Global Change Biology

celebrating 20 years

Global Change Biology (2015) **21**, 594–604, doi: 10.1111/gcb.12756

Long-term growth-increment chronologies reveal diverse influences of climate forcing on freshwater and forest biota in the Pacific Northwest

BRYAN A. BLACK[1], JASON B. DUNHAM[2], BRETT W. BLUNDON[3], JAYNE BRIM-BOX[4] and ALAN J. TEPLEY[5]

[1]Marine Science Institute, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX 78373, USA, [2]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA. [3]Bureau of Land Management, Eugene District, 3106 Pierce Parkway Suite E, Springfield, OR 97477, USA, [4]Confederated Tribes of the Umatilla Indian Reservation, Pendleton, OR 97801, USA, [5]Department of Geography, University of Colorado at Boulder, Boulder, CO 80309, USA

Abstract

Analyses of how organisms are likely to respond to a changing climate have focused largely on the direct effects of warming temperatures, though changes in other variables may also be important, particularly the amount and timing of precipitation. Here, we develop a network of eight growth-increment width chronologies for freshwater mussel species in the Pacific Northwest, United States and integrate them with tree-ring data to evaluate how terrestrial and aquatic indicators respond to hydroclimatic variability, including river discharge and precipitation. Annual discharge averaged across water years (October 1–September 30) was highly synchronous among river systems and imparted a coherent pattern among mussel chronologies. The leading principal component of the five longest mussel chronologies (1982–2003; $\mathrm{PC1_{mussel}}$) accounted for 47% of the dataset variability and negatively correlated with the leading principal component of river discharge ($\mathrm{PC1_{discharge}}$; $r = -0.88$; $P < 0.0001$). $\mathrm{PC1_{mussel}}$ and $\mathrm{PC1_{discharge}}$ were closely linked to regional wintertime precipitation patterns across the Pacific Northwest, the season in which the vast majority of annual precipitation arrives. Mussel growth was also indirectly related to tree radial growth, though the nature of the relationships varied across the landscape. Negative correlations occurred in forests where tree growth tends to be limited by drought while positive correlations occurred in forests where tree growth tends to be limited by deep or lingering snowpack. Overall, this diverse assemblage of chronologies illustrates the importance of winter precipitation to terrestrial and freshwater ecosystems and suggests that a complexity of climate responses must be considered when estimating the biological impacts of climate variability and change.

Keywords: dendrochronology, freshwater mussels, river discharge, sclerochronology, winter climate

Received 16 May 2014; revised version received 21 August 2014 and accepted 4 September 2014

Introduction

Several recent syntheses demonstrate coherent, multi-species responses to changing climates with a focus on the role of warming temperatures (Walther *et al*., 2002; Parmesan & Yohe, 2003; Rosenzweig *et al*., 2008; Poloczanska *et al*., 2013). Yet much inconsistency remains within and among species, which confounds our ability to distinguish between influences of climatic and non-climatic factors (Walther, 2010; Parmesan *et al*., 2011). Some of this variability may be attributed to regional or local patterns in temperature (Walther *et al*., 2002; Pinsky *et al*., 2013), or alternatively, changes in other climatic phenomena, most notably the timing, amount, and type of precipitation. Thus, identifying these key climate drivers and the degree to which they influence biological processes remains a priority for understanding past and future ecosystem responses to global warming.

In terrestrial systems, one of the most widely available data sources for estimating biotic response to climate is the global network of tree-ring chronologies (Fritts, 1976; St George *et al*., 2010). These annually resolved (one value per year), exactly dated chronologies can be compared to environmental records to identify the months or seasons in which climate is most limiting to growth, the stationarity of that relationship, and interactions among multiple climate variables (Biondi & Waikul, 2004; D'arrigo *et al*., 2008; Zhang & Wilmking, 2010). Given the broad distribution of temperate forests, climate-growth relationships can be assessed from single stands to hemispheres and across landforms, topographic positions, and diverse

Correspondence: Bryan Black, tel. 361-749-6789, fax 361-749-6777, e-mail: bryan.black@utexas.edu

assemblages of species (Cook *et al*., 2001; St George *et al*., 2010).

Increasingly, techniques developed for the analyses of tree rings are being adapted to other long-lived species, particularly those living in marine (Marchitto *et al*., 2000; Butler *et al*., 2010; Matta *et al*., 2010) and freshwater (Schöne *et al*., 2004; Rypel, 2009; Rypel *et al*., 2009; Black *et al*., 2013) ecosystems. This line of work promises to contribute considerably to our knowledge of biotic responses to changing climates, as biological time series in aquatic ecosystems are strongly underrepresented in the existing literature (Rosenzweig *et al*., 2008). In freshwater systems, understanding the biotic responses to environmental variability is particularly important as global water security is already critical and the projected effects of climate change are likely to exacerbate this predicament (Vorosmarty *et al*., 2010; Carpenter *et al*., 2011; Arthington, 2012). Growth-increment chronologies of long-lived freshwater organisms should be of sufficient length (i.e., several decades) and accuracy to calibrate climate-biology relationships and evaluate the roles of such variables as temperature and precipitation, which define thermal and hydrological regimes (Lins & Slack, 1999; Heino *et al*., 2009; Arismendi *et al*., 2013). Moreover, when freshwater chronologies are integrated with other biological time series such as tree-ring chronologies, the combined dataset could yield insight into broadly shared sensitivities within a region, and whether those climate-growth relationships are in phase, out of phase, or unrelated (Black, 2009; Rypel *et al*., 2009; Haag & Rypel, 2011).

The overall goal in this study is to evaluate how a diversity of species in terrestrial and aquatic ecosystems responds to a suite of common climate forcing agents. To this end, we develop a network of growth-increment chronologies from long-lived freshwater mussels collected from river systems distributed across the climatically and hydrologically diverse Pacific Northwest region of the conterminous United States (Wolock *et al*., 2004; Wigington *et al*., 2013). We first assess the degree of synchrony among mussel growth-increment chronologies as preliminary evidence for climate forcing (Moran, 1953; Liebhold *et al*., 2004). Given past evidence as to the influence of hydrologic variability (Rypel *et al*., 2008; Rypel & Bayne, 2009; Black *et al*., 2010) we then evaluate relationships between mussel growth-increment chronologies and seasonal and annual patterns in stream discharge. Next we compare mussel growth-increment chronologies to temperature and precipitation to broadly assess the influence of regional climate drivers. Finally, we integrate the mussel data with a collection of new and existing Pacific Northwest tree-ring chronologies to describe patterns of covariability across terrestrial and aquatic ecosystems. We hypothesize that broad-scale variability in precipitation and temperature to which tree-ring chronologies in the region are sensitive (Gedalof & Smith, 2001a,b; Lutz *et al*., 2012) will induce synchrony with mussel growth. Understanding long-term variability in growth among locations, species, and ecosystems, as well as the key climate factors that drive coherent responses among them is central for assessing regional impacts of changing climates.

Materials and methods

Collection of mussels

Live freshwater mussels were collected at eleven sites across the Pacific Northwest that represented a wide range of flow regimes and supported local populations estimated at $>10^3$ individuals, a criterion included to minimize impacts of collecting the 30–40 samples required for chronology development (Fig. 1; Table S1). The largest and presumably oldest individuals were collected over a maximum of 200 m distance. Only members of the dominant species were considered, including *Margaritifera falcata* at seven sites and *Gonidea angulata* in the John Day River (Table 1).

Upon inspection of the samples, three sites were discarded from further analysis. At Lobster Creek (44°20′25.14″N 123°49′41.08″W) in the Oregon Coast Range, individuals were all insufficiently long-lived (<10 year in age) for chronology development. Samples were also collected from the Malheur River (44°1′16.49″N, 118°15′54.17″W) and Williamson River (43°38′27.9″N, 121°52′36.9″W), but the majority of sufficiently old samples had experienced severe physical damage that precluded chronology development. Note that three chronologies, Albany, Dexter, and Steamboat, have been previously published (Black *et al*., 2010).

Sample preparation and visual cross-dating of mussel growth increments

Mussel valves were embedded in JB Qwik Weld resin (J-B Weld, Co, Sulphur Springs, TX, USA) 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. For each specimen, a total of three thin sections approximately 0.5 mm in thickness were taken from both the left and right valves, mounted on glass slides, and polished using 1200 grit sandpaper, 0.9 μm and 0.3 μm lapping film. One section from each valve was stained with Mutvei's solution in an attempt to increase the visibility of annual growth increments (Schone *et al*., 2005). For *M. falcata*, growth increments in the prismatic layer of the valves were used in chronology development, whereas increments in the nacreous layer were used for the *G. angulata*. Many of the *G. angulata* experienced severe erosion of the prismatic layer, and the nacreous layer provided a much more complete record. For Steamboat Creek, acetate peels were used to enhance growth-increment contrast (Black *et al*., 2010). The

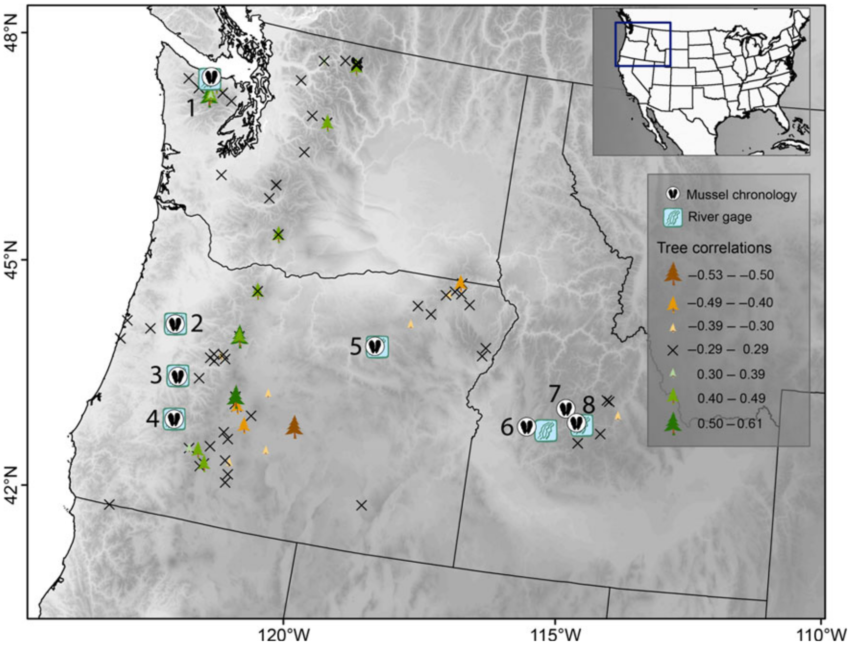

Fig. 1 Locations of river gages and freshwater mussel chronologies (numbered): (1) Elwha, (2) Albany, (3) Dexter, (4) Steamboat Creek, (5) John Day, (6) Payette, (7) Bear Valley, and (8) Stanley Lake. Also shown are locations of tree-ring chronologies and their correlations to the Bear Valley mussel chronology (1962–2003), which is a longer proxy for the leading principal component (1981–2002) of five mussel chronologies.

Table 1 Attributes of freshwater mussel growth-increment chronologies

Chronology	Lat	Lon	Ele. (m)	Span	Series†	ISC‡	MS§	Correl. $PC1_{mussel}$ ¶	Correl. $PC1_{river}$**	Correl. local disch††	Hydro-graph‡‡	USGS River gage
Bear Valley	44.427	−115.282	2037	1962–2005	28	0.62	0.26	0.83	−0.64	−0.69	Snow	13235000
Albany	44.639	−123.110	63	1979–2004	16	0.67	0.19	0.68	−0.39	−0.33	Rain	14174000
Elwha River	48.095	−123.559	66	1993–2008	15	0.74	0.31	0.49	−0.63	−0.52	Rain	12045500
Dexter	43.938	−122.834	68	1987–2005	18	0.71	0.24	0.78	−0.71	−0.65	Rain	14150000
Payette	44.104	−116.001	1016	1981–2005	14	0.57	0.27	0.64	−0.62	−0.57	Snow	13235000
Stanley Lake	44.249	−115.043	1995	1989–2005	21	0.83	0.32	0.01	0.15	−0.01	Snow	13295000
Steamboat Creek	43.350	−122.729	366	1980–2003	23	0.62	0.34	0.84	−0.80	−0.85	Rain	14316700
John Day*	44.894	−119.190	741	1974–2006	14	0.79	0.25	0.58	−0.39	−0.47	Snow	14044000

*Chronology developed from *Gonidea angulata*.
†Number of measurement time series.
‡Interseries correlation as calculated by COFECHA.
§Mean sensitivity as calculated by COFECHA.
¶Correlation (or loading) between the mussel chronology and the leading principal component of the five longest mussel chronologies.
**Correlation between each mussel chronology and the leading principal component of river discharge.
††Correlation between each mussel chronology and local river discharge over the water year.
‡‡Whether river flow is rain- or snow-dominated.

clearest thin sections (or acetate peels) from the oldest individuals were then selected for chronology development.

Images were captured with a Leica DC300 3.1 megapixel digital camera attached to a Leica MZ95 dissection scope. For each sample, multiple overlapping pictures were taken and tiled together into a single panorama. Within each collection, mussels were visually cross-dated by matching synchronous patterns beginning at the marginal increment formed during the known calendar year of capture through the inner increment formed during the first year of life (Yamaguchi, 1991).

Once visual cross-dating was complete and all increments assigned the correct calendar year of formation, growth-increment widths were measured continuously from the margin to as close to the umbo as possible using the program ImagePro Plus v. 6.0 (Media Cybernetics, Silver Spring, Maryland). When possible, one axis was measured per valve (left and right) for a total of two measurement time series per individual, though the innermost increments were often excluded due to shell erosion.

At each site, the visual cross-dating was statistically verified using the International Tree-Ring Data Bank Program Library program COFECHA, available through the University of Arizona Laboratory of Tree-Ring Research http://www.ltrr.arizona.edu/pub/dpl/ (Holmes, 1983; Grissino-Mayer, 2001). This procedure involved isolating high-frequency variability in each set of measurements via a detrending process, 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. 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 (Holmes, 1983; Grissino-Mayer, 2001). Each detrended set of mussel measurements was then correlated with the average of all other detrended sets of mussel measurements in the sample, the mean of which is reported as the series intercorrelation. Through this process, the high-frequency growth pattern of each individual was compared to the high-frequency growth pattern of all other individuals at that site. Isolating only the high frequency, serially independent growth pattern prevented spuriously high correlations among individuals, and also mathematically mimicked the process of visual cross-dating. Any measurement time series with unusually low correlations was double checked for errors.

Mussel chronology development

Once cross-dating was verified the separate but related procedure of chronology development was begun. First, the original mussel measurement time series were detrended with negative exponential functions. Detrending with negative exponential functions removed age-related growth declines while preserving as much remaining low-frequency variability as possible. Note that this contrasts with the 22-year spline detrending used in COFECHA to isolate only high-frequency variability. 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 and the 'standard' chronology was retained (developed by Ed Cook and Paul Krusic; available at http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html) (Cook, 1985). 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 nonzero value is adjacent to a zero value; i.e., a missing increment) (Fritts, 1976). This value is commonly reported in dendrochronology studies and is presented here to facilitate comparison with properties of other growth-increment datasets.

Comparisons with river and climate records

Monthly averaged records of mean daily discharge were obtained from the closest US Geological Survey (USGS) gage considered most representative (i.e. not a small tributary to the main channel) of each mussel collection site. At two sites (Bear Valley and Payette), the nearest gage records were of insufficient length, so a reference gage with a longer record (South Fork of the Payette River) was chosen to maximize chronology overlap (Fig. 1; Table 1). To examine relationships between mussel growth patterns and river flows, all eight chronologies were correlated with total discharge over the water year (October 1–September 30). The five longest chronologies, all >24 year in length, were correlated with monthly averages of river discharge to investigate whether growth was related to seasonal flow patterns. These five chronologies were also entered into a principal components analysis to examine synchrony and identify the dominant pattern of variability shared among them. The leading mussel principal component ($PC1_{mussel}$) was then correlated with quarterly (January–March, April–June, July–September, October–December) CRUTS3.1 0.5° precipitation and air temperature data averaged across the study region, −125°W to −112°W and 42°N to 48°N. For those quarters in which relationships were significant ($P < 0.01$), correlation maps between climate and $PC1_{mussel}$ were generated in the KNMI Climate Explorer (http://climexp.knmi.nl) (Trouet & Van Oldenborgh, 2013) using the CRUTS3.1 gridded temperature and precipitation data. This analysis was then repeated with the leading principal component of annually averaged (water year) discharge. Finally, time series of air temperature, precipitation, and discharge that significantly ($P < 0.01$) correlated against $PC1_{mussel}$ were entered into a stepwise regression to identify the environmental variable(s) with the most explanatory power.

Tree-ring data

All available data sets in the NOAA International Tree-Ring Databank were acquired for Washington, Oregon, and Idaho. Chronologies were developed by detrending ring-width measurement time series with 50-year 50% frequency cutoff cubic splines, which contrasts with the negative exponential detrending used for mussel chronologies. Even when using negative exponential functions, low-frequency patterns greater than approximately one-third the length of the average measurement time series are lost in the detrending process (Cook *et al.*, 1995). Thus, 50-year cubic splines were applied to tree-ring data so the resulting chronologies would have comparable spectral properties to the much shorter mussel chronologies. Only those tree-ring datasets collected after 1985 ($n = 113$) were retained to maximize overlap with mussel datasets. We also incorporated eleven previously unpublished tree-ring chronologies from the Oregon Coast Range and western Oregon Cascade Mountains (Table S1). All chronology development was conducted using the program ARSTAN and the 'standard' chronology was retained in all cases (Cook, 1985). To further increase overlap with tree-ring chronologies, the much longer Bear Valley mussel chronology was used as a proxy for the very closely related $PC1_{mussel}$ ($r = 0.83$; $P < 0.001$). Tree-ring chronologies were also correlated against the leading principal component of river discharge, which provided even greater overlap and could corroborate patterns identified in correlations between trees and mussels.

Results

Mussels cross-dated within each site, allowing the development of exactly dated chronologies ranging from 16 to 44 year in length (Table 1). Interseries correlations were strongly positive and comparable in value among all eight datasets ($r = 0.57–0.83$), underscoring the high levels of growth synchrony within each mussel collection (Table 1). On average, approximately 10% to 30% of samples were too heavily distorted by physical damage for cross-dating. Moreover, erosion often affected early growth increments and precluded accurate aging.

Among the eight chronologies developed, the leading principal component of the five longest chronologies (1982–2003; $PC1_{mussel}$) accounted for 47% of the variability in the dataset, indicating that growth was not only synchronous within sites but also among sites (Table S1). The Stanley Lake chronology did not follow the common pattern, however, as illustrated by its weak correlation ($r = 0.01$) to $PC1_{mussel}$ (Table 1). Correlation with $PC1_{mussel}$ ranged from $r = 0.49–0.84$ for all other chronologies.

Mussel chronologies were negatively associated with river discharge, as averaged across the water year (Table 1). At a monthly timescale, there were variable patterns in the seasonality of both stream discharge and mussel-discharge relationships, though stronger correlations often occurred near or shortly after the timing of peak flow (Fig. 2). At the annual scale, river discharge

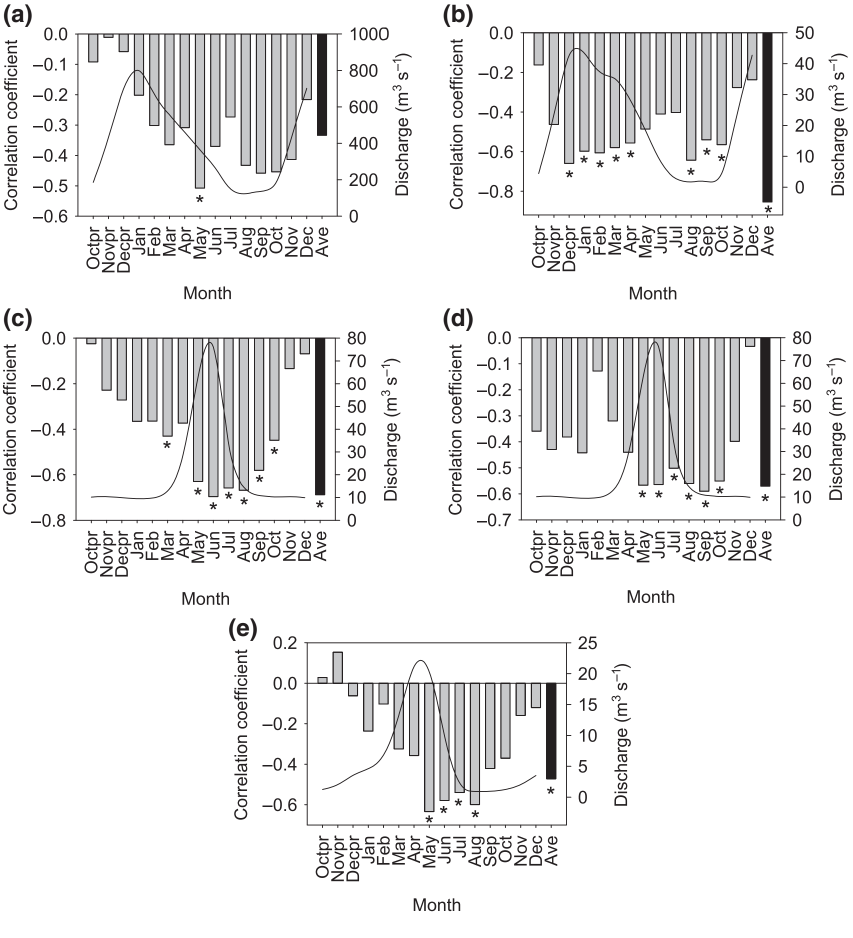

Fig. 2 Correlations between the five longest mussel chronologies and monthly averaged (gray bars) and water-year averaged (black bars) river discharge. Mean monthly river discharge is also shown (lines). (a) Albany; 1979–2004, (b) Steamboat; 1980–2003, (c) Bear Valley; 1962–2005, (d) Payette; 1981–2005, (e) John Day; 1974–2006. $^*P < 0.01$.

was highly synchronous among sites such that the leading principal component ($PC1_{discharge}$) accounted for 90% of the variability in the dataset. The relationship of mean annual river discharge to the dominant pattern of mussel growth $PC1_{mussel}$ was negative and highly significant ($r = -0.88$; $P < 0.0001$; 1981–2003) (Fig. 3). With respect to broad atmospheric drivers, $PC1_{mussel}$ was negatively correlated with precipitation in the Pacific Northwest region from the prior October (the start of the water year) through March (Fig. 4a and b) and positively related to temperature averaged from April to June (Fig. 4a and c). In the case of $PC1_{discharge}$, seasonal correlations with precipitation and temperature mirror those between $PC1_{mussel}$ and precipitation and temperature (Fig. 4d–f). Thus, $PC1_{mussel}$ tracks $PC1_{discharge}$ which is in turn related to winter and springtime precipitation as well as springtime temperature in the Pacific Northwest. Mean April–June temperature and mean October through March temperature were correlated ($r = -0.55$, $P = 0.007$) over the 1981–2003 interval shared with $PC1_{mussel}$. However, in a stepwise regression including April–June temperature and October–March precipitation ($P < 0.05$ to enter), only precipitation is retained in the final model ($R^2 = 0.59$; $P < 0.001$). Similarly, in a stepwise regression including April–June temperature and the $PC1_{discharge}$, only $PC1_{discharge}$ is retained ($R^2 = 0.75$; $P < 0.001$). When considered alone, temperature explains approximately 35% of the variance in $PC1_{mussel}$.

Almost a quarter of tree-ring chronologies (23%) were significantly ($P < 0.05$) correlated with the Bear Valley mussel chronology while 9.7% were correlated at a highly significant level ($P < 0.01$). There was no obvious spatial pattern in the correlations between the Bear Valley mussel chronology and tree-ring chronologies, though the strongest positive correlations tended to occur along the Cascade Mountain crest (Fig. 1). These relatively high-elevation chronologies consist almost exclusively of mountain hemlock (*Tsuga mertensiana*) and subalpine fir (*Abies lasiocarpa*) (Fig. 5a). The few significantly negative correlations occurred in western juniper (*Juniperus occidentalis*) and ponderosa pine (*Pinus ponderosa*) on the eastern side of the Cascades (Figs 1 and 5a). Overall, correlations between the Bear Valley mussel chronology and the tree-ring chronologies followed a weak elevational gradient, though notable outliers to this trend included low-elevation Douglas-fir or western hemlock (*Tsuga heterophylla*) sampled in westernmost Oregon, as well as extremely high-elevation sites, which were all whitebark pine (*Pinus albicaulis*) and Engelmann spruce (*Picea engelmannii*) from Idaho. Patterns in correlation between trees and the Bear Valley mussel chronology were mirrored by patterns in correlation between trees and $PC1_{discharge}$, as calculated over the longer 1957–2011 interval (Fig. 5b).

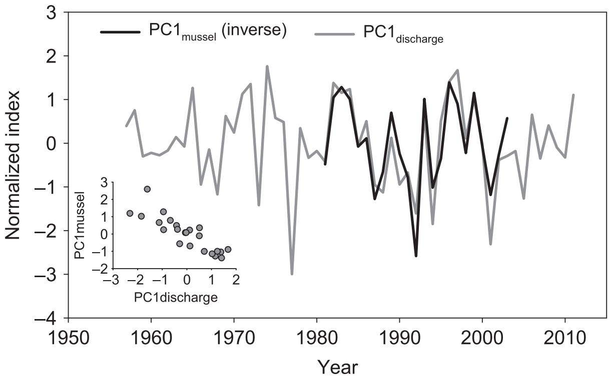

Fig. 3 The leading principal component of the five longest mussel chronologies ($PC1_{mussel}$; inverted) and the leading principal component ($PC1_{discharge}$) of river discharge from associated gage stations, as averaged over the water year. Inset: bivariate plot of $PC1_{mussel}$ and $PC1_{discharge}$; $r = -0.87$; $P < 0.001$.

Discussion

Mussel climate-growth relationships

Results of this study indicate that regional climate variability can act to synchronize growth of long-lived species across broad extents. In contrast to previous reviews (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Rosenzweig *et al.*, 2008; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013), however, we find that biotic responses are more strongly tied to patterns of precipitation than temperature. In rivers, variation in the quantity and timing of precipitation translates into patterns of stream discharge (Poff & Ward, 1989), which have been reported to strongly influence growth of riverine mussels (Rypel *et al.*, 2008, 2009; Black *et al.*, 2010; Haag & Rypel, 2011). Higher annual river discharges corresponded to narrower growth increments, consistent with climate-growth relationships observed in a network of 42 chronologies developed for a range of mussel species in the southeastern United States (Rypel *et al.*, 2008, 2009; Haag & Rypel, 2011). The processes behind this responses are not clear, but could involve physical damage from high flow events (e.g., direct injury, dislocation, or burial in stream sediments), reductions in primary productivity, or difficulty feeding in turbulent water (Henley *et al.*, 2000; Howard & Cuffey, 2003; Rypel *et al.*, 2008, 2009; Black *et al.*, 2010).

When correlations between annual growth and stream discharge are evaluated on a monthly basis, the importance of seasonality is evident, as peak correlations occur from as early as the winter

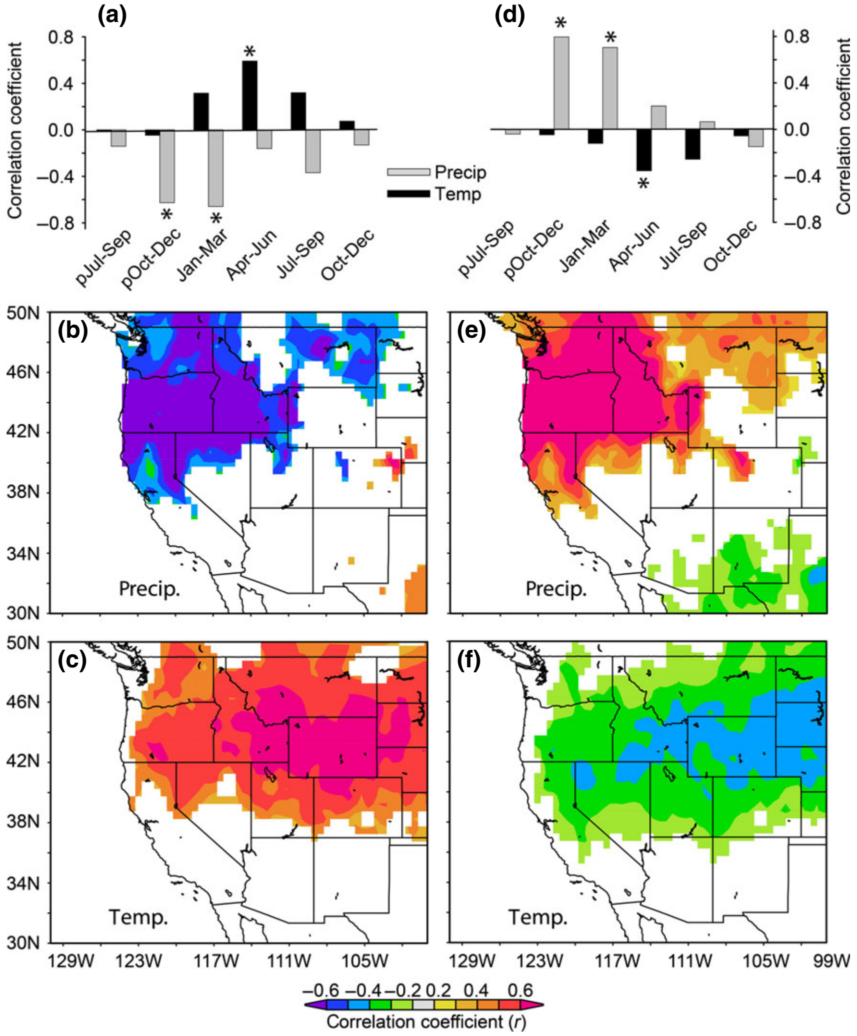

Fig. 4 (a) Correlations (*r*; 1981–2003) between the leading principal component of the five longest mussel chronologies ($\mathrm{PC1_{mussel}}$) and quarterly averaged precipitation and air temperature data bounded by the region 112°W–125°W and 42°N–48°N; *$P < 0.01$, (b) Correlations (*r*; 1981–2003; $P < 0.1$) between $\mathrm{PC1_{mussel}}$ and gridded prior October–March precipitation and (c) gridded April–June air temperature. Correlations (*r*; 1957–2011) between the leading principal component of river discharge ($\mathrm{PC1_{discharge}}$) and (d) quarterly averaged precipitation and air temperature data bounded by the region 112°W–125°W and 42°N–48°N; *$P < 0.01$, (e) Correlations (*r*; 1957–2011; $P < 0.1$) between $\mathrm{PC1_{discharge}}$ and prior October–March precipitation, and (f) April–June air temperature.

(Steamboat Creek) to as late as the summer (Payette River and Bear Valley Creek) in streams with rain, or snow-dominated hydrographs, respectively. We found no evidence to suggest a single critical time period for which discharge is most important. Rather, it appears that higher discharges at any time of the year can limit growth of freshwater mussels. However, these discharge patterns and resulting mussel growth responses are linked to climate during the winter months over which the vast majority of precipitation occurs (Mote & Salathe, 2010), imparting coincident effects on flows of rain-dominated river systems and lagged effects on flows of snow-dominated river systems. Although the influence of winter precipitation patterns may vary with river hydrography, they nonetheless induce synchronous discharge patterns in rivers at the annual scale and thus synchronize growth patterns in mussels throughout the Pacific Northwest region. We were unable to assess seasonal growth patterns in mussels, including the specific times of year in which growth was fastest. More direct observation of individual growth or condition of mussels in the field and additional study of interactions among discharge, temperature, and related factors (e.g., primary productivity) may provide additional insights useful for understanding the mechanisms linking mussel growth to climate.

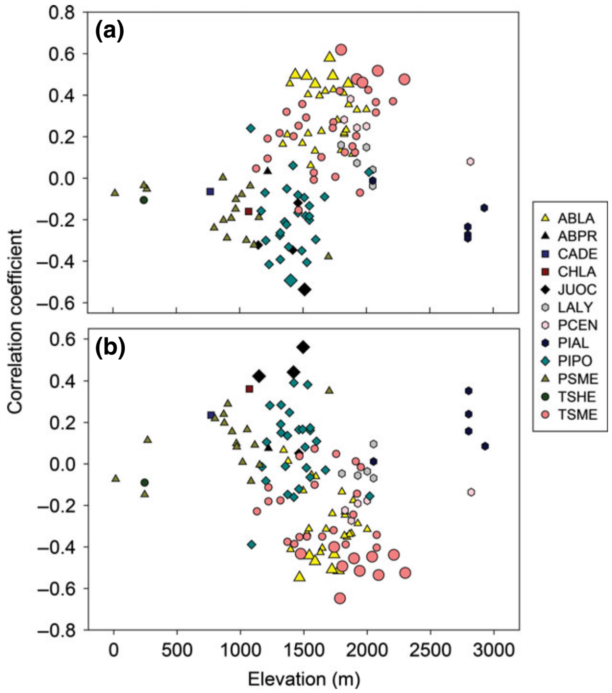

Fig. 5 (a) Elevation and species of Pacific Northwest tree-ring chronologies as well as their correlation with the Bear Valley mussel chronology. Note that the four lowest elevation tree-ring chronologies (from the Coastal Ranges) as well as the five highest-elevation chronologies (from Idaho) are outliers to the pattern followed by the majority. (b) Correlation between trees and $PC1_{discharge}$. Large symbols in each panel indicate significant correlations ($P < 0.01$). Tree species abbreviations: ABLA = subalpine fir (*Abies lasiocarpa*); ABPR = noble fir (*Abies procera*); CADE = Incense-cedar (*Calocedrus decurrens*); CHLA = Port Orford cedar (*Chamaecyparis lawsoniana*); JUOC = western juniper (*Juniperus occidentalis*); LALY = subalpine larch (*Larix lyalii*); PCEN = Engelmann spruce (*Picea engelmannii*); PIAL = whitebark pine (*Pinus albicaulis*); PIPO = ponderosa pine (*Pinus ponderosa*); PSME = Douglas-fir (*Pseudotsuga menziesii*); TSHE = western hemlock (*Tsuga heterophylla*); TSME = mountain hemlock (*Tsuga mertensiana*).

Among the collections of mussels we studied, the Stanley Lake Outlet chronology did not correlate with discharge and was the one exception to the underlying pattern of regional growth synchrony found across all other sites. Series intercorrelations at Stanley Lake were the strongest of any mussel dataset, indicating that growth was highly synchronous among individuals within the collection. A lack of correlation with environmental records or other mussel chronologies may be due the fact that these samples were collected immediately downstream from the outlet of a large lake, which likely attenuated variability in discharge (Poff & Ward, 1989). Because discharge data were unavailable for this stream, we attempted to correlate growth with discharge from a nearby gaged stream, which may have had a different flow regime. Furthermore, it has been hypothesized that food availability may be greater in lake outlets (Richardson & Mackay, 1991; Brim-Box & Williams, 2000), a factor that could also influence how mussels respond to variability in stream discharge. Aside from this location, however, mussel growth was remarkably synchronous across the sites examined considering the geographic extent of the study region and the variety of hydrographic regimes involved.

Although precipitation and river discharge were most strongly coupled with the mussel chronology network, there is little questioning that temperature is also important to the species considered here. Temperatures vary considerably across the Pacific Northwest and influences how precipitation is delivered – as rain or as snow (Nolin & Daly, 2006), which indirectly influences biotic response through effects on precipitation type and the seasonality of river flows. One possible explanation for relatively weak correlations with mussel growth could be that air and stream temperatures were poorly related (Johnson, 2003; Arismendi *et al*., 2012). However, earlier work involving the Albany, Dexter, and Steamboat chronologies indicated that some in stream temperature metrics were significantly associated ($P < 0.01$) with growth, though correlations to discharge were stronger (Black *et al*., 2010). Studies outside the study region have found that mussel growth chronologies (Schöne *et al*., 2004) and life histories (Bauer, 1992) are strongly tied to interannual variability and broad latitudinal gradients in temperature. Indeed, air temperature explained as much as 55% of the variability in *Margarifitera* growth-increment chronologies from Sweden (Schöne *et al*., 2004). These individuals were collected at relatively high latitudes where temperature may be more limiting, as is supported by the observation that temperature-growth relationships somewhat diminished from north to south (Schöne *et al*., 2004). Ultimately, how precipitation, discharge and temperature influence mussel growth remains poorly described across broader extents, and this information could be a key component in future management and climate adaptation strategies.

Terrestrial-aquatic linkages

Cool-season precipitation is not only important to mussel growth but also to tree radial growth throughout the Pacific Northwest. Shared sensitivities are sufficiently strong that mussel growth, as represented by the Bear Valley chronology, significantly ($P < 0.01$) correlated with tree-ring chronologies, illustrating climate-driven coupling between terrestrial and freshwater systems at regional scales. The climate–growth relationships observed here are consistent with those previously described in western North American forests (Lutz *et al.*, 2012). High-elevation subalpine fir and mountain hemlock along the crest of the Cascade and Olympic Mountains are likely limited, at least in part, by high snow pack, which serves as a proxy for growing season length (i.e., high snowpack suggests late snow melt and a short growing season) (Gedalof & Smith, 2001a; Peterson & Peterson, 2001; Lutz *et al.*, 2012). In contrast, ponderosa pine and western juniper in the rain shadow of the Cascade Mountains are more likely to be limited by drought (Cook *et al.*, 2004; Knapp *et al.*, 2004; Lutz *et al.*, 2012). Thus, a dry year would correspond to low discharge, low snowpack, and low-elevation drought such that mussel chronologies (robust growth) are out of phase with moisture-limited ponderosa pine and western juniper (reduced growth), but in phase with snow pack-limited subalpine fir and mountain hemlock (robust growth). Commonalities in the climate response of trees and mussels have also been identified in the United States Southeast Coastal Plain in which bald cypress (*Taxodium distichum*) was positively associated with river discharge while mussel growth was negatively associated (Rypel *et al.*, 2009).

Correlations between $\mathrm{PC1}_{\mathrm{discharge}}$ and tree-ring chronologies corroborate the relationships observed between trees and mussels. Indeed, an elevation gradient is somewhat more pronounced and characterized by negative correlations to discharge at high elevation. Notably, the four lowest elevation chronologies, all from the Oregon Coast Range, as well as the five highest-elevation chronologies, all from Idaho, are outliers to this trend (Fig. 5). Further work is needed to elucidate the exact mechanisms underlying tree-mussel relationships, but mussels and trees do independently verify the general relevance of cool-season hydroclimatic conditions across freshwater and terrestrial ecosystems of the Pacific Northwest. Just as importantly, they demonstrate differential responses to climate variability; some species or populations may be positively influenced under one set of climate conditions while others have an inverse or neutral response. These findings also underscore the importance of seasonality in climate response and add to a growing body of literature that points to the importance of winter climatic patterns on biota in western North America (Logerwell *et al.*, 2003; Black *et al.*, 2011; Schroder *et al.*, 2013).

In the Pacific Northwest, the hydrologic regimes linked to mussel and tree growth patterns appear to be changing. Over the past several decades, winters have become warmer, snowpack has diminished, and discharge in undisturbed rivers has declined, especially in the lowest quartile such that low-flow years are becoming more extreme (Mote, 2006; Luce & Holden, 2009; Pederson *et al.*, 2011). Slowing lower tropospheric winds from the west may be reducing precipitation in the higher elevations of the Pacific Northwest, a trend that is forecast to strengthen over the coming decades (Luce *et al.*, 2013). Scenarios for the region also predict that summertime blocking high pressure systems and accompanying drought will intensify while wintertime temperatures will continue to rise (Mote & Salathe, 2010). Consequently, snow pack is forecast to decline drastically (Nolin & Daly, 2006). Also, the enhanced seasonality of precipitation and increased probability of extremes could raise the amplitude of river discharge with higher flows in the winter (due to winter precipitation falling as rain or melting early) combined with lower flows in the summer (due to reduced winter snowpack) (Safeeq *et al.*, 2013).

Implications for mussel and tree growth are difficult to predict and will depend upon the interactions among temperature, precipitation, snow pack, soil moisture, and river flow, though the results of this analysis suggest that higher winter flows, as expected in rain-dominated systems, would negatively impact mussel growth. Reduced winter snow pack could also mean that high-elevation trees will eventually face summer drought stress, or that extremely low summer river flows will adversely impact mussels, especially through loss of habitat. Importantly, this study considers only one aspect of life history and does not address other issues of long-term population viability including reproductive success and survivorship, which may be dependent on other ecosystem considerations, including, for example, the status of host fish populations necessary for larval development and transport (Strayer, 2008; Haag, 2012). Thus, long-term changes in growth, should they be predictable, may not necessarily translate into changes in population size. Though much remains to be understood, broad linkages across mussel and tree growth chronologies highlight the widespread relevance of winter hydroclimate in the Pacific Northwest, the complexity of biological responses to its variability, and in so doing provide important baseline information for anticipating the impacts of future changes on the functioning of terrestrial and aquatic systems.

Acknowledgements

This study was funded by support from the U.S. Geological Survey and U.S. Forest Service, Pacific Northwest Research Station. We are grateful to the contributors of the International Tree-ring Databank and thank J. Jones and F. Swanson for comments on an earlier draft of this manuscript. Use of trade or firm names in this document is for reader information only and does not constitute endorsement of any product or service by the US Government.

References

Arismendi I, Johnson SL, Dunham JB, Haggerty R, Hockman-Wert D (2012) The paradox of cooling streams in a warming world: regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters*, **39**, L10401. doi: 10.1029/2012GL051448.

Arismendi I, Johnson SL, Dunham JB, Haggerty R (2013) Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. *Freshwater Biology*, **58**, 880–894.

Arthington AH (2012) *Environmental flows: saving rivers in the third millennium*. University of California Press, Berkeley.

Bauer G (1992) Variation in the life-span and size of the fresh-water pearl mussel. *Journal of Animal Ecology*, **61**, 425–436.

Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303–311.

Black BA (2009) Climate driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. *Marine Ecology Progress Series*, **378**, 37–46.

Black BA, Dunham JB, Blundon BW, Raggon MF, Zima D (2010) Spatial variability in growth-increment chronologies of long-lived freshwater mussels: implications for climate impacts and reconstructions. *Ecoscience*, **17**, 240–250.

Black BA, Schroeder ID, Sydeman WJ, Bograd SJ, Wells BK, Schwing FB (2011) Winter and summer upwelling modes and their biological importance in the California current ecosystem. *Global Change Biology*, **17**, 2536–2545.

Black BA, Von Biela VR, Zimmerman CE, Brown RJ (2013) Lake trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. *Polar Biology*, **36**, 147–153.

Brim-Box J, Williams JD (2000) Unionid mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia. *Bulletin of the Alabama Museum of Natural History*, **21**, 1–143.

Butler PG, Richardson CA, Scourse JD, Wanamaker AD, Shammon TM, Bennell JD (2010) Marine climate in the Irish Sea: analysis of a 489-year marine master chronology derived from growth increments in the shell of the clam Arctica islandica. *Quaternary Science Reviews*, **29**, 1614–1632.

Carpenter SR, Cole JJ, Pace ML *et al.* (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science*, **332**, 1079–1082.

Cook ER (1985) A time-series analysis approach to tree-ring standardization. Ph.D. thesis, University of Arizona, Tucson, AZ, 171 pp.

Cook ER, Briffa KR, Meko DM, Graybill DA, Funkhouser G (1995) The segment length curse in long tree-ring chronology development for paleoclimatic studies. *Holocene*, **5**, 229–237.

Cook ER, Glitzenstein JS, Krusic PJ, Harcombe PA (2001) Identifying functional groups of trees in west Gulf Coast forests (USA): a tree-ring approach. *Ecological Applications*, **11**, 883–903.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the western United States. *Science*, **306**, 1015–1018.

D'arrigo R, Wilson R, Liepert B, Cherubini P (2008) On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change*, **60**, 289–305.

Fritts HC (1976) *Tree Rings and Climate*. Academic Press, New York.

Gedalof Z, Smith DJ (2001a) Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America. *Canadian Journal of Forest Research*, **31**, 322–332.

Gedalof Z, Smith DJ (2001b) Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophysical Research Letters*, **28**, 1515–1518.

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, **57**, 205–221.

Haag WR (2012) *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. Cambridge University Press, Cambridge England. 505 pp.

Haag WR, Rypel AL (2011) Growth and longevity in freshwater mussels: evolutionary and conservation implications. *Biological Reviews*, **86**, 225–247.

Heino J, Virkkala R, Toivonen H (2009) Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, **84**, 39–54.

Henley WF, Patterson MA, Neves RJ, Lemly AD (2000) Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science*, **8**, 125–139.

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–78.

Howard JK, Cuffey KM (2003) Freshwater mussels in a California North Coast range river: occurrence, distribution, and controls. *Journal of the North American Benthological Society*, **22**, 63–77.

Johnson SL (2003) Stream temperature: scaling of observations and issues for modelling. *Hydrological Processes*, **17**, 497–499.

Knapp PA, Soule PT, Grissino-Mayer HD (2004) Occurrence of sustained droughts in the interior Pacific Northwest (AD 1733–1980) inferred from tree-ring data. *Journal of Climate*, **17**, 140–150.

Liebhold A, Koenig WD, Bjornstad ON (2004) Spatial synchrony in population dynamics. *Annual Review of Ecology Evolution and Systematics*, **35**, 467–490.

Lins HF, Slack JR (1999) Streamflow trends in the United States. *Geophysical Research Letters*, **26**, 227–230.

Logerwell EA, Mantua N, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. *Fisheries Oceanography*, **12**, 554–568.

Luce CH, Holden ZA (2009) Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophysical Research Letters*, **36**, L16401. doi: 10.1029/2009GL039407.

Luce CH, Abatzoglou JT, Holden ZA (2013) The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest USA. *Science*, **342**, 1360–1364.

Lutz ER, Hamlet AF, Littell JS (2012) Paleoreconstruction of cool season precipitation and warm season streamflow in the Pacific Northwest with applications to climate change assessments. *Water Resources Research*, **48**, W01525. doi: 10.1029/2011WR010687.

Marchitto TM, Jones GA, Goodfriend GA, Weidman CR (2000) Precise temporal correlation of holocene mollusk shells using sclerochronology. *Quaternary Research*, **53**, 236–246.

Matta ME, Black BA, Wilderbuer TK (2010) Climate-driven synchrony in otolith growth-increment chronologies for three Bering Sea flatfish species. *Marine Ecology Progress Series*, **413**, 137–145.

Moran PAP (1953) The statistical analysis of the Canadian lynx cycle, synchronization and Meteorology. *Australian Journal of Zoology*, **1**, 291–298.

Mote PW (2006) Climate-driven variability and trends in mountain snowpack in western North America. *Journal of Climate*, **19**, 6209–6220.

Mote PW, Salathe EP (2010) Future climate in the Pacific Northwest. *Climatic Change*, **102**, 29–50.

Nolin AW, Daly C (2006) Mapping 'at risk' snow in the Pacific Northwest. *Journal of Hydrometeorology*, **7**, 1164–1171.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan C, Duarte C, Poloczanska E, Richardson AJ, Singer MC (2011) COMMENTARY: overstretching attribution. *Nature Climate Change*, **1**, 2–4.

Pederson GT, Gray ST, Woodhouse CA *et al.* (2011) The unusual nature of recent snowpack declines in the North American Cordillera. *Science*, **333**, 332–335.

Peterson DW, Peterson DL (2001) Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, **82**, 3330–3345.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science*, **341**, 1239–1242.

Poff NL, Ward JV (1989) Implications of streamflow variability and predictability for lotic community structure - a regional-analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.

Poloczanska ES, Brown CJ, Sydeman WJ *et al.* (2013) Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 919–925.

Richardson JS, Mackay RJ (1991) Lake outlets and the distribution of filter feeders - an assessment of hypotheses. *Oikos*, **62**, 370–380.

Rosenzweig C, Karoly D, Vicarelli M *et al.* (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–357.

Rypel AL (2009) Climate-growth relationships for largemouth bass (*Micropterus salmoides*) across three southeastern USA states. *Ecology of Freshwater Fish*, **18**, 620–628.

Rypel AL, Bayne DR (2009) Hydrologic habitat preferences of select southeastern USA fishes resilient to river ecosystem fragmentation. *Ecohydrology*, **2**, 419–427.

Rypel AL, Haag WR, Findlay RH (2008) Validation of annual growth rings in freshwater mussel shells using cross dating. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 2224–2232.

Rypel AL, Haag WR, Findlay RH (2009) Pervasive hydrologic effects on freshwater mussels and riparian trees in southeastern floodplain ecosystems. *Wetlands*, **29**, 497–504.

Safeeq M, Grant GE, Lewis SL, Tague CL (2013) Coupling snowpack and groundwater dynamics to interpret historical streamflow trends in the western United States. *Hydrological Processes*, **27**, 655–668.

Schone BR, Dunca E, Fiebig J, Pfeiffer M (2005) Mutvei's solution: an ideal agent for resolving microgrowth structures of biogenic carbonates. *Palaeogeography Palaeoclimatology Palaeoecology*, **228**, 149–166.

Schöne BR, Dunca E, Mutvei H, Norlund U (2004) A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margarifitera*, Sweden). *Quaternary Science Reviews*, **23**, 1803–1816.

Schroder ID, Black BA, Sydeman WJ, Bograd SJ, Hazen EL, Santora JA, Wells BK (2013) The North Pacific High and wintertime pre-conditioning of California current productivity. *Geophysical Research Letters*, **40**, 1–6.

St George S, Meko DM, Cook ER (2010) The seasonality of precipitation signals embedded within the North American Drought Atlas. *Holocene*, **20**, 983–988.

Strayer DL (2008) *Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance*. University of California Press, Berkeley. 203 pp.

Trouet V, Van Oldenborgh GJ (2013) KNMI Climate Explorer: a web-based research tool for high-resolution paleoclimatology. *Tree-Ring Research*, **69**, 3–13.

Vorosmarty CJ, Mcintyre PB, Gessner MO *et al.* (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555–561.

Walther GR (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2019–2024.

Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wigington PJ, Leibowitz SG, Comeleo RL, Ebersole JL (2013) Oregon hydrologic landscapes: a classification framework. *Journal of the American Water Resources Association*, **49**, 163–182.

Wolock DM, Winter TC, Mcmahon G (2004) Delineation and evaluation of hydrologic-landscape regions in the United States using geographic information system tools and multivariate statistical analyses. *Environmental Management*, **34**, S71–S88.

Yamaguchi DK (1991) A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research*, **21**, 414–416.

Zhang YX, Wilmking M (2010) Divergent growth responses and increasing temperature limitation of Qinghai spruce growth along an elevation gradient at the northeast Tibet Plateau. *Forest Ecology and Management*, **260**, 1076–1082.

Supporting Information

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

Table S1. Attributes of previously unpublished tree-ring chronologies for western Oregon.