

Climate-induced shift in hydrological regime alters basal resource dynamics in a wilderness river ecosystem

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SUMMARY

1. We integrated a 20-year ecological data set from a sparsely inhabited, snowmelt-dominated catchment with hydrologic models to predict the effects of hydrologic shifts on stream biofilm.
2. We used a stepwise multiple regression to assess the relationship between hydrology and biofilm ash-free dry mass (AFDM) and chlorophyll-*a* (chl-*a*) under recent climate conditions. Biofilm AFDM was significantly related to the timing of peak streamflow, and chl-*a* was significantly related to the timing of median streamflow. We applied these results to output from the variable infiltration capacity hydrologic model, which predicted hydrology under a baseline scenario (+0 °C) and a range of warming scenarios expected with climate change (+1, +2 or +3 °C).
3. When compared to the baseline, the results indicated that earlier peakflows predicted under warming scenarios may lead to earlier initiation of biofilm growth. This may increase biofilm AFDM during the summer by up to 103% (± 29) in the +3 °C scenario. Moreover, interannual variability of AFDM was predicted to increase up to 300%. Average chl-*a* during the summer increased by up to 90% (± 15) in the +3 °C scenario; however, its response was not significantly different from baseline in most years.
4. Because hydrologic change may alter the temporal dynamics of biofilm growth, it may affect the seasonal dynamics of biofilm quality (i.e. chl-*a*-to-AFDM ratio). The results indicated that hydrologic shifts may increase biofilm quality during the spring, but may decrease it during the summer. Thus, we provide evidence that predicted hydrologic shifts in snowmelt-dominated streams may alter the quantity and quality of an important basal resource. However, the magnitudes of these predictions are likely to be affected by other environmental changes that are occurring with climate change (e.g. increased wildfire activity and stream warming).

Keywords: algae, climate change, resource quality, snowmelt, variable infiltration capacity hydrologic model

Introduction

Projected increases in surface air temperatures associated with climate change have the potential to alter substantially the structure and function of various ecosystem types (IPCC, 2007). Potential effects on terrestrial ecosystems have been elucidated by quantitative models that forecast changes in ecosystem distributions, population responses of organisms (Jones *et al.*, 2009) and carbon dynamics (Parton *et al.*, 1995). Climate change will also affect aquatic ecosystems by altering thermal and hydro-

logic regimes (Kaushal *et al.*, 2010; Poff *et al.*, 2010). In western North America, shifts from snow- to rain-dominated precipitation have led to reduced snowpack, earlier snowmelt and reduced peakflow and summer baseflow (Stewart, 2009; Kunkel & Pierce, 2010). From 1948 to 2002, snowmelt and associated stream run-off in this region shifted 10–30 days earlier and is expected to be up to 40 days earlier by 2100 (as compared to the period 1951–80; Stewart, Cayan & Dettinger, 2004). A recent hydrologic model also showed that the timing of spring snowmelt for the Salmon River in Idaho would have occurred

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10–30 days earlier if air temperatures had been 2 °C warmer during the time period from 1976 to 2005 and would have been 15–45 days earlier if it was 3 °C warmer (Tang *et al.*, 2012). These shifts in streamflow are predicted to have substantial consequences for stream ecosystems, such as alteration in invertebrate community composition (Poff *et al.*, 2010) and carbon processing (Acuna & Tockner, 2010).

Despite the likely effects of climate change on basal resources and aquatic food webs, quantitative predictions of such effects are lacking. Studies have used long-term data and comparative studies to assess which types of organisms may be affected directly by thermal and flow regime shifts (Durance & Ormerod, 2007; Poff *et al.*, 2010; Woodward, Perkins & Brown, 2010). These studies have produced qualitative predictions, but have not developed predictive models for a range of climate-change scenarios. Other studies have quantified effects, whereby they predicted how carbon dynamics (Acuna & Tockner, 2010; Marcarelli, Van Kirk & Baxter, 2010) or distributions of thermal habitats and taxa (Isaak *et al.*, 2010; Lyons, Stewart & Mitro, 2010; Wenger *et al.*, 2011) may respond directly to climate-change scenarios. Because consumers will be affected by altered temperature and flow, such studies increase the understanding of climate-change impacts, but these organisms will also be affected by changes in resource availability that have not been integrated into predictive frameworks. Thus, there is a need for quantitative predictions of basal resource responses to warming and consequences for aquatic food webs.

Here, we couple a predictive hydrologic model and a long-term ecological data set from a wilderness catchment presently characterised by a snow-dominated hydrology. This approach generated predictions of how expected shifts in hydrology may affect the biomass of streambed biofilm under various climate scenarios. Biofilm is composed of algae, heterotrophic microbes and detritus that are embedded in a polysaccharide matrix on aquatic surfaces (Lock *et al.*, 1984). As biofilm is affected by temperature and hydrology (DeNicola, 1996; Larned, 2010), it is likely to be sensitive to climate change. Because biofilm is an important resource for many stream consumers (Feminella & Hawkins, 1995), its alteration could have consequences for stream food webs. To help assess such effects, we used a 20-year data set of hydrology and biofilm biomass to model their relationship under contemporary climate conditions. First, we generated hydrographs using two different modelling approaches: a multiple linear regression (MLR) that reconstructed contemporary flows from 1990 to 2009 and the variable

infiltration capacity (VIC) model (e.g. Liang *et al.*, 1994; Liang, Wood & Lettenmaier, 1996) that simulated hydrographs under four temperature scenarios (+0, +1, +2 and +3 °C) for the same time period. The reconstructed MLR-generated hydrographs and long-term data set of biofilm biomass were then compared to quantify the relationship between biofilm biomass and contemporary streamflows. Next, by coupling this biofilm–hydrology relationship with VIC-generated hydrographs under several warming scenarios, we predicted biofilm response to expected hydrologic shifts, an important step in forecasting possible consequences for overall food webs.

Methods

Study site

We studied tributaries of Big Creek (Idaho, U.S.A.), a sixth-order river (mean elevation: 2117 m, catchment area: 1444 km²) that flows into the Middle Fork Salmon River (see Fig. S1). The catchment is a mosaic of forest composed of Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*), shrub-steppe dominated by grasses and sagebrush (*Artemisia* spp.) and exposed rock. Most of the annual precipitation (*c.* 40 cm) occurs as winter snow. The catchment lies in the Frank Church River of No Return Wilderness and is largely unaffected by human land use. Parts of the catchment have experienced large wildfires since *c.* 1988, which are becoming more frequent in this region due to climate change (Westerling *et al.*, 2011).

Biofilm sampling

Biofilm was sampled annually from 1990 to 2009 in six tributaries of lower Big Creek (Cave, Cliff, Cougar, Goat, Pioneer and Rush Creeks), which range from 2nd to 5th order (catchment area: 7.9–243.4 km²) (see Robinson, Minshall & Royer, 2000 for stream descriptions). Based on methods for sampling wilderness stream ecosystems (see Davis *et al.*, 2001), streams were sampled over a 4- to 5-day period within each year. The initiation of this relatively short sampling period was at approximately the same time each summer across years. This 4- to 5-day sampling window began between 20 July and 30 July in 75% of the years (median: 23 July, Julian day 204) and between 26 June and 6 August for the remaining years (median: 11 July, Julian day 192). Although the actual sampling date differed among years, the multiple regression model that compared hydrology and biofilm biomass (see Methods and Results below) identified the timing of

the sample date relative to the date of peakflow and median streamflow as the best predictors of biofilm biomass. Through this relativisation, the regression model accounted for any variation associated with shifts in the actual sampling date. Due to insufficient sample size, 1992 was excluded from the analysis.

In each stream, we sampled five permanent transects located in riffle habitat and *c.* 50 m apart. From 1990 to 2007, we scrubbed a known area (3.14 cm²) from one haphazardly collected rock per transect and filtered it onto pre-ashed glass fibre filters (0.70 µm). Each rock had 1–4 areas scrubbed until a visibly detectable mass of material was collected. In 2008 and 2009, we scrubbed the entire surface of 3–5 haphazardly selected rocks per transect, composited the slurry and subsampled it prior to filtering. To calculate biofilm biomass on a per unit area basis for the 2008–09 data, we assessed rock area by tracing its circumference onto paper, weighing the cut-out and applying a paper weight-to-surface area regression. In all years (1990–2009), we typically collected five samples per stream, resulting in *c.* 30 biofilm samples per year. Although protocols varied in some of these years, a comparison of duplicate samples collected using both biofilm sampling methods showed that they provided comparable results (C. Baxter unpublished data). Thus, changing protocols are unlikely to have affected our results.

Based on standard methods (APHA, 1998), filters from each transect were analysed for ash-free dry mass (AFDM) and chlorophyll-*a* (chl-*a*). Filters were extracted in methanol for *c.* 12 h, analysed for chl-*a* with a spectrophotometer and corrected for phaeophytin. After extraction, the filters and methanol extract containing the chl-*a* component were recombined, dried at 60 °C for at least 48 h, weighed and ashed at 550 °C for *c.* 4 h. Samples were then reweighed to calculate AFDM.

Measuring contemporary hydrology

We had to reconstruct the flows for Big Creek mainstem during the time period over which we sampled biofilm (1990–2009) because Big Creek's discharge was only consistently measured from 1944 to 58. Using a MLR approach that quantified the relationship between the historic hydrologic data from Big Creek mainstem (1944–58) and contemporaneous data from three active gauges on nearby rivers in the Salmon River catchment, we reconstructed the hydrograph for the time period that we sampled biofilm (see Table S1). Multiple permutations of the active gauges were included as candidate models (i.e. individually or with all gauges combined). Model fit was

assessed with root mean square error (RMSE), which was calculated for each candidate model by comparing modelled discharge against the measured discharge between 1944 and 1958. This approach has successfully reconstructed discharge at other locations with discontinued gauges (e.g. Nawaz & Khan, 2006). The MLR was then validated by comparing modelled and measured discharge from a new gauge on Big Creek that was installed in 2008 and not used in the initial model construction (see Appendix S1).

Assessing the relationship between biofilm and contemporary hydrology

To investigate potential relationships between biofilm biomass and the contemporary hydrographs generated by the MLR approach, we used the stepwise procedure to construct a multiple regression model (SAS v.9.2; SAS Institute, Cary, NC, U.S.A.). We used r_{adj}^2 to determine the best-fitting model out of several candidate models that incorporated multiple hydrologic predictors and all combinations of those predictors (see below). Although Bayesian methods would also be valid, we used multiple regression because parameter estimates generated by regression analysis are comparable to those generated by Bayesian approaches when these are based on uninformed priors (e.g. Ellison, 2004), as would have been the case with our data set.

We analysed AFDM and chl-*a* separately. AFDM is a measure of living and senesced autotrophs, heterotrophic microbes, detritus and the polysaccharide matrix. Because it is a measure of algal pigments, analysis of chl-*a* provides a relative index of living autotrophs that can be a higher-quality resource for consumers (i.e. lower carbon-to-nutrient ratio; Frost, Hillebrand & Kahlert, 2005). Furthermore, chl-*a* can be positively related to biofilm nutrient content (Hill, Fanta & Roberts, 2009; Fanta *et al.*, 2010) and growth of certain grazers (Stelzer & Lamberti, 2002). Thus, contrasting responses of AFDM and chl-*a* metrics could indicate coarse changes in biofilm composition and quality. However, biofilm is composed of other components, such as heterotrophic microbes, detritus and carbon exudates, that also contribute to biofilm quality (Lock *et al.*, 1984; Frost *et al.*, 2005), but would not be detected with chl-*a* analyses. Other environmental factors (e.g. water nutrient concentrations and light) can also modify the relationship between chl-*a* and nutrient content (Hill *et al.*, 2009; Fanta *et al.*, 2010). Thus, comparing chl-*a* and AFDM responses may indicate the changes in biofilm quality, but this surrogate has some limitations and should be interpreted accordingly.

For each year, we averaged AFDM and chl-*a* across all streams because we only had one annual value for each hydrologic metric and the individual samples would not be independent replicates. Applying the multiple regression to individual data points could artificially inflate the r^2_{adj} , bias parameter estimates, and would violate assumptions of regression. Conversely, our use of average biofilm values in the multiple regression would lead to a conservative estimate of the relationship between biofilm and hydrology. Based on the water year calendar, we calculated minimum daily flow, peak daily flow, average daily flow, standard deviation of daily flow and coefficient of variation for Big Creek. We then determined the median sampling date for each year separately. Using these median sampling dates, we then calculated days since the occurrence of peakflow, 75th percentile flow, 95th percentile flow, centre of mass (CT, sensu Stewart *et al.*, 2004) and median flow (defined as the day when 50% of the annual flow had occurred) for each year. All combinations of metrics were tested for inclusion in the best-fitting multiple regression model. However, we included only the interaction between peakflow and days since peakflow because including all interactions would have led to more predictors than the 20 data points. For those metrics that were found to be statistically significant in the best-fitting multiple regression model, we then calculated parameter estimates and the associated variation around those estimates.

Predicting hydrology under various warming scenarios

To predict flows from 1990 to 2009 under different temperature scenarios, we used the VIC model (e.g. Liang *et al.*, 1994, 1996), which simulates discharge based on meteorological data, vegetation cover and soil properties (see Appendix S1 in supporting information for more details). We ran a baseline scenario (+0 °C) and three warming scenarios (+1, +2 and +3 °C to daily minimum and maximum temperatures) that encapsulated the range projected for this region by 2080 (Mote & Salathe, 2010). Because flow was not measured on Big Creek during the biofilm sampling period (1990–2009), we calibrated and validated the VIC model by comparing the +0 °C scenario to subsets of flow data from the historic gauge that was located on Big Creek mainstem from 1944 to 58. Model calibration was based on Nash–Sutcliffe coefficient (E_f) (Nash & Sutcliffe, 1970) and r^2 .

Predicting biofilm biomass under four scenarios

For the time period that we sampled biofilm (1990–2009), we calculated hydrologic metrics from the VIC-generated

hydrographs under four scenarios (+0, +1, +2 and +3 °C). The VIC-generated metrics were then used in the regression equation that linked hydrology and biofilm, which predicted AFDM and chl-*a* for each year and warming scenario. For calculations that predicted biofilm biomass based on the VIC-generated hydrographs, we used the grand median sampling date of all years combined (Julian day 204). This eliminated the influence of sampling date on biomass predictions and quantified how hydrologic shifts could affect biofilm biomass on a particular date during the summer. Without such a control, biomass may differ simply due to differences in sampling date even if hydrology did not change. Because our predicted biofilm responses were based on a regression equation that incorporated both parameter estimates and associated variation, we could calculate 90% prediction intervals for each of the projected biofilm data points in all of the temperature scenarios. By comparing these 90% prediction intervals, we assessed whether biofilm levels were significantly different from baseline (+0 °C) on our specific sampling date, providing an indicator of how biofilm may respond during the overall summer. We also assessed the changes in interannual variation for biofilm biomass by calculating coefficients of variation across the 20 years in each temperature scenario.

Assumptions of the biofilm modelling approach

Our coupling of long-term ecological and hydrologic data required several assumptions. Rather than using hydrographs from the individual tributaries in the initial biofilm–hydrology comparison, we used the MLR-generated hydrograph for Big Creek mainstem as an indicator of hydrologic conditions across the sample sites. Using the hydrograph from the mainstem was necessary because the VIC model, which simulated hydrology under the various temperature scenarios, is more accurate for large catchments and can provide inaccurate hydrograph predictions for smaller streams (Olson, 2010; Wenger *et al.*, 2010). However, our study streams flow directly into Big Creek and are in relatively close proximity to each other; therefore, the mainstem of Big Creek integrates tributary hydrographs and averages hydrologic conditions at the catchment scale. For instance, even in those years when peakflows occurred earlier in Big Creek and its tributaries, distributions of peakflow timing for individual tributaries were relatively consistent around the peakflow timing for the mainstem. The distributions also exhibited overall low skewness (Olson, 2010). Thus, shifts in hydrology due to changes in snowmelt timing probably exhibit a high degree of unison across the

catchment, suggesting that similar shifts simulated by the VIC model would also be consistently applied throughout the catchment.

When assessing how biofilm responses differed under various warming scenarios, we used predictions from the VIC-generated +0 °C scenario as the baseline rather than the predictions based on the MLR-generated hydrograph. This substitution was necessary because the VIC +0 °C scenario underestimated peakflows in 2008 and 2009 when compared to the contemporary hydrograph (see Fig. S2). Using the contemporary hydrograph generated by the MLR approach as the baseline for the comparison of biofilm predictions would have introduced methodological bias for those years. In the +2 and +3 °C VIC scenarios, the dates of peakflow (45 and 50% of years, respectively) and median flow (20 and 45%, respectively) exceeded the range measured for contemporary conditions (Figs 1 and 2). We extrapolated and assumed a continued linear relationship between biofilm and hydrology in these scenarios; however, other factors (e.g. grazing, nutrient limitation or sloughing) can alter peak biofilm biomass (Biggs, 1996; Larned, 2010) and may attenuate the trajectory and magnitude of increases predicted by the model. Furthermore, climate-induced changes in hydrologic regimes are occurring in parallel with other changes that may affect biofilm biomass (e.g. stream warming and increased wildfire activity; Wenger *et al.*, 2011; Westerling *et al.*, 2011). Thus, predictions generated by our analysis are best interpreted as potential responses to hydrologic shifts alone.

Results

Contemporary hydrologic regime

Model calibration showed that the MLR successfully reconstructed Big Creek's contemporary hydrograph based on the best-fitting model that incorporated all three gauges in nearby rivers ($P < 0.0001$, $r^2 = 0.98$, Table S2, Fig. S2). After correcting for the additional catchment area at the gauging station that was installed on Big Creek in 2008, modelled flows based on this MLR approach were independently compared against recent discharge data and found to be equally accurate (RMSE = $4.82 \text{ m}^3 \text{ s}^{-1}$, $P < 0.0001$, $r^2 = 0.98$). This validated the stationarity assumption of the MLR relationship over the study period. The hydrograph displayed a snow-dominated hydrology that exhibited a spring peakflow event driven by snowmelt. When averaged across all years, peakflow occurred on 25 May (Julian day 145), ranging from 9 May (Julian day 129) to 12 June (Julian day 163).

Relationship between biofilm and contemporary hydrology

Although the stepwise regression approach tested all combinations of multiple variables, biofilm AFDM was best predicted by a single variable from the MLR-generated hydrograph, time since peakflow (Fig. 3A). Earlier peakflows resulted in increased AFDM, such that AFDM would be more than twice the average baseline in years when peakflow occurred before 4 April (Julian day 95). The next best-fitting regression model was also based on a single predictor, days since median flow ($P = 0.0003$, $r_{\text{adj}}^2 = 0.52$). Similarly, despite the multiple regression approach, the best-fitting model for chl-*a* included only one factor, the days since median flow. However, this relationship was relatively weak (Fig. 3B). Days since 95% percentile flow was the next best-fitting regression model, but was also only weakly related ($P = 0.0084$, $r_{\text{adj}}^2 = 0.30$). Thus, earlier flows would be predicted to increase AFDM and chl-*a* during the summer, but exhibited less predictive power for chl-*a* (i.e. lower r_{adj}^2).

Predicted hydrologic response to warming

The VIC +0 °C scenario effectively simulated Big Creek's hydrograph, as it was correlated with the contemporary hydrograph generated by the MLR approach ($r^2 = 0.81$) and was above the threshold considered to represent a good model fit ($E_f = 0.75$, Fig. S2). The timing of peakflow ($P < 0.0001$, $r_{\text{adj}}^2 = 0.74$), median flow ($P < 0.0001$, $r_{\text{adj}}^2 = 0.87$) and CT ($P < 0.0001$, $r_{\text{adj}}^2 = 0.84$) based on the two hydrographs were also correlated over the study period (Fig. S3). However, there were discrepancies between the modelled and observed peakflows in May, June or July for some years (Fig. S2), possibly due to input precipitation data for those years that may not have accurately represented high-elevation snow accumulation. Despite these discrepancies, the strong correlation between the timing of flow metrics from 1990 to 2009 (Figs S2 and S3) and the high E_f value indicated that the overall VIC model exhibited a good model fit.

Based on the VIC model that simulated flows under various temperature scenarios, higher air temperatures during the study period would have led to earlier peakflows and median flows, due to more precipitation arriving as rain versus snow (Figs 1 and 2). Compared to the +0 °C scenario, peakflows were predicted to be 23 ± 9 days earlier in +2 °C scenario and 46 ± 13 days (mean \pm SE) earlier in the +3 °C scenario. In the +2 °C scenario, peakflow occurred in the winter (i.e. before 22 March) for 15% of the years, but one of those years had a second high flow that followed and was >50% the

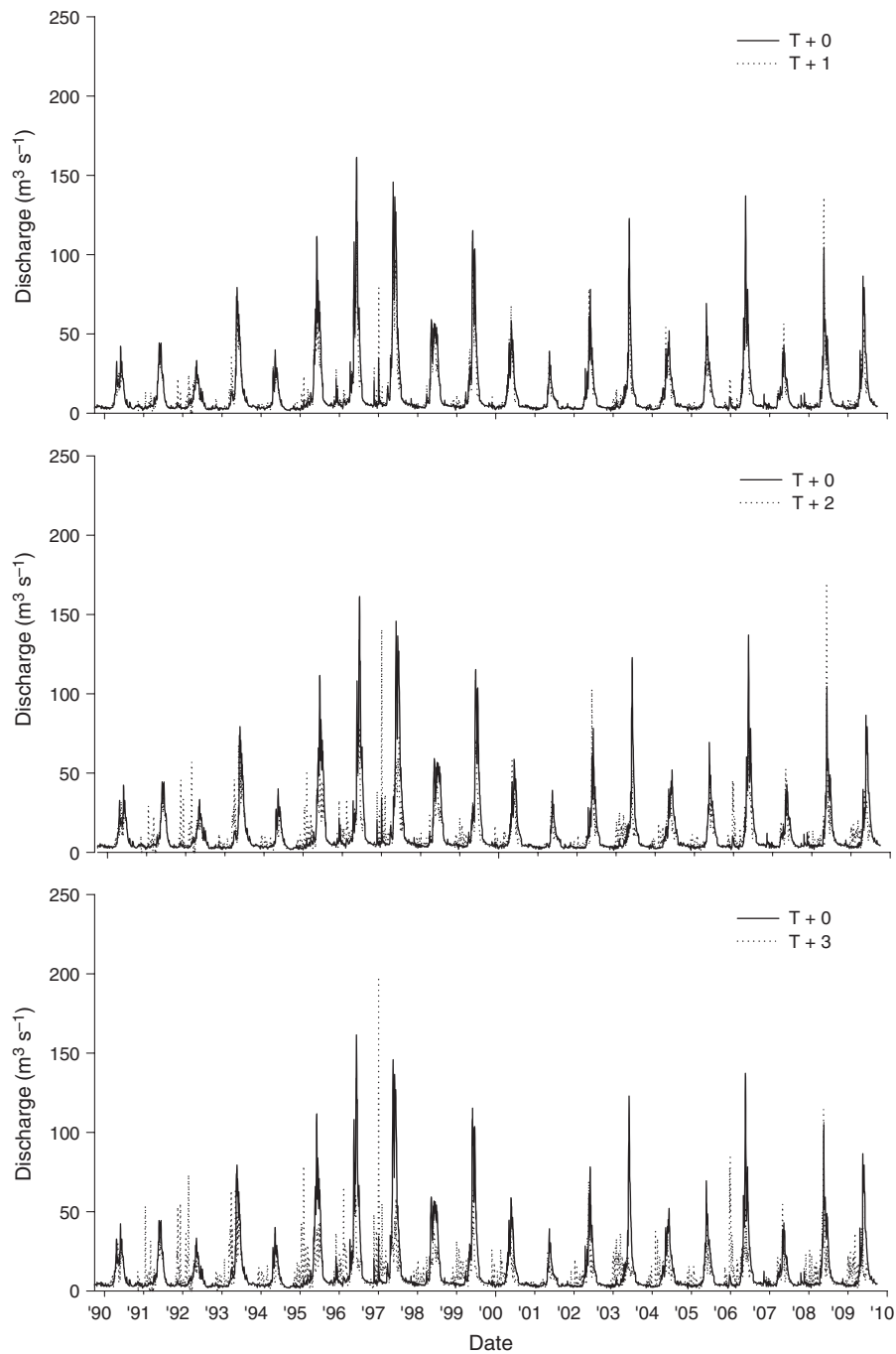


Fig. 1 Comparison of variable infiltration capacity (VIC)-generated hydrographs under four scenarios (+0 +1, +2 and +3 °C) that primarily show earlier and lower magnitude peakflows for warmer temperatures.

magnitude of the winter peakflow. Peakflow was in the winter for 35% of years in the +3 °C scenario, but two of those years had a second high flow that followed the winter peakflow. Median flows were earlier in the +2 and +3 °C scenarios (14 ± 2 and 27 ± 4 days, respectively). In the +1 °C scenario, peakflow and median flow changed little compared to the +0 °C scenario (5 ± 3 and 5 ± 1 days, respectively).

Predicted biofilm response

When VIC-generated hydrologic metrics were applied to the regression equation linking AFDM and hydrology, shifts in peakflow timing were predicted to increase summer AFDM relative to the baseline scenario (i.e. +0 °C; Fig. 4a–c). When averaged across years, AFDM was nominally higher ($12\% \pm 6$; mean \pm SE) in the +1 °C

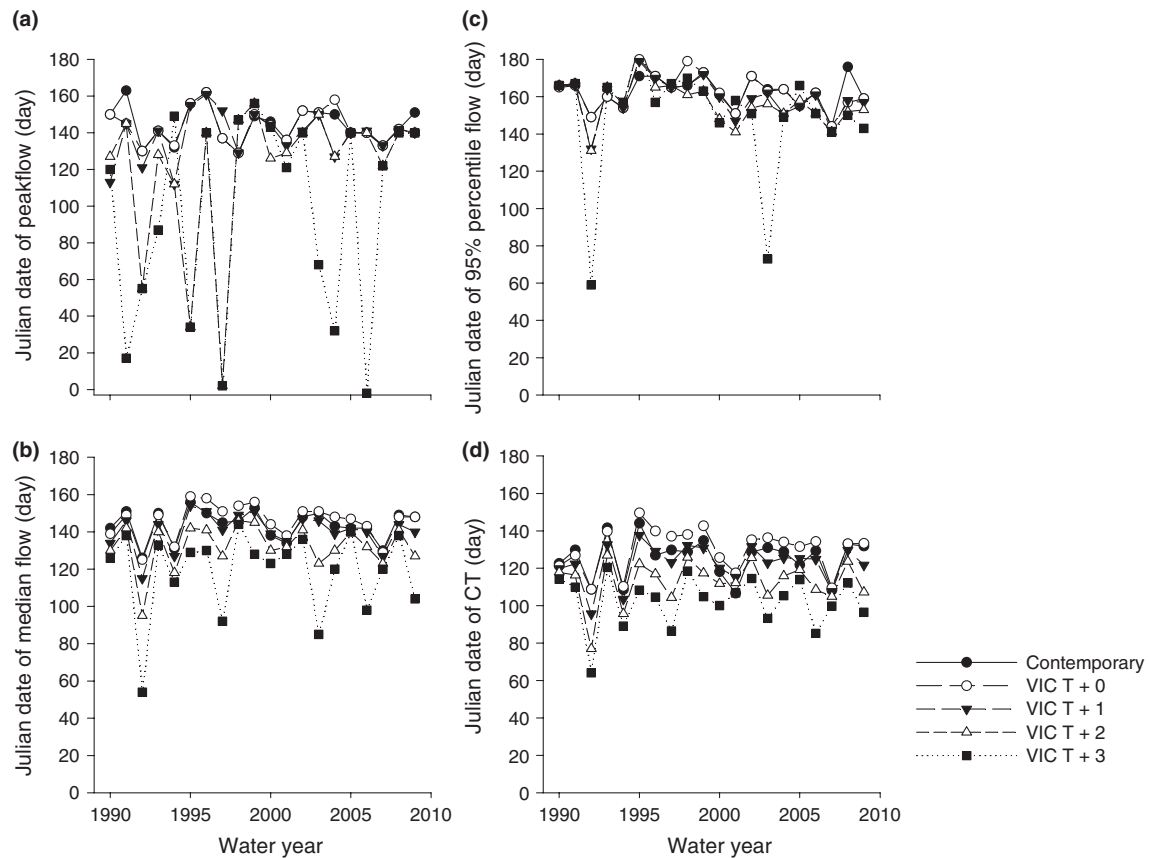


Fig. 2 Julian date of (a) peakflow, (b) median flow, (c) 95% percentile flow and (d) centre of mass (CT) for Big Creek, which were calculated from the contemporary hydrograph and the variable infiltration capacity (VIC) model under four temperature scenarios (+0, +1, +2 and +3 °C). Dates calculated based on water year, but the Julian date values on the *y*-axis are labelled based on calendar year. In the VIC +3 °C scenario, the peakflow date of 363 was converted to -2 because it was a date in the previous calendar year.

scenario, but 19 of the years had 90% prediction intervals that overlapped baseline predictions (Fig. 4a). In the +2 °C scenario, AFDM was 52% (± 20) higher than in the +0 °C baseline scenario. Also, 15% of the years had biomass that exceeded the prediction intervals and were more than twice the baseline levels (Fig. 4b). On average, biofilm AFDM in the +3 °C scenario was 103% (± 29) higher than in the baseline +0 °C scenario and outside the prediction intervals for 40% of the years (Fig. 4c). Furthermore, 30% of the years exhibited levels that were more than twice the baseline. When calculated across years and compared to the baseline scenario, interannual variability of AFDM was *c.* 2.9 and 3.0 times greater in the +2 and +3 °C scenarios, respectively (Fig. 5). If these biofilm responses were maintained throughout the summer, hydrologic shifts would be expected to increase not only biofilm AFDM but also its interannual variability during the summer months.

Although hydrologic shifts were predicted to alter average chl-*a*, responses substantially overlapped baseline (i.e. +0 °C) in many of the years. When averaged

across years, shifts in the timing of median flows under the +1 °C scenario slightly increased chl-*a* ($18\% \pm 2$, mean \pm SE), but prediction intervals in all years exhibited substantial overlap with the baseline (Fig. 4d). Chl-*a* increased under the +2 and +3 °C scenarios compared to the baseline ($46\% \pm 6$ and $90\% \pm 15$, respectively), but prediction intervals overlapped baseline in all years (Fig. 4e,f). The interannual variability of chl-*a* was similar in the +1 and +2 °C scenarios, but was *c.* 1.3 times more variable in the +3 °C scenario compared to the +0 °C scenario (Fig. 5).

Discussion

Predicted biofilm responses to hydrologic change

Our integration of hydrologic models and long-term ecological data indicates that flow regime shifts expected under changing climate could approximately double biofilm AFDM during the summer in snowmelt-dominated catchments. In particular, earlier peakflows may

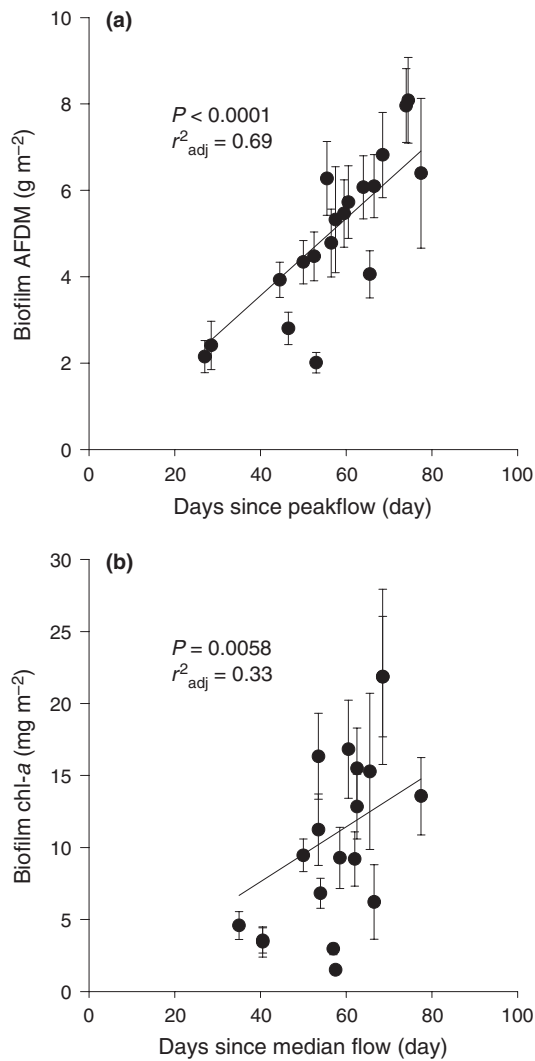


Fig. 3 Relationships between contemporary hydrologic metrics for Big Creek (see Fig. S2) and biofilm (a) ash-free dry mass (AFDM) and (b) chlorophyll-*a* (mean \pm SE) during the summer. Each data point is an average of *c.* 30 samples from six tributaries of Big Creek, Idaho.

allow biofilm to initiate growth earlier than is observed under contemporary hydrologic regimes, effectively lengthening the growing season (Fig. 6), as has been observed for terrestrial plants (Cleland *et al.*, 2007). Inter-annual variability of biofilm AFDM could also be up to three times greater under these scenarios. Biofilm chl-*a* responded similarly to hydrologic shifts, but it was not different from baseline in many of the years because of overlapping prediction intervals. As hydrology can regulate biofilm biomass (Larned, 2010), others have asserted that hydrologic shifts will affect stream food webs (Meyer *et al.*, 1999; Woodward *et al.*, 2010), but such effects have not been quantified previously. We show that climate-induced shifts in hydrologic regimes may change the

amount and temporal variability of this basal resource, with probable implications for food webs in snowmelt-dominated streams.

Potential effects on biofilm quality

Differences in responses by AFDM and chl-*a* suggest the potential for hydrologic shifts to alter seasonal patterns of biofilm quality for consumers. For instance, AFDM measures living and senesced organic matter of assorted types, including both autotrophs and heterotrophs, but chl-*a* is a relative index of living autotrophic biomass and can be positively related to biofilm nutrient content (Frost *et al.*, 2005; Hill *et al.*, 2009; Fanta *et al.*, 2010). Because the relative importance of these components can change during biofilm succession, biofilm quality can similarly change through time, such that quality can be relatively greater during early successional stages (Fisher *et al.*, 1982). If earlier peakflows lead to earlier initiation of biofilm accrual, it may affect succession and the timing of peak biofilm quality (Fig. 6). For instance, under warming scenarios, AFDM was well above baseline in many years when chl-*a* was not. Thus, hydrologic shifts may increase the relative contribution of detritus and heterotrophic microbes during these summers, potentially reducing biofilm quality. However, the predicted response for average chl-*a* sometimes exceeded that of AFDM (e.g. 2009), suggesting that summer biofilm quality could increase in other years. This, in combination with the greater interannual variability of AFDM observed in the +2 and +3 °C scenarios, indicates that biofilm quality may become less predictable under future conditions.

Although our sampling occurred in the summer, indirect evidence leads us to postulate that quality could increase during the winter and spring (Fig. 6). Under a snow-dominated hydrology with peakflow occurring in late spring, senesced material, which accumulated during the previous growing season and may be of lower quality, would not be scoured until spring. If a shift to a rain-dominated hydrology exported senesced material in the winter, faster recovery of actively growing algae (e.g. Biggs *et al.*, 1999) may increase their relative contribution during a time period previously dominated by lower-quality detritus. Although the effects could be ephemeral if AFDM continued to increase and chl-*a* levelled off, these results suggest to us that hydrologic shifts could alter seasonal patterns of biofilm quality. On the other hand, algal phenology and competitive interactions can be linked to temperature and light (Steinman & McIntire, 1986; DeNicola, 1996; Hill, 1996). Thus, earlier peakflows may decouple thermal and light regimes from contempo-

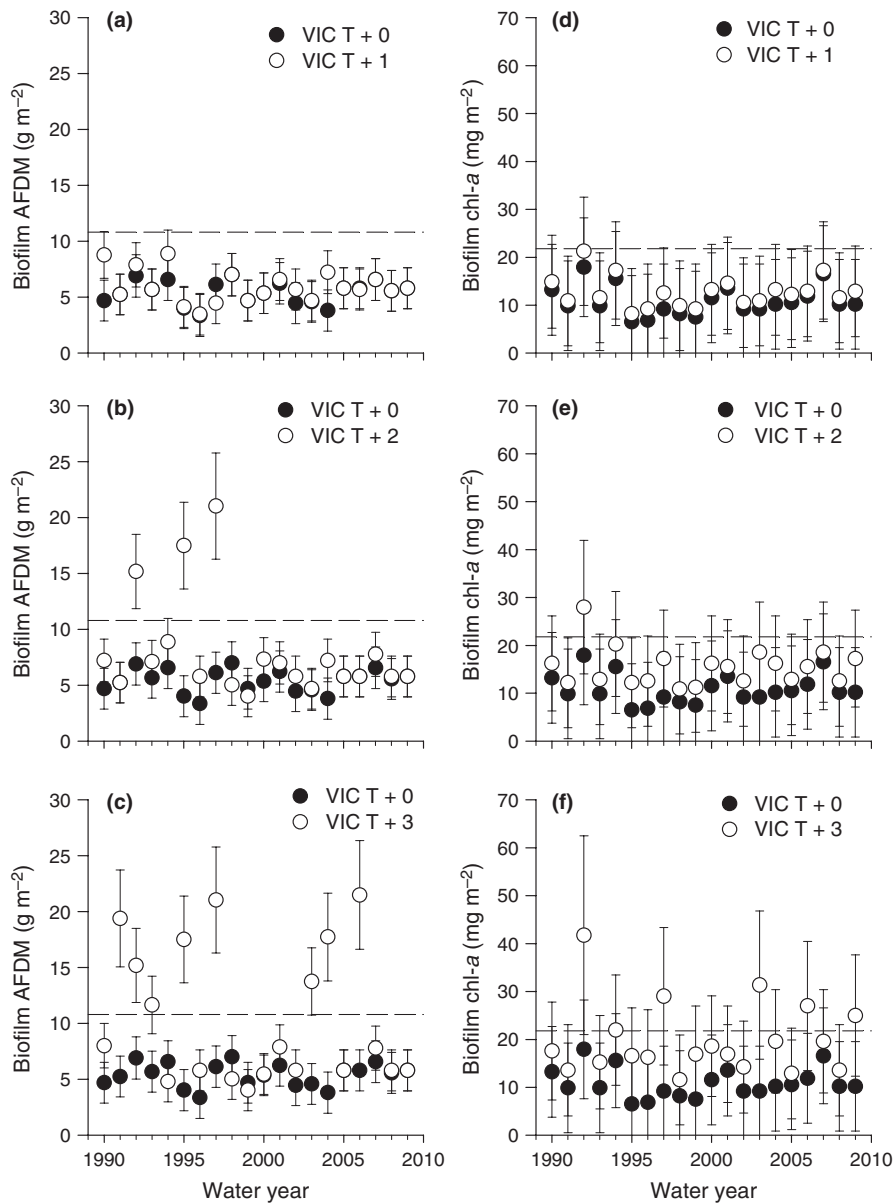


Fig. 4 Predicted biofilm (a–c) ash-free dry mass (AFDM) and (d–f) chlorophyll-*a* (mean \pm 90% prediction intervals) under four temperature scenarios (+0, +1, +2 and +3 °C). Values calculated using variable infiltration capacity-generated hydrographs (see Fig. 2) in the regression equations (see Fig. 3). The dashed line is the threshold at which AFDM or chl-*a* during the summer would be twice the average baseline levels (+0 °C).

rary hydrologic conditions, potentially altering the abiotic template for algal regrowth and the trajectory of biofilm succession. If such changes ultimately reorganised the composition of the biofilm assemblage and the new assemblage differed in cellular chl-*a* content from those currently observed, temporal patterns of biofilm quality under this new scenario may deviate from our predictions. Despite the potential influence of these other processes, our results indicate that hydrologic shifts will likely affect when biofilm biomass begins to accrue during the summer, with consequences for the timing of peak

biofilm biomass and quality in snowmelt-dominated catchments (Fig. 6).

Additional factors that may alter predicted responses of biofilm

Our analysis focussed on how expected climate-induced shifts in hydrologic regimes may alter biofilm biomass; however, other factors are likely to modify the linear relationship between biofilm and hydrology that was observed under contemporary ecological conditions and

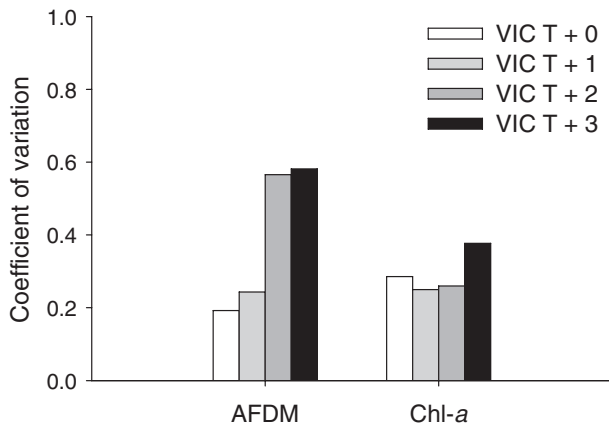


Fig. 5 Interannual variability of biofilm (a) ash-free dry mass (AFDM) and (b) chlorophyll-*a* during the summer. Calculations are based on biofilm predictions under four temperature scenarios (+0, +1, +2 and +3 °C) across the 20-year study period (see Fig. 4).

used to generate our predictions. In particular, climate change is associated with environmental changes that are likely to occur with flow regime shifts and have consequences for stream biofilm (e.g. increased wildfire activity, alteration of nutrient inputs and stream warming; Campbell *et al.*, 2009; Wenger *et al.*, 2011; Westerling *et al.*, 2011; Moritz *et al.*, 2012). For instance, wildfire can increase light flux and biofilm biomass (Minshall, Brock & Varley, 1989); thus, estimates may be conservative if climate change increases wildfire activity as projected (Westerling *et al.*, 2011). Conversely, post-scour recovery of primary production can be slower in the winter than in the summer due to seasonal differences in light and thermal regimes (Uehlinger, 2000). Thus, shifts of peak-flow from spring to winter observed in the +2 and +3 °C scenarios may temper the magnitude of our predicted increases due to changes in the abiotic template that slows algal growth. Higher air temperatures that lead to earlier peakflows are also likely to increase stream water temperatures (Wenger *et al.*, 2011), changes that are expected to have positive effects on primary producers (DeNicola, 1996; Yvon-Durocher *et al.*, 2010). Thus, warming may reinforce our predictions of increased biofilm biomass. However, stream warming has been projected to alter the composition of biofilm communities and increase the dominance of lower-quality cyanobacteria in some ecosystems (Carey *et al.*, 2012). This may attenuate increases in biofilm quality that we predicted based on earlier peakflows. Such a possibility is supported by recent evidence indicating that warming can increase the relative dominance of cyanobacteria in lake ecosystems (Kosten *et al.*, 2012), although the results from lotic ecosystems have been mixed (Wilde & Tilly, 1981;

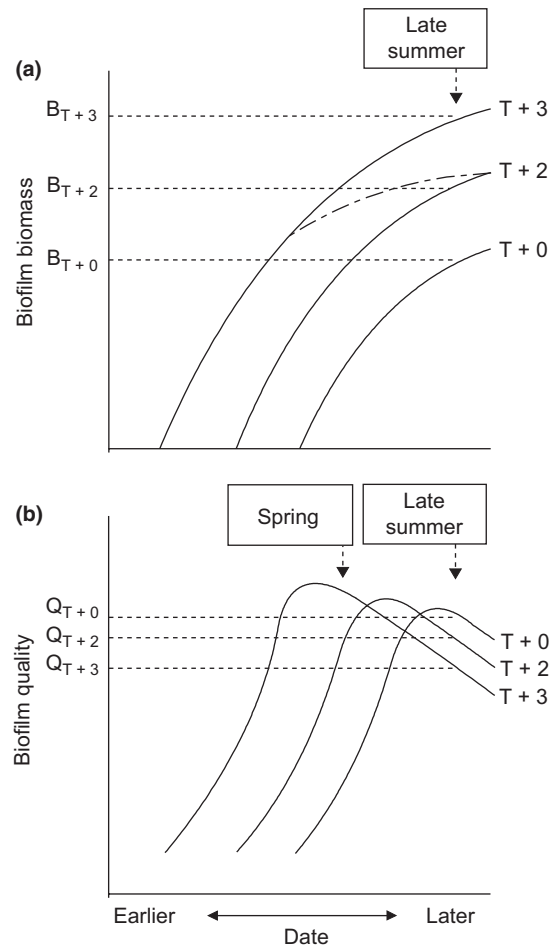


Fig. 6 Conceptual figure indicating the trajectory of biofilm biomass (a) and quality (b) responses (solid lines) under three temperature scenarios (+0, +2 and +3 °C). As predicted by the variable infiltration capacity model, warmer air temperatures are likely to lead to earlier peakflows, which could lead to an earlier initiation of biofilm growth. Therefore, warming would be predicted to increase biofilm ash-free dry mass (AFDM) and chlorophyll-*a* during the late summer; the magnitude of the AFDM response may be greater (see Fig. 4). Conversely, earlier peakflows associated with warming would be projected to decrease biofilm quality (i.e. chl-*a*-to-AFDM ratio) during the late summer, but may increase biofilm quality during the late winter or early spring. Other factors (i.e. grazing, light, sloughing, nutrient limitation) ultimately may limit biofilm biomass; therefore, biomass responses may level off under the warmest scenarios (as indicated by the dashed-dotted line in the +3 °C biomass scenario). The intersection of the dotted and solid lines for each temperature scenario indicates the level of biofilm biomass or quality predicted for a sampling date during the late summer. For clarity, biofilm responses are only shown during the time period immediately after peakflow in each scenario.

Gudmundsdottir *et al.*, 2011). Such contrasting results indicate a potential for warming to alter biofilm assemblages, but additional research is needed to understand these effects. Finally, mechanisms of biofilm sloughing can differ between periods of extended baseflow versus

periods of frequent spates (Uehlinger, Buhner & Reichert, 1996; Bouletreau *et al.*, 2006). Thus, the response of biofilm to earlier peakflows predicted by our analysis may be attenuated by sloughing and other factors (e.g. nutrient limitation and grazing; Biggs, 1996; Larned, 2010) that may not be directly linked to climate change, but may alter the biofilm–hydrology relationship once biofilm biomass reaches a certain threshold (Fig. 6).

The magnitude of increases we predicted (i.e. approximate doubling of AFDM) may not be fully attained due to other factors that could alter the biofilm–hydrology relationship observed under contemporary climate conditions. A full accounting of these effects would have required a more mechanistic modelling approach, but this was not feasible even with 20 years of ecological data. Despite the limitations of models like those we used, we were able to explain 70% of the variation in biofilm AFDM with a single hydrologic predictor variable. Thus, our effort identified a potentially important pathway by which climate change may lead to higher biofilm biomass in snowmelt-dominated stream ecosystems, representing an initial step in understanding biofilm responses to climate change. Future investigations aimed at clarifying mechanisms underpinning this relationship would help to assess confidence in predictions based on this or similar models. Furthermore, the incorporation of additional changes that may occur along with climate-induced alteration of hydrology (e.g. changes in nutrient dynamics, stream temperature and riparian vegetation) and potential shifts in biofilm assemblages would provide further insight into biofilm responses. Nevertheless, *a priori* forecasts of basal resource responses like those we present here are an important first step in quantifying predictions for organisms and food webs in streams.

Potential effects on consumers

Biofilm can be a preferred resource for many stream animals (e.g. versus leaf detritus; McNeely, Finlay & Power, 2007), and it can increase their growth rates (Mihuc & Minshall, 1995). Thus, shifts in biofilm quantity, quality and temporal variability could affect consumer populations. For example, spring is an important time for aquatic insect development as they prepare for adult emergence, which can peak between June and July in these streams (Malison & Baxter, 2010). Because higher food quality can increase growth rates even at low levels of resource availability (Boersma & Kreutzer, 2002), earlier peakflows may increase biofilm quality and insect growth rates at a critical time. On the other hand, higher temporal variability predicted by our model suggests that biofilm

quantity and quality could be less predictable in the future, with possible negative consequences for higher trophic levels. Effects of altered biofilm dynamics could also be influenced by direct impacts of hydrologic change on consumers, as egg-laying and emergence can be timed to avoid predictable spring run-off. Hydrologic shifts can have direct positive, negative or neutral effects on consumers, depending on a taxon's ability to adapt to the less predictable peakflows expected with climate change (Harper & Peckarsky, 2006; Poff *et al.*, 2010). These more direct effects of hydrologic change on consumers or the potential shifts in biofilm assemblages discussed above could attenuate or reinforce responses to shifts in biofilm quantity and quality, but further studies are needed to assess possible interactions.

*Contrasting responses of AFDM and chl-*a**

Our analysis indicated that AFDM exhibited a stronger and less variable statistical relationship (i.e. higher r^2_{adj}) with hydrologic change than chl-*a*. Assessing the mechanism underlying this difference was outside the scope of this study, but previous evidence does offer a biological explanation for these results. Differences may have been related to greater resistance and resilience of chl-*a* to scour associated with highflow and particle abrasion (Biggs & Close, 1989; Biggs *et al.*, 1999). For instance, 59% of floods in New Zealand streams reduced chl-*a* with an average decline of 8%, but 74% of floods reduced AFDM with an average decline of 21% (Biggs & Close, 1989). Conversely, AFDM is more resistant in other ecoregions (Fisher *et al.*, 1982), probably because light, temperature and nutrients can alter responses of AFDM and chl-*a* to scour (Biggs *et al.*, 1999). Chl-*a* can also be more resilient, as evidenced by its recovery within 6 days post-scour in New Zealand streams, whereas AFDM exhibited only moderate recovery even 18 days post-scour (Biggs *et al.*, 1999). As our sampling of biofilm was >27 days post-peakflow and >35 days post-median flow, chl-*a* growth may have already plateaued. AFDM recovery can be slower; thus, it may have been still accumulating when sampling occurred. Finally, algal species can differ in chl-*a* content and algal communities can undergo taxonomic succession post-scour due to seasonality (Fisher *et al.*, 1982). Thus, differences in AFDM and chl-*a* responses could also be related to shifts in the relative dominance of taxa that differ in chl-*a* content.

In conclusion, our integration of a 20-year ecological data set and hydrologic models suggests that biofilm biomass during the summer and interannual variability, as measured by AFDM, would increase with hydrologic

shifts expected under changing climate in streams whose hydrology is presently dominated by snowmelt. Average chl-*a* exhibited similar increases; however, responses substantially overlapped the baseline scenario in most years. The temporal dynamics of biofilm growth and succession may also be affected by predicted shifts of peakflow from late spring to early spring or even winter. Therefore, hydrologic shifts may affect the seasonal dynamics of biofilm quality by altering the relative dominance of living versus senesced organic matter. Because biofilm is an important resource in many streams, such changes in its quantity, quality and associated temporal variability could have considerable implications for sustaining stream productivity under future climate scenarios. Our analysis therefore identified a potentially important pathway by which climate change may alter food webs in snowmelt-dominated streams. Such quantitative predictions regarding the biomass and productivity responses of basal resources are needed to forecast food-web responses to climate change. Our analysis represents only an initial step in quantifying these effects because other ecological changes are projected to occur with climate-induced hydrologic change (Campbell *et al.*, 2009; Wenger *et al.*, 2011; Westerling *et al.*, 2011; Moritz *et al.*, 2012) and are likely to affect predicted biofilm responses. This highlights the need for similar assessments that incorporate the effects of these additional factors (e.g. stream warming and increased wildfire activity) across multiple trophic levels and ecosystem types.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods used to reconstruct and predict the hydrology of Big Creek, Idaho.

Figure S1. Locations of the six study streams (Cave, Cliff, Cougar, Goat, Pioneer and Rush Creeks) in the lower Big Creek catchment, Idaho.

Figure S2. Comparison of the VIC-generated hydrograph for the +0 °C scenario and the contemporary hydrograph reconstructed using a multiple linear regression (MLR) model.

Figure S3. Linear regressions comparing the timing of flow metrics (peakflow, median flow and centre of mass) for the contemporary hydrograph and the VIC +0 °C scenario.

Table S1. Gauging stations used to reconstruct discharges in Big Creek, Idaho.

Table S2. Root mean square error (RMSE) for four candidate models that reconstructed the contemporary discharge in Big Creek, Idaho.

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