

AN ABSTRACT OF THE DISSERTATION OF

Scott W. Miller for the degree of Doctor of Philosophy in Fisheries Science presented on August 30, 2007.

Title: The Effects of Irrigation Water Withdrawals on Macroinvertebrate Community Structure and Life History Strategies.

Abstract approved:

David Wooster

Judith L. Li

I used current water management practices in central and eastern Oregon and Washington as natural experiments to quantify the effects of irrigation water withdrawals on macroinvertebrate community structure and life history strategies. Reduced discharge had direct (e.g. decreased velocity and wetted habitat) and indirect (e.g. increased conductivity and temperature) effects on key environmental determinants of macroinvertebrate communities and life history strategies. In general, macroinvertebrate responses were more strongly related to indirect than direct environmental alterations.

For a lowland river system, the severity of community and population level responses depended on the magnitude and duration of low flow events. However, discharge reductions alone, even when exceeding 90% of ambient levels, had no effect on community composition. Rather, changes in community composition were associated with interacting thresholds of reduced discharge and altered water quality (i.e., increased conductivity and temperature). Similar responses were observed at the population level; growth and development alterations for *Brachycentrus occidentalis* appeared to reduce fitness during high-intensity, long-duration water withdrawals associated with increased

temperature. Winter discharge levels facilitated recovery of macroinvertebrate communities on an annual basis, whereas recovery was not observed after discharge and physicochemical variables returned to predisturbance conditions for only one month.

At a broader spatial scale, I examined whether macroinvertebrate responses to water withdrawals of similar magnitude and duration depended on species traits (e.g., voltinism, thermal preference, size) for 12 rivers spanning an altitudinal gradient. Species traits differed among high, mid, and low elevation reference reaches; however, compositional responses to water withdrawals were similar among rivers found at different elevations. Apart from significant density increases, I was unable to detect compositional responses above and below all 12 diversions, despite discharge reduction exceeding 75% of ambient levels. In contrast, the proportional abundance for 10 of 52 species traits (e.g., multivoltinism, streamlined, swimmers) significantly differed above and below all points of diversion.

Irrigation water withdrawals appear to impact macroinvertebrates through indirect environmental alterations that intensify with the magnitude and duration of water withdrawals. Preserving environmental conditions within natural ranges of variability, especially during low water years, appears critical to mitigating adverse biological responses to water withdrawals.

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The Effects of Irrigation Water Withdrawals on Macroinvertebrate Community Structure
and Life History Strategies

by
Scott W. Miller

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APPROVED:

Co-Major Professor, representing Fisheries Science

Co-Major Professor, representing Fisheries Science

Head of the Department of Fisheries Science

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes release of my dissertation to any reader upon request.

Scott W. Miller, Author

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CONTRIBUTION OF AUTHORS

Dr. David Wooster and Dr. Judy Li aided in data analysis and interpretation and edited all manuscripts presented herein.

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THE EFFECTS OF IRRIGATION WATER WITHDRAWALS ON MACROINVERTEBRATE COMMUNITY STRUCTURE AND LIFE HISTORY STRATEGIES

CHAPTER 1: INTRODUCTION

Agricultural productivity throughout the western United States (U.S.) is absolutely dependent on irrigation. In 2000, irrigated agriculture constituted the greatest use of freshwater in the U.S., withdrawing approximately 303 MI per day (Huston et al. 2004). In California an estimated 90% of water use is for irrigated agriculture (Allan 1995). A similar pattern exists in Oregon where half of the approximately 15,000 farms are either wholly or partly dependent on irrigation. Over 90% of irrigation water for Oregon farms comes from surface waterbodies and is delivered to agricultural fields by approximately 60,000 out-of-channel diversions (Bastach 1998). Due in part to this ubiquitous management practice, only 2% of U.S. rivers remain free-flowing and the top four threatened animal groups (mussels, crayfishes, stoneflies, and fishes) live in freshwater (Ward and Stanford 1983, Stein et al. 2000).

With human population exceeding six billion people, increased demands for freshwater resources coincide with a growing concern for the health and well-being of lotic (i.e., stream and river) ecosystems. The sustainability of irrigated agriculture is being questioned because of particular events such as the death of over 30,000 Chinook salmon in the Klamath Basin, OR (Levy 2003) and trends associated with global climate change, which are predicted to escalate water resource conflicts (Arthington et al. 2006). This growing social awareness has helped spawn a new era of 'instream flow' modeling and design (Richter et al. 1997). Whereas past determinations of ecologically meaningful flows focused on minimum levels for single species (Jowett 1997, Baron et al. 2002), contemporary efforts aim to reestablish natural patterns of hydrologic variability to promote geomorphic and ecosystem processes (Richter et al. 1997, Bunn and Arthington 2002, Arthington et al. 2006).

Environmental variability has long been recognized as playing an important role in structuring biologic communities and maintaining biodiversity (Hutchinson 1961, Menge and Sutherland 1976, Connell 1978). In lotic ecosystems, discharge is the primary driver of environmental variability (Resh et al. 1988, Poff and Ward 1990) and is characterized by the timing, frequency, duration, magnitude, and predictability of intra- and inter-annual discharge fluctuations (Poff and Allan 1997). Each of these components interact to influence environmental variables such as water chemistry, temperature, ecosystem connectivity, and geomorphology; all have direct or indirect associations with community composition, life history adaptations, and trophic structure (Leopold et al. 1964, Junk et al. 1989, Bunn and Arthington 2002). While a considerable amount of work has addressed how alterations to the timing and magnitude of high flow events affect geomorphic and ecological processes (reviewed in Allan 1995; Power et al. 1996; Vinson 2001), the effects of low flow events have received considerably less attention (Resh et al. 1988, Lake 2000).

Seasonal low flows and desiccation can be normal events for streams in arid and semi-arid regions; however, irrigation water withdrawals can exacerbate the magnitude, duration, and spatial extent of low flow conditions (Wilber et al. 1996, Eheart and Tornil 1999). Despite the ubiquity of this management practice, we currently do not understand how such alterations influence chemical, physical, and biological components of lotic ecosystems. The few studies addressing the effects of irrigation water withdrawals have focused on macroinvertebrate communities and produced inconsistent results. While some studies found strong impacts on community structure (Dudgeon 1992, Rader and Belish 1999, McIntosh et al. 2002), others found little to no impact (Castella et al. 1995, Dewson et al. 2003, McKay and King 2006, Dewson et al. 2007). Consequently, we currently do not understand when or to what extent irrigation water withdrawals alter stream ecosystems. Moreover we lack an understanding of the mechanisms that drive these responses. This dearth of knowledge inhibits our ability to manage lotic ecosystems in a way that allows water withdrawals, while minimizing ecological degradation.

The goal of this research was to investigate the effects of low flow events on benthic macroinvertebrates in agricultural settings where rivers are intensively managed for irrigation practices. I accomplished this goal through three studies addressing population, community, and species trait responses of macroinvertebrates to irrigation water withdrawals that were conducted at regional and local spatial scales. I chose benthic macroinvertebrates, for whom numerous life histories are well known, as target organisms because they are relatively sedentary, ubiquitous, and differentially sensitive to pollutants (Metclaff 1989, Barbour et al. 1999).

In the first study (Chapter 2), I intensively sampled a single lowland river system (Umatilla River) through space and time to characterize community level responses of macroinvertebrates to water withdrawals of increasing magnitude and duration (resistance). Specifically, I tested whether changes in community composition were proportional to the amount of water withdrawn or if a threshold is reached after which significant responses are observed. For each response pattern the development of management strategies designed to maximize economic benefit and minimize the degradation of aquatic systems would differ dramatically. To further understand ‘why’ or ‘how’ low flow events impose a disturbance on stream biota, I also sought to identify what environmental variables were associated with macroinvertebrate responses. Finally, I assessed resiliency by examining whether macroinvertebrate communities recovered with the restoration of flow levels after one month and following winter high flows.

In Chapter 3, community level responses observed in Chapter 2 were pursued further by focusing on responses of an individual population. Specifically, I examined how irrigation water withdrawals affect the growth and development of the filter feeding caddisfly, *Brachycentrus occidentalis* Banks. I hypothesized that hydrologic changes would have little impact on development and growth, whereas the interactive effects of increased temperature and reduced velocities would lead to faster developmental rates and smaller sized individuals. The population costs of smaller sized individuals would be density reductions due to decreased recruitment and competitive ability.

Finally, in Chapter 4 I increased the spatial scope of the study to determine the ubiquity of macroinvertebrate community responses across central and eastern Oregon and Washington. Specifically, I examined whether the resistance observed on the Umatilla River, a lowland system, was consistent for mid and high elevation systems experiencing water withdrawals of similar magnitude and duration. I predicted responses would be greater for macroinvertebrates found at high elevations compared to those at low elevations because of differences in species traits that influence resistance to disturbance. As species traits are advantageous for studies of disturbance, providing mechanistic interpretations of response patterns, I also explored how water withdrawals select for or against specific species traits. These differences could imply consequences for ecosystem processes and provide comparisons at both local and regional spatial scales (Heino 2005, Poff et al. 2006).

CHAPTER 2:

**RESISTANCE AND RESILIENCE OF MACROINVERTEBRATES
TO IRRIGATION WATER WITHDRAWALS**

Scott W. Miller, David Wooster, and Judith L. Li

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Abstract

Water withdrawal for irrigated agriculture is one of the leading uses of freshwater resources in the world; however, effects of low flow disturbances on lotic ecosystems are poorly understood. We studied an intensively managed agricultural catchment to determine: (i) how macroinvertebrate assemblages and environmental variables respond to water withdrawals of varying magnitude and duration; (ii) what environmental variables are associated with macroinvertebrate responses and (iii) the resiliency of macroinvertebrate communities to irrigation water withdrawals. Three reaches were sampled above and below four irrigation diversions that create a gradient of increasing water withdrawal from upstream to downstream (i.e., 0, 22, 87, 90, 97% water withdrawn) along a 36 km river section. Monthly samples were collected from June to September of 2004 and 2005, which represented average and drought water conditions, respectively. Irrigation water withdrawals were associated with both direct and indirect changes to the physicochemical environment. Direct effects (e.g., decreased velocity, depth and wetted habitat) were approximately proportional to the amount of water withdrawn, while indirect effects (e.g., increased conductivity and temperature) occurred when water withdrawals exceeded 85% of ambient levels. Changes in macroinvertebrate communities were more strongly related to indirect than direct effects of irrigation water withdrawals. In an average water year, community changes were associated with interacting thresholds of reduced discharge and increased conductivity. During a drought year, community changes were related to the interacting thresholds of reduced discharge and increased temperature. Between years, macroinvertebrate responses differed with the magnitude and duration of low flow conditions. In 2004, high-intensity, relatively short-duration water withdrawals (< 2 months) and alterations to the physicochemical environment changed the relative abundance of macroinvertebrate communities, while macroinvertebrate indices and proportional abundances of functional feeding groups remained unchanged. In contrast, discharge reductions exceeding 90% of ambient levels and temperatures above 30°C from July – September of 2005 were associated with shifts in community composition from a dominance of collector-gatherer and filterer EPT taxa to predatory insects, non-insect taxa, and scraping elmids beetles. On an annual basis

macroinvertebrate communities appeared resilient to the impacts of water withdrawals following winter high flows. In contrast, recovery was not observed after discharge and physicochemical variables returned to predisturbance conditions for only one month. Irrigation water withdrawals appear to impact macroinvertebrates through indirect effects that intensify with the magnitude and duration of water withdrawals and annual water availability. Preserving environmental conditions within natural ranges of variability, especially during low water years, appears critical to mitigating adverse biological responses to water withdrawals.

Introduction

Human alterations to the flow regime of river systems are one of the leading detriments to freshwater biodiversity (Dynesius and Nilsson 1994, Richter et al. 2003). The use of freshwater resources for human consumption, agricultural production and power generation has altered patterns of water quality, quantity, and ecosystem connectivity. Specifically, irrigated agriculture constitutes the largest use of freshwater resources in the world (Oki and Kanae 2006). In the year 2000 alone, an estimated 303 MI day⁻¹ of freshwater were withdrawn from surface waters within the United States for agricultural uses, which accounted for 40% of freshwater consumption (Huston et al. 2004). While research examining the effects of large dams has led to modification of continuum-based theories and development of the serial discontinuity concept (Ward and Stanford 1983), the impacts of irrigation water withdrawals are poorly understood.

Seasonal low flows and desiccation can be normal events for streams in arid and semi-arid regions. However, irrigation water withdrawals can exacerbate the magnitude, duration, and spatial extent of low flow conditions (Wilber et al. 1996, Eheart and Tornil 1999). Though periods of extreme low flow in intermittent systems can reduce taxa richness and density through altered habitat quality, quantity, and fragmentation (e.g., Boulton and Lake 1990), our ecological understanding of low flow disturbances in

perennial systems, both natural and human induced, is quite rudimentary (Resh et al. 1988, Lake 2000).

The few studies investigating the effects of irrigation water withdrawals on macroinvertebrate communities in perennial streams have produced inconsistent results. While some studies found strong impacts on community structure (Dudgeon 1992, Rader and Belish 1999, McIntosh et al. 2002), others found little to no impact (Castella et al. 1995, Dewson et al. 2003, McKay and King 2006, Dewson et al. 2007). Inconsistencies among studies might result from differences in the magnitude, duration and timing of irrigation water withdrawals. Poff and Allan (1997) suggest that these factors and the predictability of historic hydrologic variability influence the adaptive strategies of stream biota, constraining their response and recovery to disturbance events.

Although not directly tested, Corrarino and Brusven (1983), Rader and Belish (1999), and Dewson et al. (2003) provide evidence for threshold responses of macroinvertebrate communities to water withdrawals differing in magnitude (i.e., low to moderate withdrawals have little impact, while high intensity withdrawals result in large impacts). Threshold phenomena offer a potential explanation for inconsistent responses among studies; Rader and Belish (1999) and Dewson et al. (2007) also suggest that the duration of low flow events might influence the magnitude of macroinvertebrate responses. Rader and Belish (1999) found no significant differences in macroinvertebrate density or community composition during periods of high-intensity, short-duration water withdrawal, but high-intensity, long-duration water withdrawals significantly reduced densities and altered community composition.

Our inability to predict how irrigation water withdrawals of varying magnitude and duration affect freshwater biota compromises our ability to balance economic and ecological needs for freshwater resources. With half of the world's population located in water stressed areas and global warming altering the availability of freshwater resources, there is a growing need to understand such disturbance, response, and recovery patterns

(Oki and Kanae 2006). Therefore, we used an intensively managed agricultural catchment as a natural experiment to characterize the resistance and resilience of macroinvertebrate communities to irrigation water withdrawals. Specifically, we asked: (i) how do macroinvertebrate assemblages and environmental variables, of a fifth order river, respond to water withdrawals of increasing magnitude and duration; (ii) what environmental variables are associated with macroinvertebrate responses and (iii) what is the resiliency of macroinvertebrate communities to surface water withdrawals?

Methods

Study area

The study was conducted on a 36 km lowland section of the 143 km Umatilla River located in Northeastern Oregon, U.S.A. (Fig. 2.1). The climate of the study area is cold continental, characterised by hot dry summers (average maximum temperature 31.3°C) and cold winters (average maximum temperature 7.5°C). Average annual precipitation for the lower Umatilla River at Hermiston, OR is 226 mm. The Umatilla River is a fifth order tributary of the Columbia River that drains a catchment of 5,930 km². The hydrograph is typical of a snow-pack hydrologic regime, with maximum flows (~150 m³s⁻¹) occurring from March through May and base flows (~6 m³s⁻¹) dominating from June through October. Irrigated agriculture is the dominant land use adjacent to the study area, yet the stream is buffered by a corridor of *Populus*, *Alnus*, and *Salix*. Upriver of the study section, the mainstem is free flowing with no major dams or impoundments.

Within the 36 km study section there are four irrigation dams from river kilometre 56 to 20 (Fig. 2.1) that create a gradient of decreasing instream flow with distance downstream (i.e., a longitudinal gradient) (Fig. 2.2). The disparity in discharge between upstream and downstream river segments increases from June to September, as spring runoff recedes and agricultural demands increase. Diversions are operated from approximately March to October, with maximum withdrawals occurring from June to September. Diversion structures are concrete and timber dams that span the entire bankfull width; they are ~1.8

m high and have withdrawal capacities ranging from 4 to $6.3 \text{ m}^3\text{s}^{-1}$. All points of diversion have been operating since the early 1900s.

Study design

The 36 km river section was separated into five river segments for our study (Fig. 2.1). We located one control segment above all points of diversion and one treatment segment below each of the four points of diversion. From upstream to downstream, river segments are referred to as control, 1, 2, 3, and 4. River segment lengths were equal to the distance between two diversion structures (Table 2.1), except for the control and segment four, which lacked upstream and downstream diversions respectively. The length of these segments was approximately equal to the minimum distance between any two points of diversion (4.5 km). We located three sample reaches within each segment for a total of 15 reaches in 2004 and 12 in 2005. The three reaches in segment one were not sampled in 2005 because low water levels impeded operation of the diversion. Sample reaches were equal to 10 x bankfull width (Table 2.1) and were located immediately downstream (A), midway between each point of diversion (B), and immediately prior to the next diversion (C) (Fig. 2.1). Reaches were sampled once per month in June, July, August, and September of 2004 and 2005.

River segments differed in flow volume but were otherwise similar in physical structure, riparian vegetation, geology, soils, and adjacent land use, with the exception of segment four, which had an average bankfull width half as wide as other river segments and a median particle size (D_{50}) greater by 23 mm on average (Table 2.1). Despite higher median particle sizes at the segment scale, increases were limited to reaches B and C within segment four (D_{50} by reach for segment four: A = 49 mm; B = 72 mm; C = 74 mm).

Sampling: Biological variables

Within each reach, a Surber sampler (0.09 m^2 , 500 μm mesh) was used to collect six randomly located benthic macroinvertebrate samples from arbitrarily located riffle

habitats to a depth of 10 cm. We constrained sampling to riffle habitats because they are thought to be most affected by low flow events (Stanley and Fisher 1997). The six Surber samples from each reach were composited, preserved in 70% ethanol and processed using a 500 count subsampling procedure (Caton 1991, Vinson and Hawkins, 1996). When possible, we identified macroinvertebrates to genus (Merritt and Cummins 1996). Chironomidae midges, however, were identified to tribe, and all non-insect taxa were identified to either order or family (Thorp and Covich 1991). All identified insects were assigned functional feeding groups (FFGs) according to Merritt and Cummins (1996), while Thorp and Covich (1991) was used for non-insect taxa. Total abundance, taxonomic richness, Ephemeroptera, Plecoptera and Trichoptera (EPT) taxonomic richness, Shannon's diversity index (Magurran 1988) and the proportional abundance of non-insect taxa were computed for each sample and are referred to as macroinvertebrate indices.

We collected periphyton samples by randomly selecting six rocks from riffle habitats adjacent to Surber locations. Periphyton was removed from a 6.5 cm² portion of each rock, placed into a light-sealed bottle and stored frozen. Defrosted samples were split with a plankton splitter for determination of ash-free dry mass (AFDM) and biomass of chlorophyll-*a*. AFDM was determined according to the methods of Steinman and Lamberti (1996). To measure chlorophyll-*a* biomass we used the hot ethanol extraction method (Sartory and Grobbelaar 1984) followed by spectrophotometry of the filtrate. Subsequent chlorophyll-*a* concentrations were determined using the equation of Steinman and Lamberti (1996).

Sampling: Environmental variables

We measured discharge at the top and bottom of each reach using a Marsh McBirney digital flow meter during each sampling event. Depth and velocity (0.6 water depth) were measured at a minimum of 20 points across the stream or at intervals that ensured one cell (depth x width) did not contain greater than 5% of total discharge. From the instantaneous discharge estimates, we computed instantaneous discharge on the day of

sampling (Q_{instant}), the difference in discharge between successive sampling events (Q_{diff}), and a summation of the Q_{instant} up to and including the date of sampling (Q_{duration}). In addition, we used continuous discharge estimates from available United States Geological Service (USGS) or Bureau of Reclamation (BOR) gauging stations to verify that instantaneous measurements accurately represented monthly discharge levels. For all river segments, we found no significant differences between median monthly flows and instantaneous discharge measurements.

During each sampling event, we also measured stream velocity (0.6 water depth) and depth at all Surber sampler locations. Wetted width, bankfull width, reach slope and percent solar radiation were measured at the top, middle and bottom of each sample reach. Percent solar radiation ($\text{kWh m}^{-2} \text{day}^{-1}$) was calculated for the interval between sampling events and was measured using a Solar PathfinderTM (Solar Pathways, Colorado Springs, Colorado) positioned in the centre of the river channel. The Solar Pathfinder quantifies site specific shading (e.g., riparian vegetation or topographic features) and combines this with solar radiation data compiled by the National Renewable Energy Lab (<http://rredc.nrel.gov/solar/>) to estimate insolation values on an hourly to annual basis. Median particle size of the substrate (D_{50}) was also quantified for the sample reach using the Wolman (1954) pebble count method. The ratio of wetted to bankfull width was used to quantify the contraction of available wetted habitat (i.e., % habitat loss) for each reach and date of sampling.

Temperature was monitored at 30 min intervals within each reach from June to September using thermal data loggers. From the continuous temperature data we computed average temperature for the interval between sampling events ($\text{temperature}_{\text{average}}$), degree days (sum of average daily temperature above 0°C) ($\text{temperature}_{\text{degree-days}}$), and the seven day average of the maximum daily temperature ($\text{temperature}_{7\text{-day}}$). A single in-situ measurement of specific conductance at 25°C and turbidity were also obtained during each sampling event.

Analyses: Environmental and macroinvertebrate response gradients

We used Kendall's tau correlation coefficients to assess longitudinal relationships (i.e., upstream to downstream) of environmental variables and macroinvertebrate indices with stream kilometer for each individual month sampled in 2004 and 2005. Stream kilometer was chosen instead of discharge because we were interested in all longitudinal gradients, not just those related to water withdrawals. We did not adjust alpha levels using Bonferroni corrections because they are overly conservative, increasing the chance of dismissing ecologically meaningful results (Moran 2003). We recognize that the probability of interpreting spurious results increases with the number of test performed; however, the 33 of 60 significant results for environmental variables, and nine of 40 for macroinvertebrate indices, have very low probabilities of occurrence (2.5×10^{-27} and 1.0×10^{-4} , respectively).

Community level changes in macroinvertebrates were examined independently for 2004 and 2005 with non-metric multidimensional scaling (NMS). Specifically, we tested whether gradients in community structure related to the longitudinal water withdrawal gradient were stronger than expected by chance alone. NMS was run with Sørensen's distance in PC-ORD version 5 (McCune and Mefford 2005) using log transformed ($\log_{10}(x+1)$) macroinvertebrate densities. We assessed dimensionality by evaluating the relationship of final stress versus the number of dimensions; in addition, a Monte Carlo test with 250 runs of the randomized data quantified the probability of obtaining the observed stress by chance alone. We used Kendall's tau correlation coefficients to quantify relationships between macroinvertebrate abundances and ordination axes scores (McCune and Mefford 2005). A value of 0.30 was chosen as a cutoff for interpreting ecologically meaningful correlations, which was more conservative than the Kendall's coefficient corresponding to statistical significance (0.25).

Analyses: Linking macroinvertebrate and environmental response gradients

Relationships of environmental variables with ordination axis scores were assessed with Kendall's tau correlation coefficients. Using HyperNiche version 1.0 (McCune and

Mefford 2004), we also modelled macroinvertebrate responses to irrigation water withdrawals with non-parametric multiplicative regression (NPMR) (McCune 2006). We adopted a non-parametric habitat model because environmental and biological variables exhibited both linear and complex non-linear relationships with stream kilometer. Furthermore, we anticipated multifactor responses of macroinvertebrate communities to water withdrawals because of interactions between discharge and the physicochemical variables.

NPMR differs from traditional modelling tools by avoiding a global model where coefficients are sought in a fixed mathematical equation (McCune 2006). Rather, NPMR relies on the data to specify model form by using a local multiplicative smoothing function with a leave-one-out cross-validation. We used a local mean estimator and Gaussian weighting function in a forward step-wise regression, where data points closer to the target point receive greater weight. In model generation, a minimum average neighbourhood size of three was specified to set the minimum amount of information (i.e., data points) bearing on the weighted estimate. Fit was assessed with a cross-validated R^2 (xR^2), which is more conservative than traditional R^2 because each data point is excluded from calculating the residual sums of squares for the response at that point.

We used a sensitivity analysis to assess the relative influence of individual explanatory variables within a selected model (McCune 2006). Sensitivities are generated by nudging values of individual predictor variables up and down to measure resulting change in the response variable at that point. The accumulation of sensitivity values across all data points are averaged and expressed as a proportion of the range of the response variable. A value of 1.0 indicates equal change in the response per unit change in the predictor; whereas a value of 0 indicates that nudging a predictor has no effect on the response.

NPMR models were developed individually for NMS axis two scores from the 2004 and 2005 ordinations and macroinvertebrate indices that demonstrated significant longitudinal gradients with stream kilometer. Except for stream kilometer, the 11 environmental

variables in Table 2.3, in addition to Q_{diff} and $Q_{duration}$ were included as potential explanatory variables in all NPMR models. NPMR models were developed separately for 2004 and 2005, with data from all months combined within a year. To ensure variance explained by NPMR models was related to longitudinal (i.e., upstream to downstream) and not temporal (i.e., June to September) gradients, we examined bivariate relationships between all explanatory and response variables, with data points grouped by month. In addition, month was included as a categorical variable within the pool of potential explanatory variables.

Analyses: Macroinvertebrate resilience to water withdrawals

We assessed resilience of macroinvertebrate communities to irrigation water withdrawals at two temporal scales. First, recovery was assessed after a one month increase in $Q_{instant}$ (i.e., September 2004) following two months of high-intensity water withdrawals during July and August of 2004 (Fig. 2.2). As water withdrawal is a seasonal occurrence on the Umatilla River separated by unaltered winter high flows, for our second approach we assessed whether macroinvertebrate communities were reset on an annual basis in June of 2005. We calculated average Sørensen's dissimilarity among all reaches for each individual month sampled in 2004 and 2005 using log transformed ($\log_{10}(x+1)$) macroinvertebrate densities. We hypothesised that macroinvertebrate community composition would be most similar in June, the start of the irrigation season and that dissimilarity would increase over the irrigation season. Recovery was assessed at one month and annual time scales by evaluating whether differences among reaches (i.e., Sørensen's dissimilarity values) approached June 2004 levels in September of 2004 and June of 2005, respectively. Because Sørensen's dissimilarity values could be comparable, while actual community composition could be quite different, we tested for differences in community composition between June of 2004 and 2005 using a multiple response permutation procedure (MRPP) (Mielke and Berry 2001) and indicator species analysis (ISA) (Dufrene and Legendre 1997).

Results

Longitudinal gradients: Discharge

The magnitude of downstream discharge reductions varied among months within a year and the duration differed between years (Fig. 2.2). In 2004, the water withdrawal gradient was greatest in July, whereas reduced water withdrawals, summer rains and releases from an upstream tributary reservoir allowed for partial recovery from August to September. In contrast, 2005 was an ‘extreme’ drought year as measured by the Palmer Hydrologic Drought Index; for 58 years of record (USGS gauge #14026000) average 2005 discharge levels had a 2% ($9.7 \text{ m}^3\text{s}^{-1}$) probability of occurrence, as compared to 75% ($22.6 \text{ m}^3\text{s}^{-1}$) in 2004. Drought conditions increased the magnitude, duration, and spatial extent of low flows, with discharge reduced below $0.3 \text{ m}^3\text{s}^{-1}$ in each river segment from July – September.

Longitudinal gradients: Environmental variables

Environmental variables exhibited gradual changes in turbidity, velocity and depth, and threshold changes in temperature, conductivity and percent habitat loss with distance downstream (Fig. 2.3). During both years, the significance and direction of downstream changes depended on month, whereas the duration of downstream changes differed between years (Fig. 2.3). In 2004, downstream changes were greatest in July and August for most environmental variables, with patterns weakening or even reversing in September (temperature, velocity, depth). In contrast, downstream gradients in 2005 were generally of greater magnitude and duration, persisting for all of July, August, and September (e.g., temperature, conductivity, velocity). For both years, correlations of percent habitat loss with distance downstream were low because the greatest losses occurred in segment two, which resulted in a hump-shaped pattern. We found no consistent downstream patterns for chlorophyll-*a* concentration and periphyton biomass.

Longitudinal gradients: Macroinvertebrate indices

In 2004, we found no consistently significant longitudinal gradients for all macroinvertebrate indices and a high degree of within segment variability (Fig. 2.4). In

contrast, density and the proportion of non-insect taxa significantly increased with distance downstream in 2005, while EPT richness significantly decreased (Fig. 2.4). As in 2004, richness and diversity showed no significant gradients. Except for density, the significance of downstream patterns was generally minimized in June and increased in strength from July through September. Non-insect gradients were largely driven by increased Turbellaria, Oligochaeta, and Nematoda. In contrast, taxa losses from the orders Plecoptera (e.g., *Skwala* and *Classenia*) and Ephemeroptera (e.g., *Epeorus*, *Choroterpes* and *Dipheter*) contributed to the decline of EPT taxa in segment four; Trichoptera remained relatively unchanged.

Longitudinal gradients: Macroinvertebrate communities

Separate 2004 and 2005 NMS ordinations revealed two significant gradients that represented 88 and 89% of the variation in macroinvertebrate communities, respectively. The stress of both ordinations was below 12, corresponding to a satisfactory solution with little risk of false inference (McCune and Grace 2002). Ordination solutions were rotated to maximize macroinvertebrate community gradients along axis one, which represented a strong temporal gradient from June to September (Fig. 2.5a, c) and accounted for 70% of macroinvertebrate community variability in 2004 and 73% in 2005. Correlations of macroinvertebrate indices with axis one revealed increased proportions of scraper taxa (e.g., *Petrophila*, *Optioservus*, *Helicopsyche*) from June to September (2004, tau: 0.38; 2005, tau: 0.45), whereas the proportion of collector-gatherers (e.g., *Attenella*, *Baetis*) decreased (2004 tau: -0.49; 2005 tau: -0.51) (Table 2.2). Macroinvertebrate densities increased from June to September of both years (2004, tau: 0.36; 2005, tau: 0.43), with increases largely driven by *Fallceon*, *Tricorythodes*, *Cheumatopsyche*, *Oecetis* and *Helicopsyche* (Table 2.2).

Sample reaches separated out by river segment along axis two (Fig. 2.5b, d), which represented 18% of macroinvertebrate community variation in 2004 and 16% in 2005. However, sample reaches did not separate sequentially from upstream to downstream or from low to high levels of water withdrawal. Instead, control and segment one reaches

were located in the middle, segment two and three reaches at the top, and segment four reaches at the bottom of axis two for 2004 and 2005. Dissimilarities among sites within a month were lowest in June and peaked in September of 2004 and 2005 (Fig. 2.6).

Dissimilarities between river segments were largely driven by EPT taxa richness in 2004 (tau: 0.34) and 2005 (tau: 0.36), densities of EPT taxa in both years, and the proportion of non-insect taxa in 2005 (tau: -0.31).

While most taxa were correlated with either axis one or two, several insect taxa in 2004 and several insect and non-insect taxa in 2005 were correlated with both ordination axes (Table 2.2). Correlations with both axes indicates that densities of these taxa changed as a function of both season and water withdrawal intensity.

Linking macroinvertebrate and environmental gradients: Correlations with NMS axes
Conductivity, temperature_{7-day}, and chlorophyll-*a* increased from June to September (axis 1) of both years, while Q_{instant} and associated hydrological variables decreased (Table 2.3). Stream kilometer in 2005 was the only strong, positive correlation along axis two for either year. Negative correlations with axis two included increased conductivity, percent habitat loss, and median particle size in segment four for both years (Table 2.3). Some correlations (e.g., Q_{instant} and temperature_{7-day}) appeared low because their associations with axis two were unimodal rather than linear.

Linking macroinvertebrate and environmental gradients: NPMR regression models
Variation in the 2004 ordination axis two scores was best explained by the interaction of conductivity and Q_{instant} ($xR^2 = 74\%$) (Table 2.4). Q_{instant} levels below $1.0 \text{ m}^3\text{s}^{-1}$ and conductivity levels less than $50 \mu\text{S cm}^{-1}$ resulted in positive axis two scores (segments two and three), whereas axis scores abruptly shifted to negative values (segments three and four reaches) when conductivity exceeded $175 \mu\text{S cm}^{-1}$ at similar discharge levels. In the 2004 model, axis two scores were more sensitive to changes in conductivity than Q_{instant} (Table 2.4).

In 2005, the drought year, the interaction of temperature_{7-day} and Q_{instant} best explained variability in axis two scores ($xR^2 = 56\%$) (Table 2.4). Q_{instant} levels below 0.3 m³s⁻¹ and temperature_{7-day} between 24 and 28°C resulted in positive scores (segments two and three), but when temperature_{7-day} exceeded 30°C at similar discharge levels abrupt changes (i.e., threshold responses) to negative axis scores were observed (segment four reaches at the bottom of the ordination). Axis two scores were more responsive to changes in temperature_{7-day} than Q_{instant}.

Longitudinal gradients in EPT richness, proportion of non-insect taxa, and macroinvertebrate densities in 2005 were best explained by temperature_{7-day} (Table 2.4). Increased temperature_{7-day} was related to lower EPT richness, greater proportions of non-insect taxa, and increased macroinvertebrate density. EPT richness declined and the proportion of non-insect taxa exponentially increased at a temperature_{7-day} of approximately 30°C. However, a two variable model provided the optimum balance between variance explained and parsimony for the proportion of non-insect taxa and EPT richness; temperature_{7-day} had a greater impact than secondary variables of month and turbidity, respectively (Table 2.4). Models were not developed for macroinvertebrate indices in 2004 because they did not show consistently significant patterns with stream kilometre (Fig. 2.4).

Macroinvertebrate resiliency to water withdrawals

In September of 2004, water withdrawal activities declined and Q_{instant} levels increased within all segments (Fig. 2.2); however, differences in macroinvertebrate community composition among sample reaches were not reduced (Fig. 2.6). In contrast, we found evidence for recovery between years, as dissimilarity values for June, 2005 returned to June, 2004 levels after peaking in September of 2004 (Fig. 2.6). Despite this trend, significant differences in community composition existed between June of 2004 and 2005 for both control and treatment segments (MRPP blocked by river segment: Chance-corrected within-group agreement (A) = 0.17; $p < 0.001$; N = 24). For example, *Skwala* and *Brachycentrus* were significantly more abundant at control reaches in 2004, whereas

Petrophila, *Glossosoma*, *Acentrella* and *Fallceon* were significantly more abundant in 2005.

Discussion

Macroinvertebrate and environmental responses to irrigation water withdrawals

Macroinvertebrate communities of the Umatilla River were highly resistant to irrigation water withdrawals. We observed threshold responses to the interactive effects of reduced discharge and indirect environmental changes. Indirect environmental changes included increased water temperature and conductivity, as compared to the direct effects of reduced velocity, depth, and amount of wetted habitat area. Environmental and macroinvertebrate responses varied with month and year according to annual water availability and the magnitude and duration of water withdrawals. Physiochemical responses paralleled changes predicted to occur during droughts by Lake (2003).

Macroinvertebrate communities were not adversely affected by reduced discharge levels, in the absence of indirect environmental changes. For example, reducing Q_{instant} from $4.5 \text{ m}^3 \text{ s}^{-1}$ (control) to below $0.3 \text{ m}^3 \text{ s}^{-1}$ (segment two) for three months in 2005 had no impact on EPT taxonomic richness or densities of EPT taxa. In addition, velocity, depth, and percent habitat loss did not significantly explain variability in macroinvertebrate community composition or macroinvertebrate indices. These results contrast with findings by Rader and Belish (1999) and Dewson et al. (2003) who observed decreased EPT taxa when discharge was reduced below $0.1 \text{ m}^3 \text{ s}^{-1}$. However, it is unclear whether macroinvertebrates responded to the direct or indirect effects of water withdrawals in their studies, as increased conductivity and temperature levels were reported, but not correlated with observed responses.

There are at least two potential explanations for the observed resistance of macroinvertebrate communities to the direct effects of water withdrawals. First, reduced velocity and wetted habitat are natural, seasonal phenomena for lowland systems in semi-arid regions that act as filters for the determination of successful life history strategies.

Because the hydrologic history of the Umatilla River included periods of extreme low flow and intermittency, we would expect some degree of macroinvertebrate resistance to low flow events. The broad ecological tolerances of several ubiquitous, community dominants (e.g., *Hydropsyche*, *Baetis*, *Tricorythodes*) reflect adaptations to variable environments. In addition, water withdrawals on the Umatilla River did not change the timing or predictability of low flow events, but rather their magnitude and duration. Preserving historic patterns of temporal variability are critical to mitigating negative biological responses, as they are thought to define the biota's resistance to disturbance (sensu Poff and Ward 1990, Wallace 1990).

Secondly, the resistance of macroinvertebrate communities to hydrologic alterations in segment two might result from increased microhabitat diversity. The spatial heterogeneity of the stream benthos was significantly greater in segment two compared to all other segments (ANOVA of coefficients of variation for D_{50} among river segment: $F = 9.02$; $P = 0.002$). Increased microhabitat diversity can result in greater biotic diversity (Poff and Ward 1990, Minshall 1984) and also provide refugia during low flow events (Boulton 2003). However, we are uncertain whether increased microhabitat diversity or spatial refugia might be operating to maintain macroinvertebrate diversity.

On the Umatilla River, the resistance of macroinvertebrates was compromised by the indirect effects of water withdrawals (i.e., increased conductivities and temperatures), which appeared to render habitat physiologically unfit. Increased conductivity levels are prevalent in arid and semi-arid regions managed for irrigated agriculture (Williams 1987, Silvia and Davies 1997). Of particular interest to our study, Rader and Belish (1999) and Dewson et al. (2003) detected increased conductivity levels below points of water withdrawal, with greatest increases occurring when discharge was reduced by over 90%. Macroinvertebrates have demonstrated both threshold and proportional responses to increased conductivity levels (Kefford 1998, Yuan and Norton 2003). Despite these observations, we do not believe conductivity is the primary factor related to observed changes on the Umatilla River, but rather a surrogate for other pollutants that might exist

in return flows. We observed taxa commonly found at conductivity levels above $500 \mu\text{S cm}^{-1}$ in arid and semi-arid regions (Miller et al. 2004) and conductivity in our study only increased from ~ 100 to $450 \mu\text{S cm}^{-1}$. Rather, increased conductivity levels suggest water removed for irrigation is being returned to the river through return flows that might also add nutrients (e.g., ammonia, nitrate, phosphate), pesticides or other chemical pollutants, which we did not measure, but have been found at elevated levels throughout the catchment. The well-documented impact of these pollutants on macroinvertebrate communities would likely be exacerbated under conditions of extremely reduced flow (Chessman and Robinson 1987, Caruso 2002).

In 2005, changes in macroinvertebrate community composition corroborated the association between temperature and variation in EPT richness, density, non-insect taxa, and ordination axis two scores. Macroinvertebrate communities abruptly shifted to a dominance of *Helicopsyche*, Turbellaria, and the elmids *Dubiraphia* and *Microcylloepus* in segment four, which are all indicative of warm, slow moving water, in addition to being drought tolerant (Ward 1986, Dudgeon 1992). Alterations to the thermal regime are common where flow levels are substantially reduced (Caruso 2002, Meier et al. 2003) and the influence of temperature regimes on macroinvertebrate distribution, behavior, development, and growth patterns are well established (Vannote and Sweeney 1980, Ward and Stanford 1982). Unfortunately, we were unable to separate temperature impacts from the synergistic effects of reduced flows and increased temperatures on macroinvertebrate community composition. We recognize, however, that these factors can be decoupled, and may result in different responses. For example, Gallepp (1977) found *Brachycentrus occidentalis* (Banks) capable of tolerating temperatures up to 27°C without significant behavioural changes, but the combination of increased temperature and reduced velocities significantly reduced filter feeding activity and subsequent fitness.

Macroinvertebrate responses between years

Despite similar ordination solutions between years, the magnitude and nature of macroinvertebrate gradients differed. The paucity of significant longitudinal gradients

for macroinvertebrate indices in 2004 suggests that downstream gradients were driven by changes in relative abundance and equal rates of species loss and replacement. When present, longitudinal changes in relative abundance occurred among functional equivalents within the same taxonomic family, resulting in no net change in how organic matter resources were processed across the disturbance gradient. For example, *Hydropsyche* dominated upstream sites, while *Cheumatopsyche* dominated downstream sites; both are filter-feeding Hydropsychidae. We observed similar replacements from upstream to downstream for the Baetidae collector-gathers, *Dipheter* and *Falceon*, respectively. The longitudinal separation of closely related species is common in rivers and thought to represent niche segregation across longitudinal thermal gradients (Ward 1992). On the Umatilla River, changes in relative abundance occurred over short spatial scales (< 4 km), despite only minor altitudinal changes, no changes in riparian vegetation and no tributary additions. Water withdrawals appear to be causing accelerated longitudinal rates of biological change, though impacts to ecosystem processes appeared minimal during an average water year.

In contrast, species loss and replacement from upstream to downstream was not equal or comparable in 2005. Starting in July and culminating in September, EPT taxa abruptly declined in segment four and were replaced by opportunistic insect and non-insect taxa. These changes in community composition were not among functional equivalents, as the proportion of collector-gatherers decreased (e.g., *Baetis*, *Dipheter*, *Acentrella*) and the proportion of scrapers (e.g., *Helicopsyche*, *Microcyloepus*, *Optioservus*) and predators (e.g., Turbellaria, Veliidae) increased from upstream to downstream.

In addition to compositional changes, macroinvertebrate densities also increased in segments three and four in 2005. Past studies attributed increased densities to crowding in areas of reduced habitat (Castella et al. 1995, Englund and Malmqvist 1996) or elevated temperatures that might facilitate increased food resources and fecundity (Rader and Belish 1999). Habitat loss was not associated with variation in macroinvertebrate densities in 2005; however, higher temperatures were associated with increased densities

and changes in community structure. Increased temperatures appeared to have adverse effects on EPT taxa of segment four, where community composition shifted to a dominance of opportunistic insect and non-insect taxa, capable of rapid population increases.

Different longitudinal response patterns between years likely reflect annual variation in water availability. Drought conditions in 2005 increased the magnitude, duration, and spatial extent of low flow conditions, which exacerbated the indirect impacts of water withdrawals. For example, elevated temperatures in 2004 were restricted to one month, which created a short-term stress (i.e., a pulse disturbance) to macroinvertebrate communities. In contrast, drought conditions and prolonged periods of high-intensity water withdrawals in 2005 caused the magnitude and duration of elevated temperatures to be much greater (i.e., a press disturbance). The high-intensity, long-duration disturbance event of 2005 constrained the number and type of colonists from the regional species pool by exceeding the physiological tolerances of many taxa.

The effects of drought on macroinvertebrate communities were also apparent in our study independent of water withdrawal impacts. For example, several taxa which differentiated control segments between 2004 and 2005 were the same taxa correlated with segment four sites in the 2004 ordination (e.g., *Petrophila*, *Glossosoma*, *Accentrella*). In other words, resistant taxa found only in the most impacted reaches in 2004 were found throughout the river in 2005. Thus, the impacts of water withdrawals on the Umatilla River appear to mimic the impacts of drought during average water years.

Resiliency of macroinvertebrate communities to water withdrawals

Macroinvertebrate communities of the Umatilla River appear resilient to the impacts of water withdrawals on an annual basis. As peak flows are not reduced, processes governing the physical structure are preserved and water withdrawals are limited to a temporary disturbance. Systems experiencing temporary disturbances and maintenance of physical structure are often characterized by rapid recovery (Rapport and Whitford

1999). Differences in community composition between June, 2004 and June, 2005 likely reflect biotic responses to natural ranges of environmental variability, which can confound assessments of recovery (Parker and Wiens 2005). In contrast to annual patterns, recovery of flow and subsequent environmental conditions on shorter time scales (i.e., one month in 2004) did not result in biological recovery. Rather, increased discharge levels appeared to only mitigate further divergence of upstream and downstream communities.

We hypothesize that winter high flows act to reset macroinvertebrate community composition along the longitudinal profile. Increased discharge rates homogenize previously distinct habitat patches (Fisher 1990) and increase drift rates, a primary recolonization mechanism of stream insects (Williams and Hynes 1976, Mackay 1992). On the Umatilla River, recolonization via drift seems especially plausible because the small spatial scale of the disturbance leaves an intact upstream recolonization source. Furthermore, during both high and moderate flow conditions, discharge flows over the top of all diversions and does not appear to disrupt the downstream transport of organisms, sediment, or organic matter. Resiliency could also result from the predictability and frequency of water withdrawals, which would promote temporal refugia (e.g., synchronisation of life stages). Most collected taxa were either uni- or multivoltine and are capable of completing all or critical components of their life cycle during the interval between disturbance events. In contrast, resiliency attributed to low flow refugia (e.g., substrate heterogeneity and hyporheic zone) seems inadequate to protect macroinvertebrates from increased temperatures and dissolved pollutants, despite its hypothesized role during recovery from droughts (Boulton 2003). For example, the hyporheic zone can be an important refugium during disturbances (Palmer et al. 1992); however, the stream substrate in segment four appeared heavily armoured below the superficial substrate layer.

Our study demonstrated that the magnitude and duration of discharge reductions potentially affects macroinvertebrate responses to irrigation water withdrawals.

However, hydrologic disturbance alone did not have direct, adverse impacts. Rather, the synergistic effects of multiple environmental variables substantially shifted the structure and function of macroinvertebrate communities. The likelihood of observing adverse indirect effects increased with the magnitude and duration of low flow events. Although experimental studies are needed to identify the exact mechanisms eliciting biotic responses to low flow disturbances, our results suggests a high degree of hydrologic plasticity among macroinvertebrates found in lowland, semi-arid systems. This highlights the importance of maintaining hydrologic, thermal, and water quality regimes within natural ranges of variability. However, macroinvertebrate life history strategies and ecological preferences vary within and among systems; in particular, varying qualities of resistance and resilience among macroinvertebrate communities might result in differential responses to low flow events (Poff and Allan 1995, Stanley and Fisher 1997). To better understand disturbance, response, and recovery patterns in catchments managed for irrigated agriculture, comparisons are needed among other lowland systems and across different physiographic regions.

Table 2.1. Average physical characteristics (\pm standard deviation) for the three sample reaches per river segment sampled on the Umatilla River, Oregon between June and September, 2004 - 2005.

Physical variable	River Segment				
	Control	1	2	3	4
Altitude (m a.s.l.)	216 (2.1)	202 (2.8)	189 (4.2)	168 (5.5)	157 (2.0)
Riffle slope (%)	0.8 (0.4)	1.0 (0.3)	1.1 (0.3)	0.7 (0.3)	0.8 (0.5)
Bankfull width (m)	61.0 (8.1)	64.9 (5.5)	80.2 (2.6)	60.7 (2.5)	31.6 (8.0)
Particle size - D_{50} (mm)	46.3 (6.8)	42.3 (7.5)	40.7 (2.3)	38.7 (8.3)	65.0 (12.9)
Solar input (%)	93.0 (3.5)	91.0 (1.0)	88.0 (9.8)	85.0 (15.3)	86.0 (3.5)
Segment length (km)	4.7	7.4	4.5	15.1	4.3
Reach length (m)	610 (81.3)	650 (55.4)	802 (26.5)	607 (71.0)	316 (17.2)

Table 2.2. Relationships of macroinvertebrate taxa with axes one and two of the 2004 and 2005 NMS ordinations. Macroinvertebrate taxa sorted by Kendall's tau with values of 0.30 or greater. Bolded taxa indicate axis correlations unique to a particular year, 2004 or 2005.

	Axis 1		Axis 2	
	2004	2005	2004	2005
<i>Cheumatopsyche</i> (0.64)	<i>Fallceon</i> (0.66)	<i>Skwala</i> (0.56)	<i>Epeorus</i> (0.53)	
<i>Fallceon</i> (0.57)	Tanypodinae (0.61)	<i>Epeorus</i> (0.38)	<i>Paraleptophlebia</i> (0.50)	
<i>Petrophila</i> (0.55)	<i>Optioservus</i> (0.54)	<i>Paraleptophlebia</i> (0.32)	<i>Dipheter</i> (0.50)	
<i>Optioservus</i> (0.49)	Turbellaria (0.54)	<i>Choroterpes</i> (0.31)	<i>Choroterpes</i> (0.47)	
<i>Oecetis</i> (0.44)	Acari (0.53)	<i>Dipheter</i> (0.30)	<i>Skwala</i> (0.47)	
<i>Argia</i> (0.43)	<i>Microcylloepus</i> (0.51)	Nectopsyche (-0.31)	Classenia (0.44)	
<i>Tricorythodes</i> (0.43)	<i>Petrophila</i> (0.50)	Oligochaeta (-0.31)	Ordobrevia (0.40)	
Hydropsyche (0.40)	<i>Argia</i> (0.49)	Petrophila (-0.42)	Tanytarsini (0.35)	
Physidae (0.38)	<i>Tricorythodes</i> (0.47)	<i>Glossosoma</i> (-0.43)	Physidae (0.33)	
<i>Microcylloepus</i> (0.37)	<i>Cheumatopsyche</i> (0.41)	Acentrella (-0.43)	Attenella (0.30)	
Nectopsyche (0.37)	<i>Oecetis</i> (0.39)	<i>Helicopsyche</i> (-0.52)	Nematoda (-0.31)	
Psephenus (0.35)	<i>Helicopsyche</i> (0.39)		Veliidae (-0.36)	
Paraleptophlebia (0.34)	Corbicula (0.34)		<i>Microcylloepus</i> (-0.30)	
<i>Helicopsyche</i> (0.31)	Physidae (0.33)		Turbellaria (-0.32)	
<i>Attenella</i> (-0.34)	Veliidae (0.33)		<i>Helicopsyche</i> (-0.37)	
Cnephia (-0.44)	Tanytarsini (0.32)		Dubiraphia (-0.40)	
<i>Ecdyonurus</i> (-0.53)	Dubiraphia (0.31)		<i>Glossosoma</i> (-0.57)	
	Chydoridae (0.31)			
	Copepoda (0.30)			
	Nematoda (0.30)			
	<i>Attenella</i> (-0.37)			
	Baetis (-0.39)			
	<i>Ecdyonurus</i> (-0.61)			

Table 2.3. Correlations of environmental variables with ordination axis scores for the 2004 and 2005 NMS ordinations. Variables with a Kendall's tau of 0.30 or greater are indicated by bold text.

Environmental Variable	Axis 1		Axis 2	
	2004	2005	2004	2005
River kilometre	-0.23	-0.25	0.07	0.38
Conductivity	0.25	0.33	-0.38	-0.34
Turbidity	0.10	-0.12	0.05	0.11
% Habitat loss	-0.14	-0.20	-0.30	-0.23
Velocity	-0.24	-0.59	-0.10	0.05
Depth	-0.18	-0.65	-0.16	0.01
Temperature _{7-day}	0.30	0.60	0.02	-0.08
Chlorophyll- <i>a</i>	0.35	0.28	-0.13	-0.04
Periphyton AFDM	-0.18	-0.28	-0.05	0.07
Q _{instant}	-0.26	-0.58	-0.10	0.09
Particle size - D ₅₀	0.05	0.09	-0.46	-0.31

Table 2.4. NPMR model results for estimating variation in axis two scores of the 2004 and 2005 NMS ordinations and macroinvertebrate indices having significant correlations with stream kilometer. Final selected models for each response variable are bolded.

Response	Predictors	Sensitivities	$\times R^2$
2004: Axis two scores	Conductivity	0.91	0.13
	Conductivity and Q_{instant}	0.68, 0.26	0.74
	Conductivity, Q_{instant} and D_{50}	0.32, 0.31, 0.09	0.75
2005: Axis two scores	Temperature _{7-day}	1.14	0.15
	Temperature_{7-day} and Q_{instant}	0.78, 0.17	0.56
	Temperature _{7-day} , Q_{instant} and D_{50}	0.46, 0.16, 0.06	0.60
2005: Proportion of non-insects	Temperature _{7-day}	0.42	0.48
	Temperature_{7-day} and Month	0.40, 0.26	0.71
	Temperature _{7-day} , Month, Turbidity	0.21, 0.23, 0.18	0.75
2005: log Density	Temperature_{7-day}	0.96	0.58
	Temperature _{7-day} and Chlorophyll- <i>a</i>	0.87, 0.16	0.63
	Temperature _{7-day} , Chlorophyll- <i>a</i> and Turbidity	0.49, 0.13, 0.16	0.66
2005: EPT richness	Temperature _{7-day}	1.53	0.44
	Temperature_{7-day} and Turbidity	0.75, 0.23	0.52
	Temperature _{7-day} , Turbidity and % Habitat loss	0.27, 0.25, 0.11	0.57

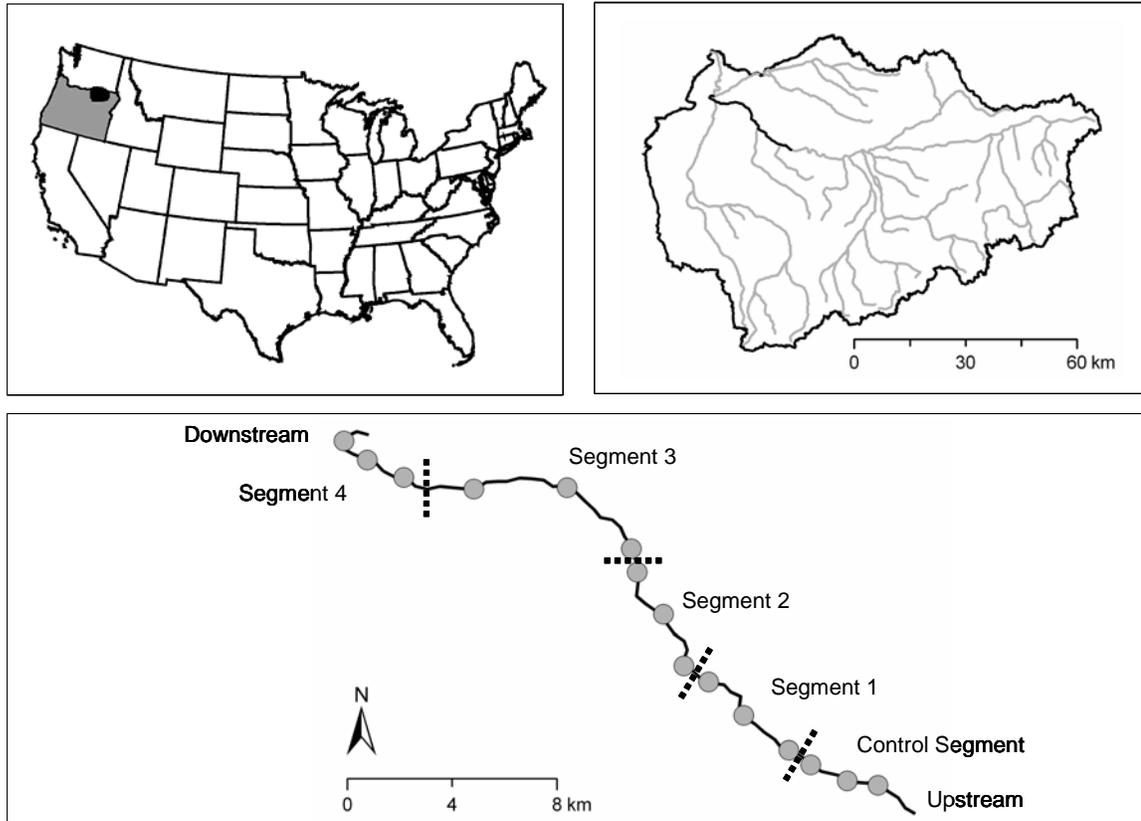


Figure 2.1. Location of study river and sample reaches. Upper left: location of Umatilla catchment in northeastern Oregon, U.S.A. Upper right: location of the 36 km study section, shown as bold line, within the Umatilla catchment. Lower panel shows the 36 km study section, with locations of river segments, sample reaches (grey dots), and points of diversion (dashed black lines).

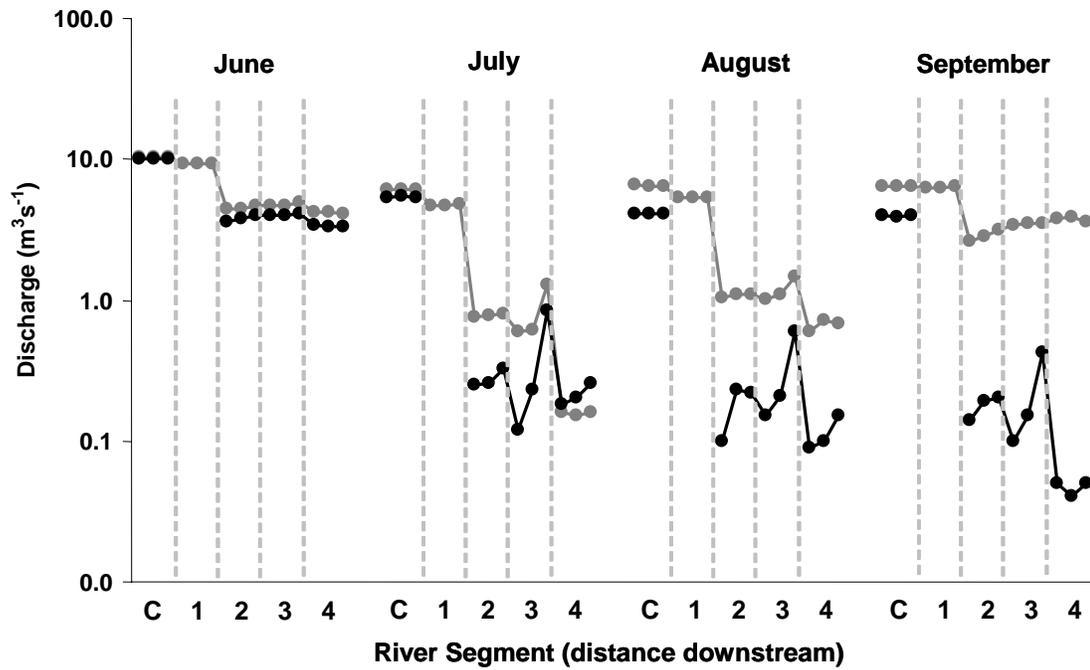


Figure 2.2. Longitudinal discharge (Q_{instant}) gradients (upstream to downstream) among months (June, July, August, September) and between years (2004: grey line and 2005: black line). River segments are indicated as C=Control, 1=Segment 1, 2=Segment 2, 3=Segment 3, 4=Segment 4. Dashed vertical lines indicate points of water withdrawal. Because segment one was not sampled in 2005, the points are not connected between the control and segment two.

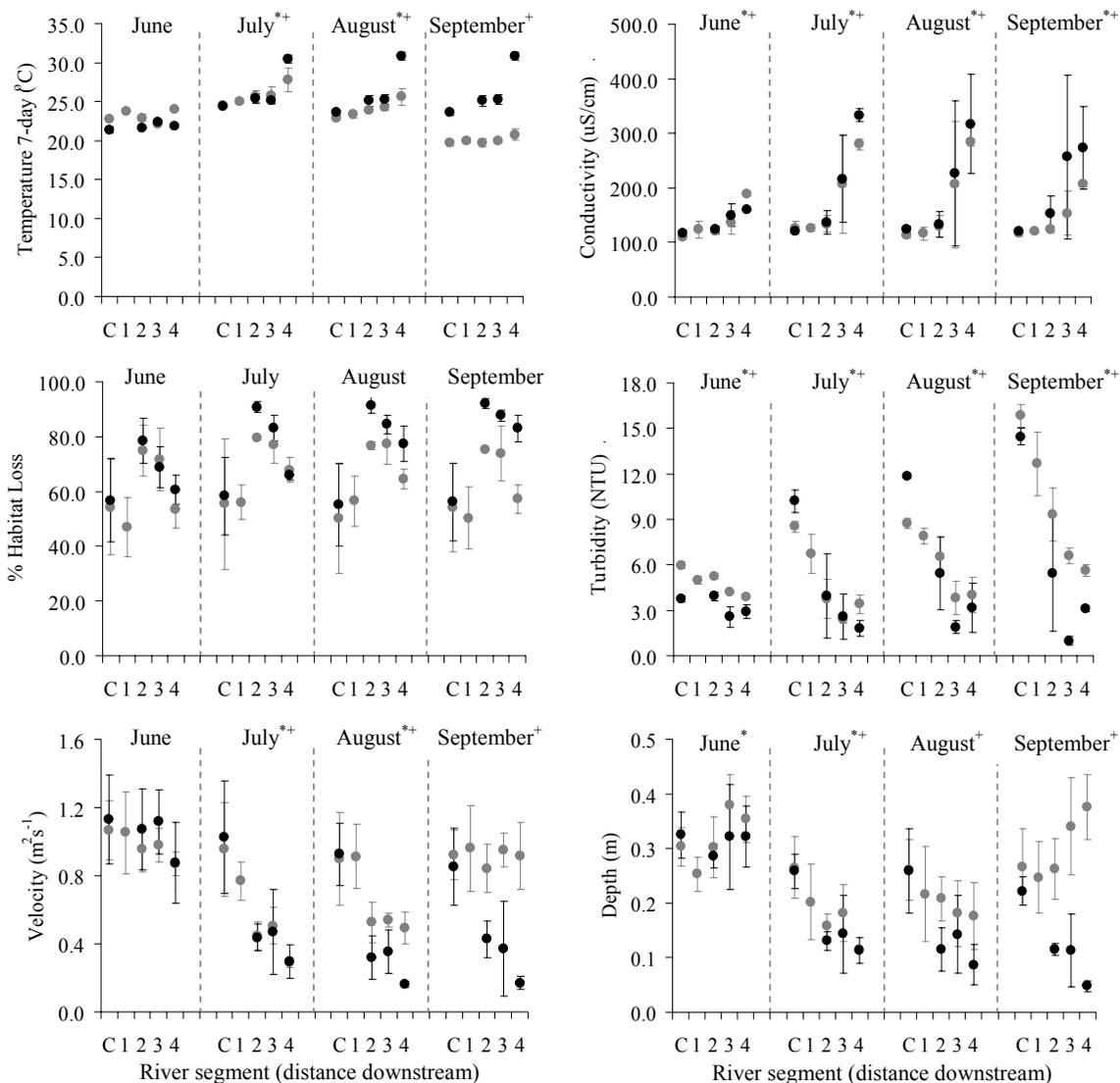


Figure 2.3. Longitudinal gradients of change for measured environmental variables among months (June, July, August, and September) and between years (2004: grey dots and 2005: black dots). Average values (\pm standard deviation) for the three reaches per segment within an individual month are presented. Significant relationships of stream kilometer with environmental variables by month and year at the 0.05 alpha level are indicated by (*) for 2004 and (+) for 2005. Significance of Kendall's tau correlation coefficients is based on 15 sites in 2004 and 12 sites in 2005. Dashed vertical lines separate individual months.

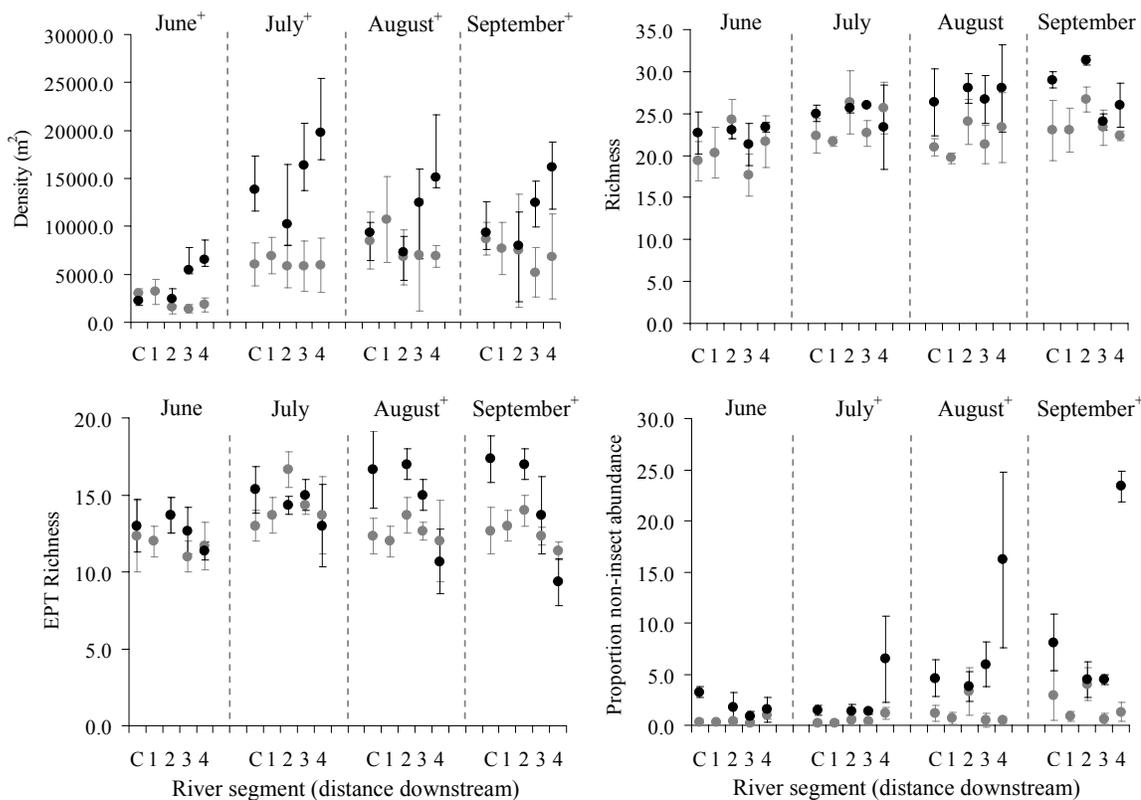


Figure 2.4. Longitudinal gradients of change for macroinvertebrate indices among months (June, July, August, and September) and between years (2004: grey dots and 2005: black dots). Average values (\pm standard deviation) for the three reaches per segment within an individual month are presented. Significant relationships of stream kilometer with macroinvertebrate indices by month and year at the 0.05 alpha level are indicated by (+) for 2005. Significance of Kendall's tau correlation coefficients is based on 15 sites in 2004 and 12 in 2005. Dashed vertical lines separate individual months.

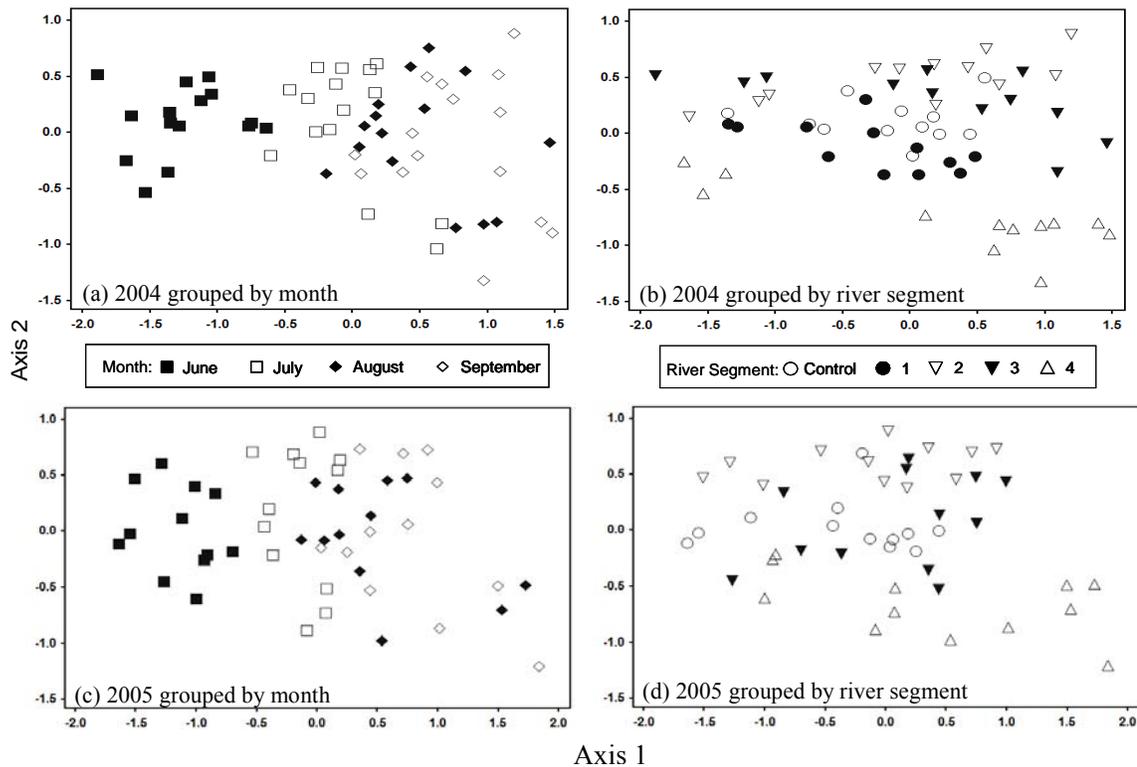


Figure 2.5. NMS ordinations of macroinvertebrate communities sampled across different river segments in June, July, August, and September of 2004 (a and b) and 2005 (c and d). Plots a and c code sample reaches by month, while plots b and d code sample reaches by river segment (i.e., magnitude of water withdrawal, with three reaches per segment).

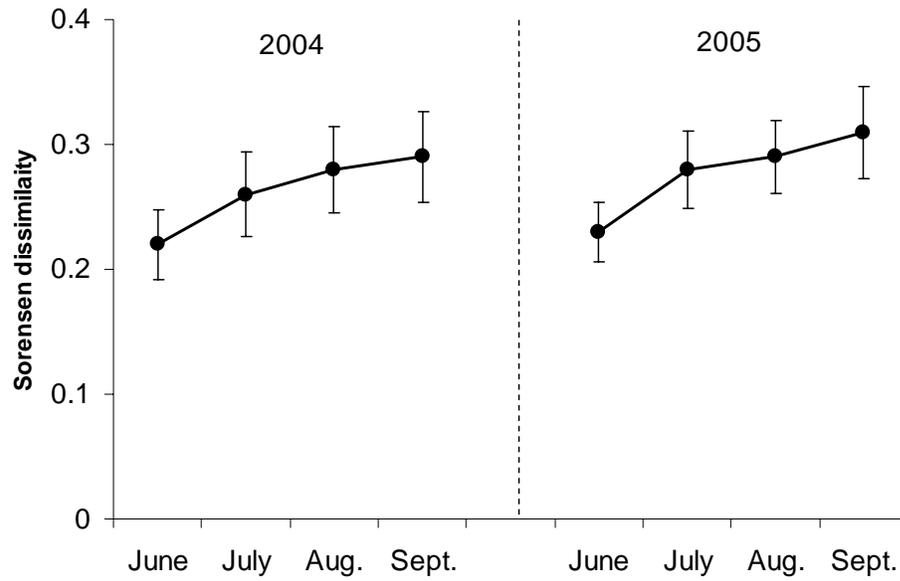


Figure 2.6. Average difference (\pm standard deviation) in macroinvertebrate community composition, measured as Sørensen dissimilarity among all reaches within an individual month, for June, July, August, and September of 2004 and 2005.

CHAPTER 3:

**DEVELOPMENTAL AND GROWTH RESPONSES OF A RIVER
DWELLING CADDISFLY (*BRACHYCENTRUS OCCIDENTALIS*) TO
IRRIGATION WATER WITHDRAWALS**

Scott W. Miller, David Wooster, and Judith L. Li

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Abstract

Irrigation water withdrawals can alter the hydrologic and thermal regimes of lotic systems, which represent two of the most important drivers of biological patterns and processes. Though irrigated agriculture is the largest consumer of freshwater resources in the world, impacts of these activities on macroinvertebrate life histories remain unknown. We sought to determine how hydrologic and thermal alterations associated with irrigation water withdrawals affect larval development and growth of *Brachycentrus occidentalis* (Banks) on the Umatilla River, Oregon. We sampled three river segments representing: (i) reference conditions above all points of diversion, (ii) hydrologic alterations below a first diversion, and (iii) hydrologic and thermal alterations below a second diversion. The three river segments were sampled monthly from June to September during average and drought water years. During the average water year, *B. occidentalis* initially developed and grew faster below both points of water withdrawal; however, significant deviations from reference conditions did not persist through September. In contrast, water withdrawals interacted with drought conditions in 2005 to increase the magnitude and duration of hydrologic and thermal alterations. *B. occidentalis* responded with increased developmental rates below both diversions; however, the rate of growth only differed below the second diversion, resulting in significantly smaller sized 4th and 5th instar individuals. Growth and developmental variability was best explained by degree day accumulations in 2004, while in 2005 the interaction of degree day accumulations and maximum temperature provided the optimal model. We provide evidence that the ubiquitous practice of managing river systems for irrigated agriculture can affect development and growth patterns of a river dwelling caddisfly. While degree day accumulations are commonly used to model responses of stream insects to elevated temperatures, our results highlight the interactive roles of degree days and absolute temperatures on life history patterns.

Introduction

Hydrologic and thermal regimes are two of the most important abiotic drivers of biological patterns and processes in river systems (Vannote and Sweeney 1980, Allan 1995, Poff and Allan 1997). Over evolutionary time organisms have evolved strategies to maximize fitness under different hydrologic and thermal regimes (Ward and Stanford 1982), while in contemporary time these variables constrain the distribution, density, development, and growth of aquatic organisms (Vannote and Sweeney 1980, Hauer and Benke 1987, Newbold et al. 1994). Natural hydrologic and thermal regimes are frequently altered by dams and water diversions, which represent primary threats to lotic ecosystems (Dynesius and Nilsson 1994, Richter et al. 2003). Though a considerable amount of work has been done to understand the abiotic and biotic impacts of large dams (reviewed in Allan 1995; Power et al. 1996; Vinson 2001), far less work has focused on the impacts of irrigation water withdrawals.

Irrigation water withdrawals alter hydrologic regimes by changing the magnitude, duration, and timing of low flow events (Wilber et al. 1996, Eheart and Tornil 1999, Miller et al. 2007). Abiotic responses include increased temperatures, reduced habitat availability, altered near-bed hydraulics, fragmented longitudinal connectivity, and reduced water quality (Benstead et al. 2005, Rader and Belish 1999, Meier et al. 2003, Miller et al. 2007). Impacts to stream biota have largely been assessed in terms of compositional responses of macroinvertebrates (Rader and Belish 1999, McKay and King 2006, Dewson et al. 2007), while life history responses of individual populations have been neglected. To our knowledge, the effects of water withdrawals on macroinvertebrate life histories have only been examined by McIntosh et al. (2003), who found fewer summer generations and lower individual biomass of a filter feeding caddisfly below a point of water withdrawal in a Hawaiian stream.

Water withdrawals have the potential to alter the growth, development, and emergence timing of aquatic insects by reducing discharge and habitat availability, increasing temperatures, and altering food quality and quantity. Aquatic macroinvertebrates play

critical roles in river systems, serving as important conduits between basal resources and higher trophic levels of both aquatic and terrestrial ecosystems (Nakano and Murakami 2001, Baxter et al. 2005). Therefore, changes to the growth, development, and timing of aquatic insect emergence can alter energy fluxes within and among lotic and riparian ecosystems. As irrigated agriculture constitutes the largest use of freshwater resources in the world (Oki and Kanae 2006) and global warming is predicted to increase the frequency of droughts and lethal water temperatures (Hogg and Williams 1996, Knowles et al. 2006), there is a growing need to understand how altered hydrologic and thermal regimes will affect macroinvertebrate life histories.

In this study, we sought to determine if irrigation water withdrawals alter the life history strategy of the filter feeding caddisfly, *Brachycentrus occidentalis* Banks. Specifically, we assessed developmental and growth responses to water withdrawals varying in magnitude and duration between average and drought water years. We hypothesized that hydrologic changes would have little direct impact on development and growth, whereas the interactive effects of increased temperature and reduced velocities would lead to faster developmental rates at the cost of smaller sized individuals. We predicted developmental and growth responses would be exacerbated by drought conditions.

Methods

Study Area

The study was conducted on a 36 km lowland section of the 143 km Umatilla River located in Northeastern Oregon, U.S.A. (Fig. 3.1). The Umatilla River is a 5th order tributary of the Columbia River that drains a catchment of 5,930 km². The hydrograph is typical of a snow-pack hydrologic regime, with maximum flows ($\sim 150 \text{ m}^3 \text{ s}^{-1}$) occurring from March through May and base flows ($\sim 6 \text{ m}^3 \text{ s}^{-1}$) dominating from July through October. The climate of the study area is cold continental, characterized by hot dry summers (average maximum temperature 31.3°C) and cold winters (average maximum temperature 7.5°C). Average annual precipitation for the lower Umatilla River at Hermiston, OR is 226 mm.

There are four irrigation dams present within the 36 km study section from river kilometer 56 to 20 (Fig. 3.1) that create a gradient of decreasing instream flow with distance downstream (Fig. 3.2). The disparity in discharge between upstream and downstream river segments increases from June to September, as spring runoff recedes and agricultural demands increase. Irrigation diversions are operated from approximately March to October, with maximum withdrawals occurring from June to September. Diversion structures are concrete and timber dams that span the entire bankfull width; they are ~1.8 m high, and have withdrawal capacities ranging from 4 to 6.3 m³s⁻¹. All points of diversion have been operating since the early 1900s. Upriver of the study section, the mainstem is free flowing with no major dams or impoundments.

Study Design

A previous study of all four diversions identified significant hydrologic alterations below the 2nd, 3rd, and 4th diversions, while thermal alterations were limited to below the 4th diversion (Miller et al. 2007). To quantify developmental and growth responses of *B. occidentalis* to altered hydrologic and thermal regimes we located one reference (R) segment above all points of diversion and two treatment segments, one below the 2nd diversion (T1 – hydrologic alterations only) and one below the 4th diversion (T2 – hydrologic and thermal alterations) (Fig. 3.1). Within each segment, three sample reaches equal to 10 x bankfull width were established (Table 3.1). Sample reaches within treatment segments were located at distances approximately 0, 2, and 4 km downstream of the diversion. Reaches within the reference segment were located at similar intervals above the first diversion. All reaches were sampled once per month in June, July, August, and September of 2004 and 2005.

Environmental conditions are relatively homogenous within the 36 km study section of the Umatilla River. Irrigated agriculture is the dominant land use; however, the river is buffered by a corridor of *Populus*, *Alnus*, and *Salix*. The river has a very low gradient, changing only 59 m over 36 km and no perennial tributaries are present. Furthermore, all river segments are similar in physical structure, riparian vegetation, geology, soils, and

adjacent land use. The only differences exist within segment T2, which has an average bankfull width half as wide as other river segments and a median particle size (D_{50}) greater by 22 mm on average (Table 3.1). Irrigation water withdrawals also create seasonal environmental differences (e.g., increased conductivity, reduced turbidity) among segments, which are described in detail by Miller et al. (2007).

Data collection: Environmental variables

We measured discharge at two transects per sample reach using a Marsh McBirney digital flow meter during each sampling event. Depth and velocity (0.6 water depth) measurements were made at a minimum of 20 points across the stream or at intervals that ensured one cell (depth x width) did not contain greater than 5% of total discharge (Buchanan and Somers 2005). Velocity (0.6 water depth) and depth were also measured at all Surber sampler locations. From these measurements we calculated Froude number (Fr), the ratio between inertial and gravitational forces, as:

$$Fr = \frac{\bar{U}}{\sqrt{gD}}$$

Where \bar{U} is the average current velocity, D is the average water depth, and g is the acceleration due to gravity ($9.8 \text{ m}^2\text{s}^{-1}$). Fr was used because Wetmore et al. (1990) identified it as the best predictor of *B. occidentalis* densities and it provides information on near-bed hydraulics (Statzner et al. 1988); analyses with other hydraulic descriptors incorporating depth and velocity produced similar results.

Temperature was continuously monitored at 30 min intervals within each sample reach from June to September. From the continuous temperature data we calculated the seven day average of the maximum daily temperature (temperature_{7-day}) to assess impacts of potentially lethal temperatures on *B. occidentalis*. In addition, temperature is monitored year-round at a single point within each river segment by the Bureau of Reclamation (BOR) (<http://www.usbr.gov/pn/hydromet/umatilla/index.html>). Using this data, we calculated cumulative degree days ($>0^\circ\text{C}$) from the average time of *B. occidentalis*

oviposition on the Umatilla River (~April 1st) to the date of each individual sampling event.

Data collection: Biological variables

Within each reach, a Surber sampler (0.09 m², 500 µm mesh) was used to collect six randomly located benthic macroinvertebrate samples from riffle habitats to a depth of 10 cm. The six Surbers from each reach were composited, preserved in 70% ethanol, and processed using a 500 count subsampling procedure (Caton 1991, Vinson and Hawkins 1996). *B. occidentalis* was identified to species using the taxonomic key of Flint (1984) and all individuals were placed into a pool of potential candidates for measuring development and biomass for a given reach and date. Based on a power analysis of data collected in 2003 (Miller, unpublished data), we randomly selected 15 individuals from each of the three reaches and pooled the data for a total of 45 individuals per segment. With this sample size, we could detect when 20% or more individuals changed developmental or biomass categories with a power of 80% at an alpha level of 0.05.

B. occidentalis head width, head length, and body length were measured using a dissecting microscope (6.7 – 40 x magnification) and ocular micrometer to the nearest 0.05 mm. Dry mass (mg) was estimated from body length following Benke et al. (1999) and was categorized according to eight biomass size classes, each having a maximum dry mass approximately double the previous category (Table 3.2). Developmental stages (i.e. instars) were determined by plotting head widths versus head lengths, which resulted in discrete groupings (Mackay 1978).

Statistical analyses

Discharge, temperature_{7-day}, and Fr were compared among rivers segments within a month using analysis of variance (ANOVA). Alpha levels ($p = 0.05$) were corrected for the number of tests (4) run per variable ($\alpha = 0.013$). Small sample sizes prohibited the use of a repeated measures design testing for the time x treatment interaction. Also, formal statistical comparisons were not made between years because samples were

collected during different time periods. Finally, cumulative degree days were not statistically compared among river segments due to a lack of replication.

We used loglinear models to determine if proportions of individuals within a given developmental or biomass category were dependent upon month, treatment, and the month by treatment interaction (Agresti 2002). Models were performed separately for each individual year and response variable. A likelihood ratio of the chi-squared statistic (χ^2) was used to assess contributions of all first and second order effects when terms were removed (backward elimination) from the model. A Pearson χ^2 goodness-of-fit test was used to assess the performance of the final model. Again, formal comparisons were not made between years because samples were collected during different times. Significant interactions were followed-up with two-way contingency table analyses using χ^2 to test for equal proportions of individuals within developmental and biomass categories among river segments within an individual month. Significant results were followed by pairwise comparisons to evaluate differences among individual river segments. Alpha values were corrected for the number of tests (4) run per response variable ($\alpha = 0.013$). The strength of associations was quantified using *gamma* (γ), since we treated both row (treatments) and column (developmental or biomass categories) variables as ordinal. All statistical tests were run using SPSS version 10.0 (SPSS 1999).

Relationships between development and biomass of *B. occidentalis* with environmental variables were modelled with non-parametric multiplicative regression (NPMR) (McCune 2006) within the program HyperNiche version 1.0 (McCune and Mefford 2004). NPMR differs from traditional modelling tools by avoiding a global model where coefficients are sought in a fixed mathematical equation (McCune 2006). Rather, NPMR relies on the data to specify model form by using a local multiplicative smoothing function with a leave-one-out cross-validation. Consequently, NPMR facilitated the detection of non-linear developmental or biomass responses to the interactive effects of multiple environmental variables. We used a local mean estimator and Gaussian weighting function in a forward step-wise regression, where data points closer to the

target point receive greater weight. Fit was assessed with a cross-validated R^2 (xR^2), which is more conservative than traditional R^2 because each data point is excluded from calculating the residual sums of squares for the response at that point.

We used a sensitivity analysis to assess the relative influence of individual explanatory variables within a selected model (McCune 2006). Sensitivities are generated by nudging values of individual predictor variables up and down to measure resulting change in the response variable at that point. The accumulation of sensitivity values across all data points are averaged and expressed as a proportion of the range of the response variable. A value of 1.0 indicates equal change in the response per unit change in the predictor; whereas a value of 0 indicates that nudging a predictor has no effect on the response.

NPMR models were developed individually for 2004 and 2005 using the response variables of development and biomass. Cumulative degree days, temperature_{7-day}, discharge, and Fr were included as potential explanatory variables in all NPMR models. Explanatory and response variables represented average conditions for the three reaches per segment for each of the four months sampled (n = 12).

Target organism

Within North America, *B. occidentalis* occurs over a broad geographic area, ranging from the state of Wisconsin to the west coast of the United States (Gallepp 1977). *B. occidentalis*, like all Trichoptera genera, is holometabolous having an egg, larvae, pupa, and adult stage. Larvae have numerous morphological and behavioral adaptations for filter feeding, but are also known to consume periphyton from the stream benthos (Gallepp 1977, Hauer and Stanford 1986). The distribution (Hauer and Stanford 1986), as well as hydrologic (Wetmore et al. 1990) and thermal (Gallepp 1977) preferences of *B. occidentalis* are well known; making it an ideal organism for studies of irrigation water withdrawal. Within the study area, *B. occidentalis* exhibits a univoltine life cycle and is the only species found from the family Brachycentridae. Furthermore, *B. occidentalis* is one of several community dominants within reference reaches, comprising up to 30% of

total benthic densities. In contrast, densities of *B. occidentalis* are significantly reduced within reaches experiencing irrigation water withdrawals (Fig. 3.3).

Results

Differences among river segments: Environmental variables

Discharge within segments T1 and T2 was significantly lower than the reference from June through September of 2004 and 2005 (All *p-values* < 0.013) (Fig. 3.4). T2 generally had greater discharge reductions than T1; however significant differences did not occur in all months of both years. Discharge reductions were generally of greater magnitude and duration in 2005 due to ‘extreme’ drought conditions as measured by the Palmer Hydrologic Drought Index; for 58 years of record (USGS gage #14026000) average 2005 discharge levels had a 2% ($9.7 \text{ m}^3\text{s}^{-1}$) probability of occurrence, as compared to 75% ($22.6 \text{ m}^3\text{s}^{-1}$) in 2004.

Despite significant discharge reductions for segments T1 and T2, Fr and temperature_{7-day} did not differ among segments in June of 2004 and 2005 (All *p-values* > 0.40) (Fig. 3.4). In subsequent months Fr was significantly reduced in segments T1 and T2, whereas temperature_{7-day} significantly increased in T2 only. Fr and temperature_{7-day} differences were of greater magnitude and duration for 2005, the drought year.

Annual degree day accumulations for segments T1 and T2 were higher than the reference during all months *B. occidentalis* is known to occur in aquatic stages (Table 3.3). Prior to significant water withdrawals, T1 had the highest degree day accumulations; however, this trend switched to favor T2 in later months. Differences between T2 and T1 and the reference segment appeared greater in 2005 than 2004.

B. occidentalis Life History

We identified four instars of *B. occidentalis* in 2004 and in 2005. The range of head capsule widths for each instar were: 2nd: 0.49 – 0.53mm, 3rd: 0.65 – 0.83mm, 4th: 0.95 – 1.1mm, and 5th: 1.15 – 1.25mm. Midpoints of head capsule widths increased by a factor

of 1.33 for each molt. A single cohort progressed through the sampling season at all sites indicating a univoltine life cycle. Larvae were present in the system in June as 2nd and 3rd instars during both years (Fig. 3.5 and 3.6). Larvae developed rapidly, reaching the 5th and final instar as quickly as July in both 2004 and 2005. By September, the vast majority of individuals were 4th or 5th instars. Within all segments and across all months, development appeared slower in 2004 as compared to 2005, despite sampling three weeks later in 2004 (Table 3.3).

Differences among river segments: Development and biomass

Loglinear analysis identified significant relationships between month, river segments (i.e. treatment), and the response variables (development and biomass) for 2004 (Development: $\chi^2 = 40.6, p = 0.002$; Biomass: $\chi^2 = 31.4, p < 0.001$) and 2005 (Development: $\chi^2 = 46.4, p < 0.001$; Biomass: $\chi^2 = 98.5, p < 0.001$). The significant two-factor interaction and analysis of residuals indicated that the proportion of individuals within a given developmental stage and biomass category was best explained by the month by treatment interaction for both years.

In June 2004, the proportion of individuals within developmental stage two and three did not differ among segments (Table 3.4, Fig. 3.5). A majority of individuals were in the 3rd instar and less than 10% in the 2nd instar. However, the proportion of individuals in larger biomass categories significantly differed among all river segments, with T2 having the greatest proportion of larger individuals (Table 3.4, Fig. 3.5). In July and August, developmental stage significantly differed among segments; again T2 had the greatest proportions of individuals in later instars. By September, proportions of individuals in the 3rd, 4th, and 5th instars were similar among all segments. Despite initially faster developmental rates for T1 and T2, biomass within individual instars did not differ among the three river segments in August or September ($p = 0.409$).

In contrast to 2004, both development and biomass significantly differed among reference and treatment segments in June of 2005 (Table 3.4, Fig. 3.6). All T1 and T2

individuals were in the 3rd instar, whereas the reference had 40% of individuals in the 2nd instar. Biomass also significantly increased from the reference to T2 (Table 3.4, Fig. 3.6). Developmental and biomass differences persisted through July, at which time a reverse trend began for T2. Starting in August, T2 had higher proportions of individuals in smaller ($\gamma = -0.53$) and not larger size classes, as in June ($\gamma = 0.80$) and July ($\gamma = 0.27$). These differences increased in September, when T2 had significantly higher proportions of individuals in the 3rd instar ($\gamma = -0.16$) and individuals in smaller size classes ($\gamma = -0.67$). Overall, individuals within 4th and 5th instars for T2 were significantly smaller than those in T1 and the reference in 2005 (Fig. 3.7); these differences were not found in 2004.

In 2004, cumulative degree days was the best predictor of development and biomass (Table 3.5). Both variables exhibited linear increases with increasing degree days. Variance explained was related to differences among months and not among river segments, as all segments showed similar biomass increases within a month. In contrast, the interaction of cumulative degree days and temperature_{7-day} best explained variance in development and biomass in 2005 (Table 3.5). As observed for 2004, biomass increased as degree days accumulated; however, the rate of increase was lower for river segments experiencing temperature_{7-day} above 27°C (T2).

Discussion

Water withdrawals significantly altered the hydrologic and thermal regimes of the Umatilla River, which appeared to influence development and growth of *Brachycentrus occidentalis*. Reduced velocity, depth, and habitat area are commonly associated with water withdrawals (McIntosh et al. 2002, McKay and King 2006, Dewson et al. 2007), whereas significant temperature alterations are less common (Rader and Belish 1999, Miller et al. 2007). Decreased discharge levels, minimum riparian and topographic shading, high rates of incoming solar radiation, and a high width-to-depth ratio (summer range 52 - 227) likely combined to elevate temperature on the Umatilla River. Greater temperature increases for segment T2 as compared to T1 likely reflect higher magnitude

discharge reductions for T2, which exposed larger substrates to the atmosphere and increased conduction to the remaining water (Cassie 2006).

Elevated degree day accumulations for segments T1 and T2 prior to significant water withdrawals (March – June) suggest additional drivers of temperature differences among segments. We believe groundwater inputs and/or increased rates of hyporheic exchange increased winter temperatures within segments T1 and T2; both have been shown to increase average daily winter temperatures (Baxter and Hauer 2000, Poole and Berman 2001). O'Daniel (2005) identified segment T1 as an area of active groundwater inputs and hyporheic exchange due to the depth of the alluvial aquifer, greater valley width, and greater sinuosity. These local inputs likely propagate downstream and contribute to elevated degree day accumulations for segment T2, which does not share similar physical conditions. Overall, water withdrawals interacted with annual water availability to influence the magnitude and duration of environmental alterations. For example, temperature_{7-day} increases in 2004 were restricted to one month, which created a short-term stress (i.e., pulse disturbance), while in 2005 drought conditions and prolonged periods of high-intensity water withdrawal increased the magnitude and duration of temperature_{7-day} alterations (i.e., a press disturbance).

Increased water temperature associated with both groundwater inputs and water withdrawals appeared to accelerate developmental rates of *B. occidentalis* and decrease the amount of time for larval growth. However, our hypothesis of *B. occidentalis* developing faster at the cost of reduced biomass was not consistently observed among segments or between years. In 2004, we did not observe ecologically significant impacts of water withdrawals on the life history of *B. occidentalis*. Developmental rates for segments T1 and T2 were accelerated during July and August, but they did not come at the expense of reduced biomass for 3rd, 4th, or 5th instars. Furthermore, individuals within developmental and biomass categories were identical come September, suggesting the timing of development differed among segments but not the growth rate. Development exhibited a similar pattern among segments in 2005, whereas biomass of 4th and 5th

instars was significantly reduced within segment T2. Consequently, in 2005 the fecundity of *B. occidentalis* was likely reduced through reductions in mean individual biomass within segment T2.

Variable responses among segments and between years likely reflect how the thermal regime was altered, in addition to the magnitude and duration of alterations. For example, groundwater inputs increased degree day accumulations during early instars of *B. occidentalis*, but did not impact maximum daily temperatures. Such changes likely explain both accelerated development and increased biomass for T1 and T2 prior to significant water withdrawals. Furthermore, the timing of increased degree days may have contributed to the magnitude of observed changes; increased winter temperature has been shown to impact growth and development more than summer increases (Rader and Ward 1989, Gregory et al. 2000, Cassie 2006). Water withdrawals subsequently increased temperature_{7-day} for both T1 and T2 in July of 2004 and 2005; however, the thermal tolerance of *B. occidentalis* was not exceeded for T1 in both years and T2 in 2004. When the thermal tolerance of *B. occidentalis* was not exceeded, growth rates appeared to simultaneously increase and compensate for faster development (Sweeney 1984, Gregory 2000). Consequently, biomass was not reduced within individual instars for T1 and T2 in 2004, despite faster developmental rates.

In contrast, water withdrawals combined with drought conditions in 2005 to produce prolonged periods of low flow conditions, which increased the magnitude and duration of thermal alterations. During this time, the thermal tolerance of *B. occidentalis* was exceeded from July through September and biomass of 4th and 5th instars was significantly reduced within segment T2. Different growth responses between T1 and T2 highlight the interactive effects of increased degree days and absolute temperatures on life history patterns. We hypothesize that growth rates initially increased with developmental rates for both T1 and T2 (positive *gamma* for biomass); however, abnormally high temperatures for T2 likely changed behavioral patterns of *B. occidentalis* and reduced ingestion rates necessary to sustain increased growth (negative

gamma for biomass). Gallepp (1977) observed reduced feeding rates of *B. occidentalis* when temperatures exceeded 27°C due to more time spent withdrawn in their case. Alternative explanations for differential responses among segments include altered food quality and quantity, differential mortality of 4th and 5th instars, and earlier egg hatching among segments.

Decreased size can affect population densities through reduced fecundity and decreased competitive ability (Ward and Stanford 1982, Sweeney 1984). Similarly, the thermal equilibrium hypothesis predicts densities will be maximized in areas where thermal conditions are most favorable and the tradeoff between development and growth is optimized (Vannote and Sweeney 1980). On the Umatilla River we did not observe this pattern, as densities of *B. occidentalis* significantly differed between the reference and segment T1, however, mean individual biomass did not differ among the two reaches come September for either year. Differences in density, not growth, suggest thermal conditions within T1 were still optimal relative to the control and some other environmental variable is reducing population densities. Furthermore, consistent density differences among months despite changing hydrologic conditions suggest density reductions are not related to hydrologic alterations. Alternatively, density patterns of *B. occidentalis* might reflect over 100 years of water withdrawal on the Umatilla River. Persistent annual temperature and hydrologic alterations in segments T1 and T2 may have greatly reduced populations of *B. occidentalis* with recovery and annual recruitment constrained by its life history strategy. Miller et al. (2007) found evidence for annual recovery of community composition on the Umatilla, but recovery was largely driven by asynchronous emerging, multivoltine taxa with high drift propensities. In contrast, *B. occidentalis* is univoltine, exhibits synchronous emergence, has a low propensity for drift, and the critical time period for growth and development coincides with the height of water withdrawals.

In addition to altering thermal regimes, water withdrawals also significantly altered hydraulic conditions within segments T1 and T2. While growth and developmental

responses to temperature alterations are well documented (Vannote and Sweeney 1980, Hauer and Benke 1987, Rader and Ward 1989, Harper and Peckarsky 2006), the role of stream hydraulics is less certain. The distribution, behavior, and feeding efficiency of filter feeding insects, including *Brachycentrus*, have been linked to near-bed hydraulics (Gallepp 1977, Statzner et al. 1988, Wetmore et al. 1990) indicating suboptimal hydrologic conditions can affect growth rates. In contrast, developmental responses to altered hydrologic regimes are less well understood. Harper and Peckarsky (2006) demonstrated through both observational and experimental studies that temperature and not discharge was a proximate cue for emergence of *Baetis bicaudatus*. This response was attributed to the high spatial and temporal variability of velocity, which makes it an unlikely proximate cue for emergence or molting. Our measurement of near-bed hydraulics, Fr , was not an important predictor of development or growth; however, altered near-bed hydraulics could interact with temperature to impact growth through reduced feeding efficiency or time spent feeding, but is unlikely to alter developmental rates.

While the univoltine life history of *B. occidentalis* did not deviate from past studies (Gallepp 1974, Hauer and Stanford 1986), the appearance of 1st and 2nd instars appears to vary regionally. Regional variation likely reflects annual degree day accumulations and timing of spring runoff. For example, Hauer and Stanford (1986) observed 1st and 2nd instars in July, 5th instars by November, and emergence during May and June on the Flathead River, MT, which experiences ~2050 annual degree days (>0°C). We collected 2nd instars in June, 5th instars as early as July, and have observed emergence in late March (Miller, unpublished data) for the Umatilla River which has ~4500 degree days. Within the Umatilla River, we also detected variability between years, with greater development and growth rates in 2005, the drought year.

Conclusion

We provide evidence that the ubiquitous practice of water withdrawals for irrigated agriculture is capable of altering developmental and growth patterns of a river dwelling

caddisfly. While degree day accumulations are commonly used to model responses of stream insects to elevated temperatures (Vannote and Sweeney 1980, Hauer and Benke 1987, Rader and Ward 1989, Harper and Peckarsky 2006), our results highlight the interactive roles of degree days and absolute temperatures on life history patterns when dealing with anthropogenic disturbances. Increased maximum temperature led to decreased biomass of the 5th and final instar of *B. occidentalis*, which suggests the size of emerging adults will also be reduced. Decreased size at reproductive maturity can reduce fecundity (Ward and Stanford 1982, Sweeney 1984) and subsequently affect population viability, as well as energy fluxes within and among ecosystems (McIntosh et al. 2003, Baxter et al. 2005). Given the potential exacerbation of this already pervasive management practice by global climate change, there is a growing need to understand how other insect populations will respond to altered hydrologic and thermal regimes, as well as consequences for ecosystem processes.

Table 3.1. Average physical characteristics (\pm standard deviation) for the three sample reaches per reference and treatment segments on the Umatilla River, Oregon between June and September, 2004 - 2005.

Physical variable	River Segment		
	Reference	T1	T2
Altitude (m)	216 (2.1)	189 (4.2)	157 (2.0)
Riffle slope (%)	0.8 (0.4)	1.1 (0.3)	0.8 (0.5)
Bankfull width (m)	61.0 (8.1)	80.2 (2.6)	31.6 (8.0)
Particle size - D_{50} (mm)	46.3 (6.8)	40.7 (2.3)	65.0 (12.9)
Solar input (%)	93.0 (3.5)	88.0 (9.8)	86.0 (3.5)
Segment length (km)	4.7	4.5	4.3
Reach length (m)	610 (81.3)	802 (26.5)	316 (17.2)

Table 3.2. Size categories used to classify biomass (mg) of *B. occidentalis*. The maximum size of each category is double the size of the next smallest category. Size categories modified from Delucchi and Peckarsky (1989).

Category	Biomass range (mg)
1	0 - 0.089
2	0.09 - 0.183
3	0.184 - 0.369
4	0.37 - 0.759
5	0.76 - 1.49
6	1.5 - 2.9
7	3.0 - 5.9
8	6.0 - 12.0

Table 3.3. Annual degree day accumulations (>0°C) from April 1st to the June, July, August, and September sampling dates for each of the three river segments.

	Sample Date	River Segment		
		Reference	T1	T2
2004	June 22nd	1434.3	1616.7	1538.5
	July 21st	1907.3	2129.7	2056.5
	Aug. 19th	2499.3	2764.7	2747.5
	Sept. 20th	3056.3	3321.7	3370.5
2005	June 9th	1210.2	1336.4	1335.0
	July 7th	1731.2	1860.4	1906.0
	Aug. 3rd	2283.2	2455.4	2574.0
	Sept. 1st	2873.2	3064.4	3187.0

Table 3.4. Results of two-way contingency table analysis testing whether proportions of *B. occidentalis* within each of the developmental and biomass categories were similar among reference and treatment segments. Tests performed individually for each of June, July, August, and September following significant month*treatment interactions from loglinear models.

Year	Month	Developmental Stage						Biomass Category					
		Main effects			Post-hoc comparisons			Main effects			Post-hoc comparisons		
		χ^2	<i>p-value</i>	<i>Gamma</i>	Reference	T1	T2	χ^2	<i>p-value</i>	<i>Gamma</i>	Reference	T1	T2
2004	June	0.2	0.898	0.14	A ¹	A	A	50	<0.001	0.7	A	B	C
	July	45.1	<0.001	0.90	A	B	C	12.8	0.012	0.34	A	B	A
	August	15.0	0.005	0.48	A	B	B	4.9	0.552	0.11	A	A	A
	September	3.3	0.511	0.09	A	A	A	6.8	0.337	0.03	A	A	A
2005	June	51.7	< 0.001	1	A	B	B	56.2	< 0.001	0.80	A	B	C
	July	32.7	< 0.001	0.52	A	B	B	20	0.01	0.27	A	AB	B
	August	2.8	0.59	-0.04	A	A	A	22.3	0.001	-0.53	A	AB	B
	September	19.5	0.001	-0.16	A	A	B	51.3	< 0.001	-0.67	A	A	B

Table 3.5. NPMR model results for estimating variation in developmental stage and biomass categories among river segments and months for 2004 and 2005. Final selected models for each response variable are bolded.

Response	Predictors	Sensitivities	$\times R^2$
2004: Developmental stage	Cumulative degree days	0.86	0.61
	Cumulative degree days and Fr	0.80, 0.07	0.59
2004: Biomass category	Cumulative degree days	0.87	0.76
	Cumulative degree days and Fr	0.83, 0.07	0.73
2005: Developmental stage	Cumulative degree days	0.95	0.64
	Cumulative degree days and Temperature_{7-day}	0.82, 0.16	0.71
2005: Biomass category	Cumulative degree days	0.94	0.37
	Cumulative degree days and Temperature_{7-day}	0.82, 0.19	0.61

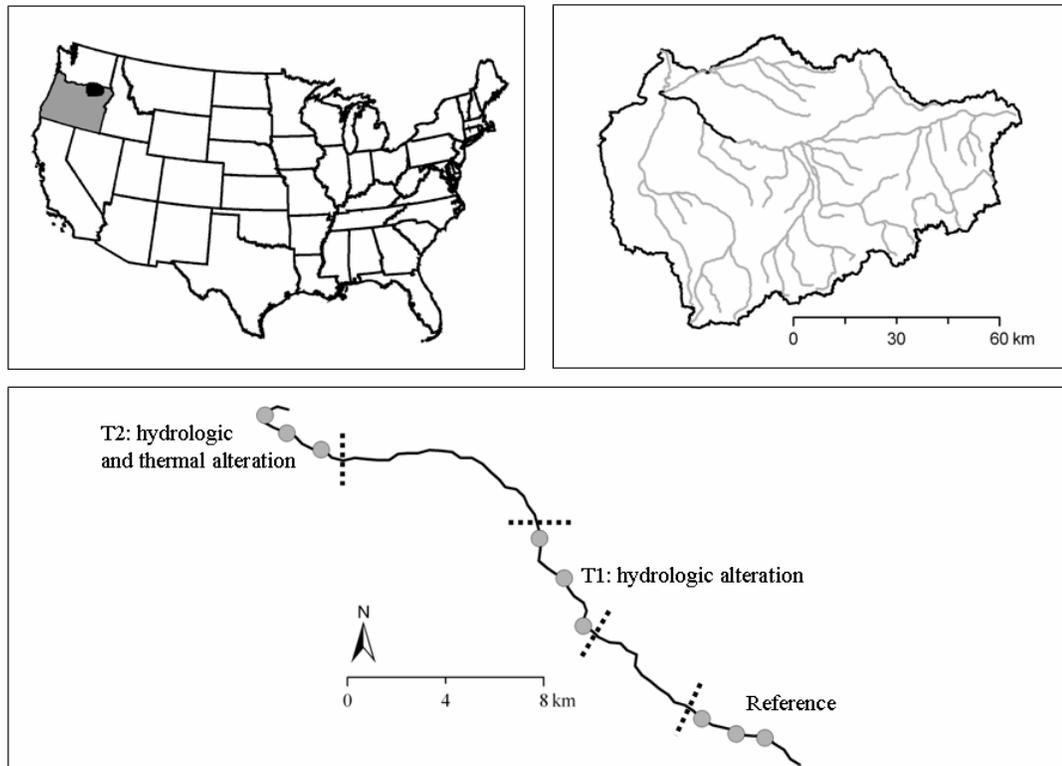


Figure 3.1. Location of catchment, study section, points of diversion, and sample reaches. Upper left: location of Umatilla catchment in northeastern Oregon, U.S.A. Upper right: location of the 36 km study section, shown as bold line, within the Umatilla catchment. Lower panel shows the 36 km study section, with locations of river segments, sample reaches (grey dots) and points of diversion (dashed black lines).

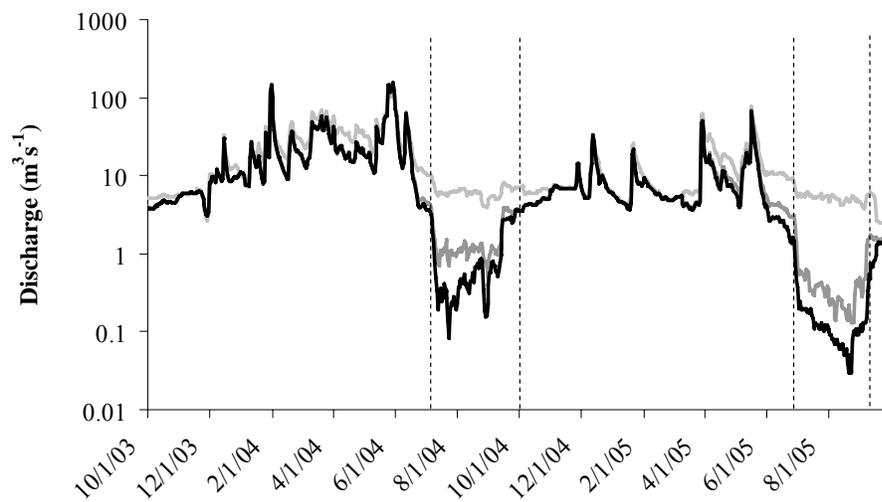


Figure 3.2. Average daily discharge values for the 2003 and 2004 water years within the reference (light grey), T1 (dark grey), and T2 (black) river segments of the Umatilla River. Dashed vertical lines bracket periods of data collection.

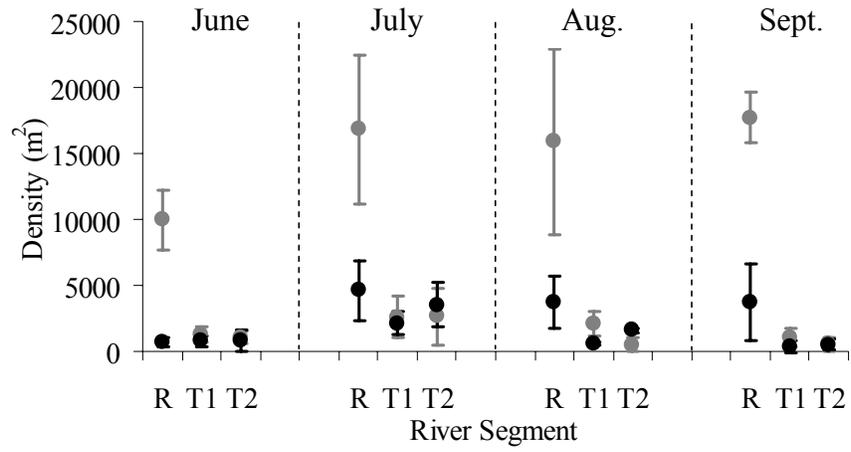


Figure 3.3. Average *B. occidentalis* densities (\pm SD) among river segments by month for 2004 (grey) and 2005 (black).

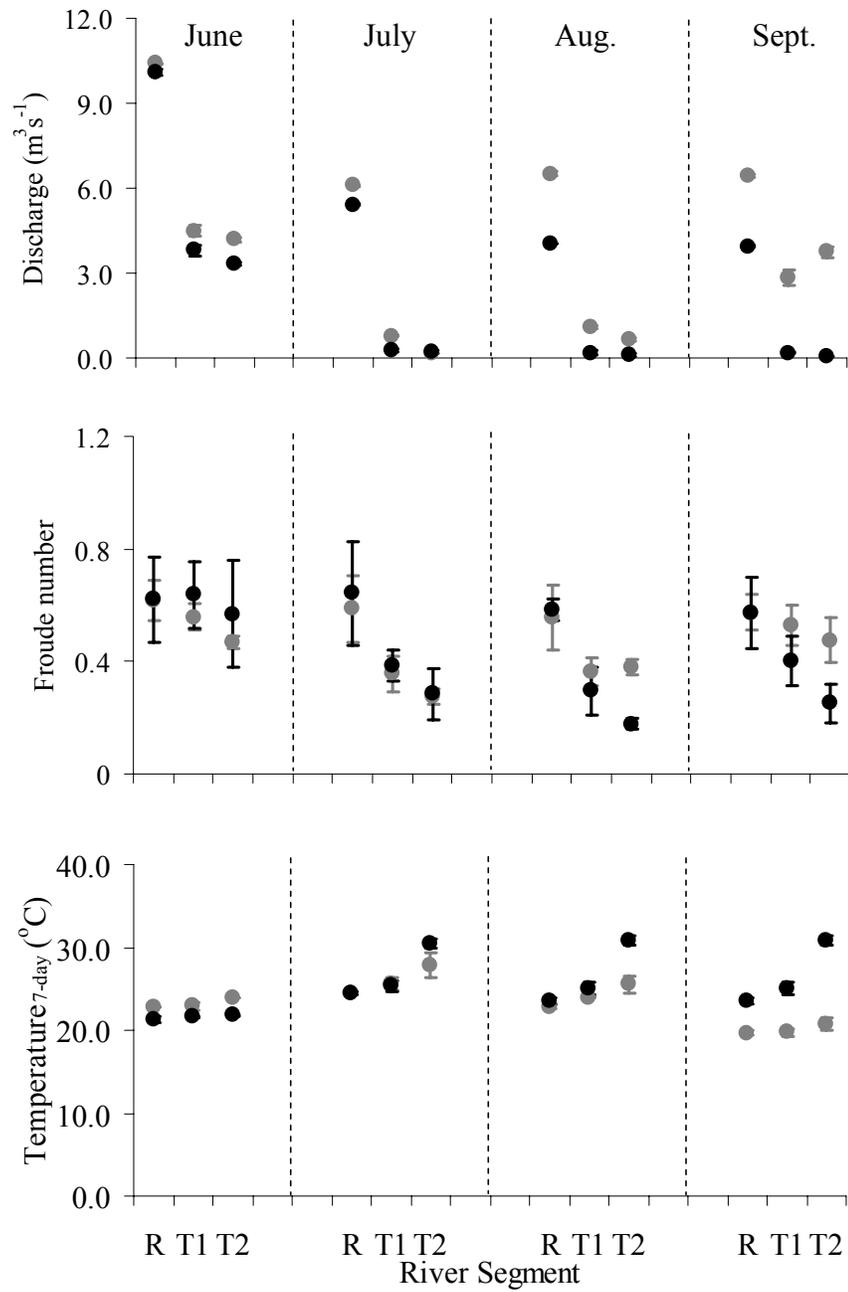


Figure 3.4. Average discharge, Froude number, and temperature_{7-day} values (\pm SD) among river segments by month for 2004 (grey) and 2005 (black).

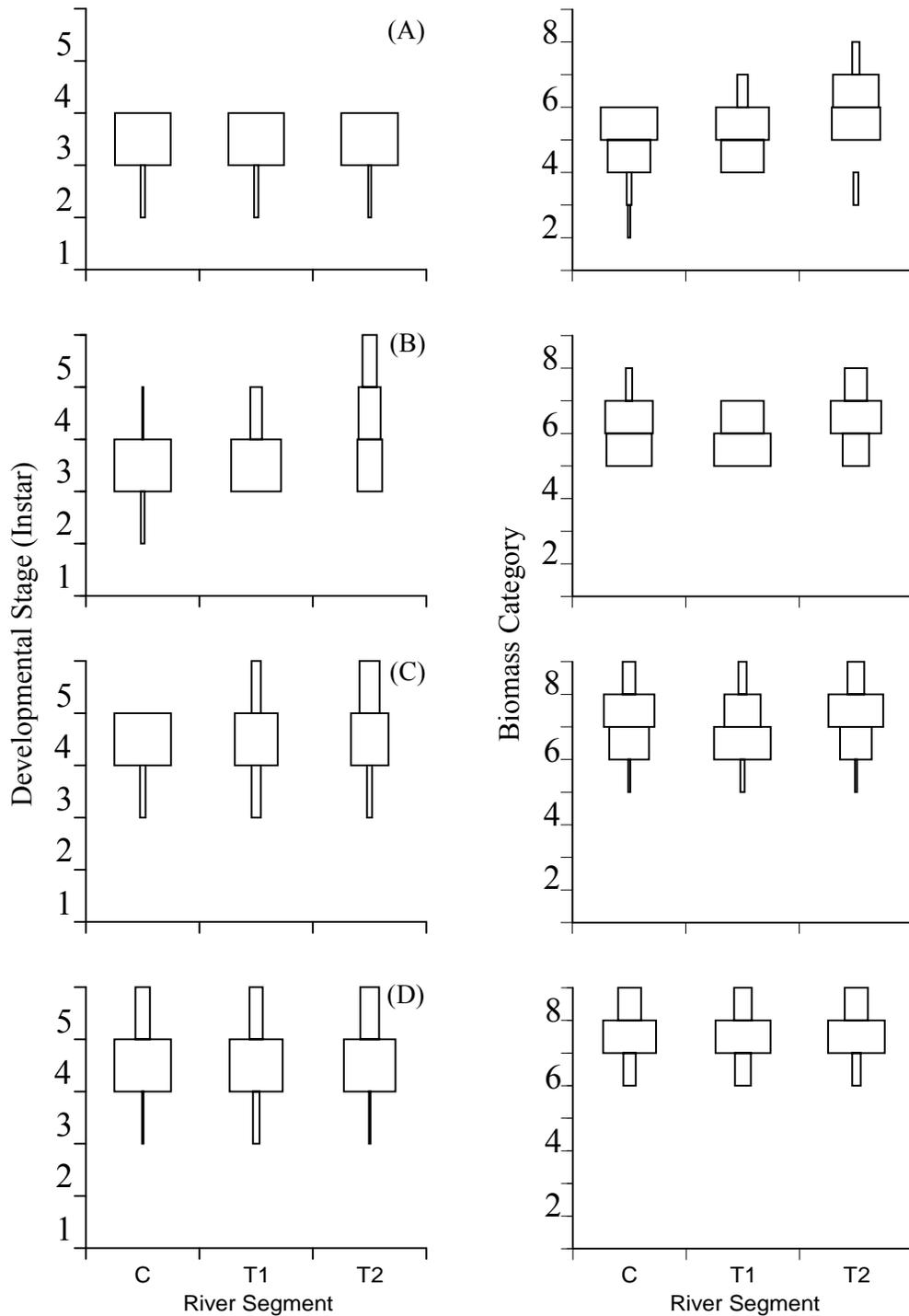


Figure 3.5. Frequency distributions for developmental stages (left) and biomass categories (right) of *B. occidentalis* among treatments for June (A), July (B), August (C), and September (D) of 2004. Width of each bar represents the relative proportion of individuals found in a development or size class.

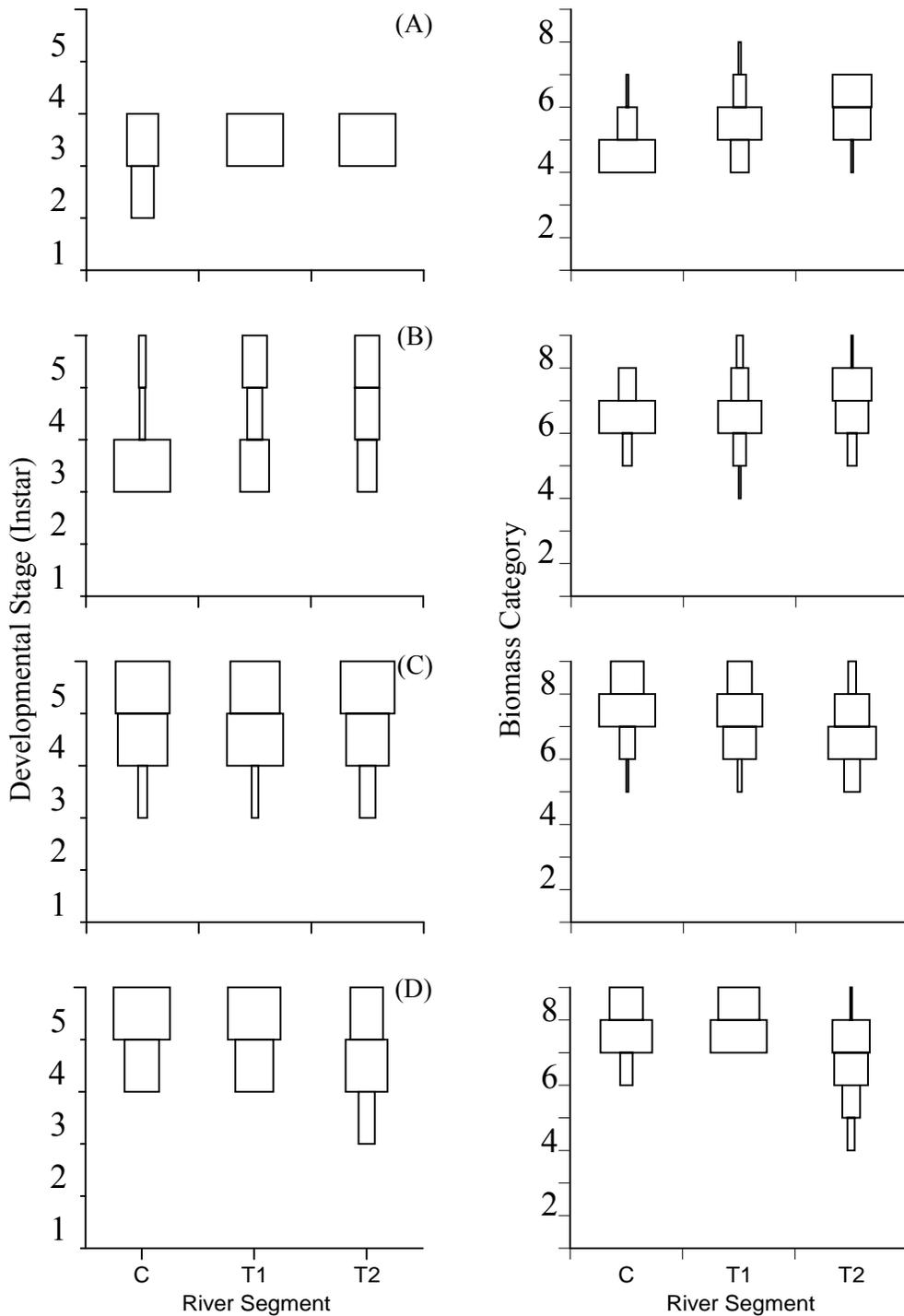


Figure 3.6. Frequency distributions for developmental stages (left) and biomass categories (right) of *B. occidentalis* among treatments for June (A), July (B), August (C), and September (D) of 2005. Width of each bar represents the relative proportion of individuals found in a development or biomass category.

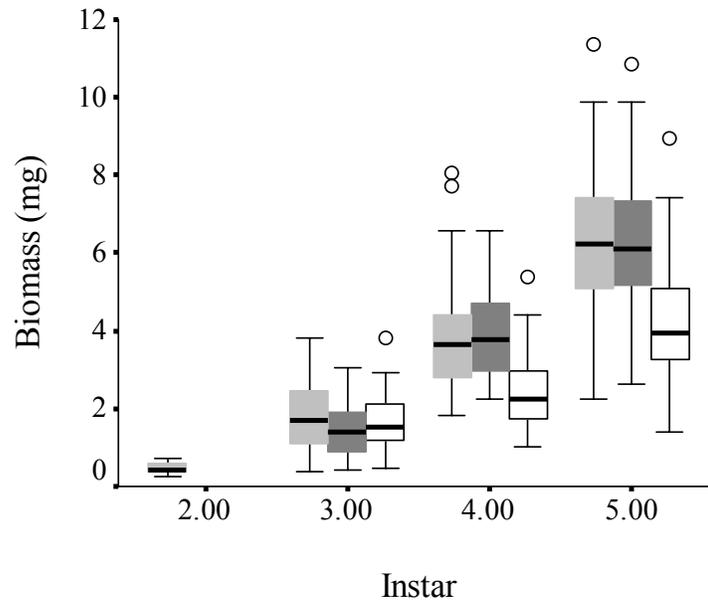


Figure 3.7. Boxplot of *B. occidentalis* biomass within individual instars among river segments for 2005. Reference segment displayed in light grey, T1 in dark grey, and T2 as transparent. The line within the box represents the median, the box spans data within the 25th and 75th percentiles, the whiskers denote maximum and minimum values unless outliers (circles) (1.5x interquartile range) were present.

CHAPTER 4:

**STRUCTURAL AND FUNCTIONAL RESPONSES OF STREAM
INVERTEBRATES TO IRRIGATION WATER WITHDRAWALS**

Scott W. Miller, David Wooster, and Judith L. Li

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Abstract

Irrigation water withdrawals are ubiquitous in arid and semi-arid regions; however, predictable macroinvertebrate responses have not emerged. Inconsistent responses have been attributed to the amount of water withdrawn in addition to the physicochemical and biological composition of studied systems. We sought to determine if species traits (e.g., voltinism, thermal preference, dispersal, size) influence macroinvertebrate responses to irrigation water withdrawals of similar magnitude and duration. We sampled above and below water diversions on 12 rivers in central and eastern Oregon and Washington, USA that spanned an altitudinal gradient. For each river discharge was reduced by 75% or more by a single point of withdrawal. When we considered all 12 rivers independent of species traits, macroinvertebrates were highly resistant to irrigation water withdrawals. We observed significant alterations to the quality and quantity of the hydrologic environment, in addition to increased algal standing stocks and minimum temperatures; however, macroinvertebrate responses were limited to increased downstream densities, as indices (e.g., diversity, richness) and community composition did not significantly change. Functionally, species traits were more sensitive than structural indices; proportional abundance for 10 of 52 species traits significantly differed above and below all points of diversion. Trait changes suggest a shift in functional composition to compensate for hydrologic alterations (e.g., decreased streamlining and swimmers) and reduced habitat area (e.g., increased predators). To further assess the influence of species traits, we clustered reference reaches (upstream) by density weighted species traits to identify groups of rivers with similar species traits (i.e., trait-based groups). Rivers grouped according to high, mid, and low elevation reaches and represented a strong gradient of increasing resistance and resilience from high to low elevations; however, we did not find evidence for differential susceptibility to water withdrawals among the three trait-based groups of rivers. Though species traits appear to influence macroinvertebrate responses to low flow disturbances, frequencies of trait states most vulnerable to water withdrawals were too homogenous to elicit differential responses at the spatial scale encompassed by our study.

Introduction

Agriculture is the most common land use in the world and accounts for 90% of total freshwater consumption (Meyer and Turner 1992, Oki and Kanae 2006). In arid and semi-arid regions, agricultural production depends on surface and groundwater withdrawals, which represent primary causes of hydrologic alterations to river systems (Allan and Flecker 1993, Dynesius and Nilsson 1994, Bunn and Arthington 2002). For example, surface water withdrawals for irrigated agriculture can change the magnitude, duration, timing, and spatial extent of low flow conditions (Wilber et al. 1996, Eheart and Tornil 1999, Miller et al. 2007). These changes can significantly impact river ecosystems by altering water quality, thermal regimes, ecosystem connectivity, and geomorphology (Meier et al. 2003, Benstead et al. 2005, Dewson et al. 2007), all of which directly or indirectly affect community composition, life history adaptations, and trophic structure (Junk et al. 1989, Allan 1995, Bunn and Arthington 2002).

The ubiquity of surface water withdrawals, at both global and regional scales is highlighted by the geographic diversity of recent studies investigating impacts to macroinvertebrate communities (e.g., U.K.: Castella et al. 1995, United States: McIntosh et al. 2002, Australia: McKay and King 2006, New Zealand: Dewson et al. 2007). Despite increasing study, predictable biological responses have not emerged. While some studies observed detrimental impacts to macroinvertebrate communities (Dudgeon 1992, Rader and Belish 1999, McIntosh et al. 2002, Miller et al. 2007), others found little to no impact (Castella et al. 1995, Dewson et al. 2003, McKay and King 2006, Dewson et al. 2007). Both the paucity of adverse impacts at low withdrawal levels and variability in responses among studies are often attributed to threshold response patterns, as well as physicochemical and biological differences among systems (Castella et al. 1995, Rader and Belish 1999, Dewson et al. 2003). Corrarino and Brusven (1983), Rader and Belish (1999), and Miller et al. (2007) all provide evidence for threshold responses, with only high levels of withdrawal having adverse impacts. In contrast, the role of functional composition or species traits (i.e., life history strategies, ecological preferences,

morphological adaptations) in explaining variable macroinvertebrate responses to low flow disturbances remains less certain.

Species traits vary at local and regional scales according to differences in physical selective forces, including both natural patterns of spatiotemporal variability (Poff and Ward 1990, Townsend and Hildrew 1994, Richards et al. 1997, Heino 2005) and anthropogenic alterations (Chessman and Royal 2004, Doledec et al. 2006). This physical template determines the susceptibility of macroinvertebrates to disturbance (resistance), as well as their ability to recover following removal of a stressor (resilience) (Townsend and Hildrew 1994). For example, macroinvertebrate communities found in disturbance-prone areas typically have higher proportions of small, highly fecund, mobile individuals with broad habitat requirements (Townsend and Hildrew 1994, Townsend et al. 1997b, Doledec et al. 2006). Such differences in species traits may cause two geographically separated systems or stream reaches exposed to the same low flow event to respond in very different ways. Consequently, differences in species traits within or among systems could confound the exclusive use of community composition to quantify water withdrawal impacts (Resh et al. 1988, Townsend et al. 1997a, Lake 2000). We hypothesize that regional and local differences in species traits of macroinvertebrate communities influence responses to water withdrawals and may explain variable responses among studies.

Our objectives were to: (i) assess the impacts of irrigation water withdrawals on a diversity of lotic systems; and (ii) determine if macroinvertebrate communities differing in species traits respond similarly to water withdrawals of equal magnitude and duration. We predicted responses of macroinvertebrate communities would depend on species traits, thus resulting in inconsistent biological responses among systems or locations in a watershed. For example, we anticipated natural differences in species traits among rivers according to elevation or stream size, with traits conferring resistance and resilience (e.g., small body size, desiccation tolerance, generalist feeding strategies) increasing from high to low elevations. Consequently, adverse responses to water withdrawals (e.g., reduced

richness and lower Ephemeroptera, Plecoptera, and Trichoptera (EPT) density) were expected to be greatest at high elevation reaches, that we predicted to be inhabited by taxa with narrow habitat requirements (e.g., preference for cold – stenothermic thermal regimes and erosional habitats), specialized feeding strategies (e.g., predators or shredders), and low dispersal abilities.

In addition to examining compositional responses of macroinvertebrates, we also sought to determine if water withdrawals reduce or eliminate the occurrence of specific species traits. We hypothesized water withdrawals would act as strong environmental filters since they alter similar environmental variables (e.g., hydrologic conditions, thermal regime, organic matter resources) that filter suites of traits from the regional species pool. Specifically, we predicted the representation of traits related to thermal and velocity preferences, mobility, desiccation tolerance, voltinism, and shape would significantly change above and below points of water withdrawal.

Methods

Study Area

We studied 12 rivers within the Blue Mountains, Columbia Plateau, and Cascade Foothills ecoregions (Omernik 1987) of central and northeastern Oregon and southeastern Washington, U.S.A (Fig. 4.1). The 12 rivers span a gradient of watershed areas, elevations, and physicochemical conditions (Table 4.1). In general, watershed area and stream order were inversely related to elevation. The 12 rivers encompass a variety of vegetation types, ranging from sagebrush grasslands and dry land agriculture at lower elevations to Ponderosa pine (*Pinus Ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), spruce (*Picea*), and fir (*Abies*) with increasing elevation. All rivers are dominated by a snowmelt hydrologic regime with maximum flows occurring from March to June; however, two rivers located in the Cascade Foothills ecoregion, Squaw and Tumalo, are moderately influenced by springs due to a young volcanic geology.

Summer discharge is intensively managed for irrigated agriculture in all study systems, with a single diversion withdrawing greater than 75% of ambient flow levels (Table 4.1); no other major dams or diversions exist upstream of study sites. Water withdrawals operate from approximately March to October and interact with summer low flows to produce minimum flow levels in late August or early September. Diversion structures are concrete, rock, or timber dams that span the entire bankfull width and range in height from 0.5 to 1.8 m.

We sampled each individual river once over a 24 h time period during late August or early September of 2005 or 2006. However, the Walla Walla River was sampled in late June to meet the 75% discharge reduction criteria. Three individual reaches were sampled above (reference) and below (treatment) each diversion, with reach length equal to 10 x bankfull width. Reaches were located immediately above and below the diversion structure and at distances 25 and 50 x bankfull width. Individual reaches were named by river (Table 4.1), location above (A) or below (B) the diversion, and distance from the diversion (1 – 0 x bankfull, 2 – 25 x bankfull, and 3 – 50 x bankfull – e.g. FIA3).

Data collection: Biological variables

Within each reach, a Surber sampler (0.09 m², 500 µm mesh) was used to collect six randomly located benthic macroinvertebrate samples from riffle habitats to a depth of 10 cm. We constrained sampling to riffle habitats because they are thought to be most affected by low flow events (Stanley and Fisher 1997). The six Surbers from each reach were composited, preserved in 70% ethanol, and processed using a 500 count subsampling procedure (Caton 1991, Vinson and Hawkins 1996). When possible, we identified macroinvertebrates to genus (Merritt and Cummins 1996). Chironomidae midges, however, were identified to tribe and all non-insect taxa were identified to either order or family (Thorp and Covich 1991). Macroinvertebrate density, richness, Shannon's diversity index (Magurran 1988), and EPT and Non-insect richness, density,

and relative abundance were computed for each reach and are referred to herein as macroinvertebrate indices.

We collected periphyton samples by randomly selecting six rocks from riffle habitats adjacent to Surber sample locations. Periphyton was removed from a 6.5 cm² portion of each rock, placed into a light-sealed bottle, and stored frozen. Defrosted samples were split with a plankton splitter for determination of ash-free dry mass (AFDM) and biomass of chlorophyll-*a*. AFDM was determined according to the methods of Steinman and Lamberti (1996); to measure biomass of chlorophyll-*a* we used the hot ethanol extraction method (Sartory and Grobbelaar 1984) and spectrophotometry of the filtrate. Subsequent chlorophyll-*a* concentrations were determined using the equation of Steinman and Lamberti (1996).

Data collection: Species traits

The 136 unique taxa collected from all 12 rivers were coded according to 17 species traits having a total of 52 states (Table 4.2). The 17 traits represent life history, mobility, and morphological traits, in addition to ecological preferences. Traits were selected based on hypothesized responses to the direct or indirect effects of irrigation water withdrawals, resistance or resilience to low flow disturbances, and recommendations of Poff et al. (2006) addressing the evolutionary lability of species traits and their likelihood for independent responses. Some traits considered less plastic by Poff et al. (2006) (desiccation resistance, emergence synchronization, development, female dispersal, swimming ability, and shape) were included because of their hypothesized susceptibility to flow alterations or ability to facilitate recovery following flow alterations. Because responses of both insects and non-insects were of interest, we also included the ‘number of reproductive cycles per individual’ and ‘life span’ as traits to further differentiate life history strategies of non-insect from insects.

Each unique taxon was assigned a single trait state for each of the 17 traits based on predominant values from the literature (Finn and Poff 2005, Poff et al. 2006). We did not

implement ‘fuzzy coding,’ which allows for variation within a taxon on a specific trait (Chevenet et al. 1994), because available biological and ecological information was insufficient for the geographic region. Traits were assigned at the genus level for all insect taxa except for some Diptera according to Poff et al. (2006); chironomidae traits were assigned at the level of tribe. Non-insects were assigned at the family or class level according to Thorp and Covich (1991) and literature sources therein.

Data collection: Physicochemical variables

We measured discharge at two transects (top and bottom) per reach using a Marsh McBirney digital flow meter. Depth and velocity (0.6 water depth) measurements were made at a minimum of 20 points across the stream or at intervals that ensured one cell (depth x width) did not contain greater than 5% of total discharge (Buchanan and Somers 2005). In addition, stream velocity (measured at 0.6 water column depth and at the water-substrate interface and averaged for analyses) and depth were measured at all Surber locations. Wetted width, bankfull width, and solar exposure were measured at the top, middle, and bottom of each reach. Solar exposure was measured using a Solar Pathfinder™ (Solar Pathways, Colorado Springs, Colorado) positioned in the center of the river channel for each of three transects. Channel slope was measured over the length of each reach, and median particle size of the substrate (D_{50}) was quantified using the Wolman (1954) pebble count method. In addition, embeddedness and silt cover were estimated at each Surber location using a categorical scale. Embeddedness was recorded as particles could be picked-up with: no resistance (i), minor resistance (ii), strong resistance (iii), and could not be moved (iiii). Silt cover was recorded based on percent cover as: 0-10% (1), 11-25% (2), 26-50% (3), 51-75% (4), >75% (5).

Temperature was continuously monitored at 30 min intervals within each reach over a 24 hour period that encompassed collection of macroinvertebrates using thermal data loggers. We computed three temperature statistics of potential relevance to macroinvertebrate communities: sum (temperature_{sum}), minimum (temperature_{min}), and

maximum (temperature_{max}) of 24 h temperature readings. A single in-situ measurement of specific conductance at 25°C and turbidity were also obtained from each reach.

Statistical analyses: Responses among all rivers

We used a nonparametric Wilcoxon signed rank procedure to test for above and below differences in environmental variables, macroinvertebrate indices, and proportions of trait states among all twelve rivers. Average percent change above and below each diversion was used as the response variable, which was calculated as:

$$\%change = \frac{(below_{avg.} - above_{avg.})}{above_{avg.}} \times 100$$

Nonparametric procedures were chosen because average percent change values were not normally distributed and transformations did not improve normality. Because averages were used for above and below comparisons among all rivers, we ensured all significant differences exceeded the average percent change among reference reaches (i.e., background rates of change). We recognize that as more tests are conducted, the probability of finding significant results by chance increases; however, Bonferroni procedures were not used to correct alpha levels ($\alpha = 0.10$) because they are overly conservative and therefore increase the chance of ignoring ecologically meaningful results (Moran 2003). In all cases, the number of observed significant results was greater than expected by chance alone (significant result expected by chance: environmental variables < 1; macroinvertebrate indices < 1; and proportions of trait states 2.5).

Prior to conducting statistical analyses we used rarefaction to standardize richness estimates to the density of the least abundant reach (HUA3), which had a density of 12,595 individuals. We performed rarefaction standardizations because density estimates varied within and among rivers by over an order of magnitude and richness estimates are known to increase with the number of individuals processed (Gotelli and Colwell 2001). Rarefaction standardizations were performed by randomly subsampling 12,595 individuals from each of the 71 other reaches using Ecosim simulation software (Gotelli

and Entsminger 2006). Average species richness from 100 randomizations was used in subsequent analyses pertaining to richness estimates.

We tested for differences in community composition above and below diversions using a multiple response permutation procedure (MRPP) blocked by river with Euclidean distance (Mielke and Berry 2001). MRPP is a nonparametric permutation procedure that tests for differences among two or more groups. A p -value assesses the probability of observed group differences under the null hypothesis, while an A -statistic quantifies effect size and within group homogeneity (McCune and Grace 2002). MRPP tests were run on the log transformed ($\log_{10}(x+1)$) reach x species density matrix (72 x 136).

Statistical analyses: Grouping rivers by species traits – ‘trait-based groups’

To identify groups of rivers with similar species traits for comparison of invertebrate responses to water withdrawals, we clustered reference (above) reaches by species traits using hierarchical agglomerative cluster analysis in PC-ORD version 5 (McCune and Mefford 2005). Reference reaches were grouped by dissimilarity using Sørensen’s distance and the flexible beta linkage method with $\beta = -0.25$. Prior to conducting this analysis, a series of relativizations, matrix multiplication, and transformations was performed. First, the reference reach x species density matrix (36 x 123) was relativized by reach totals because density estimates varied by an order of magnitude among rivers. All species were retained within this matrix because the deletion of rare species did not increase the signal to noise ratio (McCune and Grace 2002). Second, we multiplied the reference reach x species density matrix (36 x 123) by the species x trait matrix (136 x 52) to obtain the relative abundance of a trait state within a reach. Lastly, the resulting matrix (36 x 52) was transformed using arcsine-squareroot to improve distributional properties of the data. Indicator species analysis (ISA) was used to quantitatively determine the most ecologically meaningful point for pruning the cluster analysis dendrogram (Dufrene and Legendre 1997). For our application, this technique identifies the grouping level at which trait states have maximum discriminatory efficiency among groups of rivers. Specifically, an average p -value for all 52 trait state indicator values

was obtained at each grouping level in the dendrogram. The dendrogram was pruned at the grouping level yielding the lowest average p -value.

To identify which trait states were characteristic of the trait-based groups derived from cluster analysis, we overlaid groups onto an NMS ordination of reference reaches ordinated by the relative abundance of species traits (i.e., same reference reach x species trait matrix (36 x 52) used in cluster analysis). NMS is an indirect gradient analysis technique that uses rank community dissimilarities and iteratively searches for the optimal arrangement of sample objects in as few dimensions as possible (McCune and Grace 2002). NMS was run with Sørensen's distance in PC-ORD version 5 (McCune and Mefford 2005). We assessed dimensionality by evaluating the relationship of final stress versus the number of dimensions; in addition, a Monte Carlo test with 250 runs of the randomized data quantified the probability of observing a stress as low as or lower than that observed through chance alone. Ordination solutions were rigidly rotated to maximize loadings of environmental variables with individual ordination axes. Pearson correlation coefficients for the relationship of individual trait states with ordination axis scores were used to assess the relative abundance of trait states within groups. A value of 0.40 was chosen as a cutoff for interpreting ecologically meaningful correlations, which was more conservative than the Pearson coefficient corresponding to statistical significance (0.32).

Statistical analyses: Differential responses among 'trait-based' groups

We compared percent above and below change in environmental variables, macroinvertebrate indices, and trait proportions among trait-based groups with a Kruskal-Wallis test. Again, we used a nonparametric procedure because transformations did not alleviate departures from normality and unequal variances. In contrast, above and below differences in community composition among trait-based groups were compared using compositional vectors (McCune 1992). Compositional vectors dissect changes in community composition into the amount and direction of change. For our application, we assessed whether the amount or direction of change above and below points of

diversion differed among the three trait-based groups. The amount and direction of change were computed using Sørensen's distance of log transformed ($\log_{10}(x+1)$) macroinvertebrate densities and were compared among trait-based groups with MRPP.

Results

Responses among all rivers: Environmental variables

Discharge reductions ranged from 75 to 99% among all 12 rivers (Table 4.1). Although continuous discharge data were not available, withdrawal amounts exceeded 75% of ambient levels from June to September for all rivers except the Walla Walla, at which 75% discharge reductions occurred in June only (personal communication with irrigation districts). Mean velocity, depth, and wetted width significantly decreased below diversions, while chlorophyll-*a* and AFDM of periphyton communities and temperature_{min} significantly increased (Table 4.3).

Responses among all rivers: Macroinvertebrate communities

Macroinvertebrate density, EPT density, and non-insect density significantly increased below diversions (Table 4.4, Fig. 4.2). In contrast, proportional abundances of EPT taxa significantly decreased below diversions by 8.6% on average; however, reductions were not greater than the average percent change among reference reaches (10.7%). Whereas density increases were positively correlated with wetted width reductions, the proportional abundance of EPT taxa was negatively correlated with wetted width reductions (Fig. 4.3); no other environmental variables showed significant relationships with macroinvertebrates indices.

Differences in macroinvertebrate community composition above and below individual diversions was greater than expected by chance alone (blocked MRPP by river: $p = 0.019$); however, observed differences were weak ($A = 0.016$).

Responses among all rivers: Species traits

Ten out of 52 trait states representing each of the four major trait categories (life history, mobility, morphological, and ecological) significantly differed above and below all points of diversion. Trait states exhibiting significant differences were related to voltinism (multivoltine increased, $p = 0.065$), emergence synchronization (poorly synchronized decreased, $p = 0.065$; well synchronized increased, $p = 0.025$), dispersal (strong swimming ability decreased, $p = 0.065$; low adult dispersal decreased, $p = 0.092$; high crawling rate increased, $p = 0.092$), streamlining (streamlined decreased, $p = 0.055$), functional feeding groups (predators increased, $p = 0.078$), and habit (swimmers decreased, $p = 0.065$; sprawlers increased, $p = 0.005$) (e.g., Fig. 4.4).

Grouping rivers by species traits – ‘trait-based groups’

We distinguished three groups of rivers from the cluster analysis of 32 reference reaches by the relative abundance of species traits. We refer to these as high, mid, and low elevation reaches, which correspond to small, medium and large river systems (Table 4.1). Reaches within a river formed initial groupings and were subsequently joined by different rivers having similar functional attributes.

According to NMS ordination, rivers within the three trait-based groups were separated by two major gradients, which retained 93% of the original variability (Fig. 4.5a). Axis one retained 71% of the variance and represented a gradient of increasing resistance and resilience from high to low elevations (elevation: $r = -0.88$) or small to large drainages ($r = 0.67$). For example, low and some mid elevation reference reaches had higher relative abundances of taxa characterized by: (i) high adult dispersal and drift rates; (ii) multiple unsynchronized generations per year; (iii) preference for cool to warm, depositional habitats; and 4. small sized individuals (Fig. 4.5b). Along this gradient of elevation, substrate size ($r = -0.56$) and slope ($r = -0.64$) decreased, whereas temperature_{sum} ($r = 0.69$), wetted width ($r = 0.65$), chlorophyll-*a* ($r = 0.63$), and chlorophyll AFDM ($r = 0.55$) increased from high to low elevations. The NMS ordination had a stress of 9.67 and instability of 0.00001, corresponding to a stable solution with low risk of false interpretation (McCune and Grace 2002).

The second trait gradient, axis 2, retained 22% of the variance and further distinguished mid elevation from high and low reference reaches (Fig. 4.5a). Mid elevation reaches were associated with: (i) higher proportions of semivoltine taxa, slow or nonseasonal development, and desiccation tolerance; (ii) preferences for erosional habitats; and (iii) nonstreamlined individuals with low swimming capabilities (Fig. 4.5b). Environmental gradients along axis two included decreased incoming solar radiation ($r = -0.59$) temperature_{min} ($r = -0.52$), turbidity ($r = -0.44$), and discharge ($r = -0.41$), whereas alkalinity was the only variable to increase along axis 2 ($r = 0.41$).

Differential responses among trait-based groups: Environmental variables

The magnitude of above and below differences for velocity, temperature_{min}, and D₅₀ significantly differed among the three trait-based groups (Table 4.3). Velocity reductions were significantly greater for high elevation reaches, whereas temperature_{min} showed little change above versus below diversions for high elevation reaches and increased below diversions for mid and low elevation reaches. Conversely, median particle size was reduced below diversions in high elevation reaches, but showed little change in mid or low elevation reaches.

Differential responses among trait-based groups: Macroinvertebrate communities and trait proportions

Above and below changes in macroinvertebrate indices did not differ among the three trait-based groups (Table 4.4, Fig. 4.2). In contrast, the amount of change in macroinvertebrate community composition differed among the three groups (MRPP: $p = 0.06$; $A = 0.104$), while the direction of change did not differ (MRPP: $p = 0.22$; $A = 0.06$). For the amount of change, high elevation reaches changed significantly more than mid and low elevations (Fig. 4.6). The above and below response of only two trait states, common occurrence in drift ($H = 6.37$, $p = 0.041$) and low crawling rate ($H = 5.8$, $p = 0.05$) significantly differed among trait-based groups; however, the number of observed significant results was less than the 2.5 significant results expected by chance alone given

the total number of tests performed. Common occurrence in drift increased and low crawling rate decreased to a greater extent for high elevation reaches.

Discussion

Responses among all rivers: Macroinvertebrate indices and community composition

Macroinvertebrate community composition among all 12 rivers was highly resistant to irrigation water withdrawals exceeding 75% of ambient flow levels. We observed significant alterations to the quality and quantity of the hydrologic environment, in addition to increased algal standing stocks and minimum temperatures; however macroinvertebrate community composition did not change appreciably. Increased macroinvertebrate density (i.e., overall, EPT, and non-insect) was the only significant response among all rivers, as macroinvertebrate diversity, taxonomic richness, and relative abundance remained unchanged. Furthermore, most indices showed increasing and not decreasing trends below diversions (positive difference) and no taxa were consistently exclusive to upstream or downstream reaches within a river. Although the average proportional abundance of EPT taxa significantly decreased below all diversion (range: -16 to 5%), reductions were not greater than the average percent change among reference reaches for all rivers (10.7%). These results correspond to those of Castella et al. (1995), McKay and King (2006), and Dewson et al. (2007), who failed to find negative responses to water withdrawals exceeding 90% of ambient levels.

Density changes are a common response of macroinvertebrates to reduced discharge levels, both natural (Smith and Pearson 1984, Stanley et al. 1994, Suren et al. 2003) and anthropogenic (Gore 1977, Rader and Belish 1999, Dewson et al. 2007). Our observed positive linear relationship between wetted width reductions and increased density supports the hypothesis that organisms crowd into areas of reduced habitat availability during low flows (Gore 1977, Castella et al. 1995, Dewson et al. 2007). Despite the strength of this relationship, the direction (i.e., increase or decrease) and magnitude of density responses to width reductions has varied among studies. For example, density can increase in the absence of width reductions (Rader and Belish 1999, Dewson et al.

2003 and 2007), but in other studies density decreases accompanied wetted width reductions (McIntosh et al. 2002, McKay and King 2006, Miller et al. 2007). Rader and Belish (1999) attributed increased densities to elevated water temperatures in the absence of width reductions, which could increase rates of both primary and secondary production. We observed significant increases in minimum temperatures, periphyton AFDM, and biomass of chlorophyll-*a*, but they were not related to density increases ($r = 0.2$, $r = 0.03$, $r = 0.02$ respectively). Water quality conditions within remaining wetted habitats might explain variability in the direction and magnitude of change among studies. Boulton (2003) suggests densities will increase in areas of reduced habitat availability until water quality declines and exceeds threshold tolerances of individual taxa.

Despite density increases below diversions on a per m² basis in our study, the total number of invertebrates was reduced by 13% on average after scaling estimates to total wetted habitat availability (i.e., total riffle area). Thus, the reduced habitat appeared unable to accommodate all organisms displaced by wetted width reductions. Consequently, downstream reaches experienced a net loss of organisms compared to upstream reaches, although reductions were relatively small compared to the extent of habitat loss. Density dependent mechanisms (e.g., increased competition and predation) resulting from reduced habitat area, food quality, and food quantity may explain decreased densities (reviewed in Dewson et al. 2007).

Responses among all rivers: Species traits

Human alterations to river systems can represent new and sometimes novel selection forces, both on ecological and evolutionary time scales (Lytle and Poff 2004). We asked if irrigation water withdrawals act as such forces by altering the representation of trait states from the regional species pool. The proportional abundance for 10 of 52 (20%) trait states representing 8 of 17 traits significantly differed above and below all points of diversion. Despite ecologically insignificant changes in community composition, we believe select traits differed above and below diversions because specific traits co-

occurred in several ubiquitous and abundant taxa affected by water withdrawals. For example, the baetidae mayfly *Baetis* constituted 16 percent of average abundance above all diversions and only 9 percent below; all traits significantly decreasing below diversions occur in *Baetis* (e.g., multivoltine, poorly synchronized, low adult dispersal, strong swimmer, streamlined). Similar patterns were observed for the less abundant and ubiquitous baetids *Acentrella*, *Dipheter*, and *Fallceon*. Doledec et al. (2006) found similar results when only 8% of species responded to a land-use gradient in comparison to 26% of species traits.

Trait changes suggest a shift in functional composition to compensate for hydrologic alterations imposed by water withdrawals. For example, traits facilitating mobility within the water column and avoidance of high flow environments through dorsoventral flattening decreased, whereas the relative abundances of sprawlers, predators, and high crawling rates increased below points of water withdrawal. Crawlers might have an advantage over swimmers during low flow conditions because of a greater ability to seek out favorable habitats or utilize spatial refugia (Extence 1981, Delucchi 1989, Townsend and Hildrew 1994). Predators may also be able to exploit low flow conditions as prey concentrate into reduced habitat areas and benign environmental conditions prevail; both have been shown to increase predator-prey interactions (Powers et al. 1988, Peckarsky et al. 1990, Lake 2003). Responses of individual trait states parallel responses to the microhabitat variables of stream hydraulics, periphyton cover, and substrate composition in other studies (Gayraud et al. 2003, Lamouroux et al. 2004, Heino 2005, Doledec et al. 2006), all of which were significantly altered by water withdrawals in our study.

Conversely, proportional changes in trait states did not always accompany changes in environmental conditions, and some trait changes appear counterintuitive. For example, we observed fewer multivoltine taxa with poorly synchronized emergence below points of diversion, though these traits commonly infer resistance and resilience to disturbance (Townsend and Hildrew 1994, Mackay 1992); Townsend et al. (1997b) found taxa with these traits to increase in highly variable habitats. Such anomalies demonstrate the need

for caution when interpreting changes in multiple trait states across environmental gradients (Doledec et al. 2006, Poff et al. 2006). Results presented herein and findings by Poff et al. (2006) demonstrate that suites of traits can co-occur in taxa as syndromes of highly correlated trait states. This lack of independence can potentially inflate the number of trait responses and lead to spurious interpretations. Correlations among traits may also constrain responses of individual traits along environmental gradients. For example, the proportion of grazers did not increase in our study below diversions, despite significant increases in the quantity of benthic biofilms. The response of this trait might be limited because grazers in our study tended to be streamlined and prefer high flow environments, which represent reduced trait states below diversions.

Grouping rivers by species traits – ‘trait-based groups’

In support of our first hypothesis, macroinvertebrate species traits differed among reference reaches found at different elevations. Trait-based gradients were driven by both ecological and biological traits (i.e., life history, mobility, and morphology) reflecting changes in habitat conditions and disturbance regimes from high to low elevations. For example, proportions of warm-water taxa, collector filterers and gatherers, and preferences for depositional areas increased from high to low elevations. These changes paralleled observed environmental gradients of increasing temperature, wetted width, and biomass of periphyton and chlorophyll-*a*; and decreased median particle sizes from high to low elevations. Such changes demonstrate that multiple species traits in addition to functional feeding groups mirror longitudinal habitat gradients outlined in the River Continuum Concept (RCC) (Vannote et al. 1980).

Gradients of increasing resistance and resilience traits from high to low elevations are likely driven by the interaction of temporal variability and human impacts (i.e., disturbance regime). Although long-term data were not available for all rivers, annual variability (i.e., annual maximum minus minimum) for discharge and temperature was inversely related to elevation and watershed area for six of the studied rivers (unpublished data, Miller). Horwitz (1978) and Stanford and Ward (1981) observed

similar spatial patterns of variability for temperature and discharge respectively, in snowmelt rivers of the Rocky Mountains. Thermal- and discharge-driven variability are often used to define the temporal component of Southwood's habitat template (1977) (Chessman and Royal 2004), with variable environments having similar functional composition to that found for our lowland reference reaches (Townsend and Hildrew 1994, Townsend et al. 1997a). Despite the exclusive use of 'reference' reaches for developing trait-based groups these sites were not free from human impacts of thermal pollution, sedimentation, and nutrient loading. Human impacts increased in intensity at lower elevations across the study region (personal observations) and likely interacted with natural altitudinal differences in disturbance magnitude to increase numbers of disturbance adapted organisms at lower elevations.

Differential responses among trait-based groups

Despite differences in species traits among high, mid, and low elevation reference reaches, we observed only weak evidence for differential responses to water withdrawals across elevations. High elevation reaches exhibited greater above and below rates of change, but macroinvertebrate communities were not adversely impacted. Indices typically sensitive to disturbance (e.g., richness, proportion and density of EPT taxa) exhibited non-significant increases and not decreases below diversions for high elevation reaches. The paucity of significant differences among groups could reflect low statistical power resulting from high within group variance. Statistical power ranged from 0.09 – 0.88 for detecting a 25% change in macroinvertebrate indices among trait-based groups at the 0.05 alpha level.

Increased amounts of above and below change in macroinvertebrate community composition at high elevation reaches was likely caused by greater environmental changes, not necessarily reflecting species traits. Velocity and substrate size class reductions were significantly greater at high elevation reaches, and percent above and below change in velocity had the only significant correlation coefficient ($r = 0.57$) with the amount of above and below change in macroinvertebrate community composition

(Sørensen's distance) of all environmental variables. If greater rates of change were related to species traits we would expect above and below differences in trait states to be greater for high elevation reaches, which were not observed.

Inconsistent responses of stream macroinvertebrates to water withdrawals have been attributed to the amount of water withdrawn in addition to the physicochemical and biological composition of studied systems. When controlling for the amount of water withdrawn, we did not find evidence for differential macroinvertebrate responses among elevations related to species traits. The paucity of significant results, in lieu of frequencies for 10 of 52 trait states significantly differing below points of water withdrawal suggests sensitive trait states had a homogenous distribution across the study area.

Though our study spanned a range of stream types across three ecoregions, our results should be interpreted with caution since the temporal variability of hydrologic regimes was limited to differences in magnitude and duration, not frequency or predictability, which are known to be strong selective forces (Lytle and Poff 2004). Literature cited herein encompasses a greater range of hydrologic regimes, which potentially differ in frequency and predictability of temporal variability, in addition to magnitude and duration. Consequently, we would expect greater disparity in species traits across larger geographic areas and thus an increased potential for differential responses to disturbances of similar magnitude and duration. Our results suggest that systems exhibiting geographic variability in the frequency traits related to adult dispersal, swimming ability, shape, and emergence synchronization are most likely to exhibit differential responses to water withdrawals.

Our findings demonstrate the potential advantages of trait-based monitoring programs, which aid in the identification of indicator taxa, provide a mechanistic understanding for their presence or absence, and identify shifts in functional attributes of lotic ecosystems (Richards et al. 1997, Usseglio-Polatera et al. 2000, Doledec et al. 2006). In our study,

changes in trait states such as reduced streamlined body forms and high swimming capabilities identified obvious and expected responses to hydrologic alterations. In contrast, increased frequencies of predators downstream of diversions offered a potential density dependent explanation for overall reduced macroinvertebrate densities associated with wetted width reductions. Finally, because comparisons of macroinvertebrate responses to flow alterations and other disturbances across multiple spatial scales are confounded by high species turnover, species traits provide an improved approach to landscape scale studies of disturbance.

The observed resistance of macroinvertebrates to water withdrawals likely reflects how and when habitat conditions are altered relative to ambient levels. In our study, water withdrawals altered hydrologic variables and periphyton standing stocks, but they did not significantly alter thermal regimes, dissolved constituents, or siltation levels. As long as desiccation does not occur and water quality conditions are kept at tolerable levels, macroinvertebrates appear tolerant of low flow conditions (Dewson et al. 2007, Miller et al. 2007). For example, Miller et al. (2007) found macroinvertebrates highly resistant to hydrologic alterations, while the synergistic effects of reduced discharge and increased temperature significantly altered community structure and function. Furthermore, alterations to habitat quality and quantity imposed by water withdrawals are expected to have less effect when they mimic seasonal patterns of low flow levels, as they did in our study (Resh et al. 1988, Poff and Ward 1990, Wallace 1990). The antecedent hydrologic conditions for the studied systems included periods of low flow and even intermittency during summer months, which would favor life history strategies with resistance to low flow events. Water withdrawals that do not occur in concordance with predictable seasonal patterns of hydrologic variability will likely have far greater impacts.

Table 4.1. Physical characteristics and site abbreviations for the 12 target rivers. Land cover classes are coded as: Douglas-fir (D), spruce (S), fir (F), Ponderosa pine (PP), sagebrush grasslands (SG), agriculture (AG), and residential (RES).

River	Trait-based group ¹	Elevation (m)	Stream order	Watershed area (km ²)	Land cover class	Slope ² (%)	Bankfull width ² (m)	Discharge (m ³ s ⁻¹) Above	Discharge (m ³ s ⁻¹) Below	Discharge % Change
Fish (FI)	High	2031	2	21.0	DSF	5.2	6.0	0.27	0.01	-94.8
Big Sheep (BS)	High	1884	2	34.2	DSF	4.0	5.8	0.46	0.03	-93.5
Little Eagle (LE)	High	1596	2	23.5	DSF	8.3	5.2	0.53	0.03	-94.3
Hurricane (HU)	High	1366	3	75.7	DSF	3.2	12.4	1.5	0.01	-99.3
Tumalo (TU)	High	1119	3	152.6	PP	1.3	12.4	1.0	0.21	-79.0
North Powder (NP)	Mid	1101	3	150.2	PP / AG	2.4	18.4	0.37	0.04	-89.2
Pine (PI)	Mid	1036	2	77.1	SG / AG	3.4	5.6	0.18	0.01	-94.4
Squaw (SQ)	Mid	1019	3	354.5	PP	3.1	12.0	1.2	0.30	-75.0
South Fork John Day (SFJD)	Mid	701	4	1752.1	SG / AG	2.2	16.0	0.43	0.09	-79.1
Walla Walla (WW)	Low	253	4	336.7	AG / RES	2.1	20.0	3.1	0.70	-77.4
Umatilla (UM)	Low	192	5	5895.0	SG / AG	1.4	35.0	5.3	0.12	-97.7
Touchet (TO)	Low	123	4	1916	SG / AG	1.0	18.0	0.59	0.07	-88.1

¹Results of hierarchical agglomerative cluster analysis for the relative abundance of trait states within a reach

²Values represent average for six reaches per river (three above and three below point of water withdrawal)

Table 4.2. Species traits (17 total) and states (52 total) used for development of trait-based reference groups and for comparisons above and below points of diversion. See Poff et al. (2006) for descriptions of trait states.

Trait	Trait State
<i>Life History</i>	
Voltinism	Semivoltine Univoltine Multivoltine
Life Span	One year > one year
Reproductive cycles/individual	Iteroparous Semelparous
Development	Fast seasonal Slow seasonal Nonseasonal
Emergence synchronization	Poorly synchronized Well synchronized NA*
Desiccation	Yes No
<i>Mobility</i>	
Female dispersal	Low High NA ¹
Occurrence in drift	Rare Common Abundant
Max crawling rate	Very low Low High
Swimming ability	None Weak Strong
<i>Morphological</i>	
Shape	Streamlined Not streamlined
Size at maturity	Small Medium Large
Armoring	None Poor Good

Table 4.2. (Continued)

Trait	Trait State
<i>Ecological</i>	
Rheophily	Depositional only Depositional/erosional Erosional
Thermal preference	Cold stenothermic/cool eurythermal Cool/warm eurythermal Warm eurythermal
Functional feeding group	Collector-gather Collector-filterer Herbivore Predator Shredder
Habit	Burrow Climb Sprawl Cling Swim Skate

¹NA – Trait not applicable. NA was assigned for taxa that do not possess one of the trait states.

Table 4.3. Results of Wilcoxon signed rank tests comparing average percent change in environmental variables above and below points of diversion and results of Kruskal-Wallis tests for differences in percent change among trait-based groups. Significant differences at the 0.10 α level are in bold text.

	All rivers			Trait-based groups			H	P
	Average % change (SD)	W ₊	P	High Average % change (SD)	Mid Average % change (SD)	Low Average % change (SD)		
Discharge	-88.6 (9.0)	0	0.003	-91.3 (9.6)	-85.8 (8.8)	-87.6 (10.3)	0.54	0.762
Conductivity	-0.7 (8.6)	6.0	0.855	-5.3 (11.9)	1.2 (2.4)	4.5 (4.1)	3.47	0.176
Turbidity	171.9 (407.2)	40.0	0.221	356.8 (580.0)	-16.4 (37.3)	114.9 (275.9)	1.19	0.552
Wetted width	-40.3 (17.4)	0	0.003	-33.0 (17.5)	-45.3 (11.9)	-45.9 (24.7)	1.19	0.515
Velocity	-48.7 (17.3)	0	0.003	-60.4 (11.0)A	-33.3 (17.5)B	-49.8 (11.1)AB	5.66	0.059
Depth	-47.6 (15.8)	0	0.003	-55.1 (12.7)	-43.0 (14.4)	-41.2 (22.2)	1.91	0.386
Siltation	85.9 (155.0)	5.0	0.423	98.9 (158.6)	379.2 (516.6)	0 (0)	1.4	0.496
Embeddedness	0.29 (18.4)	26.5	0.959	0.95 (76.2)	16.4 (55.7)	-22.2 (69.4)	0.91	0.635
Temperature _(max)	3.0 (2.0)	60.0	0.108	-0.8 (8.0)	7.8 (5.2)	3.1 (1.2)	2.48	0.289
Temperature_(min)	2.6 (6.7)	65.0	0.045	-1.7 (6.7)A	6.1 (6.7)B	5.0 (3.3)B	5.62	0.060
Temperature _(sum)	2.7 (6.9)	58.0	0.147	-1.2 (8.2)	7.2 (5.3)	3.3 (2.3)	1.86	0.395
Solar radiation	1.2 (21.5)	39.0	1.0	-1.4 (11.6)	7.4 (37.5)	-2.6 (8.0)	0.80	0.671
Chlorophyll-a	162.3 (189.0)	78.0	0.003	244.6 (199.7)	145.6 (225.5)	47.3 (54.7)	1.72	0.424
AFDM	88.7 (123.0)	68.0	0.025	134.9 (124.8)	77.3 (142.6)	27.0 (101.1)	2.47	0.291
D50	-10.2 (19.0)	20.0	0.147	-24.3 (14.9)A	-5.7 (18.7)AB	7.4 (3.7)B	5.8	0.055

^ADifferent letters indicate statistical significance at the 0.10 α level.

Table 4.4. Results of Wilcoxon signed rank tests comparing average percent change in macroinvertebrate indices above and below points of diversion and results of Kruskal-Wallis tests for differences in percent change among trait-based groups. Significant differences at the 0.10 α level are in bold text.

	All rivers			Trait-based groups			H	P
	Average % change (SD)	W ₊	p	High Average % change (SD)	Mid Average % change (SD)	Low Average % change (SD)		
Density	44.3 (29.3)	77.0	0.003	37.0 (18.7)	59.3 (22.7)	36.5 (48.5)	1.44	0.484
Richness	5.4 (12.7)	56.5	0.196	10.4 (12.7)	-1.3 (7.9)	9.2 (9.3)	2.89	0.236
Diversity	2.2 (11.2)	49.0	0.456	6.9 (11.6)	-6.5 (9.5)	5.9 (3.0)	3.96	0.138
Non-insect density	242.9 (481.3)	61.4	0.092	353.8 (678.9)	250.3 (413.6)	48.2 (88.1)	2.03	0.363
Non-insect proportion	116.4 (313.4)	51.0	0.367	221.0 (477.2)	67.5 (148.5)	7.5 (39.2)	0.21	0.898
Non-insect richness	11.9 (26.0)	44.0	0.113	21.8 (21.4)	-4.1 (19.7)	16.7 (37.9)	4.19	0.123
EPT density	30.2 (25.0)	73.0	0.009	38.4 (22.3)	28.8 (19.8)	18.3 (38.4)	0.54	0.762
EPT proportion	-8.6 (15.2)	13.0	0.045	1.7 (13.1)	-17.1 (4.1)	-14.3 (21.1)	4.18	0.124
EPT richness	2.3 (11.8)	41.0	0.505	11.02 (8.3)	-5.5 (7.3)	-1.9 (14.6)	4.15	0.125

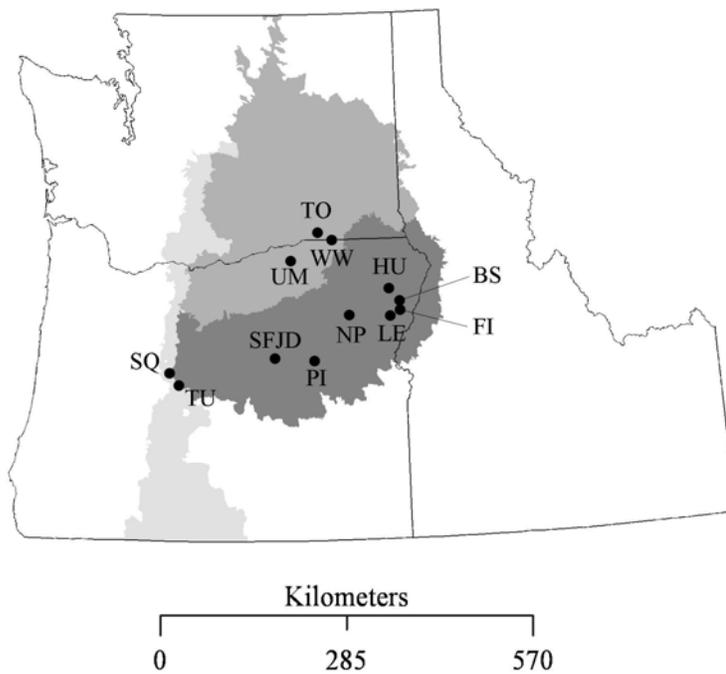


Figure 4.1. Location of the 12 study rivers within the Cascade Foothill (light grey), Columbia Plateau (medium grey), and Blue Mountain (dark grey) ecoregions of Oregon and Washington, U.S.A. Table 1 provides site abbreviations and physical characteristics.

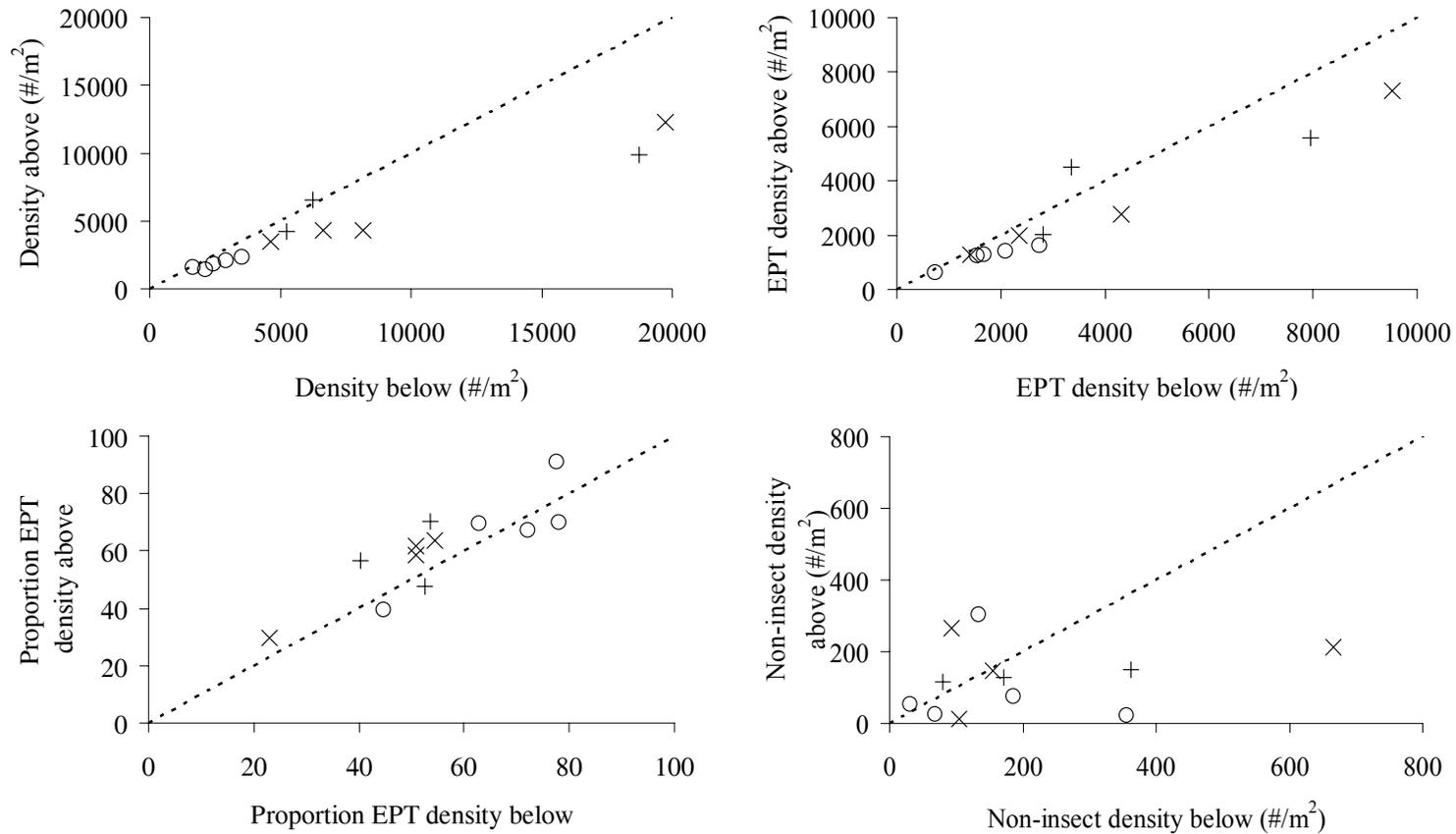


Figure 4.2. Comparison of average macroinvertebrate density, EPT density, proportional abundance of EPT taxa, and non-insect density above and below points of water withdrawal. Points grouped by trait-based groups: High – circles; Mid – Xs; and Low elevation – plus signs. Dashed line represents the one-to-one line. Points falling below the line represent increases and points falling above the line represent decreases below the point of water withdrawal.

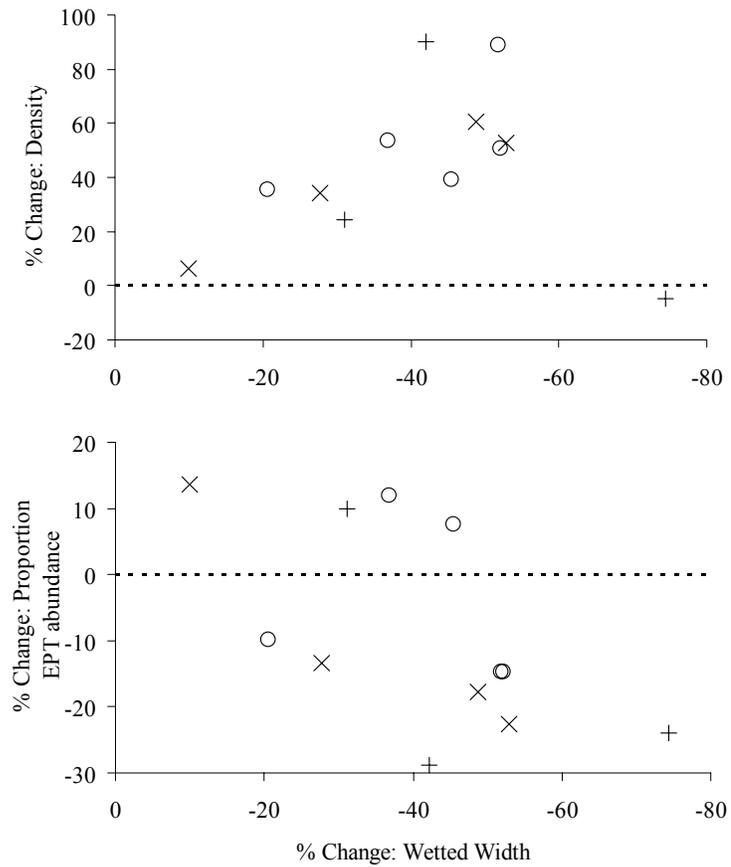


Figure 4.3. Relationship between percent change in wetted width and density (left: R^2 with outlier = 0.02; R^2 without outlier = 0.52) and the proportional abundance of EPT taxa (right: $R^2 = 0.35$). Dashed horizontal line indicates point of no change for the y-axis variable; points falling above the line indicate an increase below the diversion. Point codes are described in figure 4.2.

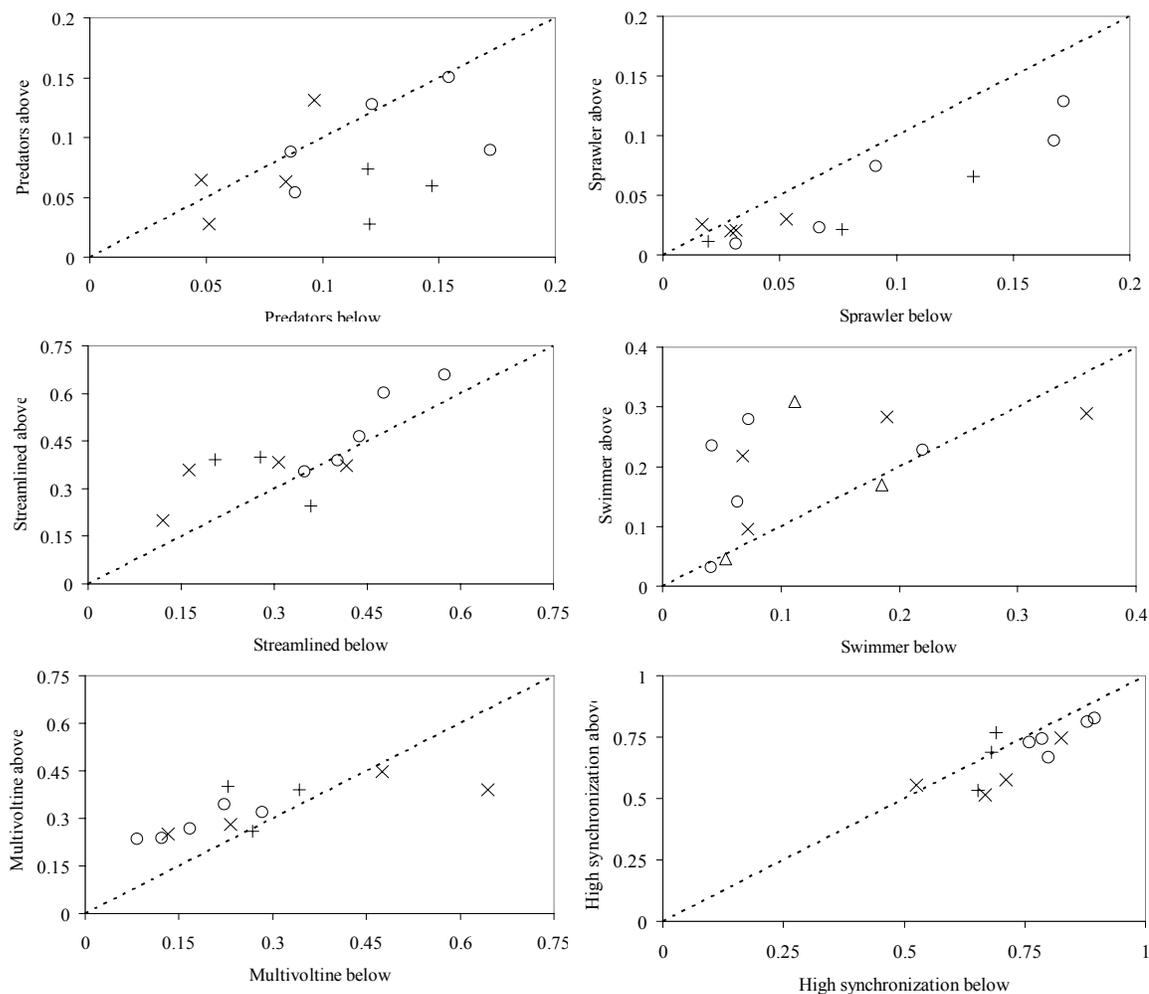


Figure 4.4. Examples of trait states showing significant differences above versus below points of diversion. Points are average proportions for each river. Point codes as in Fig. 4.2.

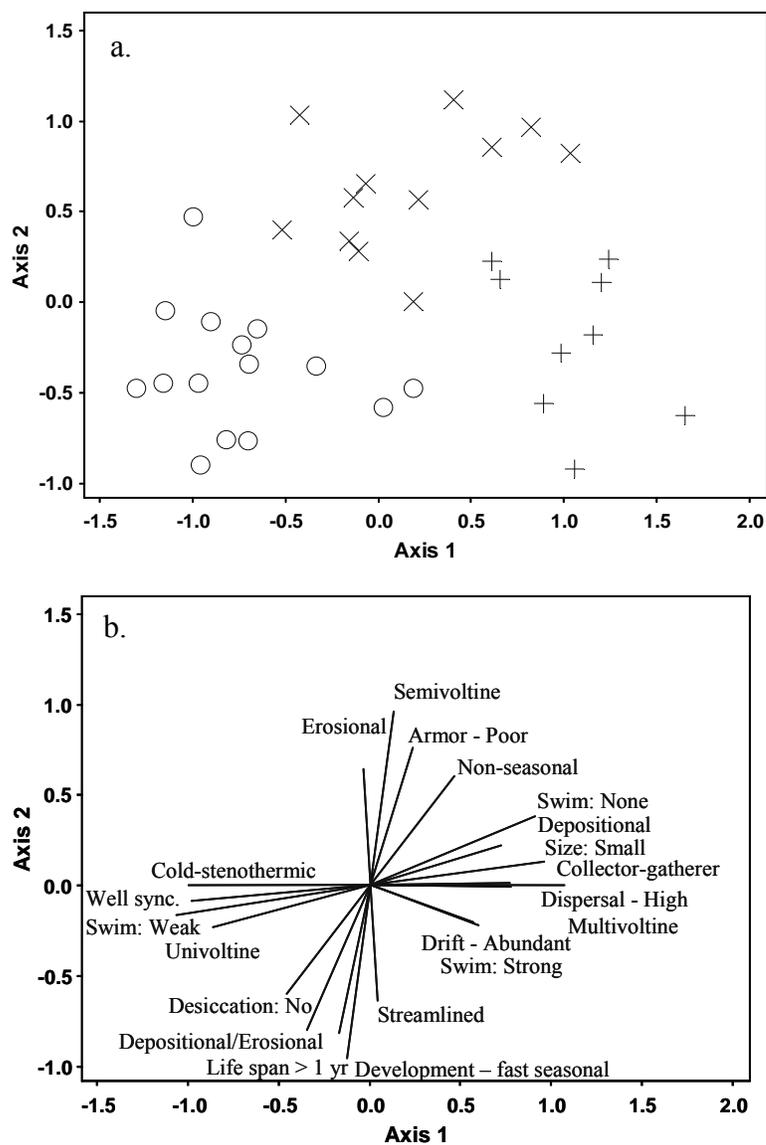


Figure 4.5. NMS ordination of the relative abundance of trait states for the three reference reaches within each of the 12 rivers (a.) and a joint plot overlay of trait states correlated with a Pearson correlation coefficient above 0.40 (b.). Reaches coded by trait-based groups: High – circles; Mid – Xs; and Low elevation – plus signs.

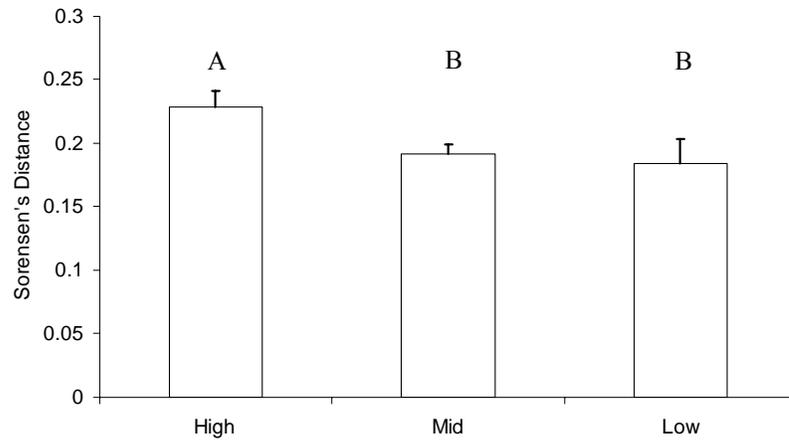


Figure 4.6. Average Sorensen's distance (+SD) measuring amount of change in community composition between reference (upstream) and treatment (downstream) reaches among trait-based groups. Letters indicate statistical significance at the 0.10 α level.

CHAPTER 5: SUMMARY

In the preceding chapters, I used water management practices in the semi-arid West as large scale experiments to understand how irrigation water withdrawals affect benthic macroinvertebrates. I found irrigation water withdrawals have the potential to alter key environmental determinants of the density, distribution, and life history strategies of macroinvertebrates. Environmental alterations included both direct (e.g. decreased velocity, depth, and wetted habitat) and indirect (e.g. increased conductivity and temperature) responses to reduced discharge. Direct effects were found ubiquitously throughout high and low elevation reaches and the magnitude of change appeared proportional to the amount of water withdrawn. In contrast, indirect effects occurred more frequently at low elevations and responses were only observed at high levels of water withdrawal below a series of multiple diversions. The severity of indirect effects also increased with the duration of low flows, which varied with annual water availability. In general, community and population level responses of macroinvertebrates were more strongly related to indirect than direct environmental alterations.

In Chapter 2, I identified disturbance, response, and recovery patterns for macroinvertebrate communities of the Umatilla River. The severity of community and population level responses depended on the magnitude and duration of low flow events. Specifically, macroinvertebrates exhibited threshold responses to the synergistic effects of reduced discharge and indirect environmental alterations. Similar responses were observed at the population level; alterations to the growth and development of *B. occidentalis* appear most likely to reduce fitness during high-intensity, long-duration water withdrawals associated with increased temperature. Despite significant alterations to community composition during summer months, winter discharge levels facilitated recovery of macroinvertebrate communities on an annual basis, whereas recovery was not observed after discharge and physicochemical variables returned to predisturbance conditions for only one month.

Balancing risk to ecological systems relies on understanding biotic responses to increasing levels of stress, as well as the mechanisms eliciting responses (Kelly and Harwell 1990). Threshold responses to increasing discharge reductions suggests all levels of water withdrawal do not have adverse impacts; however, applying this finding to balance instream flow needs with those of irrigated agriculture is confounded by the mechanisms eliciting macroinvertebrate responses. Despite the well established view that discharge and associated near-bed hydraulics directly influence benthic communities (Statzner et al. 1988, Townsend et al. 1997a), population and community level responses on the Umatilla River did not respond to discharge reductions alone. Rather, temperature increases associated with reduced discharge levels (i.e., indirect effect) appeared most detrimental to macroinvertebrates. Furthermore, the likelihood and magnitude of observing water quality alterations appeared to increase with the duration of low flow levels, as in the drought year of 2005. These results suggest the maintenance of thermal and water quality regimes within natural ranges of variability are equally as important as maintaining natural patterns of hydrologic variability.

Finally in Chapter 4, I assessed the consistency of macroinvertebrate responses across a diversity of river systems experiencing water withdrawals of similar magnitude and duration. High, mid, and low elevation reference reaches significantly differed in species traits, with traits inferring greater resistance and resilience increasing from high to low elevations; however, compositional responses of macroinvertebrates were similar among rivers found at different elevations. More surprisingly, I failed to find ecologically significant differences in macroinvertebrate community composition among all 12 rivers, despite discharge reductions greater than 75% of ambient level. Macroinvertebrate responses were limited to increased densities below points of water withdrawal and were associated with reductions in wetted habitat.

I believe the absence of indirect effects can explain inconsistent response patterns between the Umatilla River (Chapter 2) and the 11 other rivers encompassed by this study (Chapter 4). When I restricted sampling to a single diversion per river (see Chapter

4) direct environmental alterations (e.g., reduced velocity and wetted habitat) had minimal impact on macroinvertebrate communities. In contrast, the Umatilla and several other rivers included in this study have multiple downstream diversions in close proximity (e.g., Umatilla, Walla Walla, South Fork John Day). Samples collected below consecutive diversions revealed increasing water quality alterations and subsequent adverse impacts to macroinvertebrate communities (Miller, unpublished data). Consequently, rivers such as the Umatilla, which have multiple downstream diversions in close proximity, appear most susceptible to water withdrawals because of the increased likelihood of indirect effects on water quality. However, it remains unclear whether response to indirect environmental alterations will be consistent among high, mid, and low elevation systems.

Over three water years and across twelve catchments I have examined what levels of water withdrawal impact river systems, the mechanisms eliciting biotic responses, and the extent to which populations and communities of macroinvertebrates are altered. This work was initiated by a desire to help manage water resources in a more sustainable way and recognized from its inception that the needs of irrigated agriculture and other out-of-stream uses need to be balanced with those of freshwater ecosystems. Based on the variability of responses among catchments and between years I believe accomplishing this goal requires the development of a mechanistic understanding of how low flow disturbances elicit biotic responses through experimental studies. Such an understanding is critical to making accurate predictions about when low flows are detrimental to aquatic biota and for comparing responses among systems and organisms.

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