THESIS

ON THE DEVELOPMENT OF FLOW-ECOLOGY RELATIONSHIPS FOR STREAMS IN COASTAL WATERSHEDS OF SOUTHERN CALIFORNIA

Submitted by

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ABSTRACT

ON THE DEVELOPMENT OF FLOW-ECOLOGY RELATIONSHIPS FOR STREAMS IN COASTAL WATERSHEDS OF SOUTHERN CALIFORNIA

Linking hydrologic alteration to the biotic responses of streams is essential for understanding and managing the effects of land use changes and other human influences on aquatic ecosystems. This study develops flow-ecology relationships for wadeable streams in coastal watersheds of southern California to understand the ecological effects of urbanization and other sources of hydromodification. Streams in this region are predominately flashy, seasonally intermittent, and fine grained; hence, the inherently harsh disturbance regime is a major determinant of biotic composition. I match biological and geomorphic data with proximate U. S. Geological Survey streamflow gages to examine flow-ecology relationships between benthic macroinvertebrates and the hydrologic and hydraulic regimes of 32 biomonitoring sites spanning a gradient of watershed urbanization. Associations between landscape, streamflow, and biotic metrics indicate that flow permanence and urbanization are overarching and interacting influences on benthic macroinvertebrate assemblages in this region. In particular, flow intermittency and flashiness are significant predictors of both taxonomic and traits-based measures of biotic composition. Urban land cover and road density are significantly correlated with higher flow flashiness and decreasing measures of biotic integrity. Hydraulic metrics describing streambed mobility are strongly positively associated with measures of biotic integrity as a result of high intercorrelation with flow permanence. Thus, it appears that benthic macroinvertebrate assemblages are fundamentally influenced by flow intermittency and urban-induced flashiness in this region. Use of daily discharge data analyzed 3 yrs prior to biological sampling events appears to result in little to no loss of resolution in flow-ecology relationships

compared to sub-daily (15-min) and long-term (decadal) flow records. Results also underscore the utility of traits-based analyses and stratification of sites by flow permanence and dominant substrate in revealing mechanistic relationships between flow and biotic metrics. By using gaged sites to identify the flow metrics best describe biological variation, this study provides insight into which elements of the flow regime are most important to model accurately in future efforts to develop a regional hydrologic foundation that will allow the inclusion of ungaged biomonitoring sites in refining flow-ecology relationships.

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Symbols:

D_{50}	=	median diameter of bed material (m)
n	=	Manning's roughness
q	=	unit discharge
q_p	=	mean of the annual peak specific discharges
Q	=	flow
Q_{mean}	=	fraction of the record above average flow for the record
Q_p	=	mean day of water year when peak flow occurs
R	=	hydraulic radius of channel (m)
S	=	bed slope (m/m)
γ	=	specific weight of water (N/m^3)
γ_s	=	specific weight of sediment (N/m^3)
τ	=	shear stress (Pa)
τ_*	=	dimensionless shear stress
τ_{*c}	=	critical dimensionless shear stress
ω_*	=	dimensionless unit stream power

Statistical Terms:

p	p value
R^2	coefficient of determination
ρ	Spearman's rank correlation coefficient

UNITS OF MEASURE

cfs	cubic feet per second
cms	cubic meter(s) per second
km	kilometer(s)
km/km^2	kilometer(s) per square kilometer
km^2	square kilometer(s)
L/s	liter(s) per second
m	meter(s)
m/m	meter(s) per meter
min	minute(s)
mm	millimeter(s)
N/m^3	Newton(s) per cubic meter
%	percent
Pa	pascal(s)
yr(s)	year(s)

CHAPTER 1 INTRODUCTION

Natural variations in streamflow and sediment regimes shape aquatic community composition, a key indicator of overall health in riverine ecosystems (Poff *et al*., 1997; Bunn and Arthington, 2002). Urbanization, agriculture, water extraction and/or augmentation, and other human activities alter the streamflow and sediment regimes of receiving water bodies to which aquatic biota respond. In particular, urbanization can result in decreased biodiversity and lost or replaced species (Paul and Meyer, 2001; Walsh *et al*., 2005), as well as diminished ecosystem goods and services (Arthington *et al*., 2006).

Water resources managers are challenged with developing and administering regulatory programs that meet human demands, while complying with the Clean Water Act which aims to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters." Many states, in the United States (U. S.), for example California, have developed or are in the process of developing bio-objective programs, with the goal of assessing the ecological integrity of streams through sampling of benthic macroinvertebrates and other biological indicators (Norris and Hawkins, 2000; U. S. Environmental Protection Agency (EPA), 2003; California Environmental Protection Agency, State Water Resources Control Board, 2014). Such programs can inform the development of environmental flow thresholds or recommend limits on hydromodification, in order to prevent unacceptable levels of ecological degradation. In developing defensible bio-objective programs and environmental flow standards, managers and policy-makers need a scientific basis that mechanistically links streamflow, hydraulic regimes, and the biological indicators that are commonly used to assess stream health.

Flow regimes in southern California streams are predominately flashy and seasonal (Hawley and Bledsoe, 2011); hence, the natural and urban induced in-stream disturbance regimes are likely major determinants of biotic composition. Flow-ecology relationships typically relate statistics describing departures in stream discharge from some reference condition to biological response (Poff *et al*., 2010); however, this approach has limitations because stream discharge is used as a surrogate for hydraulic and bed mobility conditions that are mediated by local channel characteristics and geomorphic setting. Hydraulic parameters quantify erosive forces relative to the substrate size and channel morphology and, as a result, provide a more physically-based description of habitat dynamics and disturbance.

Development of flow-ecology relationships in southern California is needed to inform state bio-objective programs, hydromodification management, and other efforts to understand and mitigate the effects of urbanization and other human influences on in-stream biota. In this study, I examine relationships between measures of watershed urbanization, streamflow and hydraulic regimes, and benthic macroinvertebrates to better understand the effects of urbanization on biological communities in southern California. The specific objectives of this study are as follows:

1. Identify relationships between flow regime and benthic macroinvertebrates in gaged stream systems of southern California using both taxonomic and species trait composition.
2. Explore effects of watershed- and local-scale land cover on flow alteration and biotic response.
3. Evaluate whether hydraulic metrics describing bed mobility and substrate disturbance explain more variation in benthic macroinvertebrate assemblages than simpler discharge-based metrics in assessing the influence of urbanization.

4. Compare the relative influence of stream intermittency versus substrate disturbance on benthic macroinvertebrate assemblages.

To achieve the foregoing objectives, I match existing biomonitoring data in southern California to nearby U. S. Geological Survey (USGS) streamflow gages. Watershed, flow, and hydraulic metrics are related statistically to taxonomic and traits-based metrics calculated from the biomonitoring data at each site as described in Chapter 3. In Chapter 2, I provide examples of other regional flow-ecology development studies and a brief review of hydrologic, hydraulic, and biotic metrics used to quantify flow-ecology relationships.

CHAPTER 2 BACKGROUND

2.1 Measures of biotic response to flow alteration

The ecological response variable in flow-ecology relationships is often derived from fish, benthic macroinvertebrate, periphyton, or riparian vegetation data. Although ecological response to flow alteration can be measured using a variety of biological indicators, this study will focus on the use of benthic macroinvertebrates. Benthic macroinvertebrate samples are collected in streams throughout California through state biomonitoring programs and represent the best available data set for a regional study in southern California. Assemblages of benthic macroinvertebrates can be described in taxonomic terms such as abundance of intolerant taxa or Ephemeroptera, Plecoptera, and Trichoptera (EPT) percent richness. EPT taxa are commonly used to indicate less disturbed stream conditions because these taxa are thought to be sensitive to urban induced stresses. Similarly Benthic Index of Biotic Integrity (B-IBI) metrics are used to assign a score to biomonitoring sites, which indicates ecological health at the stream sites. Macroinvertebrates can also be described in terms of the specific traits they possess that allow them to survive and thrive in their environments. For example, the ability to breathe air can be advantageous to macroinvertebrates in streams that experience frequent drying. Traits-based metrics can, therefore, improve insight into the causal relationships between benthic macroinvertebrates and stream environments (McGill *et al*., 2006; Poff *et al*., 2006).

2.2 Regional flow-ecology studies using benthic macroinvertebrates

Many studies have focused on benthic macroinvertebrates to quantify flow-ecology relationships (Poff and Zimmerman, 2010). Quantile regression is a useful tool for identifying limits on macroinvertebrate assemblages imposed by hydrologic regimes across the western

U. S. (Konrad *et al*., 2008). Hydrologic variables such as high-flow frequency, low-flow pulse count and variation, and minimum April flows were significantly correlated with total, EPT, and Trichoptera richness in a study spanning 13 states in the northeastern U. S. (Kennen *et al*., 2010). Flow variability and minimum flows explained the most variance in macroinvertebrate communities in the semiarid, Mediterranean, Segura River basin in Spain, a climatic setting similar to southern California (Belmar *et al*., 2013). Regional flow-ecology studies also link stream flashiness to the response of benthic macroinvertebrates. Increased flashiness, as measured by a decrease in $T_{Qmean,}$ was associated with reduced values of B-IBI in Puget Sound lowland streams (Booth *et al*., 2004) and reduced EPT richness in North Carolina Piedmont streams (Pomeroy, 2007). Stream drying is another important control on the composition of benthic macroinvertebrate communities. Study of a longitudinally drying river in eastern France indicated that both invertebrate density (benthic and hyporheic) and richness decreased in response to increased durations of drying events (Datry, 2012). Another study in the Huachuca Mountains of Arizona (Bogan *et al*., 2013) also showed lower invertebrate richness at intermittent sites than perennial sites, but that there was no significant difference in invertebrate abundance. Intermittent reaches tended to be dominated by taxa that possess traits advantageous in drying streams. These regional flow-ecology studies underscore the importance of intermittency, low flows, and flashiness to benthic macroinvertebrates.

2.3 Hydraulic metrics and benthic macroinvertebrates

Physical disturbance of streambed substrates plays a key role in determining habitat availability and suitability for benthic macroinvertebrates (Allan and Castillo, 2007). A few studies have used benthic macroinvertebrates to predict streambed stability (Schwendel *et al*., 2011a, 2011b, 2012). In a New Zealand study that used a painted particle tracer approach to quantify intensity and frequency of streambed mobility (Townsend *et al*., 1997a), the use of bed mobility metrics supported the intermediate disturbance hypothesis (Connell, 1978) in that invertebrate richness had a "hump-shaped" relationship with increasing disturbance. Bed mobility metrics also had positive relationships with high adult mobility and streamlined or flattened body type, which are both thought to provide an advantage in disturbance-prone systems. Neither of these relationships was replicated using disturbance metrics derived from discharge (Townsend *et al*., 1997a). A similar study found that the percentage of individuals with small size, high adult mobility, clinging ability, streamlined or flattened body, or that were habitat generalists had positive linear relationships with increased intensity of stream disturbance as measured by bed mobility (Townsend *et al*., 1997b). Macroinvertebrate response to disturbance has also been examined using shear stress to describe the level of flow that mobilizes the mean substrate size (Rader and Ward, 1989), median substrate diameter (D_{50}; McElvary *et al*. (1989)), and the proportion of the substrate sizes in motion at a given discharge (Cobb *et al*., 1992; Death and Winterbourn, 1994). A negative relationship between increased substrate movement and total insect abundance was observed in a west-central Manitoba, Canada, stream where streambed stability increased from lower to upper reaches as the substrate shifted from shale- to boulder-dominated (Cobb *et al*., 1992). These studies collectively suggest that physically-based metrics describing substrate disturbance and mobility could have significant explanatory power in developing flow-ecology relationships based on benthic macroinvertebrates. Regional flow-ecology studies have been developed in various parts of the US, but not for southern California. Emerging bio-objective programs in California would benefit from an empirical basis for identifying ecologically relevant flow and hydraulic metrics in this region. In the present study, I use streamflow records from USGS gages to compute both discharge-based and hydraulic metrics for inclusion in flow-ecology relationships as described in Chapter 3.

2.4 Description of flow regimes

Variability in streamflows sets the stage for species diversity and development of different traits in aquatic biota (Bunn and Arthington, 2002). Developing flow-ecology relationships requires quantitative description of various elements of streamflow regimes including magnitude, frequency, duration, timing, and rate of change (Poff *et al*., 1997). Many software packages such as Indicators of Hydrologic Alteration (IHA; Richter *et al*. (1996)), GeoTools (Bledsoe *et al*., 2007), and the Hydroecological Integrity Assessment Process (National Hydrologic Assessment Tool (NAHAT); Henriksen *et al*. (2006)) calculate statistics or streamflow metrics that aim to describe various components of the flow regime. Flashiness metrics such as T_{Qmean} (Konrad and Booth, 2002) and Richards-Baker Flashiness Index (RBI; Baker *et al*. (2004)) can be used to relate biotic response to hydrologic variability.

Most hydrologic metrics describing flow regimes in previous studies rely on daily, weekly, or even monthly discharge records. RBI is explicitly sensitive to the time step used for calculation, and indicates greater flashiness when computed using sub-daily data (Baker *et al*., 2004). In North Carolina Piedmont watersheds, flashiness metrics derived from continuous hydrologic simulations are better predictors of EPT and B-IBI metrics when based on 15-min or hourly time steps rather than daily time steps (Pomeroy, 2007). A study comparing streams in the Raleigh, North Carolina, and Milwaukee-Green Bay, Wisconsin, metropolitan areas showed that hourly flows are necessary to detect increases in stream flashiness with increased urbanization (Knight and Cuffney, 2012). In the flashy, often urbanized coastal watersheds of southern California, sub-daily discharge records may be required to accurately describe the flow regimes.

In addition to determining the appropriate data time step for development of flow-ecology relationships in southern California, I also examine the effects of antecedent versus long-term flow conditions. Flow metrics may be calculated based on varying time periods prior to biological samplings to explore whether benthic macroinvertebrate assemblages are more reflective of antecedent conditions or long-term conditions. Streamflow metrics based on 1 yr prior to sampling, 3 yrs prior to sampling, and for the period of record were calculated for a study spanning 13 states in the northeastern U. S. (Kennen *et al*., 2010). Analysis was ultimately performed using the metrics calculated from flow records 3 yrs prior to sampling in order to maximize sample size, while adequately capturing temporal variation. Comparisons of flow metrics based on long-term (5 to 15 yrs) versus short-term (30 to 100 days) periods prior to biological sampling suggest that both time scales impose limits on macroinvertebrates in the western U. S. (Konrad *et al*., 2008). Differences in these studies suggest that calculating metrics both on a shorter and longer period of record may be informative.

CHAPTER 3 METHODS

3.1 Study area

This study focused on biomonitoring sites proximate to USGS gages (Figure 3.1) in the region of southern California bounded by the Pacific Ocean to the west, the Transverse Ranges to the north, and Peninsular Ranges to the east. Study sites were also within the "south coast" hydrologic region of California (Gotvald *et al.*, 2012), as well as the southern and Baja California pine-oak mountains and the California coastal sage, chaparral, and oak woodlands Level III ecoregions (EPA, 2014).

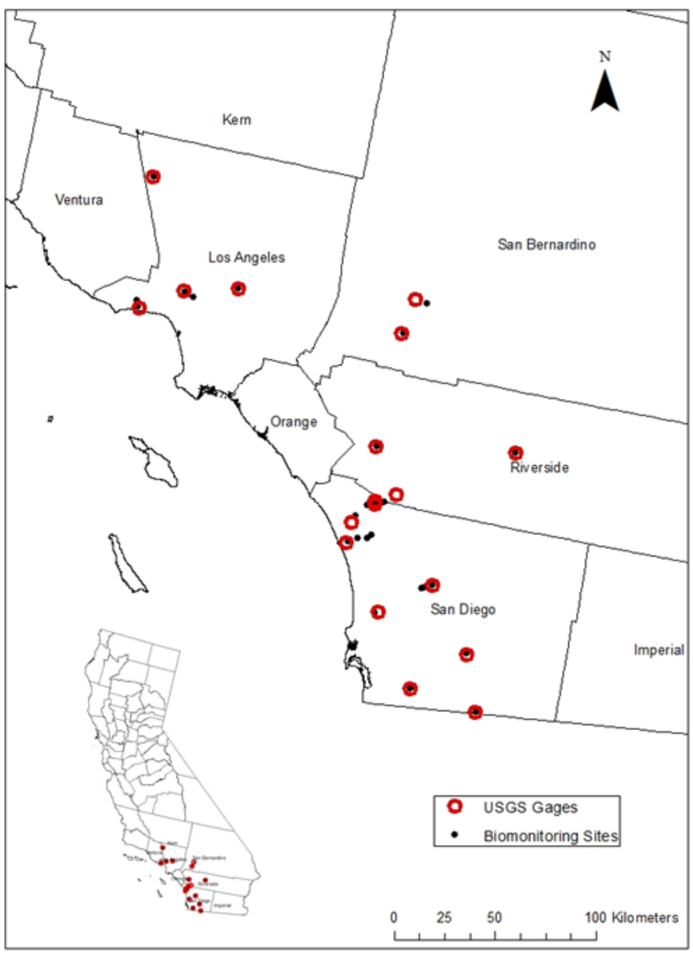


Figure 3.1 – Map of biomonitoring sites with matched USGS gages used in this study.

Study sites ranged in elevation from 10 to 1,120 m above sea level and range in watershed size from 21 to 1,877 km^2. This portion of southern California has a Mediterranean climate with mild, wet winters characterized by frontal storms and hot, dry summers often punctuated by wildfires. Vegetation cover is predominately sage brush, chaparral, and conifer forests (Stein *et al*., 2012). Stream systems in this study ranged from seasonally intermittent to fully perennial and are influenced by varying levels of urbanization.

3.2 Matching biomonitoring data to streamflow data

I utilized existing benthic macroinvertebrate data to investigate flow-ecology relationships at a mix of reference and nonreference sites sampled from 1997 to 2011 under the California Surface Water Ambient Monitoring Program (SWAMP), and the Southern California Stormwater Monitoring Coalition (SMC) Regional Monitoring Program. For sites that were sampled multiple times, data from the most recent sampling effort were used. BMI data were converted to standard taxonomic effort levels (generally genus-level identifications except Chironomidae were identified to subfamily (Richards and Rogers, 2011), and subsampled when necessary to 500-count. Along with macroinvertebrate sampling data, watershed characteristics such as percent urbanization from the National Land Cover Database (NLCD; EPA, 2001) and road density (P. Ode, pers. comm.) were provided by SCCWRP to investigate associations between urbanization, hydrologic, and hydraulic metrics influencing biological community composition.

As many biomonitoring sites as possible were matched to nearby USGS streamflow gages to describe the hydrologic and hydraulic regime at each biomonitoring site. Only USGS gages with instantaneous (15-min) flow data are used for the analysis. The following criteria were used to determine whether each biomonitoring site can be matched to a particular USGS gage and to ensure that flow data adequately represent conditions at that location:

- difference in watershed areas less than 15% relative to gage watershed area;
- USGS gage record encompassed sampling date of proposed biomonitoring site match; and
- no intervening dams, diversions, or reservoirs.

Absence of intervening dams, diversions, and reservoirs were verified using a variety of tools including Google Earth® and Bing® imagery, as well as USGS gage annual reports and the National Inventory of Dams (NID; U. S. Army Corps of Engineers (USACE) (2014)). Multiple biomonitoring sites were matched to the same USGS gage, but the converse is not allowed. In the end, 32 biomonitoring sites were matched to 18 USGS gages (Figure 3.1).

3.3 Flow metrics

I calculated flow metrics describing streambed mobility, hydraulic conditions, flashiness, stream drying, peak and average conditions, as well as, timing of peak events (Table 3.1). The final set of flow metrics was chosen through use of principal component analysis (PCA), correlation analysis, literature review, and hypotheses about which flow and biotic metrics might responds best to one another. Watershed area, median grain size, and percent sand plus fines were also recorded for each biomonitoring site. Flashiness metrics T_{Qmean} (Konrad and Booth, 2002) and Richards-Baker Flashiness Index (Baker *et al*., 2004) were both calculated, but were highly correlated so only T_{Qmean} was used in further analysis. Similarly, bed mobility metrics were calculated using both dimensionless shear stress (τ_*; Eq. (3.1)) and dimensionless unit stream power (ω_*). The resulting bed mobility metrics were also highly correlated and therefore only τ_* metrics were used in further analysis.

Table 3.1 – Flow metrics used to develop flow-ecology relationships in southern California.

	Metric Name		Description	Category
1	Average Duration of Bed Mobilizing Event	Dur. Mobile	Total amount of time bed is mobile according to a critical dimensionless shear stress (τ_{*c}) of 0.03, divided by the discrete number of bed mobilizing events in the gage record.	Bed Mobility
2	Percent of Time Bed Mobile/Percent of Time Flowing	%Mobile/ %Flowing	Percent of the time the bed is mobile according to τ_{*c} of 0.03, divided by the percent of the time with nonzero flow.	Bed Mobility
3	Time Integrated Sediment Transport Capacity	Time Int. Sed. Trans.	Time integrated sediment transport capacity. Sum of the products of binned probabilities of τ_* above 0.03 times the upper τ_* value of each bin.	Bed Mobility
4	T_{Qmean}		Fraction of the record above average flow for the record (Q_{mean}).	Flashiness
5	Mean Annual q_p	Mean Ann. q_p	Mean of the annual peak specific discharges (q_p).	Peak Events
6	Timing of Q_p	Time Q_p	Mean day of water year when peak flow (Q_p) occurs.	Peak Events
7	Mean February q	Mean Feb. q	Mean February unit discharge (q).	Average Conditions
8	Mean September q	Mean Sept. q	Mean September unit discharge (q).	Average Conditions
9	Average Duration of Zero Flow Events	Dur. Zero	Total time with zero flow divided by the discrete number of zero flow events in the gage record.	Drying
10	%SAFN		Percent sand plus fines in channel substrate.	Substrate
11	Velocity		Mean cross-section averaged velocity over period of record.	Average Hydraulic Conditions
12	Reynolds Number	Re	Mean ratio of unit discharge to kinematic viscosity over period of record.	Average Hydraulic Conditions

Bed mobility metrics and unit discharges depend on site-specific channel and substrate characteristics at the study sites, and were based on existing physical habitat (PHAB) data routinely collected alongside benthic macroinvertebrates in the biomonitoring efforts. Mean unit discharges (q) were calculated by dividing mean discharges (Q) by bankfull width at each site. Bed slope, bankfull width, and median grain size (D_{50}) were used to convert discharges to hydraulic metrics. I performed subsequent field surveys of channel cross section, longitudinal profile, and substrate for sites where existing PHAB data were previously unavailable (Harrelson *et al.*, 1994). Field surveys were also performed at nine sites where PHAB data are available, and results from the detailed field surveys and the PHAB surveys were compared. During these field surveys, I used a total station to survey a cross section and longitudinal profile. I also performed pebble counts at gravel-bed sites using a sampling frame to calculate median grain size (D_{50}; Bunte and Abt (2001)). Manning's *n* values were estimated using photographs (Barnes, 1967) of biomonitoring sites, and Manning's equation (Chow, 1959) was used to estimate discharge based on channel geometry.

Bed mobility frequency and duration were assessed by comparing τ_* occurring in the channel to a critical value of 0.03 (Parker, 2008) at each time step of discharge in the gage record. To test the sensitivity of this threshold, bed mobility metrics were also calculated using critical values of 0.06 and 0.1:

$$\tau_* = \frac{\tau}{(\gamma_s - \gamma)D_{50}} = \frac{RS}{1.65D_{50}} \qquad \textbf{Eq. (3.1)}$$

where,

τ_* = dimensionless shear stress;
τ = shear stress (Pa);
γ_s = specific weight of sediment (N/m^3);
γ = specific weight of water (N/m^3);
D_{50} = median diameter of bed material (m);
R = hydraulic radius of channel (m); and
S = bed slope (m/m).

Time-integrated sediment transport capacity was calculated by binning all of the τ_* values for each time step with $\tau_* > 0.03$ and then summing the products of each bin's probability and upper limit. Timing of peak flow was assigned a day of water year using the IHA "circular method" (Richter *et al.*, 1996). Nonperennial streams were defined as those that "lack surface flow for at least several days per year in most years" (Mazor *et al.*, 2014). Whether a site is perennial or nonperennial is based on the long-term flow record rather than the 3-yr flow record.

Sites were divided into perennial and nonperennial categories in order to further investigate the effects of flow permanence on identification flow-ecology relationships.

3.4 Data resolution and antecedent flow conditions

In order to assess the effects of data resolution, most flow metrics were calculated separately using both 15-min and daily streamflow data. Metrics calculated only from daily data were timing of annual peak flow, and monthly mean (Mean Feb. q and Mean Sept. q) metrics. Mean monthly unit discharges (q) were using instead of mean monthly discharges (Q) in order to normalize values by stream width because sites spanned a wide range of stream sizes. All metrics were also calculated using gage data from two periods: 1) from 3 yrs immediately preceding biological sampling, and 2) from the total available gage record from water years 1989 to 2013. Years of gage data available from water years 1989 to 2013 varied from 5 yrs to the entire period from October 1, 1988 to September 2013. The one gage used with only 5 yrs of data total only had streamflow data available for approximately 1.5 years prior to sampling so this length of record was used for that particular gage/biomonitoring site match.

Flow regimes at many of the sites are highly seasonal, in that many go dry for several weeks to a few months in the summer most years. Thus, I anticipated that the amount of time the site is flowing prior to sampling could have a large impact on the amount and types of organisms found in the stream; however, all sites in the study were flowing for at least 4 months prior to sampling so this potential effect was assumed to be minimal and not investigated further.

3.5 Biotic metrics

A set of taxonomic and traits-based biotic metrics were calculated using the biomonitoring data. Traits were assigned to macroinvertebrate taxa using a database developed for North American insects (Poff *et al*., 2006). Some insect and noninsect taxa recorded at biomonitoring sites were not included in this database, so traits were assigned to these missing taxa based on literature review and expert judgment (Boris Kondratieff, LeRoy Poff, and Matt Pyne, pers. comm.). Three biomonitoring sites included separate samples using both a reach-wide or targeted riffle approach, while for others the sampling method was not recorded. Since the targeted riffle result was only available at a three sites, the reach-wide result was selected in all cases except for at the seven sites which did not indicate sampling method on the only available result. An index of biotic integrity metric (Southern California Index of Biotic Integrity (SC-IBI)) was calculated using a method developed for benthic macroinvertebrates in southern California (Ode *et al*., 2005). Biotic metrics were reduced to a set of 12 using correlation analysis, PCA, literature review, and judgment (Table 3.2) for development of flow-ecology relationships. Biotic metrics were reduced to 12 from a larger set considered with the intention of eliminating redundancy and using *a priori* mechanistic understanding of which biotic traits might be responsive to flow.

Table 3.2 – Reduced set of biotic metrics used in developing flow-ecology relationships in southern California.

	Metric Name		Description	Type
1	Amphipoda		–	Percent Abundance
2	Noninsect		–	Richness
3	EPT		Insect orders Ephemeroptera, Plecoptera, and Trichoptera.	Percent Richness
4	Diptera		–	Percent Abundance
5	SC-IBI		Southern California Index of Biotic Integrity (Ode *et al*., 2005).	Value
6	Resilience to Disturbance	Dist. Resil	Composite metric to indicating if organism has one of the following traits advantageous to resilience against disturbance: (1) multivoltine, (2) fast seasonal development, (3) long adult life span, (4) strong flying ability, and (5) high adult female dispersal.	Percent Richness
7	Resistance to Desiccation	Desi. Resist	Composite metric to indicating if organism has one of the following traits advantageous to resistance against desiccation: (1) adult exiting ability, (2) desiccation resistance, (3) air breather, (4) burrowing habit, and (5) warm eurytherm (prefer warm (15-30°C) temperatures)	Percent Richness
8	Resistance to Gravel-bed Instability	Gvl. Inst. Resist	Composite metric indicating if organism has one of the following traits advantageous to resistance against bed mobilization in gravel-bed systems: (1) adult exiting ability, (2) clinger habit, (3) small size, (4) high crawling rate, and (5) streamlined shape.	Percent Richness
9	Resistance to Sand-bed Instability	Snd. Inst. Resist	Composite metric indicating if organism has one of the following traits advantageous to resistance against bed mobilization in sand-bed systems: (1) burrowing habit, (2) sprawling habit, (3) streamlined shape, and (4) adult exiting ability.	Percent Richness
10	Drift Abundant	DrftAbun	Organisms abundantly found in drift samples.	Percent Richness
11	Shredder		Organism in shredder functional feeding group.	Percent Richness
12	Collector Gatherer	CollGath	Organism in collector-gatherer functional feeding group.	Percent Richness

3.6 Landscape metrics

Landscape metrics provided by SCCWRP, including percent agriculture, urban, and non-natural vegetation, were computed using NLCD 2001 data for the watershed of each biomonitoring site (EPA, 2001). Road density for each biomonitoring site, also provided by SCCWRP, was calculated using a custom layer developed by the California Department of Fish and Wildlife (P. Ode, pers. comm.). Non-natural vegetation includes roadside plantings, cemeteries, and golf courses. All landscape metrics were quantified as a percentage of total watershed area, as well as a percentage of watershed area within 1 km and 5 km of the biomonitoring site. Correlations between flow metrics, biotic metrics, and the three types of landscape metrics were computed non-parametrically using Spearman's rank correlation coefficient.

3.7 Statistical analysis

Flow-ecology relationships were investigated using three different statistical tools: Redundancy analysis (RDA), multiple linear regression (MRA), and bivariate regression using both ordinary least squares (OLS) and quantile regression. RDA was performed on metrics from the full set of sites, as well as perennial, non-perennial, sand-bed, and gravel-bed subsets. Explanatory variables must be at least one less than the number of observations; thus, the flow metrics were further reduced to seven and biotic metrics were reduced to 11 for performing RDA on the subsets of sites. Iterative RDA was also performed to identify a reduced set of flow metrics that explained the most variance in biotic metrics of each subset of sites.

"Sand-bed" and gravel-bed sites were those with $D_{50} \leq 9$ mm and $D_{50} > 9$ mm, respectively. This threshold was chosen by examining grain-size distributions and τ_* regimes to demarcate between sand-bed sites with predominately live beds that are easily mobilized versus those that behave as threshold channels. %Mobile/%Flowing metrics at sand-bed sites ranged from 0.51 to 1, and 0 to 0.79 at gravel-bed sites. Of the total 32 biomonitoring sites, eight were perennial sand-bed sites, 13 were nonperennial sand-bed sites, six were perennial gravel-bed sites, and five were nonperennial gravel-bed sites. These categories were used to investigate the effect of stratification on strength and direction of flow-ecology relationships. Statistical analysis was accomplished using several open-source software 'packages' in R (R Development Core Team, 2013). RDA was performed using the *vegan* package, version 2.0-10 in R (Oksanen, 2013). Multiple regression analysis was performed using a linear model and the 'leaps' package, version 2.9 in R for selecting the best model for each biotic metric using up to three flow metrics for each biotic metric mode (Lumley, 2009). Categorical "dummy" variables indicating perennial or not and sand-bed or not were also examined in multiple regression analyses of each biotic response model.

Quantile regression was performed using the *quantreg* package, version 5.05 in R (Koenker, 2013). In addition to performing quantile and OLS regression on metrics from all sites, regressions were also performed for eight subsets of sites. These subsets included perennial sites, non-perennial sites, sand-bed sites, gravel-bed sites, and every combination of those four categories. Prior to regression, both flow and biotic metrics were transformed using fractional, power, root, natural log, and arcsine transformations to improve normality. The best transformation for each metric was chosen using a combination of visual inspection of histograms, as well as Lilliefors (Kolmogorov-Smirnov) and D'Agostino-Pearson tests for normality (Thode, 2002; Zar, 1999).

CHAPTER 4 RESULTS

In the following sections, I first provide an overview of the characteristics of all 32 biomonitoring sites and the gradients they represent. I then describe how the flow metrics related to biotic metrics through RDA and Spearman correlation, and used MRA models of each biotic metric to further understand which flow metrics best predicted biotic metrics. Correlations with watershed metrics are then considered in the context of understanding how flow and biotic metrics were directly affected by landscape characteristics.

4.1 Data resolution

Initially, all analyses were performed using four different versions of flow metrics (15-min, 3-yr; daily, 3-yr; 15-min, long-term; and daily, long-term). Flow metrics calculated at 15-min and daily time steps were found to be highly correlated (often $|\rho| > 0.9$). Correlations between flow and biotic metrics based on gage data 3 yrs prior versus long-term data were also very similar. Since the four different versions of flow metrics did not substantially affect RDA and regression results, the following sections focus exclusively on the daily time step, 3-yr flow metrics.

4.2 Biomonitoring site characteristics

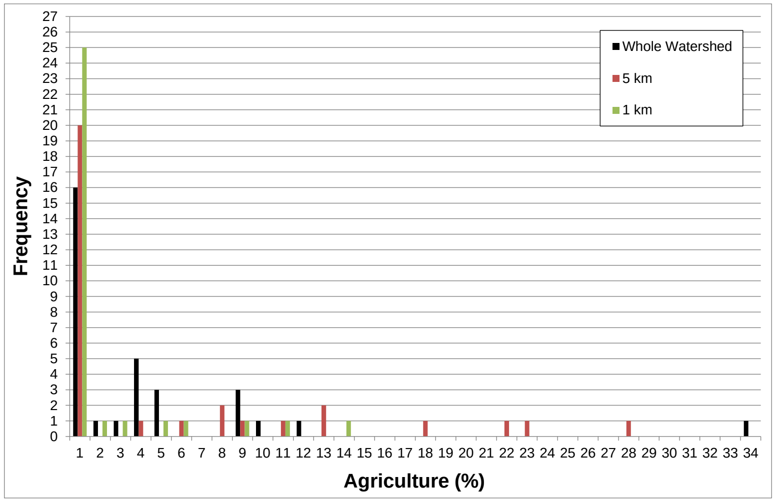
The 32 biomonitoring sites in this study represented a broad range of intermittency, substrate size, and landscape characteristics (Table 4.1). Nonperennial sites flowed 26 to 100% of the time for the 3-yr period analyzed. Perennial gravel-bed sites showed a range of bed mobility, while all but one perennial sand-bed site was mobile all of the time. %Mobile/%Flowing metric values ranged from 0.001 to 0.59 for nonperennial gravel-bed sites, and 0.51 to 1 for nonperennial sand-bed sites. Most sites had very low levels of agriculture measured at the entire watershed, within 5 km of the biomonitoring site, and within 1 km of the biomonitoring site; and were more influenced by the different measures of urbanization (Figure 4.1). With respect to human influence, only one of the 32 sites analyzed was classified "reference" condition, 24 were classified "intermediate," and 7 were classified as "stressed."

Table 4.1 – Biomonitoring site characteristics.

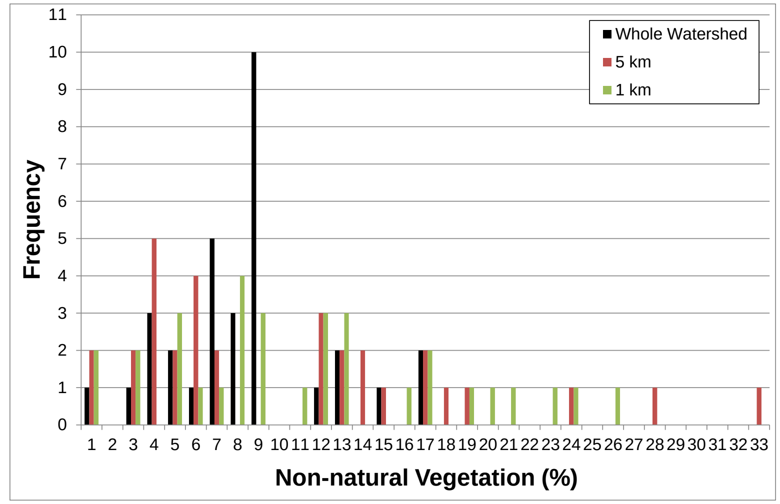
Gage No.	Station ID	Perennial/ Nonperennial	%Flowing-3yr	%Flowing-Long Term	Sand/ Gravel	Slope (m/m)	D_{50} (mm)	%SAFN	%Mobile/ %Flowing	Area (km^2)	Elevation (m)
10259000	719WE0864	Perennial	100	100	Gravel	0.04	40	43	0.79	23	257
10260500	628PS1019	Perennial	100	100	Gravel	0.02	38.5	30	0.33	311	1120
11023340	SMC00198	Perennial	100	100	Gravel	0.004	12.67	34	0.08	118	68
11092450	412CE0232	Perennial	100	100	Gravel	0.01	5660	0	0	399	200
11092450	412S02804	Perennial	100	100	Gravel	0.003	40	15	0.02	444	185
11109550	403S01136	Perennial	100	100	Gravel	0.02	125	2	0.02	769	640
11044000	902S02293	Perennial	100	100	Sand	0.02	1.03	64	1	1559	141
11044000	R5BIO-6522	Perennial	100	100	Sand	0.01	1.03	54	1	1539	145
11044300	SMSM2	Perennial	100	100	Sand	0.002	2	23	0.96	1600	107
11044300	902S04661	Perennial	100	100	Sand	0.007	1.03	38	1	1597	115
11044300	SMC00565	Perennial	100	100	Sand	0.02	1.03	66	1	1589	107
11044350	902SMSND3	Perennial	100	99	Sand	0.01	1.03	68	1	56	107
11058500	801WE1127	Perennial	100	100	Sand	0.05	9	14	1	21	536
11098000	SMC00924	Perennial	100	100	Sand	0.02	1.03	6	1	42	439
11014000	R5BIO-6524	Nonperennial	26	63	Gravel	0.005	22	21	0.05	183	157
11014000	910S06570	Nonperennial	35	63	Gravel	0.02	15	30	0.59	183	153
11042000	SMC02457	Nonperennial	89	87	Gravel	0.005	157	74	0.001	1326	37
11042000	903S00857	Nonperennial	75	87	Gravel	0.001	40	84	0.002	1365	22
11105510	404S13672	Nonperennial	69	74	Gravel	0.05	625	15	0.01	272	134
11012500	911TCAM01	Nonperennial	85	78	Sand	0.02	0.03	96	1	212	688
11014000	910S14762	Nonperennial	35	63	Sand	0.02	1.03	69	1	172	179
11015000	909SSWR03	Nonperennial	66	67	Sand	0.03	2	57	1	115	1008
11025500	905PS0026	Nonperennial	58	67	Sand	0.02	1.03	90	0.69	289	268
11025500	SMC01953	Nonperennial	56	67	Sand	0.02	1.03	80	0.94	328	203
11025500	R5BIO-6504	Nonperennial	58	67	Sand	0.01	1.03	85	0.96	331	160
11042000	903S00665	Nonperennial	75	87	Sand	0.003	1.03	84	0.99	1294	44
11042000	SMC00153	Nonperennial	100	87	Sand	0.008	1.03	83	1	1433	10
11046000	902S05173	Nonperennial	74	81	Sand	0.005	9	35	0.51	1678	64
11046000	902S00117	Nonperennial	73	81	Sand	0.01	1.03	89	0.99	1823	35
11046000	902S02357	Nonperennial	73	81	Sand	0.02	1.03	86	0.99	1662	100
11070500	SMC27709	Nonperennial	95	90	Sand	0.004	1.03	69	0.70	1877	390
11105510	SMC11406	Nonperennial	77	74	Sand	0.01	9	18	0.82	280	17

Table 4.1 (continued) – Biomonitoring site characteristics.

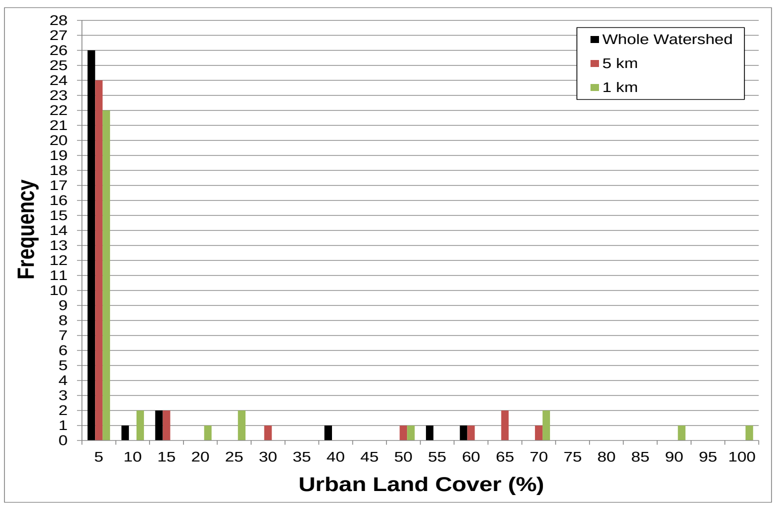
		Percent Agriculture			Non-natural Vegetation			Percent Urban			Road Density (km/km^2)		
Gage No.	**Station ID**	**1 km**	**5 km**	**watershed**	**1 km**	**5 km**	**watershed**	**1 km**	**5 km**	**watershed**	**1 km**	**5 km**	**watershed**
10259000	719WE0864	2.64	0.17	0.08	0	0	0	0	0	0	0	0	0
10260500	628PS1019	0	0	0.03	0	0.60	6.28	0	0	4.94	0	0.01	1.06
11023340	SMC00198	0	0	0.23	23.3	14.0	14.2	48.0	62.8	39.6	6.68	10.1	6.42
11092450	412CE0232	0	0.02	0.06	4.61	32.6	16.4	95.4	56.1	52.9	19.4	9.74	8.83
11092450	412S02804	0	0	0.06	25.1	18.9	16.1	69.2	67.8	55.4	12.1	12.3	9.22
11109550	403S01136	0	0.08	0.003	2.21	4.20	2.02	1.74	1.22	0.31	0.55	0.41	0.41
11044000	902S02293	0	10.8	3.46	8.94	4.36	8.47	1.39	0.43	4.95	2.24	1.50	2.58
11044000	R5BIO-6522	5.55	21.9	3.50	2.91	3.22	8.49	0.36	0.07	4.93	0.70	1.15	2.58
11044300	SMSM2	4.01	7.76	3.52	16.6	16.2	8.67	1.11	2.62	4.98	2.32	2.93	2.61
11044300	902S04661	10.4	5.96	3.48	16.3	11.3	8.59	2.83	1.30	4.97	2.27	2.61	2.60
11044300	SMC00565	0	7.50	3.52	19.3	17.3	8.63	1.04	3.01	4.94	1.06	3.00	2.60
11044350	902SMSND3	8.78	27.6	33.1	7.93	6.88	8.56	0	0.14	1.34	1.25	2.34	2.54
11058500	801WE1127	0	0	0	20.6	3.62	4.28	2.97	0.31	0.46	0.80	0.52	0.55
11098000	SMC00924	0	0	0	11.2	5.78	5.23	0.54	0.04	0.10	0	0.01	0.03
11014000	R5BIO-6524	0	0	0.08	8.71	2.36	6.12	1.07	0.19	0.64	0.98	0.62	1.32
11014000	910S06570	0	0	0.08	10.6	2.53	6.14	0.75	0.21	0.64	1.32	0.66	1.32
11042000	SMC02457	13.0	13.0	8.80	8.38	23.8	7.62	23.6	13.3	2.34	2.40	4.06	1.89
11042000	903S00857	0	22.9	9.27	6.21	16.2	7.97	89.0	46.2	3.33	9.45	5.36	1.98
11105510	404S13672	0	0.66	2.02	22.6	13.4	13.0	6.59	1.44	12.1	5.83	3.34	4.32
11012500	911TCAM01	0	0	0	15.6	6.24	6.69	0	0.53	0.26	1.62	1.03	1.42
11014000	910S14762	0	0	0.09	4.16	3.18	6.28	0	0.11	0.66	0.73	0.64	1.36
11015000	909SSWR03	0	3.72	0.86	7.14	5.80	4.40	0.00	0.24	0.14	1.31	1.49	1.26
11025500	905PS0026	0	0	0.01	7.34	3.22	3.03	0	0	0.02	2.56	0.65	0.69
11025500	SMC01953	0	0.45	0.06	5.02	5.37	3.23	0	0.39	0.07	1.81	1.37	0.74
11025500	R5BIO-6504	0	0.55	0.06	11.2	5.63	3.25	0.47	0.46	0.07	0.98	1.30	0.74
11042000	903S00665	1.63	17.2	8.72	12.7	27.0	7.29	15.9	13.5	2.15	3.43	4.25	1.84
11042000	SMC00153	0	0.37	8.92	7.41	12.7	8.11	67.8	61.2	4.71	5.88	8.71	2.11
11046000	902S05173	0	8.55	4.51	4.98	12.5	8.69	0	3.35	4.84	0.15	2.74	2.60
11046000	902S00117	0	0	4.88	11.6	3.92	8.39	21.3	2.53	4.48	3.31	1.34	2.52
11046000	902S02357	0	12.7	4.52	12.0	14.6	8.65	1.65	1.98	4.84	2.04	2.96	2.60
11070500	SMC27709	0	0	11.2	18.2	12.0	11.3	7.96	27.2	8.73	3.61	5.23	3.06
11105510	SMC11406	0	0	1.96	12.1	11.6	12.8	2.83	1.60	11.7	2.42	2.89	4.23



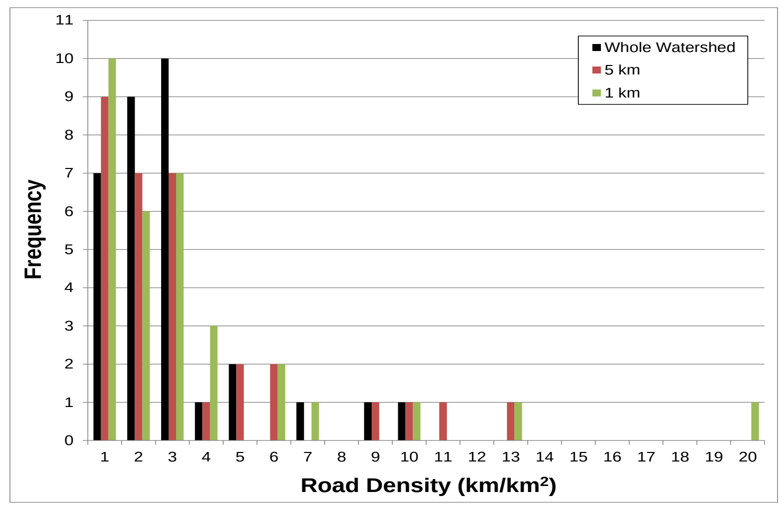
(a) percent agriculture



(b) percent non-natural vegetation



(c) percent urban land cover



(d) road density (km/km^2)

Figure 4.1 – Land-cover characteristics in watersheds delineated at biomonitoring sites. Percent land use measured for the entire watershed, within 5 km of the biomonitoring site, and within 1 km of the biomonitoring site.

A comparison of mean discharge to the level of discharge required to achieve τ_* of 0.03 showed that for sand-bed sites, this threshold was always lower than the mean flow for the 3-yr period leading up to biotic sampling (Table 4.2). Additionally, for all but three of the 11 gravel-bed sites, the bed mobility flow threshold was also lower than the mean flow for the 3-yr record.

Table 4.2 – Comparison of bed mobility threshold to mean flow for the 3-yr period analyzed for each biomonitoring site.

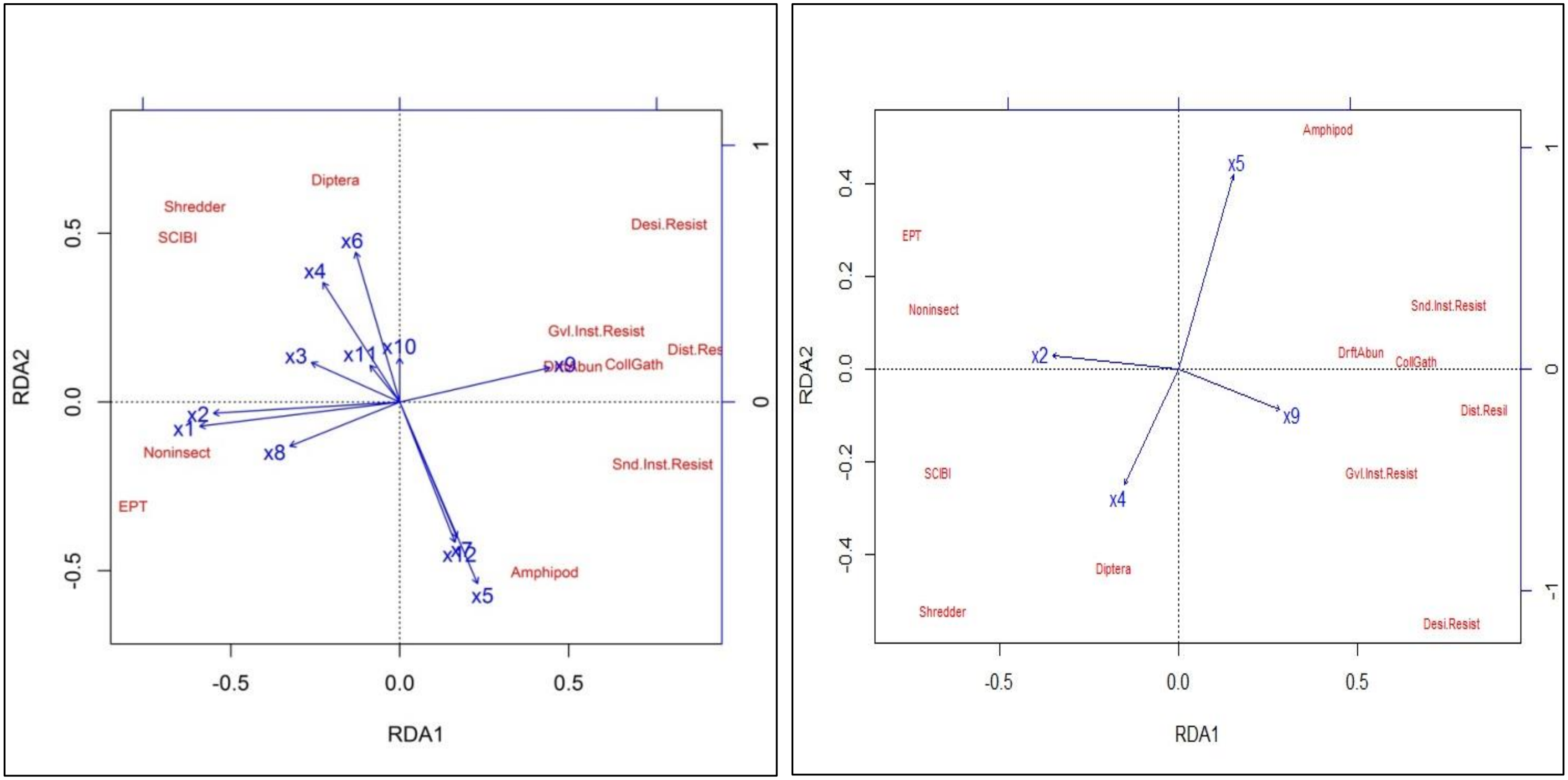
	Station ID	Q (τ_* = 0.03) (cms)	Q_{mean}	D_{50} (mm)	Slope (m/m)
1	911TCAM01	6E-10	0.3	0.03	0.02
2	902S00117	0.01	48	1	0.01
3	902S02293	0.01	29	1	0.02
4	902S02357	0.007	48	1	0.02
5	902S04661	0.003	52	1	0.01
6	902SMSND3	0.0001	7	1	0.01
7	903S00665	0.006	38	1	0.003
8	905PS0026	0.002	4	1	0.02
9	910S14762	0.0002	2	1	0.02
10	R5BIO-6504	0.0004	4	1	0.01
11	R5BIO-6522	0.003	19	1	0.01
12	SMC00153	0.01	26	1	0.008
13	SMC00565	0.0009	23	1	0.02
14	SMC01953	0.0004	4	1	0.02
15	SMC27709	0.01	9	1	0.004
16	SMSM2	0.06	12	2	0.002
17	909SSWR03	0.0001	3	2	0.03
18	801WE1127	0.0004	2	9	0.05
19	902S05173	0.4	78	9	0.005
20	SMC00924	0.006	12	9	0.02
21	SMC11406	0.1	40	9	0.01
22	SMC00198	0.4	10	13	0.004
23	910S06570	0.03	2	15	0.02
24	R5BIO-6524	0.3	0.7	22	0.005
25	628PS1019	2	112	39	0.02
26	412S02804	31	128	40	0.003
27	719WE0864	0.03	2	40	0.04
28	903S00857	77	38	40	0.0007
29	403S01136	7	49	125	0.02
30	SMC02457	48	32	157	0.005
31	404S13672	26	30	625	0.05
32	412CE0232	45156	175	5660	0.01

4.3 Relationship between flow and biotic metrics

Redundancy analysis results using all 12 flow metrics at all 32 biomonitoring sites (Figure 4.2a) showed RDA axis 1 dominated by bed mobility and Mean Sept. q metrics.

Duration of drying also weighed heavily on axis 1, but in the opposite direction of the bed mobility and Mean Sept. q metrics. RDA axis 1 explained 26.9% of the variance, while RDA axis 2 explained 9.3% of the total 50.3% constrained variance (Table 4.3). The inverse relationship between bed mobility and drying was expected because bed mobility cannot occur without flow. EPT percent richness and SC-IBI were both positively correlated with increased bed mobility, as expressed by all three bed mobility metrics, and negatively correlated with drying duration. The composite trait metrics (Desi. Resist, Gvl. Inst. Resist, Snd. Inst. Resist, and Dist. Resil) were highly positively correlated with duration of drying. T_{Qmean} and Time Q_p, countered by Mean Ann. q_p, Mean Feb. q, and Re dominated RDA axis 2, which was also highly positively correlated with percent Amphipoda. Compared to the other flow metrics, %SAFN and mean velocity did not weigh heavily on either of the first two RDA axes. Iterative RDA using all 32 biomonitoring sites (Figure 4.2b) showed that T_{Qmean}, %Mobile/%Flowing, Dur. Zero, and Mean Ann. q_p best explained the variance in biotic metrics.

Table 4.3 showed the percent of variance explained using all flow metrics for each subset, as well as, using only the flow metrics chosen after iterative RDA is performed. Explanation of variance in biotic metrics at perennial sites and gravel-bed sites seemed to be improved by stratification, but the percent constrained for all subsets was influenced by the number of observations (sites) in each stratum.



Flow Metrics:

1. Dur. Mobile	3. Time Int. Sed. Trans.	5. Mean Ann. q_p	7. Mean Feb. q	9. Dur. Zero	11. Velocity
2. %Mobile/%Flowing	4. T_{Qmean}	6. Time Q_p	8. Mean Sept. q	10. %SAFN	12. Re

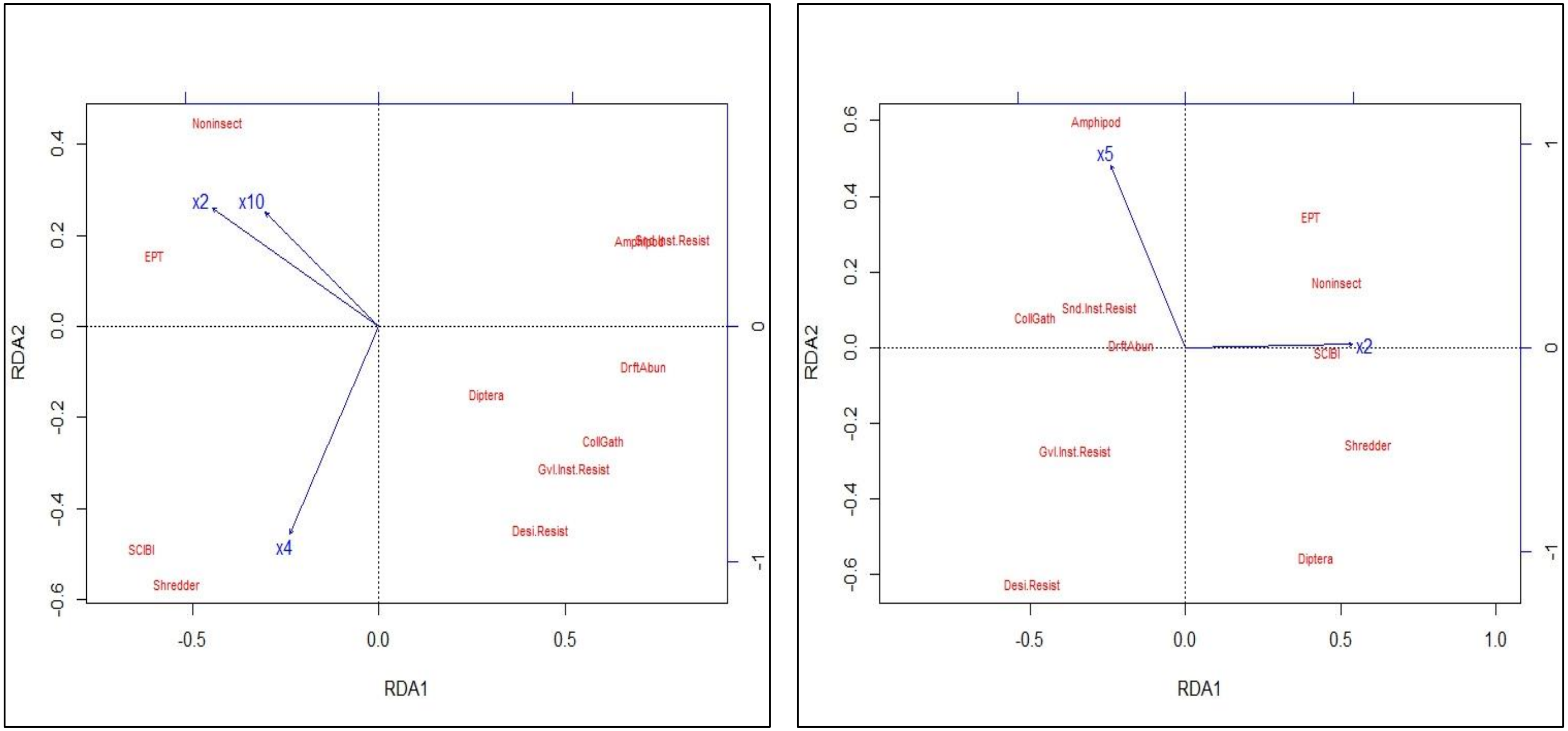
(a) RDA plot (b) final iterative RDA plot

Figure 4.2 – Redundancy analysis using all 32 biomonitoring sites.

Table 4.3 – RDA percent variance explained for regular and iterative RDA using all sites, perennial sites, nonperennial sites, sand-bed sites, and gravel-bed sites.

Sites	% Variance Explained All	% Variance Explained Iterative	No. of Sites
All	50	36	32
Perennial	63	51	14
Nonperennial	51	24	18
Sand-bed	46	33	21
Gravel-bed	80	49	11

Iterative RDA performed on four different subsets of sites (perennial, nonperennial, sand-bed, and gravel-bed) (Figure 4.3) indicated T_{Qmean}, %Mobile/%Flowing, and %SAFN best explained the variance in biotic metrics at perennial stream sites. This result suggested that in the absence of drying events, flashiness and substrate strongly influenced biotic response. At perennial sites, EPT and SC-IBI were positively correlated with increased bed mobility. Performing iterative RDA on nonperennial sites showed that Mean Ann. q_p and %Mobile/%Flowing best explained variance in the biotic metrics at sites affected by drying. Surprisingly, the duration of drying events was not chosen as one of the most descriptive flow metrics. Iterative RDA performed on sand-bed sites showed that %SAFN, %Mobile/%Flowing, and Mean Ann. q_p explained most of the variance in the biotic metrics. As seen in the other subsets, EPT and SC-IBI were positively related to bed mobility; however, EPT was strongly negatively correlated with increased %SAFN. Iterative RDA performed on gravel-bed sites reduced the flow metrics describing the biological community to T_{Qmean} and Dur. Zero.

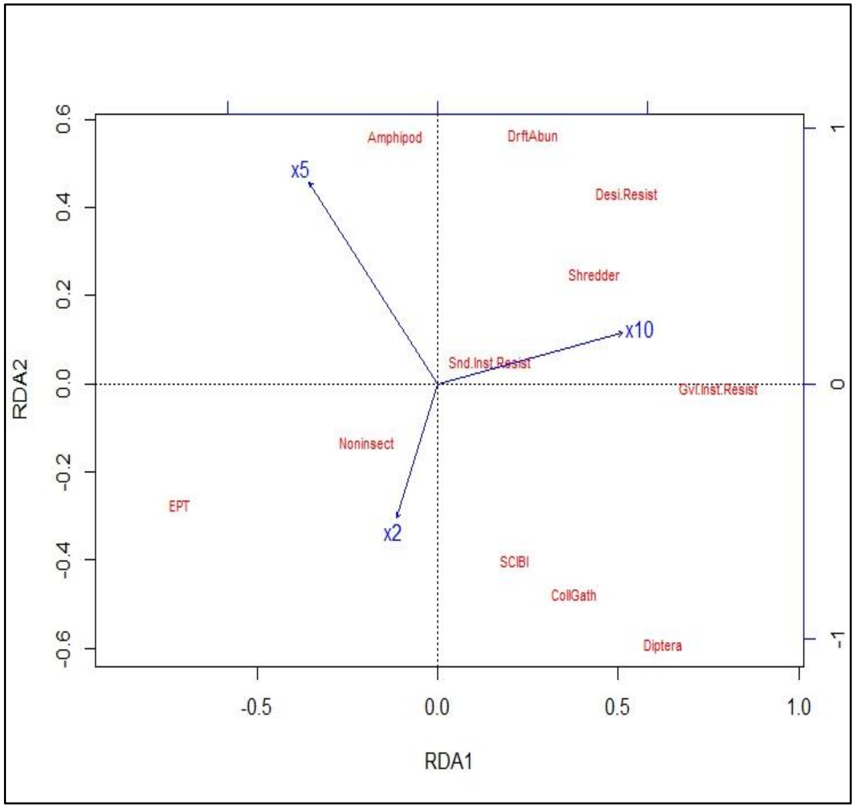


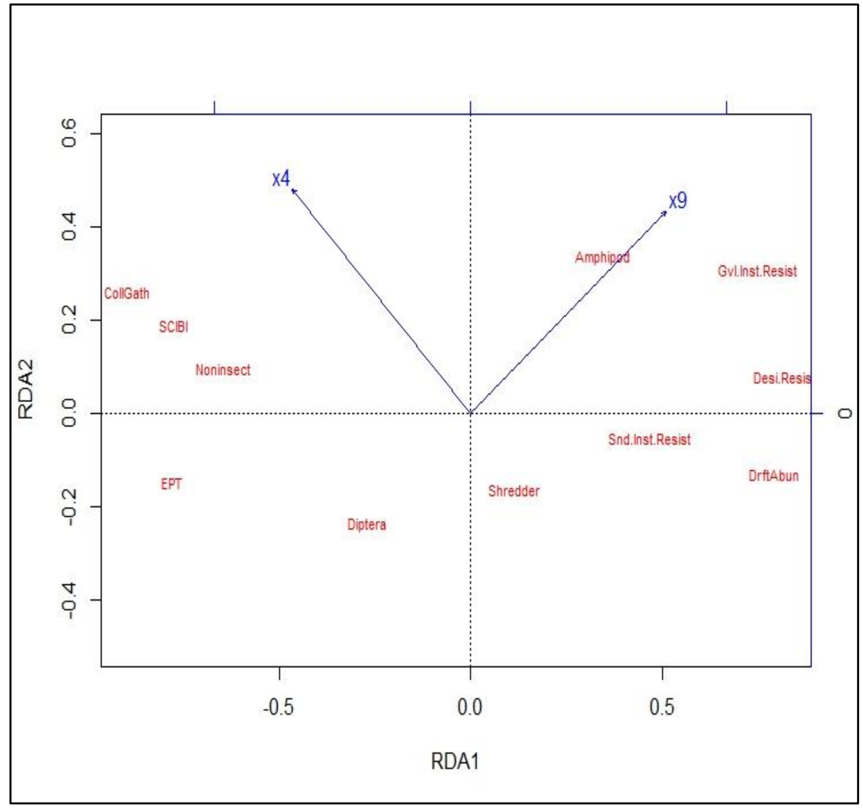
Flow Metrics:

1. Dur. Mobile	3. Time Int. Sed. Trans.	5. Mean Ann. q_p	7. Mean Feb. q	9. Dur. Zero	11. Velocity
2. %Mobile/%Flowing	4. T_{Qmean}	6. Time Q_p	8. Mean Sept. q	10. %SAFN	12. Re

(a) for perennial sites (b) for nonperennial sites

Figure 4.3 – Iterative RDA plots.





Flow Metrics:

1. Dur. Mobile	3. Time Int. Sed. Trans.	5. Mean Ann. q_p	7. Mean Feb. q	9. Dur. Zero	11. Velocity
2. %Mobile/%Flowing	4. T_{Qmean}	6. Time Q_p	8. Mean Sept. q	10. %SAFN	12. Re

(c) for sand-bed sites

(d) for gravel-bed sites

Figure 4.3 (continued) – Iterative RDA plots.

Spearman correlation revealed many significant correlations between flow and biotic metrics (Table 4.4). All three bed mobility metrics had the greatest number of significant correlations with biotic metrics; however, as in the RDA results, these relationships were counterintuitive. Velocity and %SAFN had no significant correlations with biotic metrics. As expected, increased flashiness was negatively correlated with SC-IBI, while increased drying was positively correlated with traits advantageous to resisting desiccation.

Table 4.4 – Spearman correlations between flow metrics and biotic metrics using all 32 biomonitoring sites.

	Amphipoda	Noninsect	EPT	Diptera	SC-IBI	Dist. Resil	Desi. Resist	Gvl. Inst. Resist	DrftAbun	Snd. Inst. Resist	Shredder	CollGath
Dur. Mobile	-0.18	0.57*	0.5*	0.04	0.29	-0.47*	-0.52*	-0.37*	-0.45*	-0.38*	0.33*	-0.54*
%Mobile/%Flowing	-0.28	0.55*	0.39*	0.17	0.27	-0.42*	-0.41*	-0.43*	-0.43*	-0.37*	0.40*	-0.51*
Time Int. Sed. Trans.	-0.23	0.41*	0.39*	0.09	0.26	-0.37*	-0.40*	-0.38*	-0.34*	-0.29	0.25	-0.46*
T_{Qmean}	-0.25	0.09	-0.03	0.20	0.43*	-0.24	0.06	-0.04	-0.21	-0.27	0.58*	-0.04
Mean Ann. q_p	0.59*	-0.11	0.04	-0.46*	-0.37*	0.09	-0.20	0.04	0.24	0.27	-0.52*	0.28
Time Q_p	-0.44*	-0.21	0.06	0.39*	0.33*	-0.12	0.09	0.19	0.07	-0.16	0.19	0.06
Mean Feb. q	0.42*	-0.07	-0.003	-0.33*	-0.32*	0.04	-0.18	-0.02	0.18	0.12	-0.38*	0.23
Mean Sept. q	0.13	0.36*	0.17	-0.01	-0.09	-0.45*	-0.30*	-0.20	-0.14	-0.31*	0.10	-0.17
Dur. Zero	0.09	-0.36*	-0.49*	-0.09	-0.11	0.52*	0.55*	0.25	0.24	0.48*	-0.11	0.31*
%SAFN	0.07	0.14	-0.22	0.10	0.19	0.18	0.23	-0.12	-0.002	0.11	0.23	-0.07
Velocity	-0.10	-0.09	0.28	0.10	0.26	-0.23	-0.25	-0.02	0.04	-0.26	0.05	0.11
Re	0.41*	-0.13	0.01	-0.39*	-0.31*	-0.003	-0.19	-0.003	0.16	0.13	-0.40*	0.21

*Significant at $p < 0.1$

4.4 Multiple linear regression

To maintain interpretability and parsimony, I allowed up to three of the 12 flow metrics to enter best subsets MRA models for each biotic metric. Dur. Mobile was the most common predictor metric in the biotic response models and enters eight of 12 models (Table 4.5). As in the RDA analysis, the multiple regression models showed that flashiness and bed mobility were prominent predictors of biotic metrics. Bed mobility and flashiness metrics occurred in the best models more often than drying metrics (Table 4.5).

Table 4.5 – Best multivariate models as selected by Akaike Information Criterion (AIC).

Biotic Metric	Intercept	Flow Metric1	Slope1	Flow Metric2	Slope2	Flow Metric3	Slope3	Adj. R^2	AIC
Amphipoda	1.07	Mean Ann. q_p	1.51*	Dur. Zero	0.002*	%SAFN	0.002	0.40	-1.09
Noninsect	36.89	Dur. Mobile	8*	Mean Sept. q	25.8*			0.33	301
EPT	-0.98	Dur. Mobile	0.003*	%SAFN	-0.0002*			0.42	-215
Diptera	0.45	Mean Ann. q_p	-1.13*	Velocity	1.34			0.15	12.1
SC-IBI	7.98	T_{Qmean}	4.89*	Dur. Mobile	0.22*	Time Q_p	10583	0.30	105
Dist. Resil	1.22	Dur. Mobile	-0.04*	Mean Sept. q	-0.20*	Time Q_p	-1541	0.33	-24.1
Desi. Resist	-0.76	Dur. Mobile	-0.004*	Re	-0.01*	Dur. Zero	5.84E-05	0.49	-209
Gvl. Inst. Resist	19782	%Mobile/%Flowing	-4159*	Mean Feb. q	-7082*			0.20	622
Snd. Inst. Resist	0.80	Dur. Zero	0.002*	T_{Qmean}	-0.64*	%Mobile/%Flowing	-0.07*	0.33	-31.4
DrftAbun	6.23	Dur. Mobile	-0.30*					0.11	129
Shredder	0.43	T_{Qmean}	0.62*	Dur. Mobile	0.02*			0.42	-68.1
CollGath	-0.24	Dur. Mobile	-0.01*	Mean Sept. q	-0.02			0.26	-135

*Significant at $p < 0.1$

The best multiple regression models for six out of the 12 biotic metrics included a categorical variable indicating whether a site is perennial or not (Table 4.6). In the models containing this categorical variable, %Mobile/%Flowing is the most significant and common predictor metric. Interestingly, when bed mobility metrics were not allowed in multiple regression models, Dur. Zero took the place of bed mobility metrics in most instances.

Table 4.6 – Best multivariate models as selected by AIC using categorical variable indicating whether a site is perennial or nonperennial.

Biotic Metric	Intercept	Flow Metric1	Slope1	Flow Metric2	Slope2	Flow Metric3	Slope3	Adj. R^2	AIC
Amphipoda	1.56	Peren	-0.59*	Mean Ann. q_p	1.06*	Mean Sept. q	0.70*	0.36	0.97
Noninsect	60.3	Peren	-24.9	Dur. Mobile	8.07*	Mean Sept. q	59.9	0.33	302
EPT	-0.98	Peren	0.004	%Mobile/%Flowing	0.01*	%SAFN	-0.0002*	0.43	-215
Diptera	0.46	Peren	-0.002	Mean Ann. q_p	-1.13*	Velocity	1.34	0.12	14.1
SC-IBI	7.19	Peren	2.74*	T_{Qmean}	8.00*	Mean Sept. q	-3.66*	0.29	105
Dist. Resil	1.15	Peren	-0.17*	%Mobile/%Flowing	-0.14*	T_{Qmean}	-0.51*	0.42	-28.4
Desi. Resist	-0.75	Peren	-0.01*	%Mobile/%Flowing	-0.02*	Re	-0.006*	0.52	-210
Gvl. Inst. Resist	21011	Peren	-1945	%Mobile/%Flowing	-3876*	Mean Feb. q	-5720	0.23	622
Snd. Inst. Resist	1.07	Peren	-0.17*	%Mobile/%Flowing	-0.08*	T_{Qmean}	-0.47*	0.37	-33.2
DrftAbun	6.32	Peren	-0.35	Dur. Mobile	-0.29*			0.09	131
Shredder	0.43	Peren	0.02	T_{Qmean}	0.63*	%Mobile/%Flowing	0.06*	0.42	-66.9
CollGath	-0.22	Peren	-0.02*	%Mobile/%Flowing	-0.03*			0.31	-137.6

*Significant at $p < 0.1$

When included in MRA, the sand/gravel metric was significant for seven out of the 12 biotic metric multiple regression models (Table 4.7). For the sand/gravel models, Mean Sept. q was the most common secondary metric.

Table 4.7 – Best multivariate models as selected by AIC using categorical variable indicating whether a site is sand bed or gravel bed.

Biotic Metric	Intercept	Flow Metric1	Slope1	Flow Metric2	Slope2	Flow Metric3	Slope3	Adj. R^2	AIC
Amphipoda	1.06	Sand	-0.19*	Mean Ann. q_p	1.42*	%SAFN	0.01*	0.38	-0.31
Noninsect	34.1	Sand	-9.87	Dur. Mobile	8.86*	Mean Sept. q	21.6	0.31	303
EPT	-0.98	Sand	0.01	%SAFN	-0.0002*	Dur. Mobile	0.002*	0.44	-215
Diptera	0.51	Sand	0.05	Mean Ann. q_p	-1.1*	Velocity	1.48*	0.13	13.8
SC-IBI	10.1	Sand	0.95*	T_{Qmean}	8.23*	Dur. Zero	-0.01*	0.32	104
Dist. Resil	0.88	Sand	-0.22*	Mean Sept. q	-0.27*	T_{Qmean}	-0.61*	0.40	-27.5
Desi. Resist	-0.78	Sand	-0.02*	Dur. Zero	0.0001*	Re	-0.004*	0.53	-211
Gvl. Inst. Resist	19203	Sand	-3622*	Mean Sept. q	-4412*			0.17	623
Snd. Inst. Resist	0.87	Sand	-0.12*	Mean Sept. q	-0.23*	T_{Qmean}	-0.49*	0.23	-27.1
DrftAbun	6.25	Sand	0.31	Dur. Mobile	-0.36			0.08	131
Shredder	0.55	Sand	0.07*	T_{Qmean}	0.75*	Dur. Zero	-0.001	0.43	-68.0
CollGath	-0.24	Sand	0.01	%Mobile/%Flowing	-0.04*	Mean Sept. q	-0.03*	0.27	-135

*Significant at $p < 0.1$

4.5 Hydrologic, hydraulic, and biotic correlations with landscape metrics

Spearman correlation analyses were used to assess correlation between watershed characteristics, flow metrics, and biotic metrics (Table 4.8). More significant correlations between flow metrics and watershed metrics were found at the entire watershed-scale than within 5 km and 1 km of the biomonitoring sites. T_{Qmean}, Mean Ann. q_p, Time Q_p, and Mean Feb. q were most significantly correlated with landscape measures, particularly percent urbanization and road density. In contrast, the numbers of significant correlations for bed mobility metrics were few, though the strength of correlations generally increased at the 1-km and 5-km scale watershed metrics. As anticipated, flashiness (measured by a decrease in T_{Qmean}) was significantly associated ($p < 0.1$) with increased urban land cover (ρ = -0.34 to -0.62) and road density (ρ = -0.34 to -0.65). Urbanization was also correlated with increased Mean Ann. q_p and February flows. All three bed mobility metrics were inversely correlated with all measures of percent urbanization and road density.

Table 4.8 – Spearman correlation of flow metrics and biotic metrics with watershed metrics measured at the entire watershed, within 5 km of biomonitoring sites, and within 1 km of biomonitoring sites.

		Flow Metrics											
		Dur. Mobile	**%Mobile/ %Flowing**	**Time Int. Sed. Trans.**	**T_{Qmean}**	**Mean Ann. q_p**	**Time Q_p**	**Mean Feb. q**	**Mean Sept. q**	**Dur. Zero**	**%SAFN**	**Velocity**	**Re**
Percent Agriculture	watershed	0.14	0.07	0.10	-0.22	0.37*	-0.69*	0.24	-0.07	0.09	0.37*	-0.46*	0.19
	5 km	0.23	0.13	0.17	-0.005	0.27	-0.47*	0.25	0.16	-0.04	0.27	-0.22	0.22
	1 km	0.22	0.14	0.12	0.09	0.10	-0.35*	0.09	0.42*	-0.13	0.08	-0.16	0.12
Percent Non-natural Vegetation	watershed	-0.11	-0.18	-0.09	-0.59*	0.68*	-0.43*	0.58*	0.23	-0.21	-0.21	-0.06	0.57*
	5 km	-0.13	-0.21	-0.09	-0.21	0.63*	-0.28	0.33*	0.30*	-0.01	0.06	-0.07	0.56*
	1 km	0.17	0.10	0.16	-0.27	0.17	0.05	0.12	0.06	0.005	0.03	-0.15	0.08
Percent Urbanization	watershed	-0.16	-0.25	-0.22	-0.62*	0.71*	-0.41*	0.62*	0.31*	-0.32*	-0.33*	-0.01	0.60*
	5 km	-0.25	-0.34*	-0.29	-0.34*	0.62*	-0.34*	0.60*	0.21	0.01	0.06	-0.16	0.49*
	1 km	-0.26	-0.39*	-0.43*	-0.26	0.55*	-0.31*	0.50*	0.28	-0.06	-0.13	-0.08	0.44*
Road Density (km/km^2)	watershed	-0.15	-0.20	-0.12	-0.65*	0.64*	-0.4*	0.55*	0.19	-0.17	-0.17	-0.12	0.52*
	5 km	-0.21	-0.27	-0.18	-0.43*	0.61*	-0.4*	0.59*	0.18	-0.02	0.09	-0.23	0.48*
	1 km	-0.29	-0.35*	-0.27	-0.34*	0.41*	-0.17	0.37*	0.05	0.14	0.16	-0.29	0.28

		Biotic Metrics											
		Amphipoda	**Noninsect**	**EPT**	**Diptera**	**SC-IBI**	**Dist. Resil**	**Desi. Resist**	**Gvl. Inst. Resist**	**DrftAbun**	**Snd. Inst. Resist**	**Shredder**	**CollGath**
Percent Agriculture	watershed	0.51*	0.27	-0.19	-0.40*	-0.32*	0.16	-0.02	-0.16	0.01	0.21	-0.11	-0.001
	5 km	0.25	0.39*	0.16	-0.13	-0.04	-0.23	-0.38*	-0.58*	-0.32*	-0.32*	0.003	-0.18
	1 km	0.10	0.45*	0.20	-0.14	-0.04	-0.34*	-0.33*	-0.43*	-0.35	-0.33*	-0.09	0.35*
Percent Non-natural Vegetation	watershed	0.47*	0.04	0.0002	-0.36*	-0.51*	0.18	-0.11	0.03	0.35*	0.30*	-0.48*	0.09
	5 km	0.54*	0.09	-0.18	-0.30*	-0.47*	0.08	-0.06	-0.02	0.26	0.28	-0.31*	0.21
	1 km	0.18	0.14	-0.05	-0.35*	-0.21	-0.05	0.02	0.16	0.20	0.29	-0.27	-0.10
Percent Urbanization	watershed	0.51*	0.09	0.001	-0.35*	-0.51*	0.16	-0.11	0.04	0.34*	0.28	-0.44*	0.09
	5 km	0.63*	0.02	-0.37*	-0.34*	-0.51*	0.29	0.18	0.21	0.37*	0.52*	-0.36*	0.33*
	1 km	-0.74*	0.04	-0.42*	-0.35*	-0.54*	-0.35*	0.25	0.42*	0.32*	0.53	-0.29	0.27
Road Density (km/km^2)	watershed	0.49*	0.08	-0.06	-0.32*	-0.53*	0.22	-0.06	0.04	0.36*	0.34*	-0.49*	0.09
	5 km	0.63*	0.09	-0.36*	-0.28	-0.53*	0.27	0.12	0.11	0.33*	0.45*	-0.33*	0.21
	1 km	0.65*	0.04	-0.52*	-0.17	-0.42*	0.42*	0.37*	0.43*	0.41*	0.62*	-0.22	0.21

*Significant at $p < 0.1$

Flashiness was significantly correlated with all scales of urbanization expressed as both road density and percent urban land cover. SC-IBI was inversely related to flashiness (Table 4.4) and significantly negatively correlated with all scales of percent urbanization and road density; however, EPT percent richness was uncorrelated with flashiness and only significantly negatively correlated with percent urban and road density at the 1-km and 5-km scales. T_{Qmean} was significantly correlated with road density at all scales, and percent urban at 1-km and 5-km scales. T_{Qmean} was also the best single predictor of SC-IBI in this study, whereas the best single predictor of EPT percent richness was %Mobile/%Flowing (Table 4.5).

Correlations between watershed characteristics and biotic metrics generally indicated that biotic metrics were most correlated with watershed characteristics measured within 1 km of biomonitoring sites (Table 4.8), although some biotic metrics showed mixed responses to landscape metrics of varying proximity. SC-IBI had the greatest number of significant correlations with watershed characteristics across all scales, having negative correlations with all four measures of human influence. Percent urbanization had the greatest number of significant correlations with biotic metrics. Increased urbanization also resulted in lower Shredder percent richness and surprisingly reduced Diptera percent abundance, increased percent richness of taxa abundantly found in drift and sand-bed instability resistance traits despite the fact that D_{50} increased with increased urbanization at these study sites. Counterintuitively, increased bed mobility was significantly associated with increased EPT percent richness and reduced occurrence of traits beneficial to Dist. Resil, as well as, decreased occurrence of traits benefical to Gvl. Inst. Resist and Snd. Inst. Resist (Table 4.4).

4.6 Bivariate OLS and quantile regression

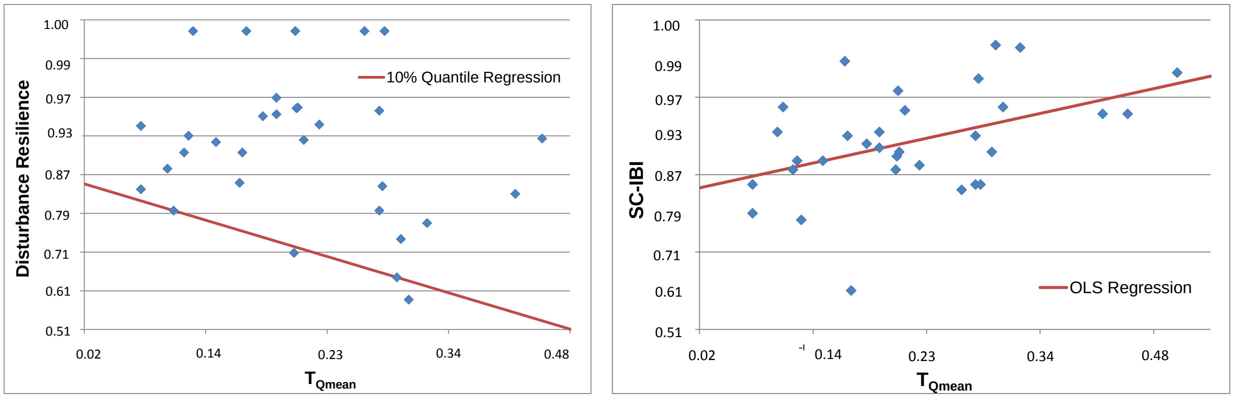
Either a bed mobility metric or a hydraulic metric were present in seven of the 12 best OLS regression models. The other best predictor metrics are T_{Qmean}, Dur. Zero, and Mean Ann. q_p.

For the lower (10%) and upper (90%) quantiles and the OLS regression, the percentage of significant relationships increased for the perennial stratum compared to all sites together (Table 4.9). In contrast, the percent of significant relationships decreased for all three regressions for the nonperennial stratum. In general, stratification by both flow and substrate type produced fewer significant relationships as a result of decreased sample size.

Table 4.9 – Percent of significant OLS and quantile regression models out of all models for nine subsets of sites.

	Sites	10% Quantile	OLS Regression	90% Quantile	No. of Sites
1	All	19	29	23	32
2	Perennial	25	37	26	14
3	Nonperennial	10	19	21	18
4	Sand-bed	19	25	19	21
5	Gravel-bed	16	18	21	11
6	Perennial Sand-bed	13	8	23	8
7	Perennial Gravel-bed	10	20	12	6
8	Nonperennial Sand-bed	11	19	17	13
9	Nonperennial Gravel-bed	8	3	8	5

Plots of biotic response to T_{Qmean} (Figure 4.4) showed that with increasing flashiness, SC-IBI scores decreased and prevalence of traits that enable organisms to be resilient to disturbance increased. Traits that lend resilience against disturbance had a negative floor relationship with T_{Qmean} (Figure 4.4a). An increasing value of T_{Qmean} indicated decreasing flashiness. This relationship showed that sites at the lower end of flashiness can support taxa with or without disturbance resilience traits, but as flashiness increased, the need for possession of these traits increased. SC-IBI increased linearly with reduced flashiness (Figure 4.4b).

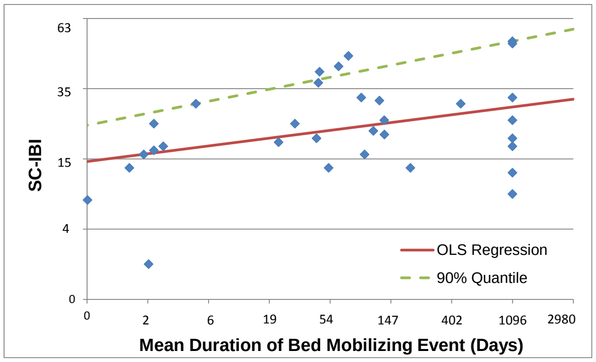


(a) Dist. Resil versus T_{Qmean}

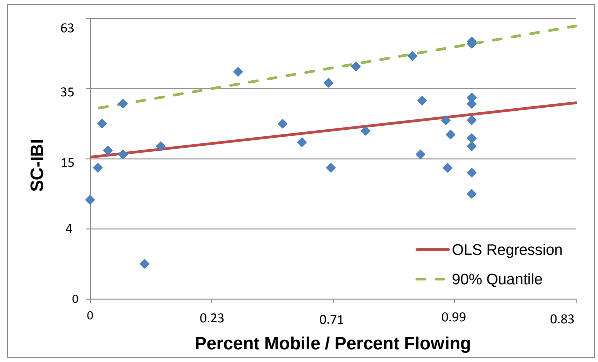
(b) SC-IBI versus T_{Qmean}

Figure 4.4 – Quantile and OLS plots.

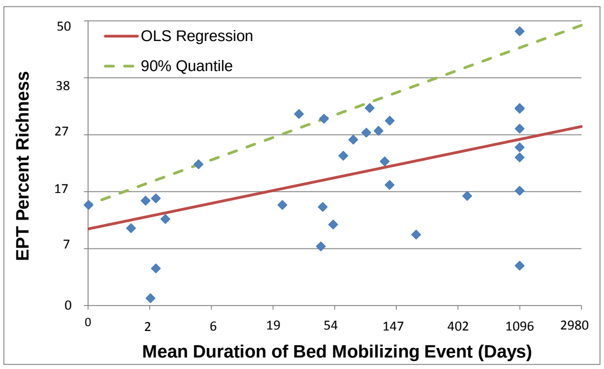
Regression plots of bed mobility metrics with SC-IBI and EPT percent richness again showed unexpected increases in SC-IBI and EPT values with increased bed mobility (Figure 4.5). All plots show significant ($p < 0.1$) models. Regression plots in Figure 4.5 showed bed mobility metrics calculated with a τ_* threshold equal to 0.03. Bed mobility metrics calculated using τ_* thresholds of 0.06 and 0.1 showed the same perplexing biotic response to increased bed mobility.



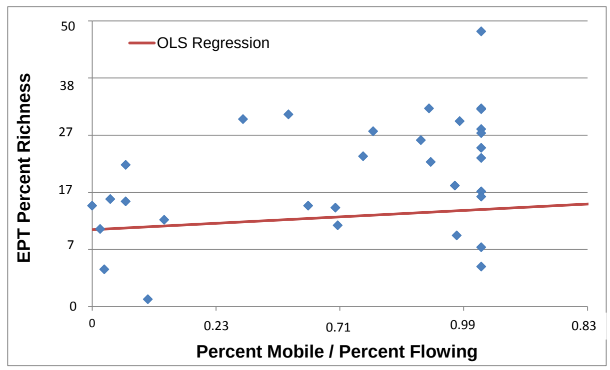
(a) SC-IBI response to Dur. Mobile



(b) SCI-IBI response to %Mobile/%Flowing



(c) EPT response to Dur. Mobile



(d) EPT response to %Mobile/%Flowing

Figure 4.5 – SC-IBI and EPT percent richness responses to bed mobility metrics.

CHAPTER 5 DISCUSSION

5.1 Data resolution and record length

Daily discharge data analyzed 3 yrs prior to sampling appear to be satisfactory for developing flow-ecology relationships for benthic macroinvertebrates in southern California, as metrics calculated at both 15-min and daily time steps are very highly correlated. These high correlations result in very similar relationships between biotic metrics and hydrologic/hydraulic metrics calculated at either 15-min or daily time steps. Many software packages used for calculating hydrologic metrics such as IHA, GeoTools, and NAHAT only accept daily data (Richter *et al*., 1996; Henrikson *et al*., 2006; Bledsoe *et al*., 2007); therefore, this finding has practical utility. Relationships described using 3 yrs of gage data versus long-term gage data also reveal similar biotic responses to both hydrologic and hydraulic metrics, with a few relationships being slightly stronger with a 3-yr period. Given the small difference in relationships resulting from different time steps and period lengths, 3 yrs of antecedent daily discharge data represent a reasonable means of reducing data requirements. This finding is consistent with a previous regional study in the northeastern U. S. that suggested using 3 yrs of data maximizes sample sites, while satisfactorily describing temporal variation (Kennen *et al*., 2010). Although all the streams in this study were flowing for at least 4 months prior to sampling, small differences between 3-yr and long-term metrics in the present study raise the possibility that even shorter records might contain more explanatory information. Other studies suggest that flow metrics based on as little as 30 to 100 days prior to sampling (Konrad *et al*., 2008) can have utility in identifying flow-ecology relationships. Therefore, future efforts may benefit from calculating flow metrics based on an even shorter record than 3-yrs prior to sampling.

5.2 Spatial scale of correlations

As anticipated, hydrologic and hydraulic metrics are most correlated with the entire watershed-scale land cover as opposed to more local conditions, with the strongest and greatest number of significant correlations occurring at the entire watershed-scale across all land-cover metrics. However, relationships between biotic metrics and land cover tend to be less straightforward, which is consistent with previous studies of land use effects on stream biota generally showing mixed results and complex patterns of scale-dependence. For example, land use within 100 m of streams in heavily agricultural watersheds in southeastern Michigan was significantly correlated with biotic response, whereas watershed-scale land use was not (Lammert and Allan, 1999). However, watershed-scale measures of historical land uses and legacy effects were better predictors of biological condition than proximate riparian land use in western North Carolina (Harding *et al*., 1998). In the present study, measures of urbanization are significantly associated with diverse biotic metrics at multiple spatial scales, yet there is no clearly discernable pattern in which scale (extent) of landscape metrics is most strongly related to biotic condition. Overall, land-cover metrics calculated within 1 km of a biomonitoring site have a greater number of significant relationships with biotic metrics compared to 5 km and entire watershed scale metrics. The more local landscape metrics could represent a variety of influences including direct channel modifications, riparian condition, and point source discharges; however, such correlations are prone to confounding factors including collinearity and spatial autocorrelation (King *et al*., 2005). Nevertheless, future development and refinement of flow-ecology relationships for this region would likely benefit from a more detailed analysis of how the effects of watershed-scale hydromodification on stream biota are mediated by more local, valley-scale factors.

5.3 Urbanization, bed mobility, flashiness, and biotic metrics

RDA and MRA models show both flashiness and bed mobility emerging as significant and largely independent predictors of variance in biotic metrics. EPT percent richness and SC-IBI decline with increasing urbanization; however, only SC-IBI is significantly correlated with $T_{Qmean.}$ Additionally, MRA models showed T_{Qmean} as the single best predictor of SC-IBI, and Dur. Mobile as the best predictor of EPT percent richness. This seems to indicate that flashiness is suppressing SC-IBI scores, but other stressors are likely causing EPT percent richness to decline as urbanization increases. Similarly, T_{Qmean} was not a good predictor of EPT richness, EPT percent richness, and B-IBI in the naturally flashy streams of North Carolina Piedmont watersheds (Pomeroy, 2007), but a B-IBI was found to decrease with increasing flashiness measured by T_{Qmean} in streams of the Puget lowlands in Washington that are not as inherently flashy (Booth *et al*., 2004). The difference in responsiveness between EPT and IBI metrics, both used to indicate the presence of sensitive taxa, could be attributed to regional differences in natural flow variability or the relative robustness of a multimetric IBI over EPT metrics based solely on the presence of three specific orders of taxa.

Metrics describing the frequency and duration of bed mobility are also negatively correlated with urbanization in this study. This result is somewhat counterintuitive given that increased urbanization would be expected to further intensify stream disturbance regimes; however, urbanization is associated with an increase in D_{50} across the sites available for this study. Coarser-bed material at the more urbanized sites increases estimates of the flow required for substrate mobilization and tends to reduce the estimated frequency and duration of bed disturbance. This could reflect urban-induced bed coarsening as a result of increased stream power and winnowing away of sand and gravels (Finkenbine *et al*., 2000; Hawley *et al*., 2013).

In addition to lower EPT percent richness and SC-IBI, increased urbanization in this study also leads to decreased Diptera percent abundance and Shredder percent richness. Increased peak flows associated with increased urbanization (Table 4.8) can lead to reduced allochthonous coarse particulate organic matter (CPOM; Aldridge *et al*. (2009)) which could explain the reduction of Shredder percent richness. Drifter percent richness and percent richness of taxa with Snd. Inst. Resist traits are also shown to increase with increased urbanization despite the bed coarsening seen as urbanization increases.

5.4 Bed mobility threshold as a surrogate for low flows

A variety of analyses indicates a counterintuitive relationship between bed mobility and biotic metrics, i.e., increased EPT percent richness and SC-IBI scores, and decreased Dist. Resil and bed instability resistance traits with greater bed mobility. As previously indicated, increasing the bed disturbance criterion to levels indicative of full bed mobility had a negligible effect on the response of biotic metrics. In contrast, many lines of evidence suggest that the bed mobility metrics are acting as a surrogate for the frequency and duration of flows above a very low-flow threshold that is critical to benthic macroinvertebrates, particularly for EPT percent richness and SC-IBI. Hydrologic analyses that were subsequently performed to investigate whether hydraulic metrics developed in this study act as proxies for flow permanence indicate that the flow threshold for bed mobility is below the mean flow for the record at all sand-bed sites (Table 4.2). Additionally, at three of the 11 gravel-bed sites, the bed mobility threshold flows are below the mean flow for the 3-yr record. Percent of time above several low-flow thresholds (0.28, 1.4, 2.8, 28, and 140 L/s), are highly correlated (ρ = 0.73 to 0.91) with the percent of time above the bed mobility threshold at sand-bed sites. The strength of correlations is substantially less (ρ = 0.17 to 0.41) when gravel-bed sites are included. Percent of time flow exceeded 28 L/s (1 cfs) is also highly correlated (ρ = -0.44) with decreased presence of Desi. Resist traits, as were all three bed mobility metrics ($p < 0.1$). %Mobile/%Flowing has a slightly weaker correlation with Desi. Resist (ρ = -0.41) than percent of time above 28 L/s. This analysis, using understanding of Desi. Resist traits, shows how traits-based metrics provide insight in the interpretation of flow-ecology relationships.

The explanatory power of the new percent of time above 28 L/s flow metric was also subsequently examined via multiple regression modeling, with the bed mobility metrics removed. The bed mobility metrics were previously selected as the primary predictor variable in seven out of the 12 best biotic response models (Table 4.5). With bed mobility metrics removed, models are dominated by the Dur. Zero and percent of time above 28 L/s metrics, and are generally slightly weaker as indicated by increased AIC value. For models in which duration of zero flow replaced bed mobility metrics as the primary predictor variable, the direction of its relationship with each biotic metric was reversed as expected.

Iterative RDA plots for perennial, nonperennial, and sand-bed sites (Figures 4.3a through 4.3c) show %Mobile/%Flowing as an important metric, but in the gravel-bed iterative RDA plot (Figure 4.3d) the Dur. Zero metric is selected instead. This indicates that, unlike sand-bed sites, a low-flow threshold well below the threshold for bed mobility is useful in describing biotic variance in gravel-bed systems. It is plausible that the optimal intermittency / low-flow thresholds for sand-bed versus gravel-bed sites could vary due to differences in low-flow movement through bed pore structures and turbulent diffusion processes. Due to larger grain size, turbulence can exist within the bed of gravel-bed channels, but flow in the surface of sand-bed channels is typically laminar (Packman and Bencala, 2000). Near-bed turbulence in gravel-bed channels allow for greater oxygenation within the bed; whereas in sand-bed channels, oxygen diffusion is more limited to the surface of the bed (Minshall, 1984). This suggests that gravel-bed channels could provide more favorable benthic habitat at very low flows than sand-bed channels (Bo *et al*., 2007; Bogan, *et al*. 2013). Differences in critical low-flow thresholds among sites could also reflect the challenge of accurately describing spatial variability in extreme low-flow conditions with streamflow gages.

5.5 Stratification of biomonitoring sites

RDA and MRA models using perennial/nonperennial and sand/gravel categorical variables underscore the importance of stratifying biomonitoring sites that span a gradient of flow intermittency and channel type. MRA shows that the sand/gravel categorical variable is significant in seven out of the 12 best biotic response models, and the perennial/nonperennial categorical variable is significant in six out of the 12 best models. These results indicate that site stratification is useful for some biotic metrics and probably unimportant for others in this study area. Presently, nonperennial streams are commonly either excluded from management or managed as “hydrologically challenged” perennial streams, as they have distinctly different biological communities and ecological functions (Larned *et al*., 2010), and macroinvertebrate assemblages have been found to be different between perennial and nonperennial sites in Mediterranean climates (Garcia-Roger *et al*., 2011). Stream drying causes habitat fragmentation resulting in oxygen depletion and elevated temperatures (Acuna *et al*., 2005). Many streams are also experiencing increased drying due to human influences; therefore, this type of stream may need to receive greater attention in future biomonitoring programs (Larned *et al*., 2010). As seen in the results, Mean Sept. q is strongly inversely related to stream drying. September is on average one of the lowest flow months for all study sites. The inverse correlation with drying would indicate that at sites with longer durations of drying events, September flows are lower. In addition, urbanization is negatively correlated with duration of drying, but positively correlated with Mean Sept. q. This might indicate urbanization increases September flows and overall flow permanence. Benthic macroinvertebrate response to substrate characteristics has also been noted in previous studies. In general, it is well-established that fine sediments can inhibit the flow of oxygenated water through streambed gravels which is detrimental to benthic macroinvertebrates and fish reproduction (Waters, 1995; Allan and Castillo, 2007). In a southeastern Michigan watershed dominated by fine- and coarse-grained moraine deposits, substrate size explained the greatest amount of variance in macroinvertebrate assemblages compared to flow stability and other habitat indices (Lammert and Allan, 1999).

5.6 Utility of hydraulic metrics in discovering flow-ecology relationships

Hydraulic metrics require additional information about geomorphic setting that is not required for metrics that are solely based on discharge. If the level of uncertainty in the physical data and parameters (i.e., slope, grain-size, cross-section, and Manning's *n*) is too large, then the additional level of measurement error introduced in the hydraulic metrics will hinder development of meaningful flow-ecology relationships. The bed mobility metrics used in this study are particularly sensitive to measurements of slope and median grain size, both of which can exhibit substantial variability among field collection methodologies and observers. Grain size and slope were compared at all sites where I perform detailed cross-section measurements and PHAB data were also available. A marked difference in grain size and slope was noted at approximately half of the sites. In locations where PHAB data were collected over multiple years at the same site, the reported slopes and grain sizes were also quite different at times. It is plausible that in some cases the channel may have switched from a gravel-bed to a sand-bed, particularly if there was a severe burn in the watershed between the two measurement dates. Reach-scale heterogeneity in substrate is also substantial in this region, and uncertainty in the previous survey location can lead to substantially different grain-size distributions (Bunte and Abt, 2001). PHAB data were collected by several different survey crews and state programs which could result in inherent inconsistencies. Minimizing inter-observer error in data collection would improve utility of geomorphic metrics in developing hydraulic-ecology relationships.

5.7 Summary

Overall, the flow and hydraulic metrics examined in this study explain substantial variation in biotic composition (taxonomic and species trait) despite complex interactions between environmental gradients and human influences in southern California. This finding using gaged watersheds appears to bode well for the development of regional flow-ecology relationships which will include ungaged basins, especially those based on low-flow and flashiness metrics. Many studies have successfully tied hydraulic metrics to macroinvertebrate communities (Statzner and Higler, 1986; Statzner *et al*., 1988; Knight and Cuffney, 2012). In the present study, relationships between bed disturbance metrics and biotic metrics were confounded by covariance with flow intermittency. Previous studies of hydraulic stream ecology and bed disturbance do not explicitly address stream intermittency (Statzner and Higler, 1986; Statzner *et al*., 1988; Cobb *et al*., 1992; Death and Winterbourn, 1994; Townsend *et al*., 1997a, 1997b; Knight and Cuffney, 2012). This study suggests that flow permanence limits discovery of flow-ecology relationships in systems with seasonal drying when not explicitly accounted for.

5.8 Future research

This study points to several potential avenues of future refinement of flow-ecology relationships in the study region. First, antecedent conditions could be investigated further by examining shorter periods prior to sampling, e.g., a few months. Traits-based analysis should also be used in future studies across complex gradients of human influences and hydrogeomorphic characteristics as it was found to aid understanding of causal linkages between flow and benthic macroinvertebrates. To better assess whether hydraulic metrics can be useful in identifying mechanisms that link landscape characteristics to the response of stream biota, a sensitivity analysis could be performed to assess signal-to-noise ratios and acceptable levels of uncertainty in the physical data. If the uncertainties in available physical data are too large, then hydraulic and bed mobility metrics are unlikely to illicit more information than metrics based on discharge alone.

Hydraulic metrics might ultimately prove useful in understanding biological response within flow intermittency and geomorphic strata; however, this appears to be predicated upon obtaining a larger sample size and regional pool of study sites. Since this study largely exhausted the pool of gaged study sites, a hydrologic modeling foundation must be developed to extend these analyses to the larger number of ungaged biomonitoring sites in the region (Poff *et al*., 2010). By identifying ecologically-relevant flow metrics at gaged sites, this study provides critical information for future hydrologic modeling efforts that will allow the inclusion of ungaged biomonitoring sites in refining these tentative regional flow-ecology relationships. For example, it is clear that calibration and testing of hydrologic models should emphasize their accuracy with respect to flow intermittency and flashiness. Further, a regional hydrologic foundation would extend this work by providing *departures* in ecologically-relevant flow metrics relative to reference conditions at both gaged and ungaged sites. Such departures and a higher spatial density of sites could help disentangle the effects of urbanization and other human influences from the broad hydrologic and geomorphic gradients encountered in this and other Mediterranean regions.

CHAPTER 6 CONCLUSIONS

Traits-based and taxonomic metrics for benthic macroinvertebrates are responsive to measures of stream drying, low flows, and flashiness in coastal watersheds of southern California. Correlations between landscape metrics and biotic metrics indicate that watershed urbanization has an overarching influence on biotic communities. Flow metrics are also significantly influenced by various measures of urbanization. These relationships can be satisfactorily described using daily discharge data and a short record length of 3 yrs prior to sampling efforts, as longer and more temporally dense flow records appear to provide little if any additional explanatory power. Stratification of sites by intermittency and substrate type can improve the strength and interpretability relationships between hydrology/hydraulics and benthic macroinvertebrate assemblages in Mediterranean regions, as well as, other regions that span interacting gradients of human influence and hydrogeomorphic characteristics. Species trait analysis also greatly aided in the interpretation of mechanisms driving flow-ecology relationships in this study. Hydraulic metrics describing streambed disturbance were significantly correlated with increases in measures of biotic integrity due to high intercorrelation with flow permanence and the frequency of discharges above critical low-flow thresholds. Thus, it appears that benthic macroinvertebrate assemblages in this region are fundamentally influenced by flow intermittency and urban-induced flashiness. Care must be taken when interpreting physically-based metrics describing bed mobility and disturbance regimes, given their potential for spurious correlations in regions characterized by flow intermittency and labile channels. Results also suggest that, in some cases, a very low, non-zero flow threshold may better describe constraints on macroinvertebrates than zero-flow thresholds. Improved consistency in geomorphic data collection would increase the utility of hydraulic metrics for development of flow-ecology relationships. The potential utility of hydraulic metrics in a given setting should be weighed against the added measurement, computational time, and resources required. Finally, by identifying ecologically-relevant flow metrics at gaged biomonitoring sites, this study informs future efforts to develop a hydrologic foundation that includes ungaged sites by identifying flow metrics that are the most important to model accurately in refining regional flow-ecology relationships.

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LIST OF ABBREVIATIONS

Acronyms:

AIC	Akaike Information Criterion
ASDSO	Association of State Dam Safety Officials
B-IBI	Benthic Index of Biotic Integrity
CPOM	coarse particulate organic matter
CRAN	The Comprehensive R Archive Network
CSU	Colorado State University
EPA	United States Environmental Protection Agency
EPT	Ephemeroptera, Plecoptera, and Trichoptera
ID	identification
IHA	Indicators of Hydrologic Alteration
MRA	multiple linear regression
MRLC	Multi-Resolution Land Characteristics Consortium
NAHAT	National Hydrologic Assessment Tool
NID	National Inventory of Dams
NLCD	National Land Cover Database
No.	number
OLS	ordinary least squares
PCA	principal component analysis
pers. comm.	personal communication
PHAB	physical habitat
®	registered

RBI	Richards-Baker Flashiness Index
RDA	redundancy analysis
SAFIT	Southwest Association of Freshwater Invertebrate Taxonomists
SC-IBI	Southern California Index of Biotic Integrity
SCCWRP	Southern California Coastal Water Research Project
SMC	Stormwater Monitoring Coalition
SWAMP	Surface Water Ambient Monitoring Program
U. S.	United States
USACE	United States Army Corps of Engineers
USGS	United States Geological Survey

Metric Abbreviations:

Adj.	adjusted
Ann.	annual
CollGath	collector gatherer
Desi.	desiccation
Dist.	disturbance
DrftAbun	drift abundance
Dur.	duration
Feb.	February
Gvl.	gravel
Inst.	instability
Int.	integrated
%SAFN	percent sand plus fines
Peren	perennial

q	unit discharge
Q	flow
Re	Reynolds number
Resil	resilience
Resist	resistance
SC-IBI	Southern California Index of Biotic Integrity
Sed.	sediment
Sept.	September
Snd.	sand
Trans.	transport
T_{Qmean}	fraction of the record above average flow for the record