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Impact of season-long water abstraction on invertebrate drift composition and concentration

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Abstract Surface water abstraction from rivers for irrigated agriculture is one of the largest uses of freshwater resources in the world. Water abstraction has important impacts on the structure of riverine assemblages. However, little work has examined the chronic, season-long impacts on ecosystem functions. Invertebrate drift is an important ecosystem function of river systems influencing nutrient cycling, food webs, and invertebrate population dynamics. We examined the season-long impact of reduced discharge resulting from multiple points of abstraction on drift assemblage composition, concentration, and total drift load. Early in the season, water abstraction had little impact on drift assemblage composition. However, later in the irrigation season, the drift assemblage at sites impacted by water abstraction diverged from upstream, control sites. The degree of change in assemblage composition at impacted sites was related to the amount of water abstracted such that sites with

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National Aquatic Monitoring Center, US Bureau of Land Management, Department of Watershed Sciences, Utah State University, 5210 Old Main Hill, Logan, UT 84322, USA the lowest discharge also had assemblages that differed most strongly from control sites. Drift assemblages at impacted sites became dominated by tolerant microcrustaceans. In addition, water abstraction resulted in an increase in drift concentration (ind./ m³). However, despite this increase in concentration at impacted sites, total drift load (# of invertebrates drifting in the river) decreased with decreasing discharge.

Keywords Drift assemblages · Agroecosystems · Water discharge · River ecosystems

Introduction

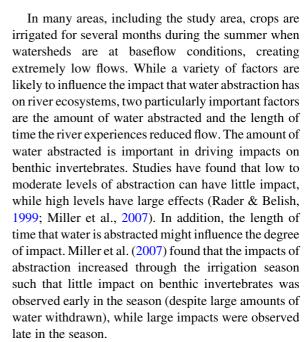
Surface water abstraction from rivers and streams for irrigated agriculture is one of the largest uses of freshwater resources in the world (Kenny et al., 2009; Wada et al., 2011). In most river systems, water abstractions occur as many relatively small points of withdrawal as opposed to a few large points, making water abstraction and the physical structures associated with it (i.e., small dams and pumps) ubiquitous features of many riverscapes. For example, 424 points of diversion were mapped along ~ 300 km of the Sacramento River in central California (Herren & Kawasaki, 2001) and the United States is estimated to have over 2.5 million small dams (<5 m), many of which are used as points of water abstraction (Poff & Hart, 2002).



Surface water abstraction can have detrimental impacts to river environments that include decreasing the extent of river and riparian wetland habitat, increasing water temperatures and sediment deposition, and changing water chemistry (Dewson et al., 2007; Baker et al., 2010). These changes in the riverine and floodplain environments in turn have important impacts on river biota. Water abstraction can influence fish assemblage composition (Benejam et al., 2010) and the density and growth rates of sensitive fish (e.g., salmonids, Harvey et al., 2006; Lange et al., 2014). Water abstraction also has important impacts on benthic invertebrate assemblages. Assemblages become dominated by tolerant taxa (Rader & Belish, 1999; Miller et al., 2007; Death et al., 2009), and invertebrate densities have been found to both increase (Rader & Belish, 1999; Miller et al., 2007) and decrease (Death et al., 2009; Matthaei et al., 2010) with water abstraction.

While a fair amount of work has considered the impacts of surface water abstraction on benthic invertebrates, less work has focused on the potential impact on drifting invertebrates despite the importance of invertebrate drift in river ecosystems. Invertebrate drift plays a key role in benthic invertebrate population dynamics (Anholt, 1995), the flow of matter from upstream reaches to downstream areas (Brittain & Eikeland, 1988; Wipfli & Gregovich, 2002), and drifting invertebrates provide an important food resource for many species of fish (Grossman, 2014). While a variety of environmental factors influence the abundance of drift, discharge is considered one of the key variables (Kennedy et al., 2014), and therefore, it is expected that invertebrate drift will be sensitive to lowered discharge resulting from water withdrawals.

Research on the effects of water abstraction on invertebrate drift has focused on drift concentration and the short-term impacts of a sudden decrease in discharge at the onset of abstraction. This work has revealed a consistent effect involving sharp increases in drift concentration at the onset of water abstraction and then a return of drift concentration to control levels after a short period of time (e.g., <1 week) (Minshall & Winger, 1968; Gore, 1977; Corrarino & Brusven, 1983; Poff & Ward, 1991; James et al., 2009). Very little work has focused on the longer-term, season-long impacts of water abstraction on drift assemblage composition and drift concentration.



We examined drift assemblage composition, concentration (ind./m³), and load (ind./s) on a river system with multiple points of abstraction that allowed an examination of the impact of decreasing discharge on drifting invertebrates. In addition, we sampled at multiple points in time during the irrigation season allowing an examination of the influence of the duration of the irrigation season on drift. Specifically, the objectives of this study were (1) to examine the relationship between decreasing discharge resulting from water abstraction and drift assemblage composition, drift concentration (ind./m³), and drift load (ind./s) and (2) to examine whether there was an increase in the impact of water abstraction through the irrigation season. In addition, because the benthos is the source of most drifting invertebrates in river systems and drift concentration can be positively related to benthic density (Walton et al., 1977; Shearer et al., 2003; Kennedy et al., 2014), we examined the impact of reduced discharge on drift concentration while taking into account the influence of benthic density.

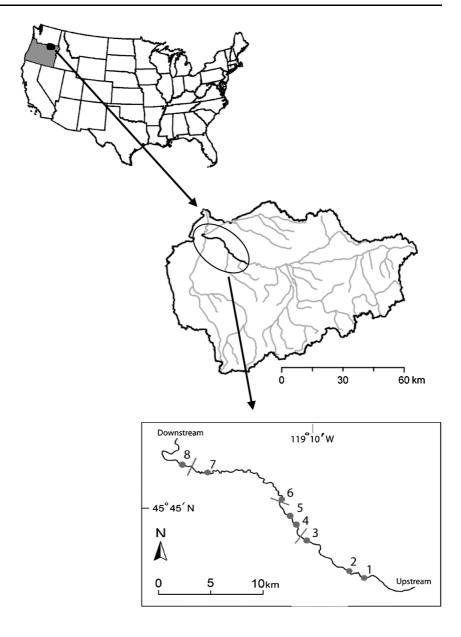
Methods

Study area and design

The study was conducted along the lower Umatilla River in northeastern Oregon (Fig. 1). The Umatilla



Fig. 1 Top panel Location of the Umatilla Basin (highlighted in black) in Oregon, USA. Middle panel Location of the 31-km study reach on the Umatilla River within the Umatilla Basin. Bottom panel The study reach on the Umatilla River (black line) and the location of the eight study sites (indicated by dots and numbers) and the three diversion dams (indicated by the solid lines crossing the river)



River is a fifth-order tributary of the Columbia River that drains a watershed of $\sim 5,900~\rm km^2$. The mainstem is 143 km long and originates in the Blue Mountains at an elevation of 710 m, and drains into the Columbia River at an elevation of 85 m. Columbia Basin basalts dominate the local geology. The climate is continental with hot, dry summers and cold winters. The lower basin is semiarid with average annual precipitation of $\sim 23~\rm cm$ and the dominant land use is irrigated cropland. The river in the study area has a low gradient (<1%).

Eight sampling sites were located across a 31-km segment of the lower Umatilla River that spanned three points of surface water diversion (Fig. 1). No tributaries enter the river along this segment; however, some irrigation return flows and groundwater inputs cause marginal surface discharge increases (Fig. 2). Geology, land use, riparian vegetation, and slope are all similar across the 31-km stretch of river. Given these similarities, the lack of tributary inputs, and that all sites were located in the same fifth-order reach, it is unlikely that longitudinal gradients (e.g., such as those



described in the River Continuum Concept [Vannote et al., 1980]) exist along the study section. The three points of water withdrawal were all low-head dams (<5 m high) constructed of concrete and timber. The irrigation season runs from April to early October; however, maximum abstraction often does not occur until June.

Three sites were located above all points of diversion and served as control sites unimpacted by surface water diversion and the five other sites spanned the diversion points and were impacted by water abstraction. Sites were numbered by elevation such that Site 1 was the most upstream and Site 8 was below the third point of diversion (Fig. 1).

Field sampling

Sampling was conducted during the irrigation seasons of 2006 and 2007. Each year drift samples were taken at each site during three time periods. The first period started in late June when discharge at the control sites

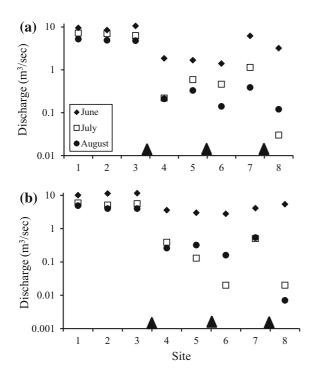


Fig. 2 Discharge at the eight study sites for each sampling period for **a** 2006 and **b** 2007. *Filled triangles* on the *x*-axis indicate the position of diversion dams. Site 1 is the most upstream and Site 8 is the farthest downstream. Note that the *y*-axis is on a log scale

had lowered (after high spring flows) to a point that made wading safe. Subsequent sampling (July and August) occurred at \sim 4-week intervals. During each sampling period, all sites were sampled within 1 week of each other.

Drift sampling occurred in the thalweg at the downstream end of riffle habitat at each site. Nets were put into position at each site by placing them onto rebar that had been driven into the substrate 7 days prior to the first sampling period. Each site had two pairs of rebar such that drift sampling was conducted at two points in the riffle. Nets were slid onto the rebar until the bottom of the net frame was in contact with the river substrate. At sites where riffles were deep, nets were stacked on top of each other such that at all sites the entire water column was sampled at the two points. Drift nets had metal frames that were 0.33 m square at the mouth and nets were 1 m long with 500 μm Nitex® mesh. During each sampling period, drift nets were set in place 30 min prior to sunrise and removed after 60 min. Drift samples were taken during this time to capture the daily increase in drift activity observed during times of low light level (Waters, 1972; Brittain & Eikeland, 1988). After removal of the nets, the depth and average velocity (measured at 6/10 depth) in the center of each pair of rebar were recorded using a Marsh-McBirney electromagnetic flow meter and stadia rod. The total volume of water sampled during the hour sampling period was estimated by multiplying the total area sampled by velocity. Drift samples were removed from the nets, composited into a single sample in the field, and preserved in 90% ethanol.

Benthic invertebrate samples were taken at each site six to 8 days after each drift sampling event. Drift nets were set at the downstream end of each riffle and during drift sampling care was taken not to walk through the riffle any more than necessary. Benthic samples were taken within the riffle upstream of the drift sampling points. Therefore, the disturbance to the benthos in the area sampled was minimal during drift sampling. Benthic sampling was conducted using a Surber sampler $(0.09 \text{ m}^2, 500 \text{ }\mu\text{m})$ at six randomly selected sites within the riffle. These six samples were composited into a single sample and preserved in 90% ethanol.

In the laboratory, random subsamples of each drift and benthic sample were taken until at least 300 individuals were picked (Caton, 1991; Vinson &



Hawkins, 1996). Organisms were identified to the lowest taxonomic category feasible, generally genus for insects (except Chironomidae, which were identified to subfamily) and family or order for noninsects, using standard keys (Merritt et al., 2008; Thorp & Covich, 2010).

In addition to collecting invertebrate drift and benthic samples, discharge measurements and continuous water temperature were recorded at each site. Discharge estimates were made at the time of drift sampling at each site using a Marsh-McBirney flow meter and cross-sectional method (Gore, 2006). Water temperature was recorded at 30-min intervals at each site using Onset Hobo dataloggers for the duration of the study. For our analyses, water temperatures were summarized as the average of the daily maximum water temperatures for the week prior to each drift sampling bout.

Data analysis

To examine the impact of water abstractions on the composition of drift invertebrate assemblages, nonmetric multidimensional scaling (NMS) ordination was used. NMS ordination is a robust ordination technique for ecological data as it does not require any assumptions of multivariate normality, yields good results even when datasets have large numbers of zero values, and has provided accurate representations of underlying data structure with test datasets (Clarke, 1993; McCune & Grace, 2002). NMS ordinations were conducted on the 2006 and 2007 data separately using Sørenson's distance on relative abundance data using the software PC-ORD v. 5.0 (McCune & Mefford, 2005). A maximum of six axes were examined, 500 iterations were conducted, and 250 runs with real data and a Monte Carlo randomization test with 250 runs were made to examine stress in relation to dimensionality.

To determine whether changes in drift assemblage composition scaled with the discharge present in the river, we first characterized the average assemblage structure in ordination space for sites not impacted by water abstraction by calculating centroids for the three upstream, control sites for each sampling month. Assemblage dissimilarity for each site relative to the control centroid was then quantified by calculating the straight line distance in ordination space between each site and the control centroid for each month. Linear

regressions with log-transformed discharge at each site were used to determine if relationships existed between discharge and assemblage dissimilarity with controls. Regressions were conducted for each month separately using assemblage composition at each of the eight study sites.

To examine the relationship between discharge and drift concentration, we conducted linear mixed effects analyses of the relationship between drift concentration as the response variable and discharge and benthic density as fixed effects. All data were used in this analysis, and therefore not all observations were independent because sites were sampled multiple times. To control for this non-independence, "Site" was used as a random effect in the models which controls for non-independence of multiple observations across sites (Zuur et al., 2009; Winter, 2013). Fixed effects in the models should not be collinear (Winter, 2013); to check for collinearity between the fixed effects, visual inspections of scatterplots and Pearson correlations on log-transformed data were conducted between discharge and benthic density for each sampling period. There was no evidence of collinearity (Pearson r < 0.50 and P > 0.20 for all comparisons) and thus both discharge and benthic density were used as fixed effects.

Four mixed models were developed—(1) a "null" model that contained site as the only explanatory variable, (2) a model that contained discharge and site, (3) a model that contained benthic density and site, and (4) a "full" model that included discharge, benthic density, and site as explanatory variables. The best model was selected using small-sample size corrected Akaike information criterion (AIC_C) weights following Burnham & Anderson (2002). Significance of the fixed effects in each model was determined using a F-distribution.

In addition to drift concentration, a parallel set of analyses were used to examine the impact of discharge and benthic density on drift load. Drift load was defined as the total number of macroinvertebrates drifting past a sampling reach per second and was calculated by multiplying drift concentration by river discharge at each site during each sampling period. Thus, drift concentration was scaled up to the entire reach at each sampling point. Benthic density was also scaled to the size of the river at each sampling point by multiplying benthic density (ind./m²) by the width of the river at each sampling point. As with drift



concentration, the same four mixed models were developed for drift load with "Site" as a random effect in each model and the best model was selected using AIC_c weights (Burnham & Anderson, 2002).

Visual inspection of residual plots indicated deviations from homoscedasticity and normality for benthic density, discharge, and drift concentration data. Log-transformations were used on all data to alleviate these deviations. Correlations and mixed models were developed and analyzed using the statistical program R (version 3.1.3; R Core Team, 2012) and, for mixed models, the package nlme (Pinheiro et al., 2015). For all analyses, the α value was set at 0.10.

Results

Environmental gradients

The three low-head dams created a similar gradient in discharge across the eight sites during both years (Fig. 2). Discharge declined at the control sites through each season, because of a natural lowering of the water table through the summer (Fig. 2). However, the absolute amount of water withdrawn remained relatively constant through the irrigation season. This, combined with the natural lowering of the water table, resulted in a greater decline in discharge at impacted sites later in the season. The multiple points of diversion created a downstream gradient in the amount of water withdrawn. In June, sites impacted by water withdrawals had discharges that ranged from 15-65% and 25-49% of the discharge at control sites in 2006 and 2007, respectively. Later in the season (July and August), impacted sites had only 0.4–17% and 0.2–12% of the discharge of the control sites in 2006 and 2007, respectively.

In June, maximum water temperatures were relatively similar among all sites (Fig. 3). By July, water temperatures showed increases below the first low-head dam (separating sites 3 and 4) and below the third low-head dam at Site 8. Water temperatures reached fairly extreme values at Site 8, climbing to 30°C in July 2006 and just over 28°C in July and August 2007 (Fig. 3). During both years, July had the highest maximum temperatures. The decline in temperatures in August resulted from releases of cold, hypolimnetic water from a tributary reservoir ~27 km upstream of the control sites. Water temperature was significantly

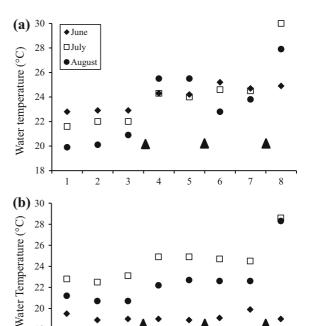


Fig. 3 Maximum water temperature for the 7 days prior to sampling drift at each site for a 2006 and b 2007. *Filled triangles* on the *x*-axis indicate the position of diversion dams

Site

and negatively correlated with discharge during all sampling periods except June 2007 (Table 1).

Drift assemblages

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A total of 70 taxa/life stage combinations were collected in 2006 and 63 in 2007. Life stages included both pupal stages of some taxa (e.g., chironomid pupae) and early instars that were identified at a coarser scale than other taxa (e.g., early instar Hydropsychidae larvae). These taxa/life stages were

Table 1 Results of Pearson correlations on the relationship between discharge (log-transformed) and maximum water temperature for each sampling period

| Year | Sampling period | r | P value |
|------|-----------------|-------|---------|
| 2006 | June | -0.77 | 0.03 |
| | July | -0.75 | 0.03 |
| | August | -0.87 | 0.005 |
| 2007 | June | 0.04 | 0.92 |
| | July | -0.77 | 0.02 |
| | August | -0.67 | 0.07 |

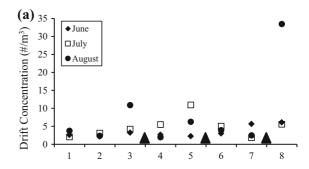


used in the NMS ordination. In terms of distinct taxa richness, a total of 53 taxa were collected in 2006 and 54 in 2007. Mayfly nymphs, chironomid larvae and pupae, and water mites (Trombidiformes) dominated the entire drift assemblage each year in June and in July 2006 (Table 2). In July 2007, additional noninsect taxa (flatworms and copepods) became dominant. In August of both years, microcrustaceans (chydorids and copepods) became dominant taxa in the drift. Chironomid larvae were dominant during all months of each year (Table 2).

The concentration of drifting invertebrates ranged from 0.2 to over 33 individuals/m³ across the two years (Fig. 4). Drift concentration increased at some sites later in the season; however, this trend was not consistent among sites within each year or within sites across years (Fig. 4).

Water abstraction and drift assemblage composition

NMS ordination conducted on the 2006 assemblage data returned a 3-dimensional solution that explained a total of 86.7% of the variation in assemblage composition among sites and sampling periods. The ordination solution had low stress (7.15) and instability (<0.001) indicating a stable solution for the final ordination. For simplicity, we examined the two dominant axes of the ordination to understand the



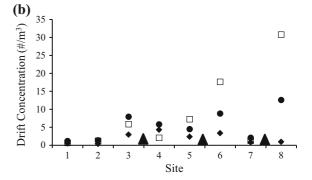


Fig. 4 Total drift concentration across the eight study sites for each month for **a** 2006 and **b** 2007. *Filled triangles* on the *x*-axis indicate the position of diversion dams

amount of difference in assemblage composition at each site through time (Fig. 5a). These two dominant axes explained a total of 72.9% of the variation in

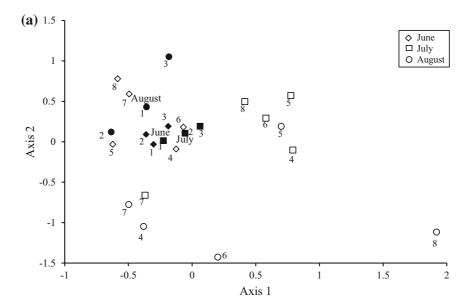
Table 2 The dominant taxa for each drift sampling period in 2006 and 2007. Values are relative abundances

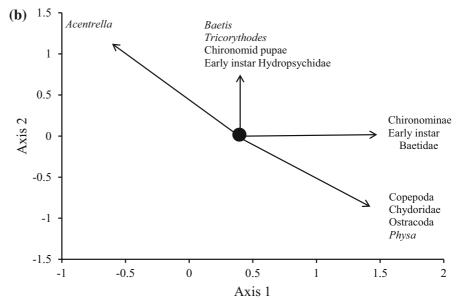
| Taxa | | | | 2006 | | 2007 | | | |
|--------------|----------------|---------------|----------------|------|------|--------|------|------|--------|
| | | | | June | July | August | June | July | August |
| Arachnida | Trombidiformes | | | 14 | 26 | - | 6 | 4 | _ |
| Branchiopoda | Diplostraca | Chydoridae | | _ | _ | 33 | _ | _ | 16 |
| Gastropoda | Basommatophora | Physidae | Physa | _ | _ | 8 | _ | _ | _ |
| Maxillopoda | Copepoda | | | _ | _ | _ | _ | 11 | 27 |
| Ostracoda | | | | _ | _ | 10 | _ | - | _ |
| Turbellaria | | | | _ | _ | - | _ | 48 | 10 |
| Insecta | Diptera | Chironomidae | Pupae | 36 | 7 | 10 | 6 | _ | _ |
| | | | Chironominae | _ | 7 | - | _ | 6 | 8 |
| | | | Orthocladiinae | 11 | 23 | 12 | 20 | 6 | _ |
| | | Simuliidae | Simulium | _ | _ | - | 5 | _ | _ |
| | Ephemeroptera | Baetidae | Baetis | 10 | 9 | - | 32 | _ | _ |
| | | Leptohyphidae | Tricorythodes | 8 | - | - | - | - | 7 |

⁻ Indicates that the taxa made up <5% of the individuals during that sampling period



Fig. 5 NMS ordination solution for 2006. a Symbols represent sites by sampling times in taxa space. Symbols are coded by whether they were above all points of abstraction (filled symbols) or were impacted by abstraction (open symbols). The words "June," "July," and "August" in the ordinations indicate the position of the centroids for the unimpacted, control sites during each month. b Taxa significantly correlated with the ordination axes. Arrows indicate the direction of increasing relative abundance





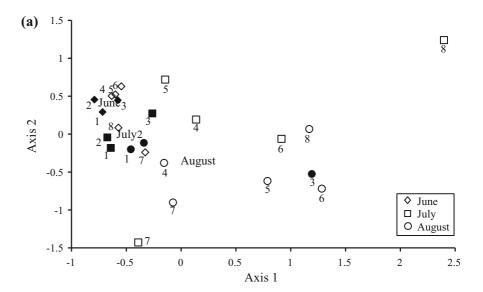
assemblage composition. The 2007 ordination returned a 2-dimensional solution (Fig. 6a) that explained 85.8% of the variation in drift assemblage composition and also had stress (10.41) and instability (<0.001) values indicative of a stable ordination solution.

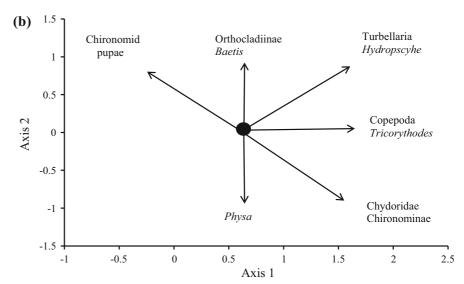
The ordinations revealed that all eight sampling sites had similar drift assemblage compositions in June. However, as the irrigation season progressed, the drift assemblage composition at sites impacted by water withdrawals diverged from the June composition (as revealed by the distance traveled through ordination space) while control sites maintained compositions similar to June (as reflected by the small distance traveled through ordination space by these sites) (Figs. 5a, 6a). The one exception to this pattern occurred in August 2007; during this period, Site 3 (a control site) had a drift assemblage more characteristic of impacted sites than the other two control sites (Fig. 6a).

For both the 2006 and 2007 ordinations, impacted sites tended to move to higher values on Axis 1 later in



Fig. 6 NMS ordination solution for 2007. a Symbols represent sites by sampling times in taxa space. Symbols are coded by whether they were above all points of abstraction (filled symbols) or were impacted by abstraction (open symbols). The words "June," "July," and "August" in the ordinations indicate the position of the centroids for the unimpacted, control sites during each month. b Taxa significantly correlated with the ordination axes. Arrows indicate the direction of increasing relative abundance





the irrigation season (Figs. 5a, 6a). Taxa correlations with Axis 1 during both years included the relative abundance of microcrustaceans (chydorids and copepods), which increased at impacted sites with reduced discharge (Figs. 5b, 6b). Other noninsects also increased in abundance at these sites (*Physa* in 2006 and Turbellaria in 2007). In contrast, both the mayfly *Acentrella* (in 2006) and chironomid pupae (in 2007) decreased in relative abundance in the drift at impacted sites later in the irrigation season (Figs. 5b, 6b). In 2006, control sites tended to have high Axis 2 values and a subset of the impacted sites had low values. Taxa correlations with Axis 2 in 2006 indicated that drift at

impacted sites tended to have lowered relative abundances of mayflies (*Acentrella*, *Baetis* and *Tricorythodes*), caddisflies, and chironomid pupae (Fig. 5b). Control sites did not separate out well from impacted sites along Axis 2 in 2007 (Fig. 6a); therefore, taxa correlated with Axis 2 in 2007 are likely responding to environmental differences among the sites other than reduced discharge.

Linear regressions of assemblage dissimilarity and discharge revealed no relationships in June of either year (Table 3; Fig. 7a, b). However, by July of both years significant relationships emerged indicating that as discharge at a site decreased, its dissimilarity to the



assemblage composition of the control sites increased (Table 3; Fig. 7a, b). This negative relationship was maintained in August 2006 but was not present in August 2007.

Drift concentration

Based upon AIC_c weights, the "Full" model that contained both discharge and benthic density as fixed effects was the best-fitting model for drift concentration (Table 4). Both fixed effects explained a significant amount of the variation in drift concentration in all models (Table 4). Discharge had a negative impact on drift concentration (estimated slope from the full model = -0.35, Fig. 8a) and benthic density had a positive impact (estimated slope = 0.55, Fig. 8b).

Drift load

As with drift concentration, the "Full" model containing both benthic density and discharge was chosen as the best-fitting model for drift load based upon AIC $_{\rm c}$ weights and both fixed effects explained a significant amount of the variation in drift load (Table 4). Both discharge and benthic density had positive effects on drift load (estimated slopes from the full model = 0.85 and 0.50, respectively; Fig. 9a, b).

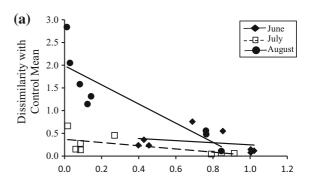
Discussion

Environmental gradients

The series of three water withdrawals had strong effects on discharge and water temperatures along our study area, and these effects tended to increase through the

Table 3 Results of linear regression analyses on the distance a site was from the control mean in ordination space, a measure of invertebrate drift compositional differences, and discharge at that site for each sampling month

| Year | Month | r^2 | P value |
|------|--------|-------|---------|
| 2006 | June | 0.07 | 0.52 |
| | July | 0.39 | 0.10 |
| | August | 0.76 | 0.005 |
| 2007 | June | 0.01 | 0.90 |
| | July | 0.49 | 0.05 |
| | August | 0.04 | 0.62 |



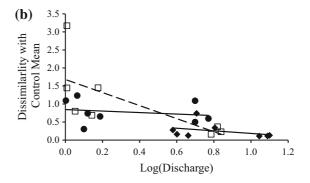


Fig. 7 Relationships between discharge at each site and the dissimilarity in drift invertebrate assemblage composition between the site and the average assemblage composition at control sites for each month a 2006 and b 2007. For all months, control sites had high discharge and sites impacted by water abstraction had lowered discharge

irrigation season. Discharge was reduced by 35–80% in June, but by July and August discharge at the impacted sites was reduced by 83-99% relative to that at the upstream, unimpacted sites. In addition, water temperatures were very similar among all the sites in June but by July and August maximum water temperatures increased by $\sim 3^{\circ}$ C at impacted sites relative to controls reaching an extreme of 30°C in August 2006 at the most impacted site. Increasing water temperatures with reduced flow is a commonly observed pattern in regulated rivers (Dewson et al., 2007). This pattern is likely exacerbated in river systems with little riparian shading and high width to depth ratios (such as the study reach on the lower Umatilla River) as the lowered volume of water rapidly heats up from solar radiation (Dymond, 1984; Meier et al., 2003).

Drift assemblage

Drift concentrations on the Umatilla River were higher than those reported for the nearby John Day Basin



Table 4 Results of mixed model analyses for drift concentration (#/m³ of water sampled) and drift load (#/s)

| Model | AIC_c | Wi | F-value | P value |
|--|---------|--------|------------|----------------|
| Drift concentration | | | | |
| Full: benthic density + discharge + site | -2.50 | 0.97 | 29.9, 9.6* | < 0.001, 0.004 |
| Benthic density + site | 4.31 | 0.03 | 25.5 | < 0.001 |
| Discharge + site | 10.98 | < 0.01 | 14.9 | < 0.001 |
| Null: site | 22.11 | < 0.01 | | |
| Drift load | | | | |
| Full: benthic density + discharge + site | -4.06 | 0.99 | 48.3, 58.1 | <0.001, <0.001 |
| Benthic density + site | 33.1 | < 0.01 | 21.7 | < 0.001 |
| Discharge + site | 9.7 | < 0.01 | 70.3 | < 0.001 |
| Null: site | 49.3 | < 0.01 | | |

In all models, "Site" was a random effect. "AIC_c" is the Akaike information criterion corrected for small-sample sizes. "wi" is the Akaike weight and was used to select the best model. For both drift concentration and drift load, the "Full" model was considered the best model

(Weber et al., 2014) as well as other systems (Alaskan low order streams: Wipfli & Musslewhite, 2004; New Zealand river: Tonkin & Death, 2013). However, they are similar to other estimates (e.g., Brewin & Ormerod, 1994; Leung et al., 2009). Early in the season, the drift assemblage was dominated by mayflies, chironomid larvae and pupae, and water mites, which are all taxa that are frequently found as dominant members of drift assemblages in other systems (Brewin & Ormerod, 1994; Musselwhite & Wipfli, 2004; Hay et al., 2008). As the irrigation season progressed, additional noninsect taxa (e.g., microcrustaceans, flatworms, and *Physa* snails) became dominant members of the overall drift assemblage and mayfly nymphs declined in dominance. Chironomid larvae were dominant members of the drift assemblage throughout the summer season of both years.

Reduced discharge and drift assemblage composition

As predicted the impact of water abstraction and reduced discharge exhibited a ramp-like effect on the invertebrate drift assemblage. Early in the season (June), no relationship emerged between discharge and the dissimilarity of drift assemblages to the mean control. In contrast, significant patterns emerged later in the irrigation season such that sites with the greatest reductions in discharge and highest water temperatures showed the greatest dissimilarity in drift

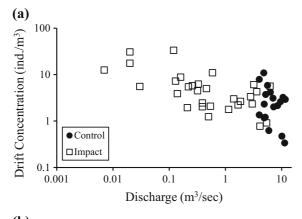
assemblage composition relative to controls. This pattern was observed during July and August 2006 as well as July 2007. However, it broke down in August 2007 as a result of one control site (Site 3) having a drift assemblage that resembled-impacted sites.

Drift assemblages were similar among all eight sampling sites early in the irrigation season. At this time, they were dominated by chironomids (both pupae and larvae), water mites, and mayfly nymphs. In contrast, later in the irrigation season (July and August), drift assemblage composition shifted at sites subject to water abstraction and, as stated above, the degree of this shift was influenced by the amount of water abstracted. This shift reflected an increase in tolerant, noninsect taxa including microcrustaceans and *Physa* snails (in 2006) and flatworms (in 2007). In addition, the shift in composition at impacted sites reflected a decline in relatively sensitive mayflies.

Tolerant microcrustaceans, *Physa* snails, and flatworms greatly dominated the impacted sites during July and August of both years. In his study of the drift of microcrustaceans, Shiozawa (1986) found the highest concentrations of these taxa in the drift during summer low flow periods. The author suggested that sediment input and low oxygen levels in interstitial spaces inhabited by these organisms force them to the surface where they are exposed to stream current and are more likely to drift. It is possible that this mechanism occurred in the Umatilla River as declines in flow from water abstractions can cause increased sediment deposition (Baker et al., 2010). It is also



^{*} indicates for the full model, F-values and P values are shown for discharge and benthic density, respectively



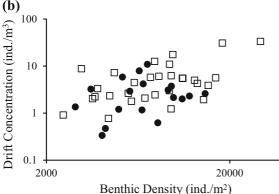
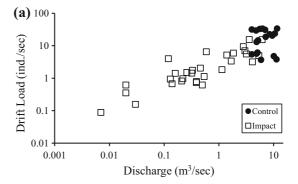


Fig. 8 Relationships between drift concentration (ind./m³) and **a** discharge and **b** benthic density. Sites impacted by water withdrawals are illustrated with *open squares* and sites above all points of withdrawal (controls) are illustrated with *closed circles*. Note that both the *x*- and *y*-axes are log scales

possible that increased water temperatures at sites impacted by water abstraction led to increased developmental rates of these organisms resulting in population blooms at impacted sites (assuming food was not limited). For example, Anderson et al. (1998) found that when raised at warm temperatures the generation times of chydorids and ostracods declined by over 50% relative to when they were raised at cool temperatures.

Both physid snails and flatworms are tolerant of human disturbances, particularly agricultural disturbances (Cuffney et al., 1997; Whittier & Van Sickle, 2010). Their high abundance in the drift later in the irrigation season at impacted sites likely reflects this tolerance. In addition, algae blooms and the extent of slow water habitat increase with water abstraction (Dewson et al., 2007; Baker et al., 2010) and it is possible these species prefer this type of habitat,



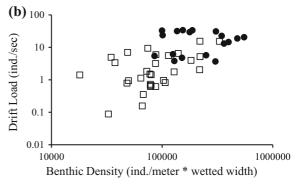


Fig. 9 Relationships between drift load (ind./s) and **a** discharge and **b** benthic density. Sites impacted by water withdrawals are illustrated with *open squares* and sites above all points of withdrawal (controls) are illustrated with *closed circles*. Note that both the *x*- and *y*-axes are log scales

resulting in high benthic abundances of these organisms in impacted reaches and concomitant increases in drift density.

As stated above, increased water temperatures associated with reduced discharge might have influenced the phenology of microcrustaceans. It is possible that water temperatures also affected the phenology of other drifting invertebrates in our study. During both years chironomid pupae tended to be associated with unimpacted, control sites while larvae of the chironomid subfamily Chironominae tended to be associated with sites impacted by water abstraction. In addition, in 2006 Baetis nymphs were associated with control sites while early instar Baetidae nymphs were associated with impacted sites. These correlations might have emerged as a result of different species of each of these groups being dominant in control sites versus impacted sites. However, they might have also resulted from changes in the developmental rates of these taxa such that at relatively cool



sites unimpacted by water withdrawals these taxa were at a different developmental stage during July and August than at the warmer, impacted sites.

While increased water temperature resulting from reduced discharge was a likely driver of changes in drift assemblage composition, our study was not designed to disentangle the impact of increased water temperature from impacts resulting from a loss of discharge per se or from other environmental variables that might have changed with water abstraction. Decreases in discharge resulting from water abstraction can influence a variety of environmental factors in river systems including concentration of toxins, filamentous algal blooms, sediment deposition, and changes in dissolved oxygen content (Dewson et al., 2007). Understanding which of these factors is influenced by water withdrawals and which are most important in driving changes in river biota is an important step in further work on the impacts of water abstraction on river reaches.

Discharge reductions and drift concentration

Drift concentration increased with decreasing discharge that resulted from water abstraction. Perhaps the most parsimonious explanation for this pattern is that a similar number of invertebrates are entering and exiting the drift at all sites regardless of discharge, but at sites with reduced discharge drifting individuals must simply pack into a smaller area of space which increases the per unit concentration. In this scenario, increased drift concentration with water abstraction does not indicate any changes in behavioral or physical dynamics that influence drift; it is a simple consequence of reduced discharge.

The packing of drifting invertebrates into a smaller area most likely played a role in increasing drift concentration in our study. However, changes in drift assemblage composition also likely played a role. The highest drift concentrations found in the Umatilla River were at sites impacted by water abstraction late in the irrigation season. At this time, these sites were dominated by microcrustaceans (ostracods, chydorids, and copepods) which have been found in other systems to drift at extremely high concentrations (Shiozawa, 1986; Richardson, 1991). It is not clear why microcrustaceans became abundant at impacted sites. However, it is possible that increases in water

temperature and the extent of slow water habitat at sites impacted by water withdrawals were conducive to population "blooms" of these organisms (Anderson et al., 1998) resulting in large numbers in the drift.

While several studies have demonstrated increased drift concentrations with reduced discharge (Minshall & Winger, 1968; Gore, 1977; Poff & Ward, 1991; James et al., 2009), they have generally only measured drift immediately following the onset of water abstraction when discharge quickly declined. However, James et al. (2009) measured drift immediately following experimental discharge reduction and for two months afterward in three New Zealand streams. The authors found a large spike in drift concentration within the first 3 days of flow reduction, but after 1 week, drift concentrations settled to those similar to control reaches. Thus, in contrast to our findings where drift concentrations were highest late in the season, there was no indication of season-long effects of water abstraction on drift concentration in the New Zealand streams despite the withdrawal of over 80% of the discharge. It is not clear why we found a season-long effect of discharge loss on drift concentration and James et al. (2009) did not. However, these variable results suggest that changes in drift concentration under conditions of water abstraction are not simply the result of packing individuals into smaller volumes of water (otherwise it would have been observed in both studies), but that changes in benthic density, invertebrate assemblage composition, drift behavior, and/or the physical processes controlling drift also change.

Benthic density was also an important variable influencing drift concentration in the Umatilla River. The positive relationship we observed is the expected pattern as the benthos is the source of most drifting invertebrates in rivers (Walton et al., 1977; Brittain & Eikeland, 1988); however, this pattern is not always observed (Waters, 1972; Tonkin & Death, 2013). Our analyses were designed to control for the effect of benthic density on drift concentration when considering the influence of discharge. Given the potential for water abstraction to influence benthic density of invertebrates (Rader & Belish, 1999; Miller et al., 2007) and the effect of benthic density on drift concentration, studies designed to examine the impact of water management on invertebrate drift should take into consideration benthic density.

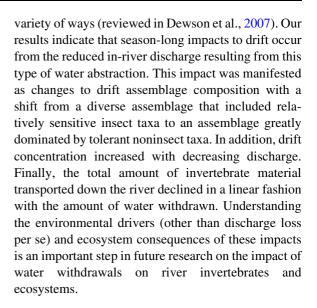


Discharge reductions and drift load

Given the increase in drift concentration with declines in discharge, total drift load might be expected to also increase as discharge declines. However, we found that drift load declined with decreasing discharge. Therefore, increases in drift concentration did not offset loss of discharge in terms of the number of invertebrates drifting down the river. These opposing trends in drift concentration and drift load have important consequences for river ecosystem function and management. For example, models of the bioenergetics of drift feeding fish indicate that individuals benefit from an increase in drift concentration (e.g., Hayes et al., 2007; Urabe et al., 2010). However, the overall loss of drift load with declines in discharge indicates that the energetic dynamics of drift feeding fish at a scale larger than that of an individual will be negatively impacted. Obviously, the loss of discharge represents a loss of habitable space for fish, including those of management concern, thus making water abstraction a concern in fisheries management simply in the sense of amount of habitat. Our results indicate that not only is habitat lost but also the delivery of food resources through drift also declines with water abstraction. Irrigation return flows and groundwater inputs recharge the Umatilla River below our study area bringing the river's discharge back up to a level more similar to that above all the points of diversion. Thus, the amount of habitable space is regained in this area for fish. However, the loss of drift load across the points of water abstraction means that the amount of energy from the drift moving into this recharged area is quite low. The consequences of this loss of drift on the dynamics of fish populations and river ecosystem in the recharged area is yet to be examined and is worthy of consideration.

Conclusions

Summer water abstraction for irrigated agriculture is a common feature of many rivers in semiarid and arid areas. The abundance of points of withdrawal and the amount of water withdrawn from freshwater systems is likely to increase in the future with a burgeoning human population and the consequences of climate change (Wada et al., 2011). This type of withdrawal can have strong ecosystem impacts to rivers in a



Compliance with ethical standards

Conflict of interest We declare no conflicts of interest with any of the editors or possible reviewers we selected.

Ethical Approval All authors agree that the following ethical standards were met when the research was conducted, the data were analyzed, the manuscript was written, and the manuscript was submitted. None of the authors of this manuscript currently have research projects or research proposals in review with any of these people. In addition, none of the authors of this manuscript have been co-authors or are currently co-authors on manuscripts in preparation with any of these people.

Human and Animal Rights Our research did not involve human or any vertebrate animal subjects. Our research involved only the collection of aquatic invertebrates, none of which, to the best of our knowledge, are threatened, endangered or in any way protected by United States federal or state laws. Finally, all authors have consented to having the manuscript submitted to Hydrobiologia.

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