

# Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States

C. P. KONRAD\*, A. M. D. BRASHER<sup>†</sup> AND J. T. MAY<sup>‡</sup>

\*U.S. Geological Survey, Washington Water Science Center, Tacoma, and The Nature Conservancy, Global Freshwater Team, Seattle, WA, U.S.A.

<sup>†</sup>U.S. Geological Survey, Utah Water Science Center, Moab, UT, U.S.A.

<sup>‡</sup>U.S. Geological Survey, California Water Science Center, Sacramento, CA, U.S.A.

## SUMMARY

1. Human use of land and water resources modifies many streamflow characteristics, which can have significant ecological consequences. Streamflow and invertebrate data collected at 111 sites in the western U.S.A. were analysed to identify streamflow characteristics (magnitude, frequency, duration, timing and variation) that are probably to limit characteristics of benthic invertebrate assemblages (abundance, richness, diversity and evenness, functional feeding groups and individual taxa) and, thus, would be important for freshwater conservation and restoration. Our analysis investigated multiple metrics for each biological and hydrological characteristic, but focuses on 14 invertebrate metrics and 13 streamflow metrics representing the key associations between streamflow and invertebrates.
2. Streamflow is only one of many environmental and biotic factors that influence the characteristics of invertebrate assemblages. Although the central tendency of invertebrate assemblage characteristics may not respond to any one factor across a large region like the western U.S.A., we postulate that streamflow may limit some invertebrates. To assess streamflow characteristics as limiting factors on invertebrate assemblages, we developed a nonparametric screening procedure to identify upper (ceilings) or lower (floors) limits on invertebrate metrics associated with streamflow metrics. Ceilings and floors for selected metrics were then quantified using quantile regression.
3. Invertebrate assemblages had limits associated with all streamflow characteristics that we analysed. Metrics of streamflow variation at daily to inter-annual scales were among the most common characteristics associated with limits on invertebrate assemblages. Baseflow recession, daily variation and monthly variation, in streamflow were associated with the largest number of invertebrate metrics. Since changes in streamflow variation are often a consequence of hydrologic alteration, they may serve as useful indicators of ecologically significant changes in streamflow and as benchmarks for managing streamflow for ecological objectives.
4. Relative abundance of Plecoptera, richness of non-insect taxa and relative abundance of intolerant taxa were associated with multiple streamflow metrics. Metrics of sensitive taxa (Ephemeroptera, Plecoptera and Trichoptera), and intolerant taxa generally had ceilings associated with flow metrics while metrics of tolerant taxa, non-insects,

dominance and chironomids generally had floors. Broader characteristics of invertebrate assemblages such as abundance and richness had fewer limits, but these limits were nonetheless associated with a broad range of streamflow characteristics.

*Keywords:* hydrologic alteration, macroinvertebrate assemblages, metrics, quantile regression, streamflow statistics

## Introduction

Streamflow regime is widely recognized as one of the most influential physical features of lotic ecosystems, having broad effects on productivity and habitat structure, and ultimately on the composition of benthic invertebrate communities (Resh *et al.*, 1988; Poff & Ward, 1989; Allan, 1995). Increasing human use of limited water resources has modified the volume, rate and timing of streamflow worldwide (Bunn & Arthington, 2002). Land use activities have also modified hydrologic processes, resulting in changes of streamflow characteristics (magnitude, duration, frequency timing and variation). While the range of ecologically-significant streamflow characteristics affected by hydrologic alteration has been well documented (Richter *et al.*, 1996; Poff *et al.*, 1997; Bunn & Arthington, 2002; Allan, 2004), the influence of specific streamflow characteristics on characteristics of benthic invertebrate assemblages is not well understood, particularly at regional scales where biological responses to flow can be generalized. Identification of the most important streamflow characteristics would allow the development of focused water management strategies that could be more achievable than complete restoration of natural streamflow patterns.

The biological effects of streamflow characteristics have been most commonly documented at the scale of a single, natural hydrologic disturbance: a flood or drought. These hydrologic disturbances typically reduce densities and richness of benthic invertebrates, but have less effect on assemblage composition and structure (Stehr & Branson, 1938; Anderson & Lehmkuhl, 1968; Fisher *et al.*, 1982; Scrimgeour & Winterbourn, 1989; Boulton & Lake, 1992; Miller & Golladay, 1996). However, generalized invertebrate responses to streamflow-mediated disturbances are not supported by these investigations except as the disturbances become more severe, frequent and spatially extensive.

In fact, links between streamflow regimes (seasonal to inter-annual time scales) and invertebrates have

been established at regional scales. Invertebrate assemblage composition and structure was related to variation in seasonal streamflow magnitude over time (Bickerton, 1995) and among a group of 83 streams in England and Wales (Monk *et al.*, 2006). Abundance, richness and diversity of macroinvertebrate communities have been positively correlated to streamflow permanence and streamflow magnitude at seasonal scales in some streams (Schlosser, 1992; Feminella, 1996; Wood *et al.*, 2001), but were negatively related to long-term mean streamflow in 62 New Zealand streams (Clausen & Biggs, 1997). Abundance and richness may be highest at intermediate streamflow magnitudes (McElravy, Lamberti & Resh, 1989) and evenness may be highest at sites with intermediate levels of streamflow stability (Death & Winterbourn, 1995). Clausen & Biggs (1997) also found that abundance and richness were positively related to daily streamflow variation, the relative magnitude of high flows ( $Q_{10}/Q_{50}$ ), and flood frequency, whereas diversity was negatively related to flood frequency.

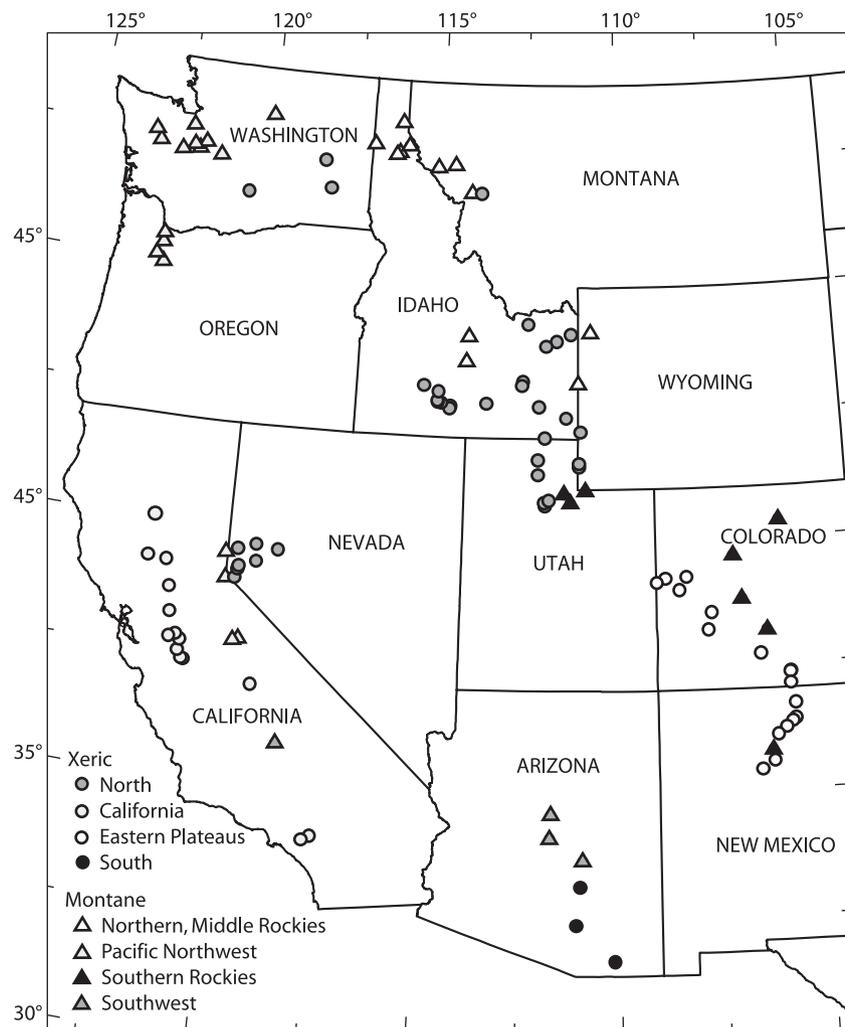
The primary objective of our study was to examine associations between streamflow patterns and characteristics of benthic invertebrate assemblages across a large geographic area: the western U.S.A. In the development of our conceptual framework for analysing streamflow invertebrate associations, we recognize that streamflow is only one factor among many others influencing biotic communities. These factors include channel form and materials, floodplain connectivity and riparian vegetation, water temperature and chemistry, availability of nutrients and energy resources, biotic interactions as well as the evolutionary history of species in the community and the legacy of past disturbance events and land use activities (Reeves *et al.*, 1995; Harding *et al.*, 1998; Allan, 2004). At the scale of the western U.S.A., invertebrate assemblages may respond to all of these factors and, as a consequence, are unlikely to display a central response (*sensu* Lancaster & Belyea, 2006) to streamflow where the values of streamflow metric and an invertebrate metric are correlated.

Nevertheless, streamflow may limit biological conditions at some sites where other factors would allow, for example, a higher abundance of organisms or greater number of taxa. The limit may take the form of a ceiling, an upper limit on an invertebrate metric that varies as a function of streamflow metric, or a floor, a lower limit on an invertebrate metric that varies as a function of a streamflow metric. Univariate or multivariate mean regression is inadequate for analysing limits in these cases (Thomson *et al.*, 1996) because streamflow would only account for variation in the biological condition along the ceiling or floor. Quantile regression, however, can address the differential effects of a factor on various quantiles of a response variable and, thus, does not require a relationship between a central tendency of a factor and a response variable (Koenker, 2005). In quantile regression, a specified quantile of a response variable

(biological condition) is fit with a continuous function of a factor, such as streamflow, (Cade & Noon, 2003; Cade, Noon & Flather, 2005; Koenker, 2005). Lancaster & Belyea (2006) used quantile regression to model maximum and minimum abundance of invertebrates in relation to hydraulic conditions and, thus, demonstrated how abundance can exhibit a 'limiting response' to a factor of interest. We extend this approach to assess less direct associations between streamflow characteristics and a broader suite of invertebrate characteristics across the western U.S.A.

## Methods

We selected sites from 11 western states (Fig. 1) where quantitative invertebrate samples were collected as part of the U.S. Geological Survey (USGS) National Water Quality Assessment (NAWQA) Program, and



**Fig. 1** Location of sites across the western U.S.A. with biome and region identified by symbols.

**Table 1** Geographical distribution of sites

Biome-Region (Omernik, 1987; U.S. EPA, 2007)	Level III Ecoregion
Montane-Northern and Middle Rockies (12 sites)	Middle Rockies (2 sites) Northern Rockies (10 sites)
Montane-Pacific Northwest (17 sites)	Cascades (4 sites) Coast Range (1 site) Puget Lowland (5 sites) Sierra Nevada (4 sites) Willamette Valley (3 sites)
Montane-Southern Rockies (8 sites)	Southern Rockies (5 sites) Wasatch and Uinta Mountains (3 sites)
Montane-Southwest (4 sites)	Arizona/New Mexico Mountains (3 sites) Southern California Mountains (1 site)
Xeric-California (14 sites)	Central California Valley (10 sites) Southern and Central California Plains and Hills (4 sites)
Xeric-Eastern Plateaus (21 sites)	Arizona/New Mexico Plateau (11 sites) Colorado Plateaus (6 sites) Wyoming Basin (4 sites)
Xeric-North (32 sites)	Columbia Plateau (3 sites) Montana Valley and Foothill Prairies (1 site) Northern Basin and Range (14 sites) Snake River Basin/High Desert (14 sites)
Xeric-South (3 sites)	Madrean Archipelago (1 site) Sonoran Basin and Range (2 sites)

where daily streamflow records were available for at least one complete water year (1 October–30 September) continuously from and including the water year of invertebrate sampling. The sites represented 22 Level III Ecoregions (Omernik, 1987; U.S. EPA, 2007) (Table 1). As part of previous NAWQA investigations, basin characteristics (Table 2) were calculated for all sites from a national 30-m digital elevation model (U.S. Geological Survey, 2006), the 1990 National Land Cover Data (Vogelmann *et al.*, 2001) and the National Inventory of Dams (U.S. Army Corps of Engineers, 2006). Habitat at sampling sites was characterized in the field following Fitzpatrick *et al.* (1998), and included information on stream depth, width, velocity, substrate and riparian vegetation. Although the analysis of associations among basin and habitat characteristics, streamflow and

**Table 2** Basin characteristics and habitat conditions

Basin characteristics	Units	Median (10th–90th percentile range)
Drainage area	km <sup>2</sup>	2136 (52–20279)
Mean basin elevation	m.a.s.l.	1930 (479–2846)
Site elevation	m.a.s.l.	1238 (21–2068)
Road density	km km <sup>-2</sup>	1 (0.33–2)
Population density	people km <sup>-2</sup>	5 (0–91)
Urban land cover	%	0.4 (0.02–5.8)
Agricultural land cover	%	4.2 (0–28)
Forest land cover	%	43 (0–80)
Number of dams		8 (0–92)
Habitat conditions at invertebrate sampling sites		
Mean depth	m	0.62 (0.3–1.7)
Coefficient of variation of depth		48 (31–73)
Mean width	m	21 (7–79)
Coefficient of variation of width		24 (10–40)
Mean velocity	m s <sup>-1</sup>	0.48 (0.09–0.8)
Coefficient of variation of velocity		51 (27–91)
Froude number		0.16 (0.04–0.37)
Sand and finer	%	16.7 (0–100)
Gravel and cobble	%	58 (0–65)
Boulder	%	5.6 (0–67)
Bank vegetation	%	58 (19–87)

benthic invertebrates was beyond the scope of this, we used to assess the extent to which other (non-hydrologic) factors were underlying the observed limits on invertebrates associated with streamflow.

Streamflow records were obtained from the National Water Information System (USGS, 2005). The hydrologic analysis was limited to streamflow records from no more than 15 years prior to invertebrate sampling. The range in record length (5–15 years) strikes a balance between a long period for characterizing inter-annual streamflow patterns and a short period during which climate, land use or water management could be considered stable for the purposes of characterizing streamflow patterns (Konrad & Booth, 2002). Most (82) sites had 15 years of streamflow record. An initial set of 50 streamflow metrics (available at <http://water.usgs.gov/nawqa/studies/mrb/pubs.html>) were selected to represent three classes of streamflow (high flows, low flows and central tendency flows) in terms of five ecologically significant characteristics: magnitude, duration, frequency, timing and variation (Richter *et al.*, 1996; Poff *et al.*, 1997). Variation was included to represent streamflow variation at temporal scales from days to

months and years (Bunn & Arthington, 2002; Biggs, Nikora & Snelder, 2005) and includes rate-of-change metrics. Metrics of magnitude, duration, frequency and variation characteristics based on streamflow for 30 and 100 days prior to invertebrate sampling were also analysed to address the possibility of strong invertebrate assemblage response to recent streamflow.

Multiple metrics were identified for each streamflow characteristic to assess whether there were preferred metrics for representing biotic responses. Kendall's rank correlation test (R Development Core Team, 2005) was applied to all pairs of streamflow metrics to eliminate highly correlated metrics (Kendall's  $\tau > 0.7$ ) that were probably to be redundant with respect to biotic responses (Clausen & Biggs, 2000; Olden & Poff, 2003). The final set of streamflow metrics was selected after screening all of the metrics for potential ceilings or floors associated with invertebrate metrics.

Quantitative samples of invertebrate assemblages were collected from the most faunistically rich habitat type at each site (typically riffles) during base flow conditions (Cuffney, Gurtz & Meador, 1993; Moulton *et al.*, 2002). Invertebrates were collected from a 0.25-m<sup>2</sup> area of the streambed using a modified Surber Sampler. In a few cases, a Hess Sampler or standard Surber Sampler was used and results were corrected for the difference in sampling area. Five samples were collected at each site and amalgamated to produce a single composite sample. Samples were enumerated and identified to the lowest practical taxonomic level at the USGS National Water Quality Laboratory in Denver, Colorado (Moulton *et al.*, 2000).

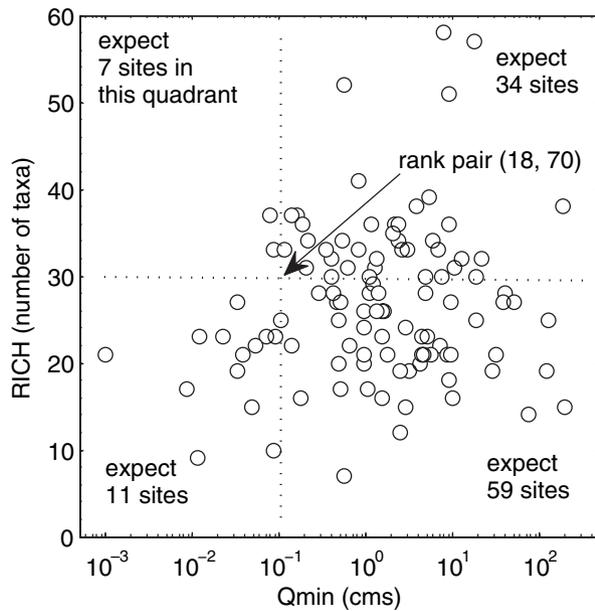
The structure and composition of benthic invertebrate assemblages was characterized using a broad range of metrics. An initial set of 157 invertebrate metrics (available at <http://water.usgs.gov/nawqa/studies/mrb/pubs.html>) was generated with the USGS Invertebrate Data Analysis System (Cuffney, 2003). Based on best professional judgement, we selected a subset of these metrics that characterize broad features of invertebrate assemblages including abundance, richness, diversity (including evenness and dominance), traits (functional feeding groups and behavioural habits), and individual taxa, to use in our analyses. Taxa were assigned to the categories of 'tolerant', 'intolerant' or 'no tolerance information available' following the U.S. Environmental Protection Agency's Rapid Bioassessment Protocol (Barbour

*et al.*, 1999) classification of taxa based on sensitivity to perturbation.

We then identified metrics that either provided complimentary information (e.g. per cent native and per cent non-native), or were subsets of another metric [e.g. abundance of Plecoptera is a subset of abundance of EPT (Ephemeroptera, Plecoptera and Trichoptera)] taxa, or were probably to produce similar species lists (e.g. tolerant species and non-insect species). When such metrics showed a similar association with the hydrologic metrics, the less inclusive invertebrate metric was eliminated. In some instances related invertebrate metrics (as in the case of Plecoptera and EPT) had associations with different hydrologic metrics, so both were retained. The final set of invertebrate metrics was selected after screening all of the metrics for potential ceilings or floors.

A nonparametric screening procedure (NPSP) was developed to identify probably ceilings and floors on invertebrate metrics associated with streamflow metrics. Ceilings and floors may be positive (the limits increase with increasing values of the streamflow metric) or negative (the limits decrease with increasing values of the streamflow metrics). NPSP is written in Visual Basic for Applications and implemented as a macro in Microsoft Excel.

Nonparametric screening procedure tests two hypotheses for each pair of streamflow-invertebrate metrics. The first hypothesis is that ranks of the data are not independently distributed such that there are fewer points than expected in some regions of the plots (as in the upper left hand region of Fig. 2). The corresponding null hypothesis ( $H_{10}$ ) is that the number of data points in each of the four quadrants centered around the rank-pair origin ( $r, q$ ) is the joint probability calculated from the ranks of the streamflow and invertebrate metric: the probability that a data point will be in quadrant 1 is  $P_1 = qr$ , in quadrant 2 is  $P_2 = (n - r, q)$ , in quadrant 3 is  $P_3 = (n - r)(q - r)$  and in quadrant 4 is  $P_4 = r(n - q)$ , where  $n$  is the total number of sites. The likelihood of the observed number of data points in each quadrant is evaluated using the binomial distribution where the total number of trials is  $n^2$  and the above specified probabilities. If the likelihood of the observed number of points is less than the desired significance level (in this case  $\alpha = 0.05$ ),  $H_{10}$  can be rejected for that rank-pair origin ( $r, q$ ) and quadrant.



**Fig. 2** Plot of invertebrate richness (number of taxa) and median annual minimum streamflow where the probability of observing 2 sites in the upper left quadrant around the rank-pair  $q = 18$ ,  $r = 70$  was highly unlikely:  $P = 0.03$  based on binomial distribution with 111 trials and probability of success was  $18/111 \times (111 - 70)/111$ . The expected number of sites is listed for each quadrant.

The first test can be applied manually for a selected rank-pair based on visual inspection of how data are distributed. To automate this routine for consistent application to all pairs of streamflow-invertebrate metrics, NPSP evaluates  $H_{10}$  for each quadrant (1–4) for all possible rank-pairs origins ( $q = 1-n$ ,  $r = 1-n$ ) for each pair of streamflow-invertebrate metrics. The result is the number of times that a given type of quadrant (lower left, upper left, lower right and upper right), had fewer observations than expected totalled for all  $n^2$  rank-pairs origins.

Although the locations of the quadrants shift with each rank-pair serving as an origin, rejecting  $H_{10}$  in quadrant type 1 for a large number of rank-pair origins, for example, indicates that in general there are fewer points than expected in the lower left region of the plot and there is probably to be a negative floor. Likewise, rejecting  $H_{10}$  in quadrant type 4 for a large number of rank-pair origins indicates that in general there are fewer points than expected in the upper right region of the plot and there is probably to be a positive ceiling. NPSP uses a second test to evaluate whether there is a statistically-significant number of rank-pair origins that had fewer data than expected in

each type of quadrant (i.e. where  $H_{10}$  was rejected for each quadrant type) to account for type I error (false rejection of  $H_{10}$ ) because of the large number of rank-pairs ( $n^2$ ) evaluated under the first test.

The null hypothesis for the second test,  $H_{20}$ , is that the number of rank-pair origins where  $H_{10}$  was rejected is not significantly greater than expected given  $n^2$  (the number of tests of  $H_{10}$ ) and  $\alpha$  (the probability of rejecting  $H_{10}$ ). For the test of  $H_{20}$ , the probability of the observed number of rank-pairs origins where  $H_{10}$  was rejected for a quadrant was evaluated using the binomial distribution with  $n^2 = 12\,321$  rank-pair origins and the probability of rejecting  $H_{10}$  of  $\alpha = 0.05$ . If the probability of the observed number of times that  $H_{10}$  was rejected less than  $\alpha = 0.05$ , then  $H_{20}$  was rejected. Because the probability of rejecting  $H_{10}$  was less than  $\alpha$  for many rank-pair origins, the second test will produce a high rate of type II errors (accepting that the number of rank-pair origins where  $H_{10}$  was rejected was not higher than expected by chance) and will not reliably detect all streamflow-invertebrate associations at a given significance level.

Streamflow and invertebrate metrics that had few ceilings or floors were eliminated from further analysis, and are not presented in this paper. Streamflow or invertebrate metrics that represented a broader group with similar patterns of ceiling and floors (e.g. metrics of streamflow magnitude or metrics of dominance, evenness and diversity) were selected while the other metrics in the group were eliminated from further analysis. A final set of 13 streamflow metrics (Table 3) and 14 invertebrate metrics (Table 4) were selected for analysis.

Most of the streamflow metrics are simple time-series statistics as defined in Table 3. Per cent daily change was calculated in terms of the absolute values of percentage change in daily streamflow and base flow recession (BFR) is the 10th percentile of all differences in the logarithms of daily streamflow,  $\log(Q_{\text{day}1}) - \log(Q_{\text{day}0})$ , which characterizes the higher end of the range of recession rates for a stream. BFR is an inverse measure with large negative value representing rapid recession. Known indicators of hydrologic alteration and non-dimensional metrics of streamflow magnitude (e.g. PDC,  $CV_{\text{month}}$ ,  $\text{High}_{\text{freq}}$ ,  $Q_{\text{max}}/Q_{\text{mean}}$ ) were included to allow comparisons among different size basins. The remaining streamflow metrics still had significant but generally weak

**Table 3** Streamflow metrics selected for analysis to represent five ecologically-significant characteristics

Magnitude
Median annual mean streamflow ( $Q_{\text{mean}}$ )
Median annual minimum daily streamflow ( $Q_{\text{min}}$ )
Duration
Median annual duration of the longest high flow event ( $\text{High}_{\text{dur}}$ )
Frequency
Median annual number of continuous periods (high-flow events) when daily streamflow exceeds $Q_{10}$ ( $\text{High}_{\text{freq}}$ )
Timing
Month of maximum monthly streamflow ( $\text{Month}_{\text{max}}$ )
Variation
Coefficient of variation of annual minimum streamflow ( $\text{CV}_{\text{min}}$ )
Per cent daily change in streamflow (PDC)
Baseflow recession rate (BFR)
Coefficient of variation of monthly mean streamflow ( $\text{CV}_{\text{month}}$ )
Median annual maximum daily streamflow as a fraction of mean streamflow ( $Q_{\text{max}}/Q_{\text{mean}}$ )
Median annual streamflow exceeded 10% of the year as a fraction of median streamflow ( $Q_{10}/Q_{50}$ )
Mean streamflow 100 days prior to invertebrate sampling divided by median streamflow (100-day $Q_{\text{mean}}/Q_{50}$ )
Minimum streamflow 100 days prior to invertebrate sampling divided by median streamflow (100-day $Q_{\text{min}}/Q_{50}$ )

**Table 4** Invertebrate metrics selected to represent five characteristics of assemblages

Abundance
Total number of invertebrates (ABUN)
Per cent of abundance comprised by Ephemeroptera, Plecoptera and Trichoptera (EPTp)
Per cent of abundance comprised by non-insects (NONINp)
Richness
Total number of taxa (RICH)
Total number of Ephemeroptera, Plecoptera and Trichoptera taxa (EPTr)
Total number of non-insect taxa (NONINr)
Per cent of richness comprised by intolerant taxa (INTOLrp)
Per cent of richness comprised by tolerant taxa (TOLrp)
Diversity and evenness
Percentage of abundance comprised by the three most dominant taxa (DOM3)
Functional feeding groups
Per cent of abundance comprised by scrapers (SCRAP)
Individual taxa
Per cent of abundance comprised by Plecoptera (PLECp)
Per cent of abundance comprised by Trichoptera (TRIp)
Per cent of abundance comprised by Coleoptera (COLEp)
Per cent of abundance comprised by Chironomidae (CHIRp)

correlations. The most strongly correlated streamflow metrics were within the same characteristic groups such as magnitude (e.g.  $\tau = 0.69$  for  $Q_{\text{mean}}$  and  $Q_{\text{min}}$ )

or variability ( $\tau = 0.65$  for  $Q_{10}/Q_{50}$  and  $\text{CV}_{\text{month}}$ ,  $\tau = 0.52$  for  $\text{CV}_{\text{month}}$  and  $Q_{\text{max}}/Q_{\text{mean}}$  and  $\tau = 0.50$  for  $Q_{10}/Q_{50}$  and 100-day  $Q_{\text{max}}/Q_{50}$ ). All other correlations among the selected streamflow metrics were relatively weak ( $\tau < 0.5$ ).

After the strongest associations among hydrologic and invertebrate metrics were identified using NPSP, selected ceilings and floors were quantified with quantile regression using the Quantreg package, version 3.84 in R (Koenker, 2005; R Development Core Team, 2005). Quantile regression addresses potential conditional relations between a factor variable and quantiles of a response variable in contrast to mean regression that assumes all quantiles follow the central tendency of the response variable. Because a biological condition may not exhibit a central response to a single environmental factors where there are multiple factors affect the biota, such as in regional-scale analyses, standard mean regression cannot adequately account for observed patterns of distribution and abundance (Cade & Noon, 2003; Lancaster & Belyea, 2006).

Quantile regression fits a continuous function through the local (with respect to the independent variable) value of the quantile of a dependent variable to account for variation in the quantile with the independent variable. In this analysis, ceilings were represented by the 90th quantile while floors were represented by the 10th quantile. These quantiles were selected to ensure an adequate number of points over the ranges of the metrics for a robust estimate of the slope of the regression line. Although smaller or large quantiles (e.g. the 1st and 99th quantiles) may be more representative of the absolute limits on invertebrate metric values, the estimates of the slopes of these quantiles are often not statistically significant in comparison to the 10th and 90th percentiles. Both linear and logarithmic forms of the quantile were tested for statistical significance in terms of the probability that the slope and intercept were zero. The functional form of the quantile with the highest statistical significance (lowest  $P$ -value) was retained in the final results.

## Results

Overall, every flow characteristic was associated with a limit on invertebrates and every invertebrate characteristic had a limit associated with at least one flow characteristic (Table 5). Streamflow variability at daily (PDC, BFR) and monthly time-scales ( $\text{CV}_{\text{month}}$ )

Streamflow metric	ABUN	EPTp	NONINp	RICH	EPTr	NONINr	INTOLrp
$Q_{\text{mean}}$	-	+C	-F	-	+F	-	-
$Q_{\text{max}}/Q_{\text{mean}}$	-	-	-	-	-	-F	+C
$Q_{10}/Q_{50}$	-	+C	-	-	-	-F	-
$\text{High}_{\text{freq}}$	-C	-	-	-	-	-	-
$\text{High}_{\text{dur}}$	-	-	-F	-	-	-	+C
$Q_{\text{min}}$	-	-	-	+C	-	-	-
$\text{CV}_{\text{min}}$	-	-	-	-	-C, -F	-	-C, -F
PDC	-F	-	-	-	-	-F	-C
BFR	-	-	-	+C	+C	-	+C
$\text{CV}_{\text{month}}$	-	+C	-F	-	-	-F	+C
$\text{Month}_{\text{max}}$	-	-	+F	-C	-C	+F	-
100-day $Q_{\text{min}}/Q_{50}$	-	-	-	-	-	-C	-
100-day $Q_{\text{mean}}/Q_{50}$	-	-	-C	-	-	-C, -F	-

Streamflow metric	TOLrp	DOM3	SCRAp	PLECp	TRIp	COLEp	CHIRp
$Q_{\text{mean}}$	-	-	-	-	-	-	-
$Q_{\text{max}}/Q_{\text{mean}}$	-	-	-	+C	-	-	-F
$Q_{10}/Q_{50}$	-F	-	-	+C	-	-	-
$\text{High}_{\text{freq}}$	-	+F	-	-	-	-	-F
$\text{High}_{\text{dur}}$	-F	-	+F	+C	-	-	-
$Q_{\text{min}}$	-	-F	-	-	+C	+C	+F
$\text{CV}_{\text{min}}$	-	-	-C	-C	-	-	-
PDC	-	+F	-	-C	-C	-	-
BFR	-	-F	+C	-	+F	+C	-
$\text{CV}_{\text{month}}$	-	-	+F	+C	-	-	-
$\text{Month}_{\text{max}}$	+F	-	-	-C	-	-	-
100-day $Q_{\text{min}}/Q_{50}$	-	-C, -F	+F	-	-	-	-
100-day $Q_{\text{mean}}/Q_{50}$	-C, -F	-	-	+C	-	-	-

Direction of ceiling or floor is indicated by: +, positive; -, negative.

was associated with limits on all invertebrate metrics except the relative richness of tolerant taxa (TOLrp) and the relative abundance of Chironomidae (CHIRp). Eight invertebrate metrics were associated with metrics of streamflow magnitude ( $Q_{\text{mean}}$ ,  $Q_{\text{min}}$ ).  $Q_{\text{mean}}$  was associated with a positive ceiling on EPTp, a negative floor on NONINp and a positive floor on EPTr, but otherwise did not appear to be particularly influential.  $Q_{\text{min}}$ , the other metric of streamflow magnitude, was associated with a positive ceiling on RICH (Fig. 2), TRIp and COLEp, a negative floor on DOM3 and a positive floor on CHIRp. Thus despite the relatively high correlation between  $Q_{\text{mean}}$  and  $Q_{\text{min}}$ , each is associated with limits for a distinct set of invertebrate metrics.

Nine of the invertebrate metrics showed both ceilings and floors of the same direction (positive or negative) associated with streamflow metrics. ABUN, for example, had a negative ceiling associated with  $\text{High}_{\text{freq}}$  and negative floor associated with PDC (Fig. 3). Although the ceiling on ABUN associated

**Table 5** Ceilings (C) and floors (F) on selected invertebrate metrics associated with streamflow metrics identified using the nonparametric screening procedure

with  $\text{High}_{\text{freq}}$  would appear to be steeper than indicated by the 90th quantile regression line (Fig. 3a), the low number of sites with  $\text{High}_{\text{freq}} > 10$  events per year do not provide enough leverage to drive the slope of the 90th quantile (Table 6). In contrast, the floor on ABUN is relatively steep with respect to PDC (Fig. 3b).

Overall, invertebrate metrics were only weakly correlated with streamflow metrics (Kendall's  $\tau < 0.3$  in for all pairs of streamflow-invertebrate metrics). Despite weak central responses, the slope of many of the limiting responses indicated the upper or lower limits on an invertebrate metric are relatively sensitive to streamflow characteristics. For example, the upper limit on EPTp shows an increase of 3% with every 0.1 increase in  $\text{CV}_{\text{month}}$  (Fig. 3c) and an increase of 4% with every 10% increase in  $Q_{10}/Q_{50}$  (Fig. 3d).

In the cases where an invertebrate metric had both a ceiling and floor of the same direction associated with a single streamflow metric, a strong correlation

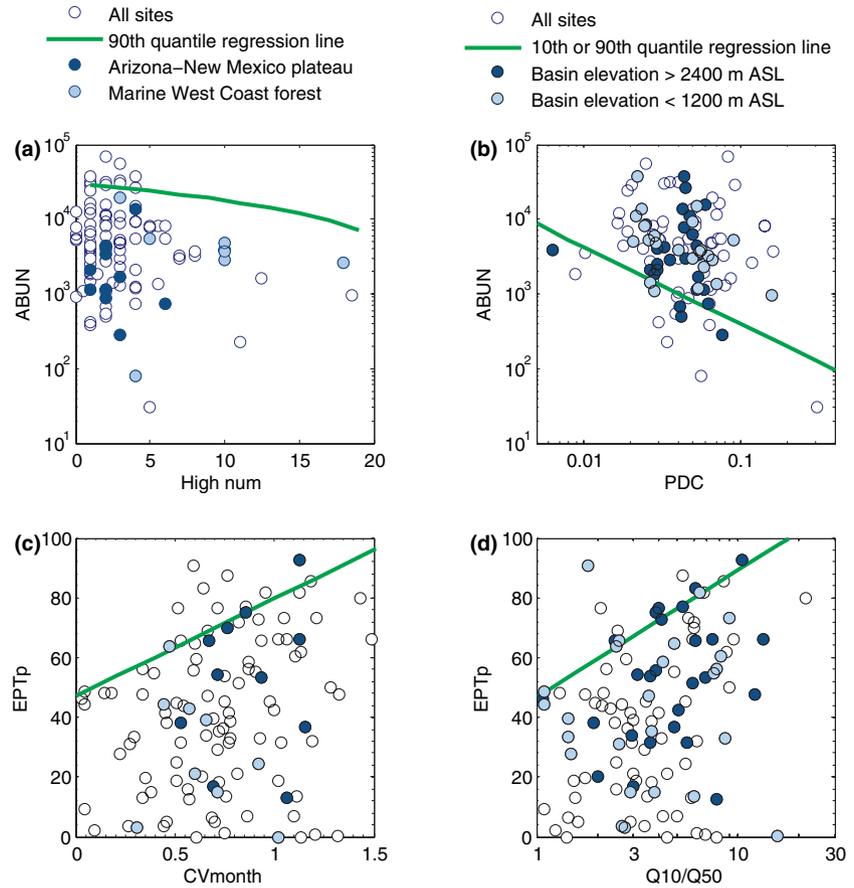


Fig. 3 Limits on abundance (ABUN) and relative abundance of EPT (EPTp) associated with selected streamflow metrics.

Table 6 Selected quantile regression equations illustrating ceilings (90th quantile) and floors (10th quantile) on invertebrate metrics

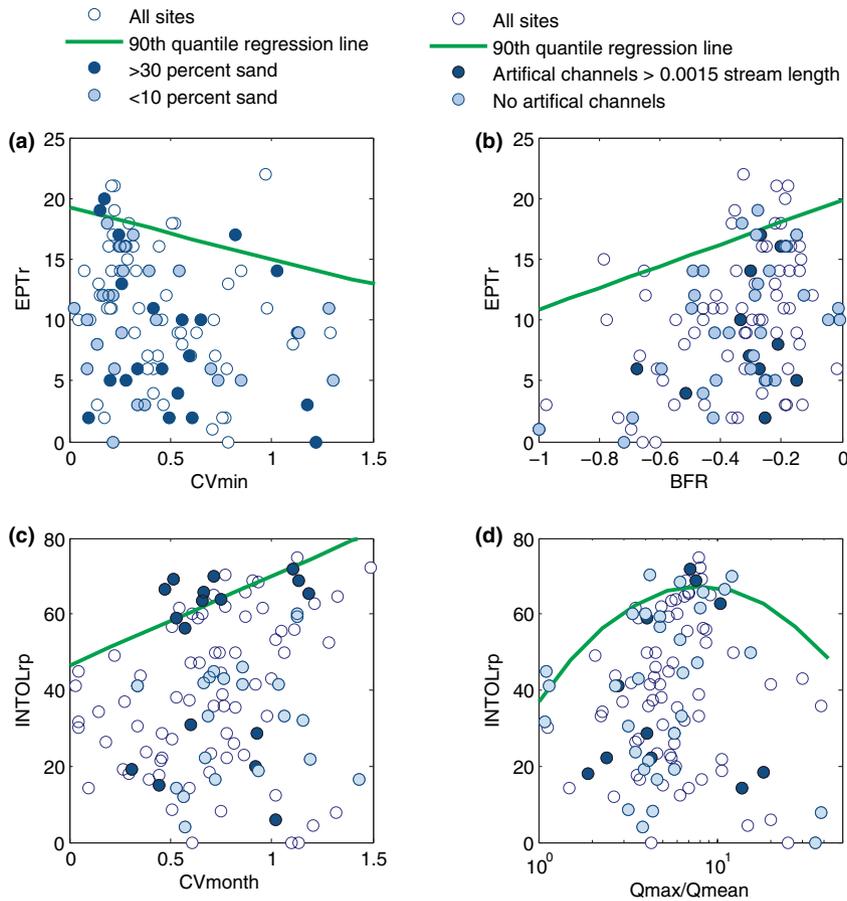
Quantile regression equation	Regression quantile	P that slope = 0
$ABUN = -1190 (High_{freq}) + 29759$	0.9	0.026
$Log_{10} (ABUN) = -1.03 [log_{10} (PDC)] + 1.57$	0.1	<0.001
$EPTp = 32.6 (CV_{month}) + 47.1$	0.9	0.003
$EPTp = 42.5 [log_{10} (Q_{10}/Q_{50})] + 46.8$	0.9	<0.001
$EPTr = -4.16 (CV_{min}) + 19.2$	0.9	0.007
$EPTr = 8.94 (BFR) + 19.8$	0.9	0.036
$INTOLrp = 23.4 (CV_{month}) + 46.6$	0.9	<0.001
$INTOLrp = -37.3 [(8 - Q_{max}/Q_{mean})^2] + 67.4$	0.9	0.006
$DOM3 = 1.08 (High_{freq}) + 40.6$	0.1	0.016
$DOM3 = -24.9 (BFR) + 35.5$	0.1	0.007
$SCRAp = 0.17 (High_{dur}) + -1.37$	0.1	<0.001
$SCRAp = -14.7 (CV_{min}) + 46.2$	0.9	<0.001

between the invertebrate and streamflow metric is possible because both the maximum and minimum values of the invertebrate metric vary in the same direction with the streamflow metric. In the case of

EPTr and  $CV_{min}$  (Fig. 4a), the 90th quantile was statistically significant ( $P = 0.007$  that slope = 0, Table 6) while the 10th quantile was not and the two metric were only moderately correlated (Kendall's  $\tau = 0.23$ ). Likewise, TOLrp had a negative ceiling and a negative floor associated with 100-day  $Q_{mean}/Q_{50}$  but these metrics were only moderately correlated (Kendall's  $\tau = -0.28$ ).

Six invertebrate metrics had limits associated with the relative magnitude of streamflow 100 days prior to invertebrate sampling. Three of these limits were unique to the recent streamflow metrics: negative ceilings on NONINp and TOLrp associated with 100-day  $Q_{mean}/Q_{50}$ , and a negative ceiling on DOM3 associated with 100-day  $Q_{min}/Q_{50}$ . Invertebrate metrics had fewer limits associated with metrics based on streamflow 30 days prior to sampling and those limits were generally the same as those for the corresponding metrics based on streamflow 100 days prior to sampling.

The shared responses of NONINp and TOLrp to recent streamflows illustrate how related invertebrate



**Fig. 4** Limits on EPT richness (EPTr) and relative richness of intolerant taxa (INTOLrp) associated with selected streamflow metrics.

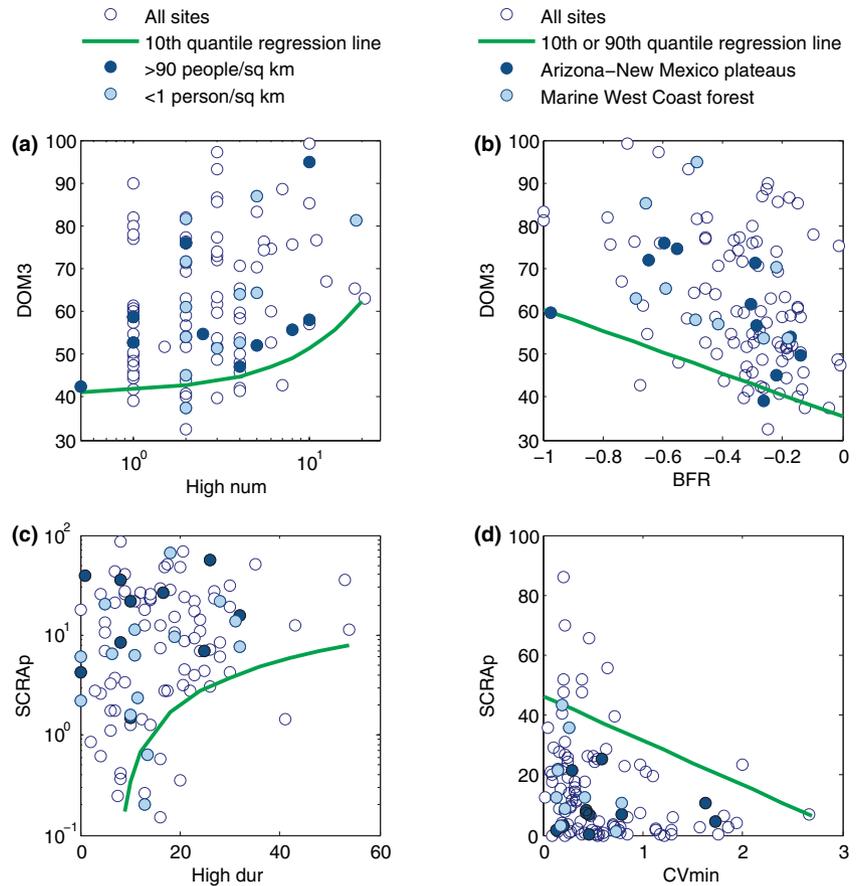
metrics (in this case because of overlap between non-insects and tolerant taxa) had similar responses. NONINp and TOLrp also shared a negative floor associated with  $CV_{\text{month}}$  and a positive floor associated with  $Month_{\text{max}}$ . RICH and EPTr shared ceilings associated with BFR (Fig. 4b) and  $Month_{\text{max}}$ , but had distinct associations with other streamflow metrics. Complementary invertebrate metrics (e.g. INTOLrp and NONINr) showed opposite responses to streamflow metrics. INTOLrp had positive ceilings associated with  $CV_{\text{month}}$  (Fig. 4c) and  $Q_{\text{max}}/Q_{\text{mean}}$  (Fig. 4d), while NONINr had negative floors associated with these streamflow metrics (Table 5). However, both INTOLrp and NONINr had negative limits associated with PDC and also had distinct limits with different streamflow metrics that distinguished one from another. Other metrics that are inversely related, such as RICH and DOM3, had opposite responses to some streamflow metrics but not with respect to all streamflow metrics (Table 5).

The upper limit on INTOLrp and  $Q_{\text{max}}/Q_{\text{mean}}$  (Fig. 4d) showed an intermediate maximum around

a value of  $Q_{\text{max}}/Q_{\text{mean}}$ . In this case, we assigned the 90th quantile a quadratic form (Table 6) that indicated low values of INTOLrp for sites where high flows are relatively low ( $Q_{\text{max}}/Q_{\text{mean}} < 3$ ) or high ( $Q_{\text{max}}/Q_{\text{mean}} > 10$ ).

The direction of invertebrate-metric responses was not consistent for all streamflow metrics. The floor on DOM3 was positive with respect to High Num (Fig. 5a) but negative with respect BFR (Fig. 5b). In these cases, the minimum level of dominance increased with the frequency of high flows and decreased in streamflows with slower recession rates (higher values of BFR). PLECP had both positive ceilings ( $Q_{\text{max}}/Q_{\text{mean}}$ ,  $Q_{10}/Q_{50}$ ,  $High_{\text{dur}}$ ,  $CV_{\text{month}}$ ) and negative ceilings ( $CV_{\text{min}}$ , PDC,  $Month_{\text{max}}$ ). In this case, the relative abundance of Plecoptera increased with streamflow variability at intra-annual time scales but decreased with daily streamflow variability (PDC) and inter-annual low flow variability ( $CV_{\text{min}}$ ).

Scrapers were the most responsive of all functional feeding groups. SCRAP had positive floors with respect to three different streamflow metrics (shown



**Fig. 5** Limits on the relative abundance of the three dominant taxa (DOM3) and scrapers (SCRAp) associated with streamflow metrics.

for  $\text{High}_{\text{dur}}$  in Fig. 5c), a positive ceiling with respect to BFR, and a negative ceiling with respect to  $\text{CV}_{\text{min}}$  (Fig. 5d). The floor resolved only very low relative abundances ( $\text{SCR}_{\text{Ap}} < 10\%$ ) while the ceiling resolved a much larger range of relative abundances ( $\text{SCR}_{\text{Ap}} \approx 10\text{--}40\%$ ).

Overall there were relatively few strong or even moderate correlations between invertebrate metrics and basin characteristics (e.g. the strongest correlation was for EPTr and population density with Kendall's  $\tau = -0.47$ ), habitat conditions (strongest correlation was EPTr and per cent of reach with sand and finer substrate with Kendall's  $\tau = -0.36$ ), or streamflow metrics. Data were coded in plots (Figs 3–5) according to other selected factors (ecoregion, elevation, substrate, artificial channel density and population density) to ascertain influences of these factors. None of the ceilings or floors appears to be dominated by the distribution of sites according to these regional, habitat or anthropogenic factors. ABUN at sites from the Arizona–New Mexico plateaus and marine west coast forests (Coast Range, Puget Lowland and Willamette Valley

ecoregions) generally showed the same patterns despite higher frequency of high flow events in marine west coast forests (Fig. 3a). The floor on ABUN associated with PDC and the ceiling on EPTr associated with  $Q_{10}/Q_{50}$  do not appear to be affected by basin elevation (Fig. 3b,d). Although EPTr and INTOLrp were moderately correlated with per cent sand and finer substrate (Kendall's  $\tau = -0.36$  and  $-0.30$  respectively), this factor did not appear to affect the ceiling on EPTr associated with  $\text{CV}_{\text{min}}$  (Fig. 4a) or the ceiling on INTOLrp associated with  $\text{CV}_{\text{month}}$  (Fig. 4c). The ceilings on EPTr associated with BFR and on INTOLrp associated with  $Q_{\text{max}}/Q_{\text{mean}}$  do not appear to depend on the density of artificial channels in the basins (Fig. 4b,d). Likewise, the floors on DOM3 and High Num and on SCRAp associated with  $\text{High}_{\text{dur}}$  do not appear to depend on population density (Fig. 5a,c).

## Discussion

Application of a NPSP in conjunction with quantile regression was effective at identifying and quantify-

ing limits on macroinvertebrate assemblages associated with streamflow. These relationships would not have been evident using mean regression because invertebrates generally did not exhibit a strong central response to streamflow. Nonetheless, streamflow characteristics appear to be ecologically significant as limiting factors on invertebrate assemblages throughout the western U.S.A.

Each of the categories of macroinvertebrate metrics (abundance, richness, diversity and evenness, functional feeding groups and individual taxa) had limits associated with streamflow characteristics (magnitude, duration, frequency, timing and rate of change). However, no single streamflow metric provides a comprehensive indicator of the effects of streamflow on the benthic invertebrate assemblages. Instead, each characteristic of benthic invertebrate assemblages responded in a distinct way to streamflow characteristics with the responses often highly specific to a particular pairing of an invertebrate metric and a streamflow metric. Consequently, it is necessary to consider a broad range of streamflow and invertebrate assemblage characteristics employing multiple hydrological and biological metrics when characterizing the influence of streamflow in lotic ecosystems.

We selected 13 hydrologic metrics and 14 macroinvertebrate metrics that demonstrate key hydro-ecological relationships. Of these, base-flow recession was associated with seven of the selected invertebrate metrics, while daily and monthly variation in streamflow were associated with six invertebrate metrics. High flow duration and minimum daily streamflow were both associated with five invertebrate metrics. Although metrics for streamflow 100 days prior to sampling had more associations than metrics for streamflow 30 days prior to sampling, we cannot separate their effects because of high correlation between flows at these time-scales. Long-term flow regime represented by multiple year (5–15 years) streamflow statistics certainly appear as important if not more important than recent flows, but again correlation of long-term flow regime and streamflow prior to invertebrate sampling limit the strength of our conclusions. The relative influence of streamflow characteristics at these different time-scales warrants further investigation.

Relative abundance of Plecoptera, richness of non-insect taxa and relative abundance of intolerant (sensitive) taxa were all associated with multiple

streamflow metrics. In general, metrics of sensitive taxa (EPT, Plecoptera, richness and intolerant taxa) had ceilings associated with flow metrics while tolerant taxa (non-insects, tolerant taxa, dominance and chironomids) had floors. Streamflow characteristics generally (but not strictly) appear to limit the maximum relative richness/abundance of sensitive taxa and the minimum relative richness/abundance of insensitive taxa. Some macroinvertebrate metrics such as richness of EPT taxa and richness of non-insects showed ceilings associated with some flow metrics and floors associated with others.

Broader characteristics of invertebrate assemblages (abundance and richness) were associated with only a few of the selected streamflow metrics (abundance with frequency of high flows and per cent daily change, and richness with median annual minimum daily streamflow, baseflow recession rate and month of maximum monthly streamflow). Although the richness metric was only statistically associated with three flow metrics, these metrics represented three different hydrologic characteristics (magnitude, duration and timing).

Complementary groups of invertebrate metrics responded predictably in opposite directions (e.g. relative abundance of EPT has a ceiling with mean annual streamflow whereas relative abundance of non-insects has a negative floor). Likewise, the relative abundance of non-insects and the per cent richness of tolerant taxa generally had inverse associations of those for the relative abundance of EPT and per cent of richness of intolerant taxa. These relationships are consistent with those described in the bioassessment literature (Resh & Jackson, 1993; Karr & Chu, 1999).

The responses of complementary invertebrate metrics were not redundant in many cases. For example, the relative richness of intolerant taxa was associated with six streamflow metrics while tolerant taxa were associated with four streamflow metrics, but there was only one streamflow metric in common (duration of high flow). These results suggest that a broad set of invertebrate and streamflow metrics may be necessary to represent fully the ecological effects of streamflow characteristics. For example, the various EPT metrics included in the analysis (relative abundance of EPT taxa, richness of EPT taxa and relative abundance of each of the component taxa) tended to each respond to different streamflow metrics. As a result, one EPT

metric alone will only provide a partial picture of the response of EPT taxa to streamflow characteristics. Overall, multiple streamflow and invertebrate metrics are needed to represent the potential range of ecologically significant streamflow characteristics.

The intent of this paper was to generalize associations among streamflow characteristics and macroinvertebrate assemblages across the western U.S.A. despite the diverse biogeography of the region. Streamflow characteristics are influenced by many natural factors (including drainage area, precipitation, basin elevation and gradient, geology and soils, vegetation, storm paths and orographical effects) and anthropogenic ones (land use, water management), so we do not presume that the limits on invertebrate assemblages described here in terms of streamflow metrics are independent of other factors. Indeed, streamflow metrics were selected to represent the effects of factors such as dams and land use that alter hydrology (e.g. BFR,  $CV_{\text{month}}$ ,  $Q_{\text{max}}/Q_{\text{mean}}$ ) as well as factors such as basin area, precipitation and elevation that account for natural hydrologic variability ( $Q_{\text{mean}}$ ,  $\text{Month}_{\text{max}}$ ) that could influence invertebrate assemblages at the scale of the western U.S.A. The limits on invertebrate assemblages did not appear to be artifacts of relations to any single other factors, such as ecoregion, elevation, substrate, artificial channels or population density. Instead, streamflow characteristics probably represented the integrated hydrologic effects of these factors. The biological influences of these and other factors not mediated by streamflow are represented by the considerable variation in invertebrate assemblage characteristics within any ceilings and floors imposed by streamflow.

Our analyses indicate that invertebrate responses could be generalized across the western U.S.A. Nonetheless, different ecoregions will have very different streamflow characteristics (e.g. desert streams in the arid Southwest, high-elevation streams, snow-melt streams and winter-rain dominated Pacific Northwest streams), and also different invertebrate assemblages with evolutionary adaptations to these flow regimes and other environmental differences. Our approach could be used at the scale of an ecoregion to resolve biotic responses to natural hydrologic variation versus anthropogenic hydrologic alteration.

The comparative responses of biota to natural streamflow characteristics, which are within the

evolutionary setting of an invertebrate assemblage, versus anthropogenic streamflow characteristics, which may be outside that setting, remain to be resolved. Many of the streamflow metrics associated with limits on invertebrate assemblages exhibit characteristic effects from human activities. For example, river regulation by dams and large storage reservoirs for flood control, power generation or water supply can redistribute streamflow in time, potentially in a number of different ways that correspond to changes in magnitude, duration, frequency, timing and rate of change. Streamflow regulation can reduce monthly variability and annual peak magnitudes (Webb *et al.*, 1999; Vinson, 2001; Bunn & Arthington, 2002), change the timing of runoff, reduce the duration of high flows and increase the duration of moderate flows (Hart & Finelli, 1999; Bunn & Arthington, 2002). At daily and shorter time-scales, hydropower production can increase streamflow variability (Gislason, 1985; Munn & Brusven, 1991; Sumioka, 2004; Wright *et al.*, 2005). Water supply projects may reduce or eliminate daily streamflow variability much of the time, increase low flows, reduce streamflow magnitude and change recession rates (Webb *et al.*, 1999; Trush, McBain & Leopold, 2000; Marchetti & Moyle, 2001; Magilligan & Nislow, 2005). Conveyance of additional water through river and stream channels to downstream users increases streamflow magnitude during natural low flow periods (Rader & Belish, 1999). The biological consequences of any of these changes at a site may depend on the deviation of the streamflow patterns from those prevailing over evolutionary history. Across a landscape with rivers having diverse hydrological regimes, however, river regulation is probably to homogenize regional differences in hydrology that may be mirrored by biota (Poff *et al.*, 2007).

The ceilings and floors on macroinvertebrate assemblages associated with streamflow characteristics are critical to efforts to conserve or restore biological resources. By comparing site conditions to these limits, resource managers can identify streamflow characteristics that are probably to be important for maintaining or achieving a specific biological condition (e.g. richness of invertebrate taxa), and will have some approximate targets in terms of metric values. These limits also demonstrate that biotic responses to streamflow may be conditional – they depend on the broader ecological state of a site. As such, an incremental change in streamflow may not in general

produce a proportionately incremental response in biota regardless of the initial ecological state of the system, though we cannot rule out this possibility. In the case of conditional responses, the biological consequences of water management or deliberate attempts to restore streamflow patterns cannot be predicted without a thorough understanding of physical and biological conditions at a site. Streamflow should be recognized as only one factor influencing lotic communities and other factors are probably to have a more influential role than streamflow at some sites. Nonetheless, a broad range of streamflow characteristics appear to be important to biota in rivers and streams across the western U.S.A., and presumably also in other equivalent large geographical areas.

### Acknowledgments

This work was supported by the U.S. Geological Survey National Water Quality Assessment Program. The conceptual framework for this paper was developed with contributions from Bob Black, Larry Brown, Terry Maret, Terry Short and Ian Waite. We appreciate the helpful comments on an earlier draft by Christine Albano, Brian Bledsoe, Steve Gingerich, Marty Gurtz and two anonymous reviewers.

### References

- Allan J.D. (1995) *Stream Ecology Structure and Function of Running Water*. Chapman and Hall, London.
- Allan J.D. (2004) Landscapes and rivers: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution and Systematics*, **35**, 257–284, 388.
- Anderson D.M. & Lehmkuhl N.H. (1968) Catastrophic drift of insects in a woodland stream. *Ecology*, **49**, 198–206.
- Barbour M.T., Gerritsen J., Snyder B.D. & Stribling J.B. (1999) *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish*, 2nd edn. EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water, Washington, D.C.
- Bickerton M.A. (1995) Long-term changes of macroinvertebrate communities in relation to flow variations: the River Glen, Lincolnshire, England. *Regulated Rivers: Research & Management*, **10**, 81–92.
- Biggs B.J.F., Nikora V.I. & Snelder T.H. (2005) Linking scales of flow variability in rivers to lotic ecosystem structure and function. *River Research and Applications*, **21**, 283–298.
- Boulton A.J. & Lake P.S. (1992) The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology*, **4**, 123–141.
- Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 4492–4507.
- Cade B.S. & Noon B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.
- Cade B.S., Noon B.R. & Flather C.H. (2005) Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology*, **86**, 786–800.
- Clausen B. & Biggs B.J. (1997) Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology*, **38**, 327–342.
- Clausen B. & Biggs B.J.F. (2000) Flow variables for ecological studies in temperate streams: groupings based on covariance. *Journal of Hydrology*, **237**, 184–197.
- Cuffney T.F. (2003) *User's Manual for the National Water-Quality Assessment Program Invertebrate Data Analysis System (IDAS) Software – Version 3*. U.S. Geological Survey Open-File Report 03-172, 103 p.
- Cuffney T.F., Gurtz M.E. & Meador M.R. (1993) *Methods for Collecting Benthic Invertebrate Samples as Part of the National Water-Quality Assessment Program*. U.S. Geological Survey Open-File Report 96-406, 66 p.
- Death R.G. & Winterbourn M.J. (1995) Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology*, **76**, 1446–1460.
- Feminella J.W. (1996) Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *Journal of the North American Benthological Society*, **15**, 651–669.
- Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, **52**, 93–110.
- Fitzpatrick F.A., Waite I.R., D'Arconte P.J., Meador M.R., Maupin M.A. & Gurtz M.E. (1998) *Revised Methods for Characterizing Stream Habitat in the National Water-Quality Assessment Program*. U.S. Geological Survey Open-File Report 98-4052, 67 p.
- Gislason J.C. (1985) Aquatic insect abundance in a regulated stream under fluctuating and stable diel flow patterns. *North American Journal of Fisheries Management*, **5**, 39–46.

- Harding J.S., Benfield E.F., Bolstad P.V., Helfman G.S. & Jones E.B.D. (1998) Stream biodiversity: the ghost of land use past. *Proceeding of the National Academy of Sciences*, **95**, 14843–14847.
- Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, **10**, 363–395.
- Karr J.R. & Chu E.W. (1999) *Restoring Life in Running Waters: Better Biological Monitoring*. Island Press, Washington, D.C., 206 p.
- Koenker R. (2005) *Quantreg: Quantile Regression*. R package version 4.17. Available at: <http://cran.r-project.org/web/packages/quantreg/index.html> (last accessed on 25 April 2008).
- Konrad C.P. & Booth D.B. (2002) *Hydrologic Trends Associated With Urban Development for Selected Streams in the Puget Sound Basin*. Geological Survey Water-Resources Investigations Report 02-4040, Western Washington, 40 p.
- Lancaster J. & Belyea L.R. (2006) Defining the limits to local density: alternative views of abundance–environment relationships. *Freshwater Biology*, **51**, 783–796.
- Magilligan F.J. & Nislow K.H. (2005) Changes in hydrologic regime by dams. *Geomorphology*, **71**, 61–78.
- Marchetti M.P. & Moyle P.B. (2001) Effects of flow regulation on fish assemblages in a regulated California stream. *Ecological Applications*, **11**, 530–539.
- McElravy E.P., Lamberti G.A. & Resh V.H. (1989) Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society*, **8**, 51–63.
- Miller A.M. & Golladay S.W. (1996) Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society*, **15**, 670–689.
- Monk W.A., Wood P.J., Hannah D.M., Wilson D.A., Extence C.A. & Chadd R.P. (2006) Flow variability and macroinvertebrate community response within riverine systems. *River Research and Application*, **22**, 595–615.
- Moulton S.R. II, Carter J.L., Grotheer S.A., Cuffney T.F. & Short T.M. (2000) *Methods of Analysis by the U.S. Geological Survey National Water Quality Laboratory – Processing, Taxonomy, and Quality Control of Benthic Macroinvertebrate Samples*. U.S. Geological Survey Open-File Report 00-212, 49 p.
- Moulton S.R. II, Kennen J.G., Goldstein R.M. & Hambrook J.A. (2002) *Revised Protocols for Sampling Algal, Invertebrate, and Fish Communities as Part of the National Water Quality Assessment Program*. U.S. Geological Survey Open-File Report 02-150, 75 p.
- Munn M.D. & Brusven M.A. (1991) Benthic macroinvertebrate communities in nonregulated and regulated waters of the Clearwater River, Idaho, U.S.A. *Regulated Rivers: Research & Management*, **6**, 1–11.
- Olden J.D. & Poff N.L. (2003) Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, **19**, 101–121.
- Omernik J.M. (1987) Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals of the Association of American Geographers*, **77**, 118–125.
- Poff N.L. & Ward J.V. (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.
- Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegard K.L., Richter B., Sparks R. & Stromberg J. (1997) The natural flow regime: a new paradigm for river conservation and restoration. *BioScience*, **47**, 769–784.
- Poff N.L., Olden J.D., Merritt D.M. & Pepin D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, **104**, 5732–5737.
- R Development Core Team (2005) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. Available at: <http://www.R-project.org>.
- Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research & Management*, **15**, 353–363.
- Reeves G.H., Benda L.E., Burnett K.M., Bisson P.A. & Sedell J.R. (1995) A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium*, **17**, 334–349.
- Resh V.H. & Jackson J.K. (1993) Rapid assessment approaches in benthic macroinvertebrate biomonitoring studies. In: *Freshwater Biomonitoring and Benthic Macroinvertebrates* (Eds D.M. Rosenberg & V.H. Resh), pp. 195–233. Chapman and Hall, New York, pp. 195–233.
- Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.
- Richter B.D., Baumgartner J.V., Powell J. & Braun D.P. (1996) A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, **10**, 1163–1174.
- Schlosser I.J. (1992) Effects of life history attributes and stream discharge on filter-feeder colonization.

- Journal of the North American Benthological Society*, **11**, 366–376.
- Scrimgeour G.J. & Winterbourn M.J. (1989) Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia*, **171**, 33–44.
- Stehr W.C. & Branson J.W. (1938) An ecological study of an intermittent stream. *Ecology*, **19**, 294–310.
- Sumioka S.S. (2004) *Trends in Streamflow and Comparisons With Instream Flows in the Lower Puyallup River Basin*. U.S. Geological Survey Scientific Investigations Report 2004-5016, Washington.
- Thomson J.D., Weiblen G., Thomson B.A., Alfaro S. & Legendre P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698–1715.
- Trush W.J., McBain S.M. & Leopold L.B. (2000) Attributes of an alluvial river and their relation to water policy management. *Proceedings of the National Academy of Sciences*, **97**, 11858–11863.
- U.S. Army Corps of Engineers (2006) *National Inventory of Dams*. Available at: <http://crunch.tec.army.mil/nid/webpages/nid.cfm> accessed on 11 October 2006.
- U.S. Environmental Protection Agency (2007) *Level III Ecoregions of the Conterminous United States*. Western Ecology Division. Available at: [http://www.epa.gov/wed/pages/ecoregions/level\\_iii.htm#Ecoregions](http://www.epa.gov/wed/pages/ecoregions/level_iii.htm#Ecoregions) accessed on 30 January 2008.
- U.S. Geological Survey (2005) *Surface-Water Data for the Nation, National Water Information System*. Available at: <http://waterdata.usgs.gov/nwis/sw> accessed on 3 January 2005.
- U.S. Geological Survey (2006) *National Hydrographic Data set*. Available at: <http://nhd.usgs.gov/index.html> accessed on 11 October 2006.
- Vinson M.R. (2001) Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecological Applications*, **11**, 711–730.
- Vogelmann J.E., Howard S.M., Yang L., Larson C.R., Wylie B.K. & VanDriel N. (2001) Completion of the 1990's national land cover dataset for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. *Photogrammetric Engineering and Remote Sensing*, **67**, 650–662.
- Webb R.H., Wegner D.L., Andrews E.D., Valdez R.A. & Patten D.T. (1999) Downstream effects of Glen Canyon Dam on the Colorado River in Grand Canyon: a review. In: *The Controlled Flood in Grand Canyon* (Eds R.H. Webb, J.C. Schmidt, G.R. Marzolf & R.A. Valdez), pp. 1–21, Geophysical Monograph, Vol. 110. American Geophysical Union, Washington, D.C.
- Wood P.J., Hannah D.M., Agnew M.D. & Petts G.E. (2001) Scales of hydroecological variability within a groundwater-dominated stream. *Regulated Rivers: Research & Management*, **17**, 347–367.
- Wright S.A., Melis T.S., Topping D.J. & Rubin D.M. (2005) Influence of Glen Canyon Dam operations on downstream sand resources of the Colorado River in Grand Canyon. In: *The State of the Colorado River Ecosystem in Grand Canyon* (Eds S.P. Gloss, J.E. Lovich & T.S. Melis), pp. 17–31, U.S. Geological Survey Circular 1282, Reston, VA.

(Manuscript accepted 3 April 2008)