484	0.97	602	818	56	62	27
Site 14	14138870	Fir Creek	OR	45.480	−122.026	0.46	439	14	56	35	34
Site 15	14139800	S_Fork Bull Run River	OR	45.445	−122.110	0.47	302	41	56	36	33
Site 16	14161500	Lookout Creek	OR	44.210	−122.257	0.52	420	62	56	61	25
Site 17	14178000	Santiam River	OR	44.707	−122.101	0.75	485	558	56	62	50
Site 18	14179000	Breitenbush River	OR	44.753	−122.129	0.63	480	273	56	62	50
Site 19	14182500	N_Santiam River	OR	44.792	−122.579	0.45	200	287	56	62	13
Site 20	14185000	S_Santiam River	OR	44.392	−122.498	0.50	236	458	56	62	28
Site 21	14211500	Johnson Creek	OR	45.478	−122.508	0.31	70	69	56	62	13
Site 22	14338000	Elk Creek	OR	42.679	−122.742	0.41	455	336	56	62	38

None of the sites have stream regulation. (http://waterdata.usgs.gov/nwis)

Baseflow index (BFI) was estimated following the method of Wahl & Wahl (1995). The value of BFI varies between 0 and 1, representing lowest and highest possible groundwater contribution, respectively at each site was obtained from daily gridded meteorological data of the Surface Water Modeling group at the University of Washington (Maurer et al., 2002).

Statistical analysis

One-day (1-d) and seven consecutive day events have been widely used to characterize both low flow (Kundzewicz & Robson, 2000; Smakhtin, 2001; Svensson et al., 2005) and stream temperature (Mohseni et al., 1998; Mantua et al., 2010) conditions. We identified both 1-d and seven-day moving average (7-d MA) maximum/minimum annual hydro-climatic events from daily mean values for stream temperature (T_{max_w}), air temperature (T_{max_a}), and stream flow (Q_{min}). Because we focused our analyses on summer and early fall events, we only used data from 1st May to 31st October each year. We defined the annual degree of synchrony as the number of days separating a pair of hydro-climatic events (i.e., T_{max_w} and Q_{min}, T_{max_a}) in a particular year. We calculated the lag between the timing of the annual T_{max} (air and water) and annual Q_{min} (# of days). In some occasions, there was more than one annual event of the same magnitude and for these cases we used the dates of the first event. Each time series was visually inspected to ensure that we were able to capture the respective annual maxima/minima; all years with data gaps between May and October were eliminated from our analysis (<5%).

We used a non-parametric Spearman's rank correlation coefficient to test the hypothesis of an increase in synchrony between the T_{max} and Q_{min} over time. We examined potential changes in the time lag between T_{max_w} and Q_{min}, between T_{max_a} and Q_{min}, and between T_{max_w} and T_{max_a}, over time. To avoid both local influences on specific sites and short inter-annual variations that may cause noise in long-term regional trends, we smoothed the timing and magnitude of the events by averaging and grouping values every 5 years (Rajagopalan & Lall, 1998; Coulibaly & Burn, 2005). To test our hypothesis of a negative relationship between the magnitude of annual Q_{min} and the magnitude of the T_{max}, we used least-squares linear regression analysis of standardized magnitude values (grouped every 0.1 standardized units). We standardized magnitude of air/water temperature and flow using a Z-transformation as follows:

$$SV_i = \frac{V_i - \mu}{\sigma}$$

where SV_i is the standardized temperature/flow at day i, V_i is the actual temperature/flow value on day i, μ is the mean, and σ is the standard deviation from the entire period of record of the respective time series. Finally, we used a Spearman's rank correlation coefficient to test trends of the standardized magnitude of hydro-climatic events over time.

Results

We observed variable synchrony between annual stream temperature maxima and annual flow minima (Fig. 2; Appendix 2 in Supplementary material). Average timing of Q_{min} among sites ranged from 34 to 89 days after the timing of the T_{max_w}. The shortest lag between the timing of the T_{max_w} and the timing of the Q_{min} across individual years ranged from 2 to 35 days and the longest lag between those events from 55 to 128 days. Sites 2, 14, and 22 each had 1 year in their record when Q_{min} occurred prior to the T_{max_w}. Site 13 showed a low variability in the timing of Q_{min} across years (average timing on day 292 ± 12 days). In contrast to Q_{min}, T_{max_a} occurred in greater synchrony with T_{max_w} across sites and years. The average timing of T_{max_a} among sites was 0–15 days before the timing of the T_{max_w}. Across years, the timing of the T_{max_a} ranged from 0 to 85 days before the timing of the T_{max_w} and up to 10 days after. Sites had an average of 4 years of complete synchrony between T_{max_a} and T_{max_w} events.

We found a significant negative trend in the time lag (# of days) between the timing of T_{max_w} and Q_{min} over time (Fig. 3a) and there were significant decreasing trends for only the timing of Q_{min} over time (Appendix 2 in Supplementary material). The maximum time lag between average 1-d T_{max_w} and 1-d Q_{min} was 74 ± 7 days during the period 1960–1965, but by 1995–2000 was 50 ± 3 days. Similarly, the time lag between 7-d MA T_{max_w} and 7-d MA Q_{min} declined from a high of 68 ± 5 days during the period 1960–1965 to the minimum of 49 ± 3 days for the period 1995–2000. In evaluating the time lag between annual T_{max_a} and annual T_{max_w} (Fig. 3 b), we found a slight positive trend for 7-d MA events but not for 1-d. During the study period, 1-d T_{max_a} ranged from

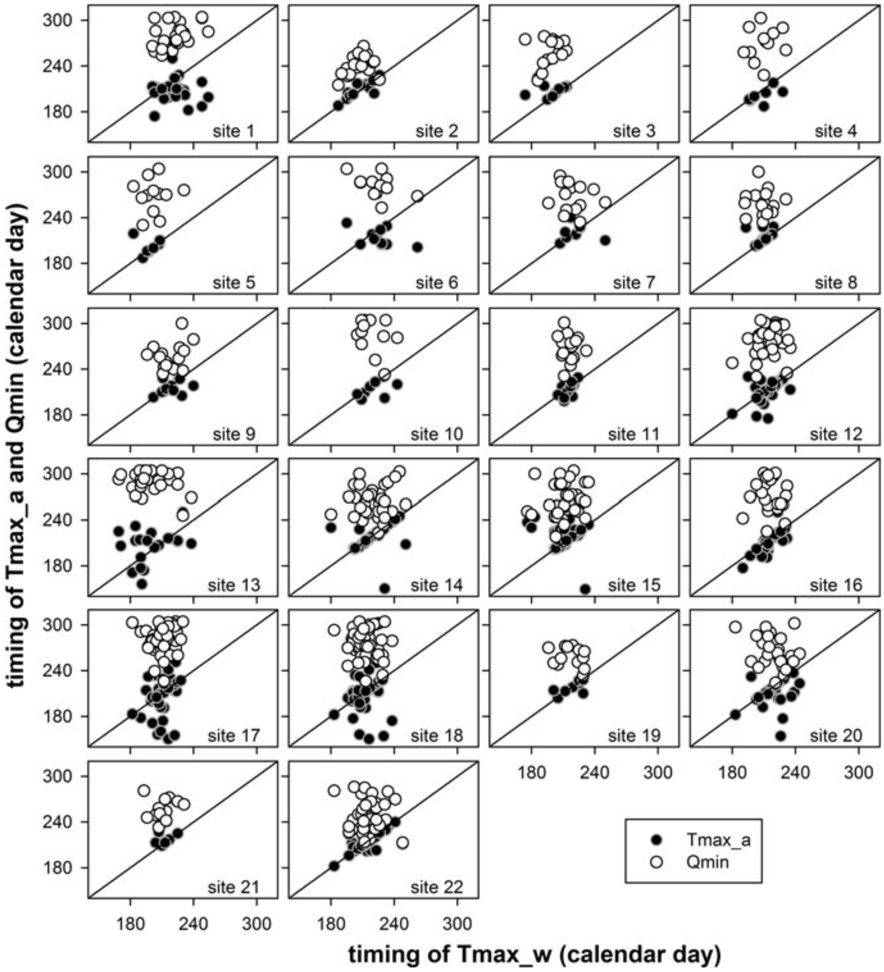


Fig. 2 Observed timing (calendar day) of the annual air temperature maxima (T_{max_a}) and annual stream flow minima (Q_{min}) compared to the timing of annual stream temperature maxima (T_{max_w}). Each *panel* shows one site with one *symbol* for each year. Points located on the 1:1 line suggest complete synchrony. All *symbols* correspond to the 7-d MA event. A similar figure for the 1-d event is included in the Supplementary material

7 ± 5 days earlier to 3 ± 6 days after the 1-d T_{max_w}; the 7-d MA T_{max_a} ranged from 9 ± 6 days earlier to 4 ± 3 days after the T_{max_w}.

There was a significant negative relationship between the magnitude of the annual T_{max_w} and the annual Q_{min} (Fig. 4a). A one standardized-level decrease in the flow was associated with an increase in stream temperature of 0.71 and 0.59 standardized units for the 1-d and 7-d MA events, respectively. Overall, the T_{max_w} events were explained by 74 and 62% of the variation in the Q_{min} for the 1-d and 7-d MA, respectively. Similarly, there was a significant negative relationship between the magnitude of the annual Q_{min} and the annual T_{max_a} (Fig. 4b). A one standardized-level increase in the air temperature was associated with a decrease in flow of 1.5 and 0.11 standardized units for the 1-d and 7-d MA events, respectively. The Q_{min} events were explained by 84 and 76% of the variation in the T_{max_a} for the 1-d and 7-d MA, respectively. Conversely, there was a significant positive relationship between the magnitude of the T_{max_w} and the T_{max_a} across periods (Fig. 4c). Specifically, a one standardized-level increase in the air temperature was associated with an increase in stream temperature of 0.49 and 0.52 standardized units for the 1-d and 7-d MA events, respectively. The T_{max_w} events were explained by 74 and 75% of the variation in the T_{max_a} for the 1-d and 7-d MA, respectively.

There was a significant negative trend in the standardized magnitude of annual Q_{min} over time (Fig. 5a). During the period 1950–1955, Q_{min} had its highest value (−0.59 ± 0.01 and −0.58 ± 0.02 for the 1-d and 7-d MA events, respectively) and during the period 1990–1995, the lowest (−0.69 ± 0.02 units for the 1-d event and −0.69 ± 0.02 units for the 7-d

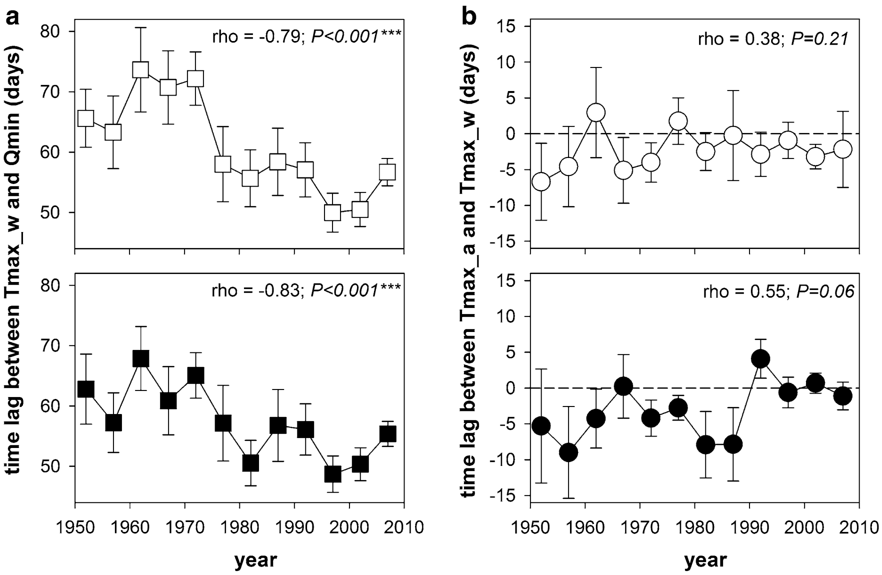


Fig. 3 Time lag (as number of days) between annual hydro-climatic events. **a** Number of days that annual stream temperature maxima (T_{max_w}) preceded annual stream flow minima (Q_{min}) for 1-d (*open square*) and 7-d MA (*filled square*) events. **b** Number of days that annual stream temperature maxima (T_{max_w}) preceded annual air temperature maxima (T_{max_a}) for 1-d (*open circle*) and 7-d MA (*filled circle*) events. Negative values indicate earlier timing of T_{max_a}. All *symbols* represent mean ± SE and include all sites grouped every 5 years. An additional figure showing individual trends for the timing of T_{max_w} and Q_{min} over time is included in the Supplementary material

MA event). The standardized magnitude of the T_{max_w} showed an increase over time, which includes a leveling off and slight decrease was evident after 1975–1980 (Fig. 5b). The standardized annual T_{max_w} was lowest during 1950–1955 (1.60 ± 0.05 and 1.51 ± 0.04 units for the 1-d and 7-d MA events, respectively) and the highest during 1975–1980 (2.20 ± 0.04 and 2.05 ± 0.04 units for the 1-d and 7-d MA events, respectively). We found non-significant trends for the annual T_{max_a} over time (Fig. 5c).

Discussion

We observed increasing synchrony between the annual stream temperature maxima and stream flow minima in minimally human-influenced streams in western U.S. As expected, years with higher stream temperature maxima and high air temperatures also showed very low stream flow minima. We also noted trends of increasing stream temperature maxima and decreasing magnitude of stream flow minima at the scale of 5-year averages over the 60 years of records.

At individual sites, the timing of stream flow minima lagged stream temperature maxima by approximately 1–4 months within the 6-month time-frame we considered (1st May to 31st October). But, in nearly all cases, stream temperature maxima preceded stream flow minima. Within sites and among years, the timing of the stream flow minima was highly variable across years, with the exception of one site (Metolius River) known to be strongly influenced by groundwater. In spite of this spatial and temporal variability, our results showed a consistent pattern of changes in the degree of synchrony between temperature maxima and stream flow minima among sites with available time series.

Increased synchrony between temperature maxima and flow minima could be due to various combinations of changes in the timing of each event. However, the significant trends that we observed were only for earlier timing of flow minima (see Fig. S3 of Appendix 2 in Supplementary material). It is possible that earlier flow minima may influence the timing and magnitude of temperature maxima. And if both flow minima and temperature maxima occur earlier, the time lapse could remain unchanged. However, we did not observe a change in the timing of temperature maxima. Therefore, our results are in agreement with the hypothesis of a shift toward earlier timing of flow minima (see Fig.

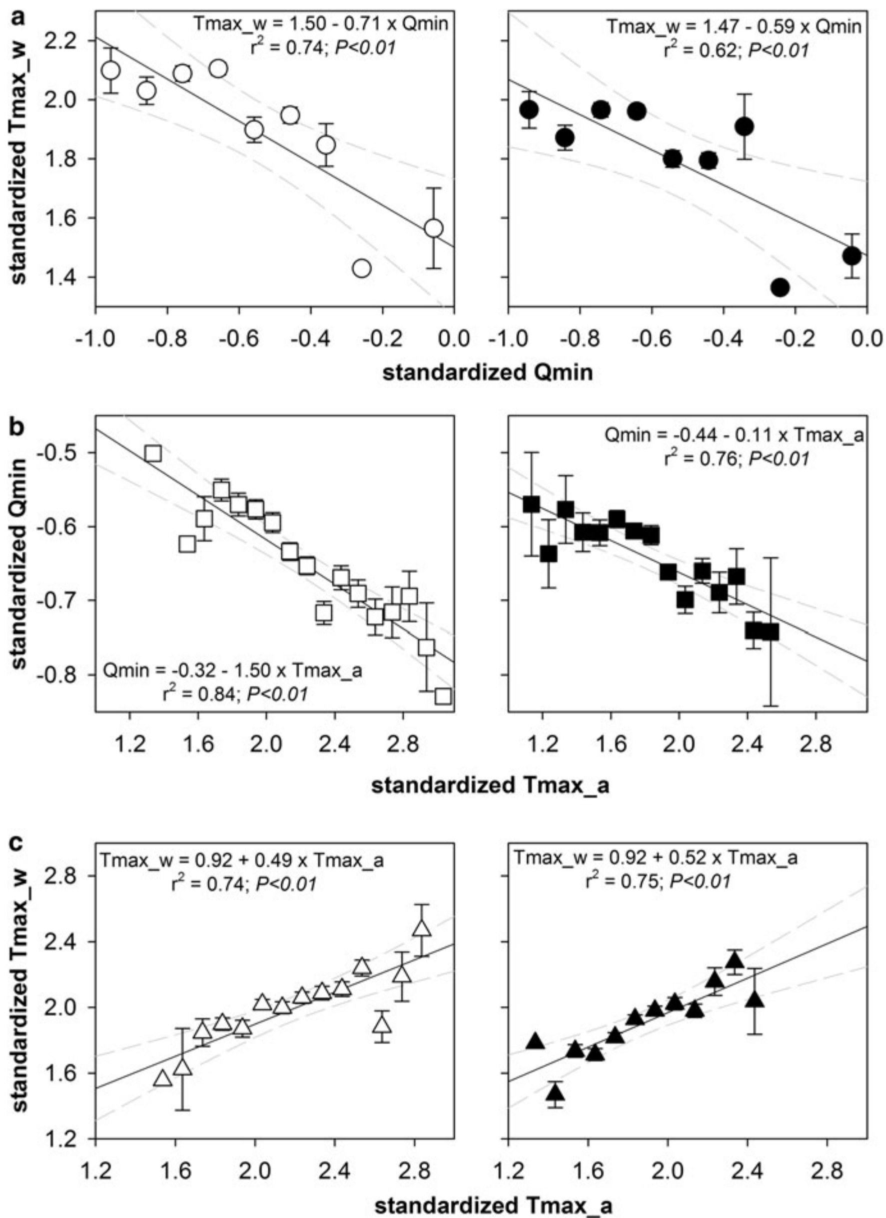
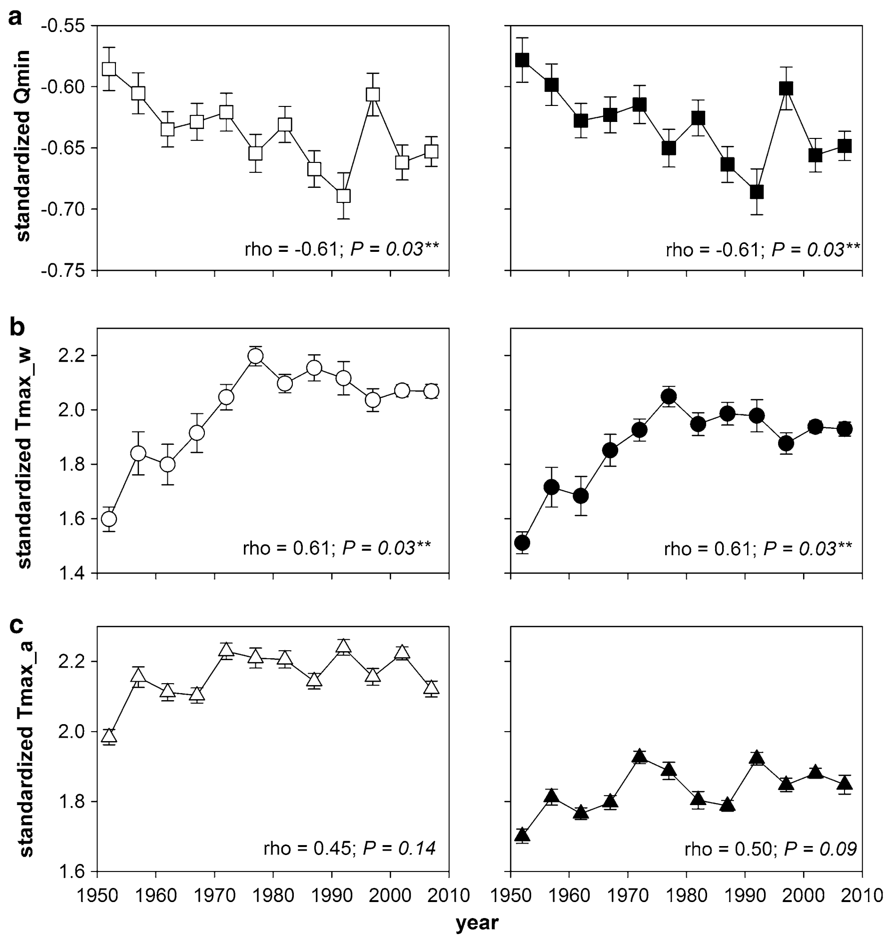


Fig. 4 Standardized magnitudes of stream temperature maxima (T_{max_w}) versus low flow minima (Q_{min}) versus air temperature maxima (T_{max_a}) for 1-d (*open symbols*) and 7-d MA events (*filled symbols*). All *symbols* represent mean ± SE of all available sites, grouped every 5 years. Standardized magnitude was grouped into classes of 0.1 units. *Dashed lines* represent 95% confidence intervals for the regression line. **a** Magnitude of T_{max_w} versus magnitude of the Q_{min} for 1-d and 7-d MA events. **b** Magnitude of Q_{min} versus magnitude of the T_{max_a} for 1-d and 7-d MA. **c** Magnitude of T_{max_w} versus magnitude of the T_{max_a} for 1-d and 7-d MA events

S3 of Appendix 2 in Supplementary material) that is leading the observed decrease in the time lag between temperature maxima and flow minima (Fig. 1). This shortening of the time lag by 20–30 days between these events is substantial and may impact a crucial period of time for aquatic biota. For example, after thermal maxima exceed levels that cause stress (e.g., McCullough et al., 2009), individuals could use the following period to recover before the stresses associated with low flows start (Matthews & Marsh-Matthews, 2003). But if there is less lag between these stressors, recovery could be shortened. Many organisms can select microhabitats to survive these stresses (Ebersole et al., 2003), but sessile organisms, that are incapable of escaping to alternative habitats, may be especially vulnerable. There could also be indirect effects for mobile organisms due to increased competition for limited resources in alternative habitats (May & Lee, 2004; Harvey et al., 2006).

Because we used a conservative approach to describe extreme annual events (i.e., daily mean values averaged every 5-year periods across sites),

Fig. 5 Standardized magnitude of the annual hydro-climatic events over time. *Symbols* represent mean ± SE of all available sites grouped every 5 years. **a** Standardized magnitude of the annual flow minima (Q_{min}) for 1-d event (*open squares*) and 7-d MA event (*filled squares*). **b** Standardized magnitude of the annual stream temperature maxima (T_{max_w}) for 1-d event (*open circles*) and 7-d MA event (*filled circles*). **c** Standardized magnitude of the annual air temperature maxima (T_{max_a}) for 1-d event (*open triangle*) and 7-d MA event (*filled triangles*)



the potential negative effects on aquatic biota may be more pronounced than we suggest. In our analyses, we focus on the timing of thermal and flow events for both 1-d and 7-d MA events but do not evaluate the duration of events or daily values throughout a summer. Years with dry and hot summers can compound these effects of low flows and high temperatures (Matthews & Marsh-Matthews, 2003). A detailed examination of historical trends in duration of events would be valuable for future research. Furthermore, a comprehensive evaluation of multiple metrics or descriptors of magnitude, variability, frequency, duration, and timing of events could be useful to better represent the full thermal experience of organisms in streams.

Although there is strong correlation between the magnitude of annual air and stream temperature maxima events, the heat budgets of streams can be quite complex (see reviews by Poole & Berman, 2001; Johnson, 2004; Caissie, 2006; Webb et al., 2008). Lower flows may have a high influence on the temperature of streams due to a decrease in the volume of stream water to buffer against air temperature fluctuations (see Poole & Berman, 2001; van Vliet et al., 2011) and slower flow with longer exposure times (Burton & Likens, 1973). Because extreme events of flow minima and temperature maxima may have greater ecological impacts than average environmental conditions, it is important to consider future changes in both the magnitude and trends of these extreme annual hydro-climatic events, in particular during hot and dry climatic periods.

Our findings of an increase in stream temperature maxima between 1950 and 1980 and a decreasing trend in stream flow minima between 1950 and 2010 in these unregulated streams are in agreement with other studies that report a long-term increase in the stream temperature in summertime in this region (Arismendi et al., 2012) and decreasing trends in the magnitude of low stream flow (Lins & Slack, 1999; Luce & Holden, 2009; Leppi et al., 2011). Since 1980, the stream temperature maxima appear to have little variation with no visible increases. Interestingly, we did not detect significant warming trends for air temperature maxima at these selected sites. This apparent incoherence between trends in stream temperature and trends in stream flow or regional climate has been observed in other western North American streams (Arismendi et al., 2012). These trends in maximum stream temperature and low flow are likely a complex response to a host of influences that cannot be inferred through simple correlations with changes in climate or hydrology.

Overall, the recent shortening of historic lags between the annual temperature maxima and annual flow minima events could lead to a disruption in species-specific variations in phenology (Noormets, 2009) and changes in the synchrony of other ecological interactions such as predator–prey, functional relationships, or changes in stream form and function. However, our understanding of how changes in synchrony of temperature and flow are affecting aquatic biota is still limited (Clews et al., 2010). Although responses are complex and context-specific, the consequences of high temperature and low flow periods on aquatic organisms have only been studied separately. We know that high temperature not only limits the metabolism and survival of aquatic organisms but also decreases the concentration of oxygen and modifies nutrient cycling (see extensive review by McCullough et al., 2009). Low flow events reduce the availability of suitable habitats (May & Lee, 1994; Hakala & Hartman, 2004; Harvey et al., 2006) and when refuge is less available, organisms are more vulnerable to predation (Steinmetz et al., 2003). Trends toward increased synchrony and magnitude of annual extreme events of temperature maxima and flow minima are recent; effects on aquatic organisms could be intensified or mediated by species-specific life histories and life stage vulnerabilities.

This study has implications for future efforts to understand the impacts of a changing climate on aquatic biota and stream ecosystems. The recent warming in this region and others has potential to affect streams via changes in the timing and magnitude of both temperature and flow; thus, it is important that future studies consider multiple environmental drivers as a new approach. Further study is needed to examine which drivers are influencing the inter-annual variability in magnitude and timing of flow and temperature in streams in many regions, and how these changes might be influencing aquatic biota and aquatic ecosystem processes in unregulated streams. Addressing these gaps in our understanding of responses to changing climate can provide a much more informed approach to sustaining key ecosystem services provided by freshwaters in the future.

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