Freshwater mussel growth-increment chronologies and relationships with stream discharge and temperature in the Pacific Northwest, USA

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Summary

1. Using dendrochronology techniques, three chronologies are developed in western Oregon using growth-increment widths from valves (shells) of freshwater mussels (*Margaritifera falcata*). Mussels were collected in the summer of 2006 in the Willamette River near Albany, OR (Albany), in the Middle Fork of the Willamette near Dexter Dam (Dexter), and Steamboat Creek in the Umpqua River basin (Steamboat).
2. Growth was highly synchronous among individuals within each site, facilitating the use of crossdating to ensure that all growth increments were assigned the correct calendar year. Final chronologies spanned 19 to 26 years in length and shared at least some degree of synchrony, though the correlation ($r = 0.6$; $p = 0.01$) between Dexter and Steamboat was by far the strongest.
3. All three chronologies negatively related to instrumental records of discharge, particularly Dexter ($r = -0.74$; $p < 0.001$) and Steamboat ($r = -0.86$; $p < 0.001$). Correlations with water temperature in terms of degree days, maximum, and mean temperature as well as air temperature were consistently positive but much weaker.
4. In a reconstruction of discharge at Steamboat Creek using stepwise linear regression, the regional Palmer Drought Severity Index (PDSI) had a partial R^2 of 0.78 while that for the Steamboat mussel chronology was substantially lower at 0.05. PDSI extended to 1895 and was a much stronger predictor of discharge than the mussel chronology. Our findings suggest opportunities for application of

mussel chronologies for reconstructing historical environmental conditions may be very limited.

5. From an ecological perspective, freshwater mussels represent a valuable indicator of biological response to climate, especially discharge, in freshwater systems. We found that responses to climate change can be very site-specific. This underscores the complex nature of biotic responses to climate change and the need to understand both regional and local processes.

Introduction

Baseline estimates of the historical range of variability in ecological systems provide critical data for evaluating current trends and establishing goals for restoration (Landres, Morgan & Swanson, 1999). Unfortunately, such information is unavailable for many systems due to the absence of long-term instrumental records or suitable proxies for reconstructing past conditions. This is particularly true of rivers, for which instrumental records are scarce (Stokstad, 1999) and the dynamic nature of fluvial processes can easily obscure or erase the signatures of past events (Miller et al. 2003). Consequently, lack of information on the natural variability of rivers poses significant obstacles to managing water resources in the face of rapid contemporary and potential future changes (National Research Council 2004).

In terrestrial systems, tree-ring data have been widely used to reconstruct various aspects of climate, disturbance, and community dynamics including droughts, snowpack, air temperature, windstorms, fires, and successional trends (Fritts, 1976, Speer *et al.*, 2001, Swetnam & Betancourt, 1990). Apart from trees, a wide range of long-lived animal species including marine and freshwater fish and bivalves also form annual growth increments, and only recently have tree-ring techniques been applied to address analogous issues in aquatic environments (Black, Boehlert & Yoklavich, 2008a, Rypel, Haag & Findlay, 2008, Strom *et al.*, 2004). In rivers, freshwater mussels are among the most useful species for chronology development given their longevity and the clarity of their growth increments (Helama & Nielsen, 2008, Rypel *et al.*, 2008, Schöne *et al.*, 2004, Schöne *et al.*, 2007). Freshwater mussel growth-increment chronologies can be annually resolved and of a quality comparable to that of tree-ring chronologies (Rypel *et al.*, 2008). Furthermore, freshwater mussel chronologies relate to broad-scale climate pattern including air temperatures, precipitation, and the El-Nino Southern Oscillation (Schöne *et al.*, 2004, Schöne *et al.*, 2007), as well as local variability in stream discharge (Rypel *et al.*, 2008, Rypel, Haag & Findlay, 2009).

Our overall objectives in this study were to critically evaluate associations between shell growth-increment width in the western pearlshell (*Margaritifera falcata*) and environmental conditions, and the potential of increments as proxies of historical variability in rivers. We specifically addressed these objectives in four stages: 1) we first evaluated the feasibility of applying tree-ring techniques to build high resolution, multi-decadal increment chronologies of mussels that captured variability on a range (inter-annual to decadal) of timescales; 2) next, we related these chronologies to long-term records of stream discharge and water temperatures available within the same river system, 3) we related both shell increment chronologies and local environmental records to regional indicators of climate to better resolve associations between local variability and regional climatic processes, and 4) we used growth-increment chronologies and instrumental climatic records as proxies reconstruct past environmental variability.

Methods

Collection of mussels.

In the summer of 2006 *M. falcata* were collected from two localities in the Willamette River basin. One collection (Albany) was made in the river near Albany, Oregon directly upstream of the confluence of the Calapooia River (N 44°38’26”; W 123°6’50”). A second collection (Dexter) was taken in the Middle Fork of the Willamette River approximately 3 km downstream of Dexter Reservoir at Elijah Bristow State Park (N 43°56’38”; W122°50’00”) (Figure 1). The latter site was chosen for its proximity to U.S. Geological Survey (USGS) gage 14150000, which provided long-term data on stream discharge and temperature. Mussels were also collected from a single locality the Umpqua River basin. This collection (Steamboat) was immediately downstream of USGS gage 14316700 (N 43°21’00”; W 122°43’40”) in Steamboat Creek, where long-term records of stream discharge and summer maximum temperatures were also available (Figure 1). We attempted to select the largest and presumably oldest individuals within each site with local populations we conservatively estimated to represent $>10^3$ individuals. This was done to avoid possible impacts of collecting 30-40 individuals per site.

Sample preparation and visual crossdating.

Mussel valves were embedded in JB Qwik Weld resin (J-B Weld, Co, Sulphur Springs, TX)[1] and thin-sectioned using a diamond lapidary saw. Sectioning followed the axis of minimum growth from the umbo to the ventral margin, perpendicular to surface growth increments. A total of three thin-sections approximately 0.5 mm in thickness were taken from both the left and right valve, mounted on glass slides, and polished using 2000 grit sandpaper and 0.5 um lapping film. One section from each valve was stained with Mutvei's solution in an attempt to increase the visibility of annual growth increments (Schöne *et al.*, 2005). Growth increments in the prismatic layer of the valves were used in chronology development due to their consistency, contrast, and the fact that the prismatic layer would not have been resorbed or altered by the mussel after it had formed. The clearest thin sections from the oldest individuals were then selected for chronology development.

Transmitted light was best for viewing the growth increments, though reflected light produced superior results in a small subset of samples. We found that staining with Mutvei's solution enhanced growth increment contrast in samples from Albany, but accented a greater degree of "noise" (sub-annual rings and stress lines) in Dexter samples (Figure 2A). Dexter specimens were best viewed without any chemical treatment. Steamboat samples were difficult to view stained or unstained or by using transmitted or reflected light, so we attempted acetate peels as an alternative preparation technique that is commonly employed in marine bivalves (Black *et al.*, 2008b). For this sample set, acetate peels were made by i) submerging the thin section in 1% HCl for one minute, ii) thoroughly rinsing and drying the specimen, iii) saturating the surface of the specimen

[1] Use of trade or firm names is for reader information only and does not constitute endorsement of any product or service by the U.S. Government.

with acetone, iv) firmly pressing a sheet of cellulose acetate film onto the soaked surface of the specimen, and v) removing (peeling off) the acetate after approximately fifteen minutes. In this process, the acetone melted the acetate into the etched surface of the thin section, capturing a three-dimensional impression of the growth increments. Peels greatly increased the clarity of the Steamboat samples and were viewed using transmitted light (Figure 2B).

Within each collection (Albany, Dexter, and Steamboat Creek), samples were visually crossdated using the “list year” technique, in which synchronous patterns were matched among samples, working back through time beginning at the marginal growth increment formed during the known calendar year of capture (Yamaguchi, 1991). Crossdating ensured that all growth increments had been correctly identified and assigned the correct calendar year.

Once visual crossdating was complete, growth increment widths were measured using the program ImagePro Plus v. 6.0 (Media Cybernetics, Silver Spring, Maryland). Images were captured with a Leica DC300 7.2 megapixel digital camera attached to a Leica MZ9$_5$ dissection scope. For each sample, multiple overlapping pictures were taken and tiled together into a single panorama. Growth increments were then measured continuously from the margin to as close to the umbo as possible, though innermost increments were often excluded due to erosion of the prismatic layer. When possible, one axis was measured per valve (left and right) for a total of two measurement time series per individual.

Statistical analysis of growth increments.

At each site, crossdating was statistically verified using the International Tree-Ring Data Bank Program Library program COFECHA, available thorough the University of Arizona Laboratory of Tree-Ring Research http://www.ltrr.arizona.edu/pub/dpl/ (Grissino-Mayer, 2001, Holmes, 1983). This procedure involved isolating high-frequency variability in each set of measurements via the process of detrending, and then cross-correlating the detrended measurements to verify that all samples aligned with one another. In COFECHA, detrending was accomplished by fitting each set of mussel measurements with a cubic spline set at a 50% frequency response of 22 years, a wavelength that provided optimal crossdating verification results in splitnose rockfish and Pacific geoduck (Black, Boehlert & Yoklavich, 2005, Black *et al.*, 2008b). Once fitted, each set of mussel measurements was divided by the values predicted by the cubic spline, thereby removing low-frequency variability, homogenizing variance, and equally weighting each set of measurements to a mean of one (Grissino-Mayer, 2001, Holmes, 1983). Each detrended set of mussel measurements was then correlated with the average of all other detrended sets of mussel measurements in the sample. Through this process, the high frequency growth pattern of each individual was compared to the high frequency growth pattern of all other individuals. Isolating only the high frequency, serially independent growth pattern prevented spuriously high correlations among individuals, and also mathematically mimicked the process of visual crossdating. Any measurement time series with unusually low correlations were double checked for errors.

After verifying crossdating, we developed a master chronology for each site by detrending the original mussel measurement time series with negative exponential functions. Detrending with negative exponential functions removed age-related growth declines while preserving any remaining low-frequency variability, much of which could have been induced by climate. At each site, all detrended series were then averaged into a master chronology using a biweight robust mean to reduce the effects of outliers (Cook, 1985). All chronology development was conducted using the program ARSTAN (developed by Ed Cook and Paul Krusic; available at http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html ; (Cook, 1985). The quality of the final chronologies was quantified using the Expressed Population Signal (EPS) statistic, which describes how well the sample means represents the mean of the theoretical population from which it was drawn. Though there is no significant threshold for this statistic, an EPS value of 0.85 or greater is considered adequate (Wigley, Briffa & Jones, 1984). Also, mean sensitivity was calculated to describe the high-frequency, between-year growth variability, which for any pair of adjacent years ranges from zero (each year is the same width) to two (when a non-zero value is adjacent to a zero value; i.e. a missing increment) (Fritts, 1976).

Local instrumental records.

Records of mean daily discharge and water temperature were obtained for the Middle Fork of the Willamette River (USGS gage 14150000), just upstream of where the Dexter mussel collection was made. Daily means of discharge ($m^3 \cdot s^{-1}$) were summarized as means for water years (1 October to 30 September) from 1 October 1978 to 30 September 2006. We also summarized the maximum of daily mean discharge in each water year. Discharges from gages downstream in the main Willamette River near Harrisburg Oregon (USGS gage 14166000) and in close proximity to the collection at

Albany (USGS gage 14174000) were also summarized for comparative purposes, but annual means among all three Willamette River gages (i.e. gages 14150000, 14166000, 14174000) were highly correlated (Pearson's $r \geq 0.98$). Thus, only the Middle Fork of the Willamette River gage was considered for subsequent analyses. Long-term water temperature data were available from this locality as well, and daily means (^{o}C) were summarized across water years. Annual summaries included the highest mean daily temperature recorded and number of days within the water year that mean daily temperatures equaled or exceeded 10 ^{o}C. Temperature records contained missing information in many years and daily traces of temperatures were examined to ensure annual maximums were captured within a given water year. If not, years with insufficient data were excluded from the analysis. To estimate the number of days within the water year equal to or greater than 10 ^{o}C (henceforth, dd10), we totaled the number of days with temperature observations and only selected years with at least 293 days of non-missing data. The number of observations used in calculating dd10 was carefully tracked in subsequent analyses to ensure years with less complete information did not bias results.

In Steamboat Creek, stream discharges were summarized from USGS daily records as described above for Willamette River gages. Temperature data were obtained from the Umpqua National Forest (Mikeal Jones and Deborah Gray, U.S. Forest Service, personal communication), and represented observations of summer maximum temperatures recorded from 1969-2005. The temperature sampling site was just upstream of the stream discharge gage and located upstream of the confluence with Canton Creek, a major tributary. Thus, stream discharge records indicated combined discharges of

Canton and Steamboat Creeks, whereas the temperature record we used only included Steamboat Creek. We examined 18 years of summer maximum temperatures provided by the Umpqua National Forest for both streams, just upstream of their respective confluence. Summer maximum temperatures were highly correlated (r = 0.76), but were on average 1-3^{o}C warmer in Steamboat Creek than Canton Creek. Temperatures from Steamboat Creek only were used to relate to mussel growth chronologies because it is larger than Canton Creek and had more complete time series of data. Using the Steamboat Creek temperature data, we selected for inclusion in subsequent analyses the single-day maximum temperature observed in each year, given the available data. This single-day instantaneous maximum temperature was different than the two metrics available from the Middle Fork Willamette River, which were based on summaries of daily means (maximum of daily mean, dd10). Different measures of annual maximum temperatures are typically highly correlated, whereas measures involving summaries of degree-days are often distinctive (Dunham et al. 2005). In addition, precipitation, mean air temperature, and Palmer Drought Severity Index (PDSI) were obtained from the NOAA National Climatic Data Center for Oregon, Division Two via [http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp]. PDSI is based on measures of precipitation, evapotranspiration, and soil properties with positive values indicating wet conditions and negative values indicating drought (Palmer, 1965).

Analysis of climate-growth relationships.

Annually resolved master chronologies of mussel growth from each site (Albany, Dexter, Steamboat) were related using Spearman rank correlation to annual summaries of stream temperature and discharges from nearby instrumental records, and climate indices. We began by examining the degree of synchrony among the three growth chronologies, and then related each to local stream discharges and temperatures, and finally to climate indices. All analyses were based on patterns of variability among years. In this work, we did not attempt to identify sub-annular (e.g., monthly, seasonal) associations between growth chronologies and environmental variables.

Reconstruction of historical environmental conditions.

The Steamboat freshwater mussel chronology and annual Palmer Drought Severity Index were entered into stepwise linear regression ($p = 0.05$ to enter) to predict Steamboat river discharge. The model was evaluated with Mallow's Cp, variance inflation factors, and Durbin Watson tests of autocorrelation in model residuals.

Results

Development of growth chronologies

Strongly synchronous growth patterns occurred among individuals within each collection, allowing for crossdating even with these relatively short-lived individuals (Figure 3A,B). We found no "missing" rings in any of the individuals used in chronology development, though some discarded samples were severely damaged and contained highly irregular and potentially incomplete growth patterns. Even the samples that were used in the final chronologies contained frequent "checks" or "false rings." These checks were generally limited to the prismatic layer, and true increments were identified by their tendency to extend through nacreous layer. Ultimately, crossdating provided the final test for distinguishing the most challenging checks and verified that all growth increments had been correctly identified.

Statistical verification of crossdating revealed highly significant correlations among samples, with inter-series correlations ranging from 0.62 to 0.71 (Table 1). Mean sensitivity, an index of year-to-year variability, was somewhat more variable among sites. Analysis of variance with Tukey's LSD mean separation indicated all sites significantly ($p < 0.05$) differed from one another, ranking from Albany which had the lowest mean sensitivity to Steamboat Creek, which had the highest year-to-year variability (Table 1). Many specimens experienced erosion through the prismatic layer and into the nacreous layer, obscuring the earliest growth increments. Two individuals from Albany were well over 40 years in age, but had experienced such significant damage that they were unsuitable for use in chronology development.

Negative exponential functions provided a good fit to the measurement time series from Albany and Dexter. However, for several individuals from Steamboat Creek negative exponential curves severely underestimated early growth and overestimated later growth, as observed during the detrending process in ARSTAN. In these cases, detrended time series contained spuriously high or low values, which could have affected the quality of the final chronology. To address this problem, we used a variation of Regional Curve Standardization in which we aligned all Steamboat Creek measurement time series with respect to age, and fit a single negative exponential function to the entire data set, described as $y = 9.9754\ e^{-0.1291*age}$. All measurement time series were then detrended using that single function. Though the chronology generated by fitting each measurement time series with a unique function differed minimally ($R^2 = 0.96$), we chose the chronology generated using a single function due to its more realistic accounting of age-related growth declines.

Final chronologies extended from 1978-2004 for Albany, 1981-2005 for the Dexter, and 1980-2003 for Steamboat Creek. The spans reported for all three chronologies included only that interval shared by a minimum of six measurement time series, the sample depth necessary to ensure EPS values greater than 0.85. In comparison to one another, all chronologies were positively correlated, yet the correlation between the Dexter and Steamboat Creek was by far the strongest (Table 2A).

Climate-growth relationships

With respect to the environment, all mussel chronologies positively related to indices of water temperature and negatively related to indices of stream discharge (Table 2B). Among the variables considered in this study, correlations were by far the greatest with discharge, especially mean discharge (Table 2B). These relationships with discharge were reflected by negative correlations with the Palmer Drought Severity Index, in which low values indicated low levels of soil moisture (Table2B). By contrast, correlations with indices of temperature were much weaker, with the exception of degree days to which the Albany chronology was positively correlated (Table 2B). Notably, correlations with discharge were the weakest for the Albany chronology in comparison to that of the other chronologies.

Reconstruction of historical environmental conditions.

The Steamboat freshwater mussel chronology and Palmer Drought Severity Index over the water year accounted for 83% of the variance in the Steamboat discharge data (Figure 5A). The relationship between actual and predicted discharge was linear, and residuals contained no significant autocorrelation (Durbin-Watson statistic of 1.802; 1st order autocorrelation of 0.048). Variance Inflation Factors were low for PDSI and the mussel chronology (VIF = 3.15 for each), indicating that multicollinearity among the predictor variables was not destabilizing the model. PDSI had the greatest partial R^2 of 0.78 ($p < 0.0001$), in comparison to an R^2 of 0.05 ($p < 0.02$) for the Steamboat chronology.

Discussion

Development of growth chronologies

Within each of the three freshwater mussel collections, growth among individuals was strongly synchronized, which facilitated crossdating and chronology development. Indeed, the level of synchrony as gauged by series intercorrelation was consistently high at each of the three sites and comparable to that found in tree-ring, Pacific rockfish, and Pacific geoduck chronologies developed elsewhere in the Pacific Northwest (Table 1) (Black *et al.*, 2008b, Black, 2009, Gedalof & Smith, 2001). Also, all three chronologies positively correlated with one another and shared the same general climate-growth relationships, but with several important differences, discussed below.

Climate-growth relationships

If climatic or other environmental conditions that drive growth are spatially correlated, patterns of growth should be synchronous between proximate locations, especially those within the same river system. However, relationships among chronologies at the three locations studied here did not appear to be a function of geographic proximity. Though Dexter and Albany both occurred in the same river system, the Steamboat and Dexter chronologies were more strongly correlated. This was in spite of the fact that the discharge regime within the Willamette River, where Dexter and Albany are located, is highly regulated whereas discharge in Steamboat Creek is unregulated (see also Rypel et al. 2008). Accordingly, differences in chronologies and their associations with climate may reflect the influence of local environmental variability on mussel growth.

All three growth chronologies positively correlated with local water temperatures, but Albany, and to a lesser degree, Dexter, related to dd10 and maximum daily temperature while Steamboat associated with instantaneous maximum daily temperature (Table 2). Relationships with discharge were much more consistent and robust, though correlations with Albany were markedly lower than Dexter and especially Steamboat. These differences in climate-growth relationships may in part have been due to variable lengths of mussel chronologies and instrumental records. For example, the Dexter chronology did not span the three coldest years observed in the instrumental records, and exclusion of certain years, especially those representing extreme events, could strongly influence climate-growth relationships. However, correlations among the chronologies were consistent with their relationships to local environmental variability. In particular, Dexter and Steamboat were much more strongly correlated to one another than with Albany, a pattern consistent with the chronologies' correlations to discharge.

With respect to climate-growth relationships, associations with temperature should be interpreted with caution. Even though Spearman rank correlations were significant, scatterplots illustrated that temperatures do not closely correspond on a linear scale (Figure 4). Chatters et al (1995) reported a much stronger relationship between mussel growth and temperature in the Columbia River Basin. However, this was based on a much smaller sample size, and there remains the possibility that the local environment was different from that at our sites. Temperature may well be more consistently limiting at higher latitudes and elevations than locations considered herein. For example, *M. margaritifera* samples in from northern Europe show more consistent associations with air temperatures (water temperature was not examined; Schöne *et al.*, 2004). Correlations with temperature at sites we sampled may also be an artifact of the inverse relationships between discharge and water temperature.

In contrast to water temperatures, growth chronologies at all sites in our study responded to stream discharge, a pattern that parallels the results of similar work on mussels in the southeastern United States (Rypel *et al.*, 2008). The consistent inverse relationships between growth and stream discharge may reflect the importance of streambed stability and potential dislodging of individuals during higher flow events (Howard & Cuffey, 2003, Rypel *et al.*, 2009, Howard & Cuffey, 2006). Even displacement of mussels through human handling has been shown to induce checks and depress growth rates in some species (Haag & Commens-Carson, 2008). At all three sites shell surfaces were often eroded and checks frequently occurred, suggesting that potentially stressful high-discharge events had occurred. One study (Schöne *et al.*, 2007) observed positive associations between summer precipitation and growth of *M. falcata* from a highly human-impacted stream. However, these results are difficult to evaluate since no metrics by which to evaluate crossdating accuracy or the signal-to-noise ratio were provided, and stream discharges resulting from precipitation were not directly examined. Overall, our results indicated that for freshwater pearlshell mussels in western Oregon, discharge exerted the greatest influence on growth.

Implications for climate reconstructions

The variable response of the three mussel chronologies to the physical environment (stream temperature, discharge) has implications for reconstructing climate. Though more research is required, this study suggests that use of mussel growth increments to estimate historical stream temperatures is questionable, especially in this region, or if extrapolations are to be made across broad geographic extents or time frames (e.g., Chatters et al. 1995). Second, it appears that freshwater mussels respond to stream discharges in ways that are qualitatively similar across species and regions in North America (Rypel *et al.*, 2008). Accordingly, changes to stream discharge regimes may be one of the most important physical factors influencing these species over longer time periods. Indeed, stream regulation was shown to disrupt associations between mussel growth and stream flow in the southeastern United States (Rypel *et al.*, 2008, Rypel *et al.*, 2009). Other work in the region on fishes has emphasized the importance of considering changes in both discharge and temperature in the context of future climate change (Crozier, Zabel & Hamlett, 2008, Mote *et al.*, 2003).

Whereas we found that freshwater mussel chronologies can be strongly tied to stream discharge, it was clear that other long-term climate indices may serve as better discharge proxies. For example, in our attempt to reconstruct discharge we found that the Palmer Drought Severity Index accounted for 78% of the variance in the Steamboat discharge record. In comparison, the Steamboat mussel chronology added a significant, yet modest, 5% to bring the total discharge variance explained to 83%. Thus, the Palmer Drought Severity Index could serve as a useful proxy for reconstructing discharges over longer timescales (e.g., >50 yr), with mussel growth chronologies potentially explaining additional variance over shorter timescales.

Despite this finding, mussels can still yield valuable data regarding stream history, particularly with respect to fine-scale variability. First, climate indices and precipitation are regional variables and would not detect local patterns. Also, major natural disturbances or significant human activity could alter the stream environment in ways that would not be captured by regional precipitation or air temperature data. For example local natural geomorphic events (e.g., floods or debris flows) and human impacts such as hydraulic mining, logging, or flow regulation could significantly affect freshwater ecosystems in ways that are not strongly reflected by broad-scale climatic indicators. In this context, freshwater mussels would be well suited to evaluate the impacts by comparing growth before and after the event or growth and affected versus unaffected regions.

Whereas mussels in this study provided relatively short chronologies, there may be opportunities to obtain longer chronologies from other locations or from historical collections. In Sweden, crossdating increments of living *M. margaritifera* with museum collections allowed the development of a partial 217-year freshwater mussel chronology sensitive to air temperatures (Schöne *et al.*, 2004). Sample sizes were low for much of the chronology due to a lack of available specimens, but this work illustrates the possible utility of historical samples. In theory, longer time series could be generated by sampling freshwater mussels preserved in sediments or ancient human middens (e.g., Chatters et al. 1995). Our experience in this work suggests that extending chronologies in such a manner may be possible, but only under a very limited range of conditions.

For the sites used in our study, crossdating unknown samples to living chronologies would be exceedingly difficult. Though the growth patterns were synchronous within sites we studied, the time series length, on average twenty years, was much too short to crossdate with "floating" (i.e. unknown date of recruitment or death) samples. In order to confidently extend a freshwater mussel chronology back in time using samples of unknown dates of origin, longer-lived samples (at least 100 years if tree-ring data are any indication) with clearly-defined increments would be required. *Margaritifera* spp. are among the longest-lived organisms in freshwater ecosystems, up to nearly 200 yr; (Helama & Valovirta, 2008, Ziuganov *et al.*, 2000), and such an approach may therefore be possible at some locations (Helama & Nielsen, 2008, Schöne *et al.*, 2004), though populations > 40 years in age are uncommon.

A second problem we encountered concerned the quality of the shells themselves. The majority of samples contained a large number of checks that would further complicate the process of crossdating. In addition, when we have examined freshwater mussel shells from ancient middens we have found them to be extremely challenging to measure, due to degradation in the prismatic layer. Given these problems, and variable climate-growth relationships we observed here, it seems unlikely that annually resolved, long-term (>100 yr) climate reconstructions (e.g., Chatters et al. 1995) can be developed with western pearlshell mussels in western Oregon.

Yet perhaps more important than climate reconstructions, freshwater mussels provide a unique opportunity to understand the multidecadal impacts of climate change in freshwater ecosystems (Hastie *et al.*, 2003, Mote *et al.*, 2003, Poff, 2002). In this study, the mussel chronologies underscore the importance of local environmental variability and site-specific climate-growth relationships. Though all chronologies were sensitive to discharge, the strength of the growth response to this variable was not equal among sites, underscoring the heterogeneous impacts of climate across the landscape. As the network of freshwater mussel chronologies is expanded throughout the region, they will undoubtedly provide valuable insight into the diversity and complexity of environmental regimes and climate-growth responses across the landscape. Such information will provide context as to how climate variability and change will affect these systems at a range of spatial scales. An important asset of these data is that they are not derived from models, but represent actual responses to past climate variability that could be used to refine estimates of climate-change impacts, especially as relates to discharge. Thus overall, these freshwater mussels represent a valuable data source regarding biological response to environmental variability in freshwater systems, establishing gradients of environmental variability across the landscape, and may also serve as a tool for climate reconstructions in limited situations.

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Figure Captions

Figure 1. Western Oregon study region and sampling location for the three freshwater mussel growth-increment chronologies, Albany, Dexter, and Steamboat. Insets show locations of USGS gages from which discharge and water temperature data were obtained.

Figure 2. Photograph of A) an Albany freshwater mussel thin section viewed with transmitted light. Section was stained using Mutvei's solution, B) a Steamboat Creek acetate peel viewed with transmitted light. Decades (the first being 2000) are dotted.

Figure 3. A) measurement time series for all Steamboat Creek freshwater mussel sampled B) detrended Steamboat Creek measurement time series (gray) and the Steamboat Creek master chronology (black). C) the Steamboat Creek, Dexter, and Albany freshwater mussel master chronologies. Minimum sample size for each chronology is six measurement time series.

Figure 4. Scatter plots of relationships between environmental variables and ring width index from *M. falcata* chronologies collected in western Oregon: Albany and Dexter chronologies vs. A) maximum mean daily temperatures and B) mean discharge over the water year for the Willamette River near Dexter Dam. The Steamboat chronology vs. C) maximum daily temperature (instantaneous) and D) mean discharge over the water year for Steamboat Creek.

Figure 5. A) Actual discharge and discharge predicted by a regression that includes the Steamboat mussel chronology and Palmer Drought Severity Index. B) Actual

discharge and predicted discharge. Gray shading denotes 95% confidence intervals on the prediction.

Table 1. Characteristics of growth chronologies for *M. falcata* chronologies developed for three locations in western Oregon (a); and summaries of measured physical characteristics at those sites (b).

a)

Location	Sample size[2]	Years recorded	Mean sensitivity[3]	Interseries correlation[4]
Dexter	18	1987-2005	0.24	0.71
Albany	16	1979-2004	0.19	0.67
Steamboat	23	1980-2003	0.34	0.62

b)

Location	Parameter	Years summarized	Mean	Range
Dexter	Mean annual discharge (m^3/sec)	1979-2005	83.26	51.74-131.98
	Number of days > 10°C	1979-1997, 2002-2005	188.43	144-246
	Maximum temperature (°C)	1979-1997, 2002-2005	16.7	14.70-19.5
Steamboat	Mean annual discharge (m^3/sec)	1979-2005	20.03	7.75-33.69
	Maximum temperature (°C)	1979-1991, 1993-1999, 2002-2005	25.14	20.56-26.82

[2] Number of measurement time series used to generate each chronology

[3] An index of high-frequency variability that ranges from 0 (no variability) to 2 (highly variable), as output by COFECHA

[4] The average correlation between each detrended measurement time series (using a 22-year cubic spline) and the average of all other detrended measurement time series as output by COFECHA

Table 2. Spearman rank correlations among *M. falcata* chronologies from Albany, Dexter, and Steamboat sites (a), and mussel chronologies and environmental variables including the regional Palmer Drought Severity Index and summaries of local water temperatures and discharges recorded from nearby locations (b). All p-values < 0.05 are in parentheses

a)

Location	Albany	Dexter
Dexter	0.20	--
Steamboat	0.35	0.60 (0.01)

b)

Parameter	Albany	Dexter	Steamboat
Palmer Drought Severity Index	-0.25	-0.62 (0.004)	-0.71 (<0.001)
Mean annual discharge	-0.46 (0.02)	-0.74 (<0.001)	-0.86 (<0.001)
Number of days > 10^{o}C	0.53 (0.01)	0.44	--
Maximum of mean daily temperature	0.43 (0.04)	0.30	--
Instantaneous maximum daily temperature	--	--	0.58 (0.005)

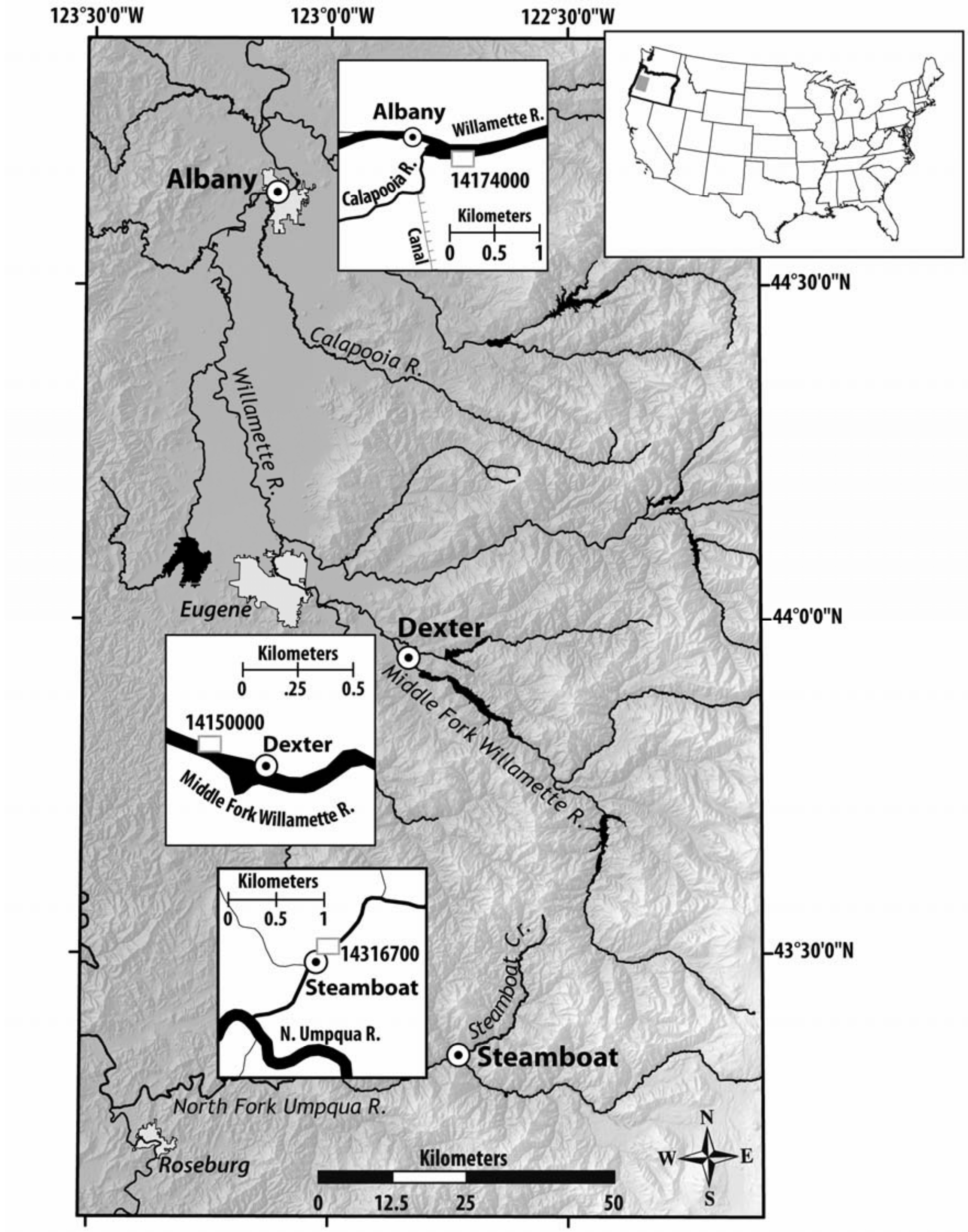

123°30'0"W
123°0'0"W
122°30'0"W
44°30'0"N
44°0'0"N
43°30'0"N
Albany
Willamette R.
Calapooia R.
14174000
Kilometers
0 0.5 1
Canal
Calapooia R.
Willamette R.
Eugene
Dexter
Kilometers
0 .25 0.5
14150000
Dexter
Middle Fork Willamette R.
Middle Fork Willamette R.
Kilometers
0 0.5 1
14316700
Steamboat
N. Umpqua R.
Steamboat Cr.
Steamboat
North Fork Umpqua R.
Roseburg
Kilometers
0 12.5 25 50
N
W
E
S

Figure 1

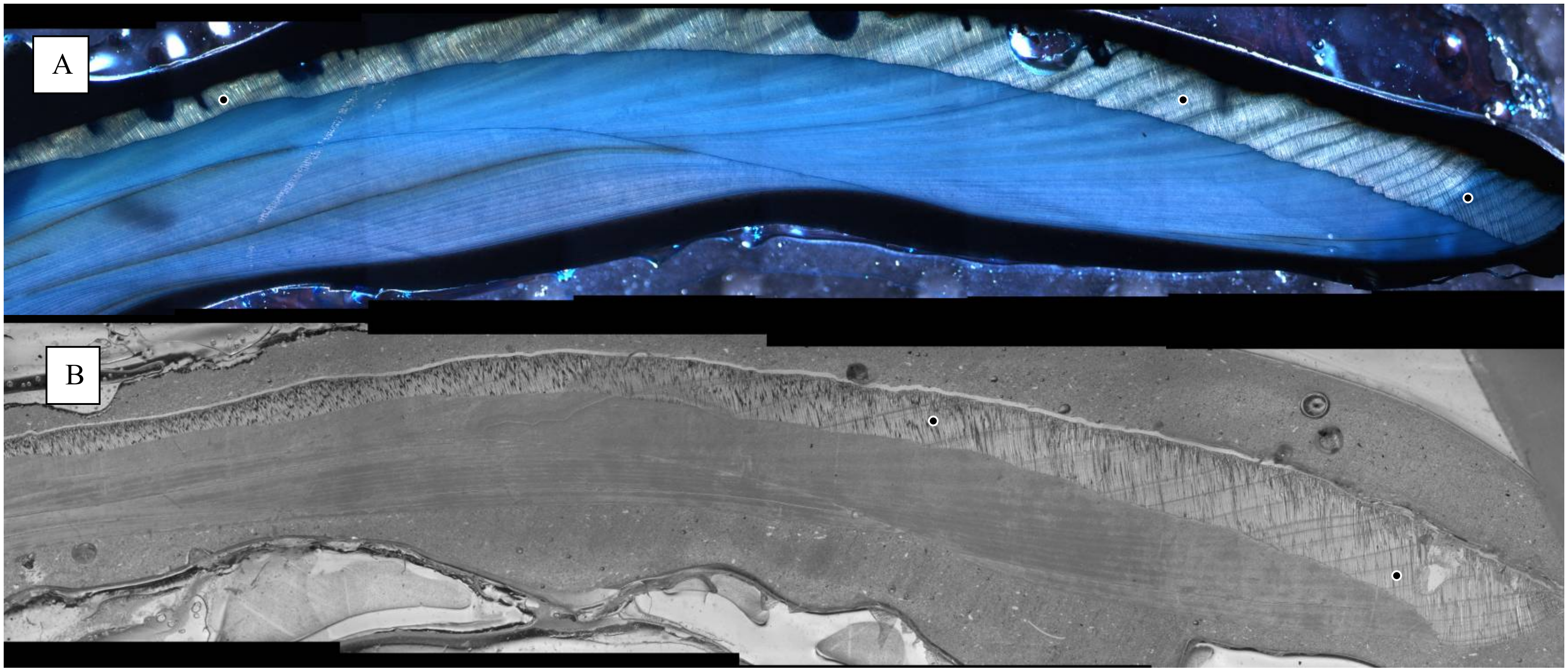
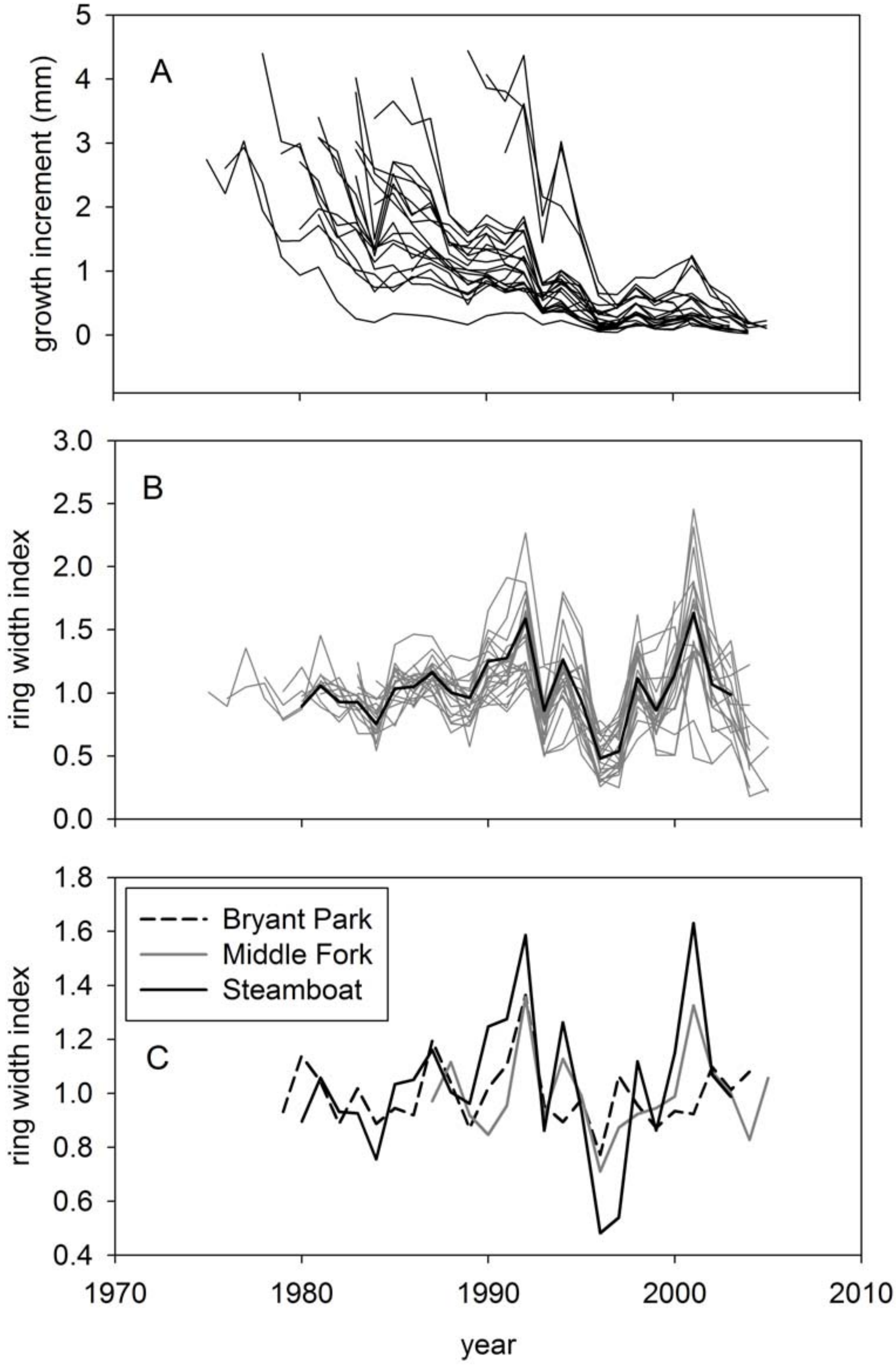
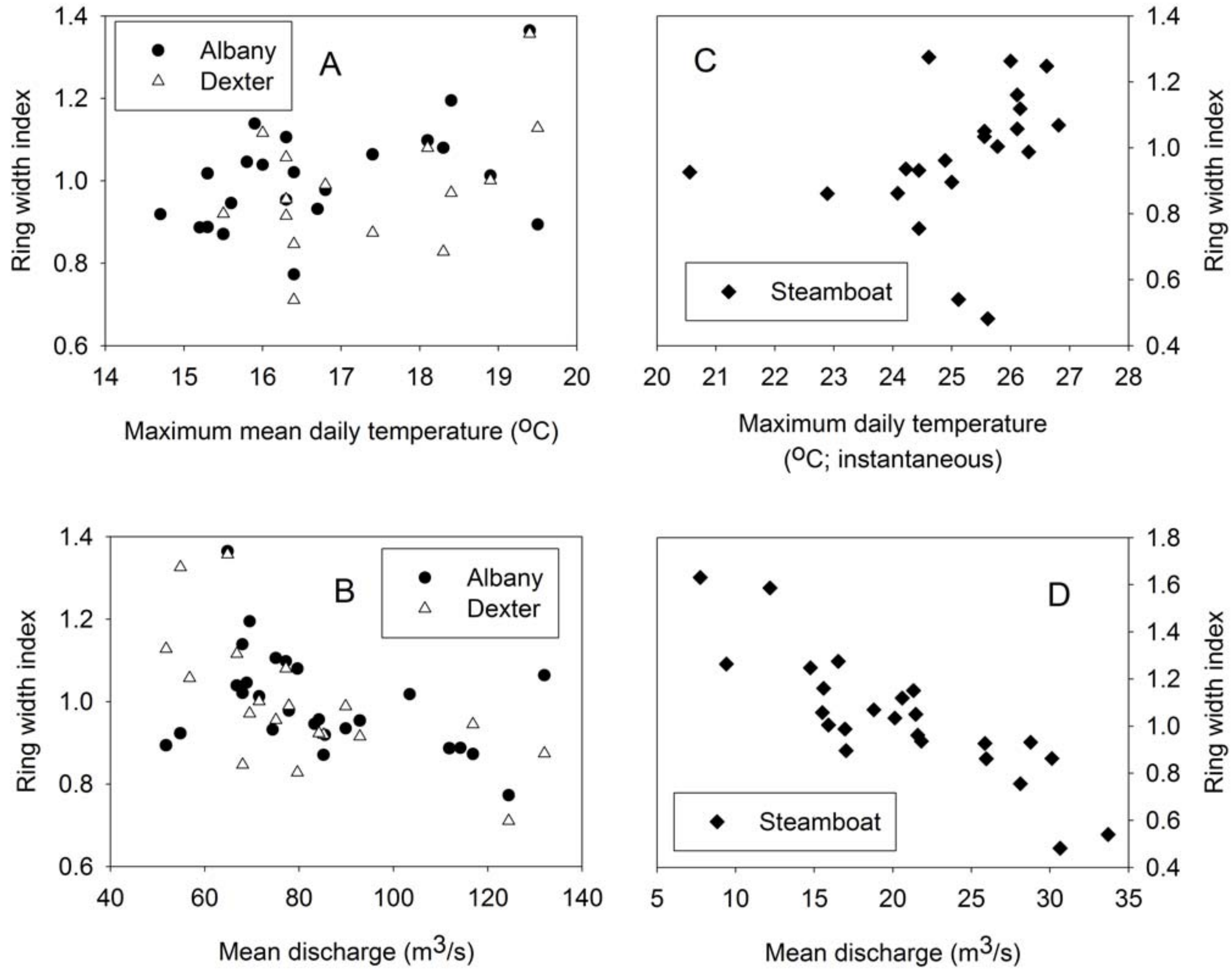


Figure 2



A
B
C
growth increment (mm)
ring width index
ring width index
Bryant Park
Middle Fork
Steamboat
year
1970
1980
1990
2000
2010

Figure 3



Albany
Dexter
A
Ring width index
Maximum mean daily temperature (°C)
C
Steamboat
Maximum daily temperature
(°C; instantaneous)
B
Mean discharge (m3/s)
D

Figure 4

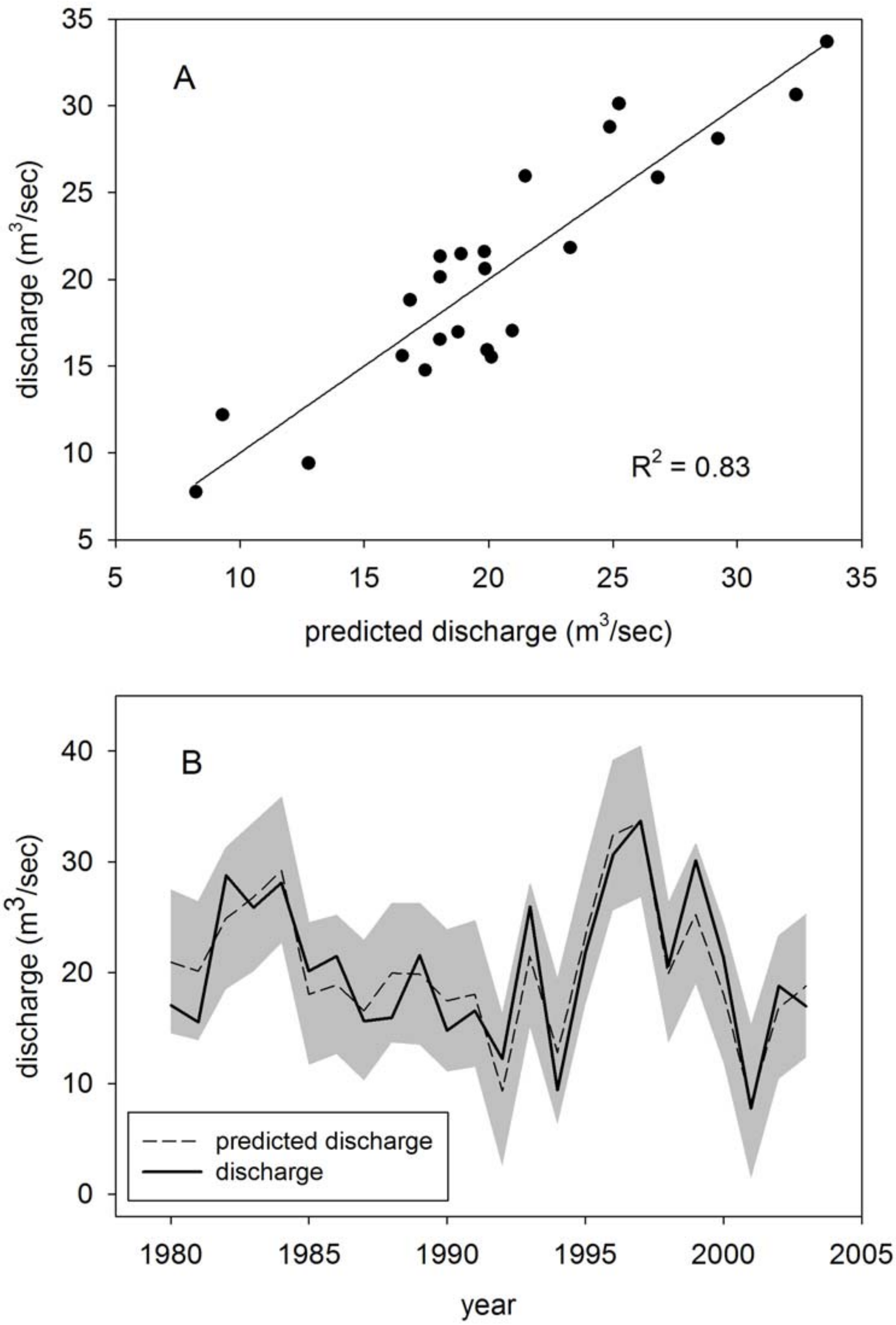

A
R^2 = 0.83
discharge (m³/sec)
predicted discharge (m³/sec)
35
30
25
20
15
10
5
B
discharge (m³/sec)
year
predicted discharge
discharge
40
30
20
10
0
1980
1985
1990
1995
2000
2005

Figure 5