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Phil D. Brown for the degree of Master of Science in Fisheries Science presented on August 14, 2008.

Title: The Effects of Water Withdrawals on the Emergence Timing, Adult Body Mass, and Total Emerging Biomass of Aquatic Insects from two Northeast Oregon Rivers.

Abstract approved:

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Small low-head diversion dams are capable of removing much of the flow of a river, often resulting in increased water temperatures and habitat loss. Warmer temperatures have been shown to accelerate aquatic invertebrate growth and development, and discharge reductions can reduce instream habitat, suggesting that water withdrawals may alter both the timing of aquatic insect emergence and the total emerging biomass from a river. To examine the influence of water withdrawals on the timing and magnitude of aquatic insect emergence, we monitored emergence continuously for 9-10 weeks during the summer of 2006 on the Umatilla and Walla Walla rivers of northeastern Oregon. Multiple sample sites were located along gradients of decreasing discharge and increasing water temperatures caused by successive diversions on each river. The emergence timing and adult body size of three holometabolous species (*Helicopsyche borealis, Petrophila confusalis,* and *Glossosoma traviatum*) were compared to discharge, water temperature, and other physical habitat variables. The emergence timing of entire taxonomic families was also compared to these variables, and the total emerging biomass was estimated for each site.

Despite reductions in discharge of up to 93% and increases in average water temperature of up to 4.6°C from upstream to downstream, emergence timing was unaltered for *H. borealis, P. confusalis,* and *G. traviatum.* However, in a laboratory experiment, higher temperatures led to earlier emergence for *H. borealis.* With the exception of Hydroptilidae, emergence timing was not correlated with discharge or water temperature for all 8 taxonomic families on each river, and the timing of total emergence remained similar among sites. Similarly, water temperature was not significantly correlated with reduced adult body size of these species, though female *P. confusalis* were 31% smaller at the warmest sample site. Total emerging biomass was reduced at sites subject to high water withdrawals, particularly on the more heavily diverted Umatilla River.

The holometabolous life histories of the three tested species and the occurrence of water withdrawals for decades prior to this study are possible explanations for the observed lack of response to seasonal alterations in discharge and water temperature. These results

suggest that the life histories of some aquatic invertebrates in Western rivers may be resistant to severe water withdrawals, but important ecological effects may exist through the reduced export of emerging biomass into the riparian ecosystem.

The Effects of Water Withdrawals on the Emergence Timing, Adult Body Mass, and Total
Emerging Biomass of Aquatic Insects from two Northeast Oregon Rivers.

by

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Phil D. Brown, Author

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GENERAL INTRODUCTION

Despite the nearly universal presence of anthropogenic disturbances in watersheds worldwide, research on the effects of human activities on lotic systems is incomplete (Malmqvist and Rundle 2002). Streams and rivers are affected by a large variety of anthropogenic influences, including pollution, impoundments, and disruptions to hydrology and habitat, each producing impacts of varying degree and character (Dudgeon et al. 2006). A common disturbance is water withdrawal for irrigated agriculture, which has seen significant increases with human population growth (Oki and Kanae 2006; Malmqvist and Rundle 2002). The influences of large hydrologic dams have been relatively well explored, but the effects of low-head agricultural diversion dams on the ecology of rivers and streams have received comparably little attention. Large dams can alter the thermal and hydrologic regimes by dampening the natural extremes of each (Vinson 2001, Poff and Allan 1997, Allan 1995), creating higher discharges and lower water temperatures during summer base flow. Low-head diversions have quite the opposite effect. Summer base flows are reduced (Rader and Belish 1999) allowing water temperatures to increase through solar warming (Rader and Belish 1999; Dewson et al. 2007a). The hydrologic and thermal regimes remain comparatively unchanged during the winter and spring, when discharges may be high and irrigation demand is low.

The effect of irrigation diversions in Oregon may be large, as approximately 1.4 million acres of farmland statewide are dependent on surface water (Bastasch 1998). Diversion of water for irrigation often occurs from late spring to autumn, a period of low natural flow in river systems. Combined with the semiarid climate of regions such as eastern Oregon, irrigation withdrawals may have serious effects on lotic ecosystems in this region by further reducing in-stream flow. Aquatic invertebrates are a crucial component of lotic ecosystems. Aquatic invertebrates have an important role in nutrient cycling and act as a bridge between primary production and higher trophic levels, providing a food source for fish (Malmqvist 2002) and terrestrial organisms in the riparian system (Nakano and Murakami 2001, Power et al. 2004).

Diversion of river water may have ramifications for aquatic invertebrate life histories by altering the discharge and temperature dynamics of streams. The life histories of individual organisms are influenced in large part by particular hydrologic events and temperature regimes, and alterations in either can affect the emergence and survival of aquatic invertebrates (Bunn and Arthington 2002). While anthropogenic reductions in discharge may alter the community composition and abundance of aquatic invertebrates (Dewson et al. 2007b; Miller et al. 2007; Rader and Belish 1999), the effect on life histories is less clear (e.g. Delucchi and Peckarsky 1989). However, intermittent streams pose specific life history challenges for invertebrates (Poff and Ward 1989), conditions that may be imposed by water withdrawals upon invertebrate communities ill-adapted to handle them in permanent streams.

Water temperature can also have a profound effect on the life histories of aquatic invertebrates. Temperature plays a direct role in the growth and development rates of aquatic ectotherms. Numerous studies suggest that aquatic insects grow and mature at a more rapid rate in higher water temperatures but achieve smaller body sizes as a result (e.g. McKee and Atkinson 2000; Hogg and Williams 1996; Giberson and Rosenberg 1992), although exceptions to one or more of these patterns have been found (Cabanita and Atkinson 2006; Gregory et al. 2000). The mechanism driving this pattern is the differential effect of temperature on development and growth rates. Increased temperatures may accelerate developmental rates more than growth rates, resulting in maturity at a lower accumulated growth (Sweeney & Vannote 1978; Vannote and Sweeney 1980). Anthropogenic decreases in discharge and resulting increases water temperature could thus have a profound effect on growth rate and size at maturity.

The effects of increased temperature on life history and emergence have particular relevance to reproductive success of invertebrates. Aquatic invertebrate fecundity is directly related to adult body size (Taylor et al. 1998; Sweeney et al. 1995). Aquatic invertebrates are believed to have a particular temperature regime that provides an optimum balance of adult body size and fecundity, and it is thought that resulting temperature changes of only 2 or 3°C could remove certain species from systems near the edge of their geographic range (Sweeney and Vannote 1978). The adult stage of some aquatic invertebrates is also very brief— particularly Ephemeroptera—and therefore differences in emergence timing of only a few days or weeks along a given section of river may have unknown effects on reproductive success. The mayfly *Dolania americana* was observed to synchronize peak emergence over a short period of time (approximately 6 to 8 days) to minimize risk of predation (Sweeney and Vannote 1982). Emergence disparities of as little as a week for such species could compartmentalize emergence and reproductively isolate river reaches between agricultural water diversions.

Potential effects on aquatic invertebrate emergence are not limited to the aquatic environment. Emerging aquatic insects can exert significant influence on food webs in the surrounding watershed. Aquatic insects provide energy sources for terrestrial organisms such as birds (Nakano and Murakami 2001; Sweeney and Vannote 1982), arachnids, lizards, and bats (Power et al. 2004). This flux of energy to the terrestrial environment is likely significant, as only 3% of emergent aquatic invertebrate biomass has been shown to return to the stream (Jackson and Fisher 1986). Peaks of emerging aquatic invertebrates may occur during periods of low terrestrial invertebrate production, providing important sources of prey for terrestrial consumers (Nakano and Murakami 2001). Reductions in discharge can shrink instream habitat (Cowx et al. 1984; Stanley et al. 1997; Brasher 2003), possibly limiting the

amount of biomass emerging from a river subjected to water withdrawals. Altered emergence timing, reduced adult body size, and instream habitat loss could modify the timing and magnitude of this subsidy to the riparian zone.

The extent and character of the impacts of water withdrawals on aquatic invertebrate life histories remains largely hypothetical. Few studies have examined invertebrates below water diversions, and those that have did not investigate the timing and size of emerging adults. Rader and Belish (1999) reported results on community composition rather than life histories downstream of diversions. Delucchi and Peckarsky (1989) investigated the role of temperature and flow on larval development rates, sizes, and emergence periods, but only on streams with natural hydrographs, and adult size and biomass were not measured. Aquatic invertebrates may respond to artificially-induced low flows and high water temperatures by altering growth rates, body size at emergence, and timing of emergence. A logical hypothesis is that growth rates will accelerate, leading to more rapid maturity, earlier emergence, and the consequent reduction in individual body size. Further study of this subject is needed for effective management of rivers impacted by diversions.

The intent of this study is to examine the effects that abiotic influences of agricultural water withdrawal have on 1) the timing of emergence of individual species and taxonomic families, 2) body size of emerged adults, and 3) the total emergent biomass. Research was conducted on two arid-land rivers with multiple withdrawal structures in succession, providing a temporal and longitudinal gradient of decreasing discharge and increasing water temperature. In Chapter 2 I explore the effects of reduced discharge and increased water temperatures on the emergence timing and adult body size of three holometabolous species. I conducted a controlled in-lab experiment with the intent of separating the influence of temperature from other abiotic factors associated with water withdrawal and to reduce natural variability inherent in field studies. In Chapter 3 I investigate the timing and magnitude of total aquatic invertebrate emergence by examining the timing of total emergence and of the component taxonomic families, and estimating the loss of instream habitat due to decreased discharge. I predicted that reduced discharge and higher water temperatures would result in 1) changes in the timing of emergence, 2) reduced average adult body size, and 3) reduced total emerging biomass from sites subject to water withdrawal.

THE EFFECTS OF WATER WITHDRAWALS ON THE EMERGENCE TIMING AND ADULT
BODY SIZE OF THREE HOLOMETABOLOUS AQUATIC INVERTEBRATE SPECIES FROM
TWO ARID-LAND RIVERS

ABSTRACT

Small, low-head diversion dams are capable of withdrawing much of the flow of a
river, often resulting in elevated water temperatures. Accelerated growth and development of
aquatic invertebrates has been demonstrated in warmer temperatures, suggesting that the
timing of insect emergence and adult body size may be significantly altered by water
withdrawals. To examine the influence of summer water withdrawals on aquatic invertebrate
life histories, emergence timing and adult body mass of three holometabolous species were
monitored continuously for 9-10 weeks on the Umatilla and Walla Walla rivers in arid
northeastern Oregon. On each river, multiple sample sites were located along gradients of
decreasing discharge and increasing water temperatures caused by successive diversions.

Despite reductions in discharge of up to 93% and increases in average water
temperature of up to 4.6°C from upstream to downstream, timing of median emergence was
unaltered for *Helicopsyche borealis, Petrophila confusalis,* and *Glossosoma traviatum.*
However, in a laboratory experiment, higher temperatures led to earlier emergence for *H.
borealis.* Water temperature was not significantly correlated with reduced adult body size of
these species, though female *P. confusalis* were 31% smaller at the warmest sample site.
Holometabolous life histories and high temperature tolerances are possible explanations for
the observed resistance of these species to life history alteration.

INTRODUCTION

River systems world wide are impacted by an array of anthropogenic influences.
Exploitation, water quality degradation, modified hydrology, and physical habitat modification
commonly degrade the biotic integrity of lotic systems (Dudgeon et al. 2006; Malmqvist and
Rundle 2002). Water withdrawal for irrigated agriculture is one such widespread disturbance
that has been increasing in severity as human populations expand throughout the world (Oki
and Kanae 2006; Malmqvist and Rundle 2002). The impacts of large hydroelectric dams on
the physical, chemical, and ecological properties of rivers have garnered much attention in the
literature, but the effects of low-head agricultural diversion dams on lotic ecology have
received far less consideration. Large dams often dampen peak discharge, elevate summer
base flow, and decrease summer water temperatures (Vinson 2001; Poff and Allan 1997;
Allan 1995). Low-head diversion dams produce distinctly different effects by reducing summer
base flow (Rader and Belish 1999), which may increase water temperatures (Cazaubon and
Giudicelli 1999; Rader and Belish 1999). Hydrologic and thermal impacts are absent or
minimized during winter and spring, when irrigation demands are low.

The growth, development, and reproductive strategies of ectothermic organisms are controlled in large part by natural hydrologic events (Lytle 2001; Lytle and Poff 2004) and water temperatures (Gallepp 1977; Sweeney and Vannote 1978; Giberson and Rosenberg 1992; Newbold et al. 1994). If water withdrawals on a naturally perennial river are severe enough to create hydrologic and thermal regimes similar to those of drying intermittent streams, some of the specific life history challenges of intermittent streams (Poff and Ward 1989) may be imposed upon an invertebrate community ill-adapted to handle them. Although such artificial reductions in discharge have been shown to alter aquatic invertebrate community composition and abundance (Rader and Belish 1999; Dewson et al. 2007; Miller et al. 2007), the effect on life histories is less clear (e.g. Delucchi and Peckarsky 1989).

Water temperature may have a significant effect on aquatic invertebrate life histories and reproductive success. Aquatic insects have been observed to grow and mature at a faster rate in warmer temperatures, but achieve smaller adult body sizes as a result (e. g. McKee and Atkinson 2000; Hogg and Williams 1996; Giberson and Rosenberg 1992), although exceptions have been found (Cabanita and Atkinson 2006; Gregory et al. 2000). Aquatic invertebrates may thus be expected to emerge earlier and at a smaller body size in water of elevated temperatures. Given that aquatic invertebrate fecundity is directly related to adult body size (Taylor et al. 1998; Sweeney et al. 1995), and some taxa (Ephemeroptera) have brief adult life stages, changes in emergence timing and body size may have significant effects on reproductive success and competitive fitness. Sweeney and Vannote (1978) proposed that aquatic insects have a narrow temperature regime within which adult body size and fecundity are optimized, and hypothesized that changes of only 2 or 3˚C could remove species from the extremities of their geographic range.

The extent and character of the impacts of water withdrawals on aquatic invertebrate life histories remains largely hypothetical. The studies that examined invertebrates below water diversions have focused on community composition (e.g. Dudgeon 1992; Castella et al. 1995; Rader and Belish 1999) rather than life histories. Conversely, research on the roles of temperature and discharge on life histories has been confined to streams with natural flow and temperature regimes (e.g. Delucchi and Peckarsky 1989; Harper et al. 1995), systems modified by large dams (e.g. Ward 1974; Vinson 2001) and industrial thermal pollution (e.g. Tennessen and Miller 1978; Coler and Kondratieff 1989) or experiments in laboratory settings only (e.g. Nebeker 1971; Giberson and Rosenberg 1992; Cabanita and Atkinson 2006). The intent of this study was to examine the effects that artificially depressed summer discharge and elevated water temperatures have on the life histories of aquatic invertebrates. Our study investigated the emergence timing and adult body mass for three holometabolous aquatic insect species in two arid-land rivers with multiple withdrawal structures creating gradients of

decreasing discharge and increasing water temperature. We expected the reduced discharge and higher water temperatures to 1) cause earlier summer emergence and 2) reduce the average adult body size of these three species from upstream to downstream.

SITE DESCRIPTION

The Umatilla and Walla Walla rivers are 5th and 4th order tributaries of the Columbia River in northeastern Oregon. The rivers originate in the forested Blue Mountains and flow through the semi-arid plains of the Columbia Basin. Large dams are absent from the mainstem of each river, although multiple low-head irrigation diversion dams (< 6 m) have been present since the early 1900s. Land use in the portion of the watershed surrounding the sample sites of each river is dominated by irrigated agriculture. The regional climate is arid with warm summers. Mean annual precipitation along the lower Umatilla River at Hermiston, Oregon is 22.7 cm, and mean maximum air temperatures range from 30.1°C in summer to -3.2°C in winter (Western Regional Climate Center, site 353847). Mean annual precipitation along the Walla Walla River at Milton-Freewater, Oregon, is 36.8 cm and mean maximum air temperatures range from 29.4 °C in summer and -3.4 °C in winter (Western Regional Climate Center, site 355593). The hydrology of the rivers is driven by snowmelt from the headwaters, with an average spring runoff (February-June) and baseflow (July-September) of 31.8 and 7.6 cubic meters per second (cms) for the Umatilla (United States Bureau of Reclamation, site YOKO) and 25.7 and 3.1 cms for the Walla Walla at Touchet, WA (United States Geological Survey, gage 14018500).

A series of four irrigation diversion dams are present along the 31 km study reach of the lower Umatilla, and two diversion dams and a zone of high surface water loss to groundwater are located along the 7 km study reach of the Walla Walla (Figure 2.1). The diversion dams and the losing reach on the Walla Walla create longitudinal gradients of decreasing discharge and increasing water temperatures during the summer months (Table 2.1). No tributaries are present within the study reaches.

METHODS
Field sampling

Emergence of adult aquatic insects was monitored at a single randomly selected riffle (sample site) above and below each diversion dam on both rivers and the losing reach on the Walla Walla during the summer of 2006. Thus, eight sample sites were located on the Umatilla, and six on the Walla Walla.   At each sample site, four floating emergence traps (Appendix A) were deployed randomly along a 50 meter transect, with two of the traps placed mid channel and two placed along the bank to capture insects that crawl ashore to emerge

(Paetzold and Tockner 2005). Emergence traps were pyramidal with a 0.25 m^2 basal area, paneled with 1 mm mesh-size screening, and tapered upwards to direct trapped insects into a sample bottle filled with 70% ethanol.

Emergence was monitored continuously and sampled weekly from 6 July – 1 September 2006 on the Umatilla and 27 June – 30 August 2006 on the Walla Walla. Water temperature was continuously monitored at each sample site using Onset HOBO temperature loggers recording at 30 minute intervals. River discharge at sites U8 through U2 on the Umatilla was obtained from the United States Bureau of Reclamation (<http://www.usbr.gov/pn/hydromet/>), and by monthly instantaneous measurements for site U1. Walla Walla discharge was determined from instantaneous measurements taken in mid-June, -July, and –August, and did not appear to change discernibly between weekly sampling periods from 5 July to the end of the sampling season, based on the recorded position of shoreline emergence traps relative to the water's edge. All instantaneous discharge measurements were made by measuring depth and water velocity (at six-tenths of depth) using a Marsh-McBirney digital flow velocity meter at a minimum of 20 points across the river. Water temperature and discharge throughout the sampling period are given in Appendices B and C. In addition to temperature and discharge, a suite of physical habitat variables were measured. Water depth at each trap and water velocity at the mid channel traps were recorded weekly. The average substrate diameter and canopy cover at each trap was recorded and remeasured if traps were moved from their original position to follow the receding water's edge.

Samples were collected from the emergence traps weekly and transported to the laboratory. The number of the snail-case caddisfly *Helicopsyche borealis* and aquatic moth *Petrophila confusalis* in each Umatilla sample and the number of *Glossosoma traviatum* in each Walla Walla sample was counted. These species were selected due to their discrete emergence periods occurring within the sampling season on the study rivers and their presence at all or most sampling sites. Body length measurements were taken from randomly selected male and female insects from the three dates of highest emergence at each site. Sample sizes are given in Table 2.2. Body length from the front of the head to tip of the abdomen was measured to the nearest 0.1 mm with an ocular micrometer for all specimens. Length measurements were converted to mass using the regression equations in Sabo et al. (2002) for *P. confusalis* and Sample et al. (1993) for *H. borealis* and *G. traviatum*. Counts and body mass measurements from the four emergence trap samples at each site were composited for each sampling date due to the patchy distribution of these species within sites.

Data analysis

We examined if the date of median emergence and average individual male and female adult body mass at peak emergence were correlated with discharge, temperature, or the habitat variables measured at each site using nonparametric multiplicative regression (NPMR) (McCune 2006) run with HYPERNICHE version 1.0 (McCune and Mefford 2004). NPMR explores relationships between a single response variable and multiple explanatory variables, but unlike parametric techniques such as multiple linear regression, it does not force the data to fit a predetermined mathematical relationship (McCune 2006). Rather, NPMR uses a local multiplicative smoothing function with a leave-one-out cross validation, allowing the data itself to predict model shape (McCune 2006). We chose NPMR for this analysis because we predicted complex nonlinear relationships between emergence timing and the environmental variables. We selected a local mean estimator and Gaussian weighting function for the local model, and specified that 3 data points (minimum neighborhood size) should be used in calculating the weighted estimate. Model fit was judged using a cross-validated R^2 (xR^2), which is more conservative than the traditional R^2.

For species with both an early and late summer emergence period (*H. borealis* and *G. traviatum*), analysis was performed on the late period only, as the initiation of this emergence occurred during the sample period and the organisms emerging at this time would have been subjected to the summer discharge and temperature regimes for a longer period of time. The date of median emergence of a species (date at which 50% of individuals have emerged) was identified at each sample site using the cumulative emergence curve of that species for the site. For NPMR, we chose discharge and water temperature averaged over the entire sampling period as metrics of discharge and temperature. Water depth, water velocity, substrate size, and canopy cover were also averaged over time. In addition to discharge, temperature, and the four habitat variables, densities of predatory benthic invertebrates and fish taxa (Wooster et al. unpubl.) from monthly surveys at the sample sites were considered for inclusion into the analysis. To avoid overfitting the model, scatterplot matrices were examined to isolate a maximum of four of the habitat and predator variables in addition to discharge and temperature that appeared to be correlated with date of median emergence. Only these variables were included in the NPMR analysis.

Laboratory experiment

Because increased temperature co-occurs with reduced discharge along the study reaches, we isolated the effect of temperature on emergence timing of *H. borealis* using a controlled laboratory experiment during the summer of 2007. Five *H. borealis* larvae collected from the Umatilla River were randomly placed into each 8 x 8 cm microcosm within temperature-controlled chambers (Sheldon Manufacturing, Inc., model 2015-ZZMFG). Eight

replicate microcosms were placed into each of four target temperature treatments (16, 19, 23, and 28˚C). The treatments represent the range of water temperatures found at the Umatilla River study sites during the summer season, and are consistent with those found in the literature for this species (Williams et al. 1983; Vaughn 1985). Microcosms were filled with a 50% blend of Umatilla River and on-site well water and were aerated with aquarium air pumps. Water was changed biweekly to control water quality. Periphyton-coated cobbles and washed sand from the larval collection site were placed in each microcosm to provide a source of food and case-building materials. Water temperature was continuously monitored with an iButton temperature logger placed in a separate microcosm within each temperature chamber. Light cycles were set to follow the ambient day length. Date of emergence was noted for each adult, and individuals were preserved in 70% ethanol.

Data analysis

Differences between the cumulative emergence curves for each temperature treatment were examined with Kolmogorov-Smirnov (K-S) tests using SYSTAT version 12. A K-S test is a goodness of fit test used to determine if two distribution curves differ, where n is the number of days (observations) between initiation and cessation of emergence. A high larval mortality rate prevented the use of microcosms as replicates to test for emergence timing among treatments. Because males and females must be measured separately due to differences in size, we had insufficient numbers to test for effects on adult body mass.

RESULTS

Emergence timing—Field

Average discharge during the sampling period decreased by 93% from upstream to downstream on the Umatilla River (Table 2.1; Appendix D), coinciding with a 4.6 ºC increase in average water temperature and a 6.8 ºC increase in average daily maximum temperature (Table 2.1). Likewise, average discharge at the downstream site on the Walla Walla River was 88% lower than the upstream site, and average temperature and average daily maximum temperature were 2.4 and 5.0 ºC higher, respectively (Table 2.1). The pronounced longitudinal gradients in discharge and temperature existed throughout the entire sampling period (Appendices B and C) because water abstraction had begun prior to emergence trap deployment.

Despite the large differences in discharge and temperature, the emergence periods for each of the three species were similar among sites (Figures 2.2 and 2.3). Initiation of *P. confusalis* emergence and peak emergence varied up to 14 days between sites (Figure 2.2), but cumulative emergence of this species did not appear related to the gradients of discharge

and temperature (Figure 2.4). Initiation of the late *H. borealis* and *G. traviatum* emergence periods varied up to 14 and 28 days between sites, and cumulative emergence curves suggest that emergence from this period may have occurred earlier at the lower sites for *H. borealis* only (Figure 2.4). NPMR analysis, however, indicates that date of median emergence was not significantly correlated with average discharge, water temperature, predatory invertebrate and fish densities, or the measured habitat variables for any of the three species (Table 2.2). All three species emerged across a broad range of accumulated degree days (Appendix E), rather than the tight clustering around a narrow range that would be expected for temperature-driven emergence timing. The abundance of each species at peak emergence varied between sites (Table 2.3).

Adult body mass—Field

Average individual adult body mass of each species varied considerably between sites, but was not significantly related to average water temperature (Figure 2.5), average discharge, or any measured habitat and predator density variable (Table 2.2). Body mass of individual insects was not related to the degree days accumulated at their emergence (Appendix E). However, average adult body mass of *P. confusalis* females was 31% lower at the warmest, lowermost Umatilla site than at the coolest, uppermost site, and markedly lower than all other sites (Figure 2.5), suggesting a possible threshold effect due to the high temperatures of this site. This pattern was not present for either *H. borealis* or *G. traviatum*.

Laboratory experiment

Water temperature within each treatment averaged 17.8, 19.4, 21.9, 27.3 ºC, which differed slightly from the target temperatures but provided clear separation between treatments. Median *H. borealis* emergence occurred 5 days earlier in the warmer temperature treatments (Figure 2.6). Cumulative proportional emergence curves differed significantly between the coolest and warmest treatments (K-S test: 27.3 ºC vs. 17.8 ºC; D = 0.56, n = 16, two-sided p = 0.006), and evidence of earlier emergence from the 21.9 ºC treatment compared to the coolest treatment is suggestive (K-S test: 21.9 ºC vs. 17.8 ºC; D = 0.44, n = 16, two-sided p = 0.065). However, the two warmer treatments did not differ significantly from each other (K-S test; 27.3 ºC vs. 21.9 ºC; D = 0.31, n = 16, two-sided p = 0.34). Mortality rates over the course of the experiment increased with temperature (17.8 ºC = 75%, 21.9 ºC = 80%, 27.3 ºC = 83%), with the exception of 19.4 ºC (95%). Emerged adults from each temperature treatment were composited for analysis, as some microcosms had 100% mortality. The sample size from the 19.4 ºC treatment was too small to include in the analysis.

DISCUSSION

Emergence timing

The similarity in emergence timing along the length of each river was unexpected, given the magnitude of differences in temperature and discharge. The effect of water temperature on the metabolic rates of insects is well documented (Cummins and Klug 1979; Ward and Stanford 1982; Robinson et al. 1983) and insects have been found to shape their life histories around discharge events (Lytle 2001; Lytle and Poff 2004), but elevated water temperatures and reduced discharge did not significantly influence the emergence timing of the species we observed at a weekly intervals. Earlier emergence of aquatic invertebrates in warmer water has been demonstrated in numerous studies with temperature differences similar to or smaller than those found in our study rivers. Giberson and Rosenberg (1992) observed that the onset of emergence occurred 180 days sooner for *Hexagenia limbata* raised in water 5 ºC warmer. Similarly, emergence of *Baetis bicaudatis* was significantly earlier for those larvae raised in water only 1.8 ºC warmer (Harper and Peckarsky 2006). In field observations, individual mayfly species initiated emergence earlier in mountain streams with average monthly temperatures a mere 1.2 – 1.6 ºC warmer year-round (Harper et al. 1995). Likewise, stoneflies (Harper and Pilon 1970; Nebeker 1971; Flannagan and Cobb 1991; Gregory et al. 2000) and a few caddisfly species (Nebeker 1971; Hogg and Williams 1996) emerged earlier in warmer temperature regimes, suggesting the effect of temperature may be geographically and taxonomically widespread.

The weekly sampling resolution may have been too coarse to detect small alterations in emergence timing, such as the 5 day difference observed during the *H. borealis* laboratory experiment. However, differences in emergence timing a week or much longer were observed in the studies cited above, suggesting that any variation in emergence timing missed by the sampling resolution in our study is comparatively small considering the gradients in temperature observed along our study rivers.

Scientific understanding of the mechanisms and processes behind the effects of temperature on growth and development is far from complete (Newbold et al. 1994; Cabanita and Atkinson 2006), and thus a number of factors may account for the similarity in emergence timing between sites. The three species in our study are holometabolous, while most published findings of emergence timing modified by temperature have examined hemimetabolous insect species. An important difference is that many caddisflies enter a diapause during the late larval or pupal stages (e.g. Hauer and Stanford 1982, Martin and Barton 1987), and this may act as a synchronizing mechanism for emergence (Otto 1981, Hogue and Hawkins 1991), a process unique to holometabolous life histories. If a pupal or pre-pupal diapause of the three species in this study acted to synchronize emergence, the

timing of emergence would remain unaltered among sites despite any difference in developmental rates of the larvae. Similar observations have been made for larval *Brachycentrus occidentalis* caddisflies along our study reach of the Umatilla River. Miller (2008) found that larval growth and development were more advanced at sites with warmer temperatures compared to sites with cooler temperatures during early and mid summer 2004 and 2005. By late summer, however, late instar growth and development had halted at the warmer sites, allowing the earlier instars at cooler sites to catch up in both developmental stage and size (Miller 2008).

The comparatively short duration of the discharge and temperature alterations, and localized evolutionary adaptation are unlikely to have caused the similarity in emergence timing. Discharge alteration occurs only during the summer months at our study sites, and while temperature at site U1 was an average of 2.3 ºC warmer than U8 during the non-irrigation season on the Umatilla (September 2005 to June 2006), the large differences in temperature occurred only in July and August. The larvae of the studied species, however, developed over a longer time period than the two months of severe temperature alteration. Yet, most growth occurs during the last 2 to 3 months of the larval stage for many aquatic insects (Hogue and Hawkins 1991), indicating that perennial temperature alteration is not required to affect larval development or emergence timing. For instance, temperatures during the final few months of the larval stage of semivoltine stoneflies can highly influence emergence timing (Flannagan and Cobb 1991, Gregory et al. 2000), and changes in emergence timing with elevated temperatures during the final month of mayfly larvae has been documented (Harper and Peckarsky 2006), suggesting the time period of highly divergent temperatures in our study is sufficient to alter development rates in many invertebrate species. It is also unlikely that subpopulations of the studied species at each site have adapted genetically to the specific local conditions (e.g. Jackson and Resh 1992), as aerial adult dispersal and larval drift during the high flows of winter and spring should prevent downstream sites from becoming genetically isolated.

Additional factors may constrain plasticity in emergence timing, including competition and emergence cues unrelated to temperature or discharge. The life histories of some aquatic insects are timed around temporal variability in food resources and the avoidance of competition (Cummins and Klug 1979), which may limit the influence of temperature or discharge in determining the timing of emergence. However, we find this scenario unlikely, as temporal resource partitioning is common primarily in shredders rather than the grazers observed in this study (Cummins and Klug 1979). Similarly, emergence may be influenced by additional synchronizing cues such as photoperiod (Lutz 1968, 1974, Pritchard 1989). However, emergence timing varied significantly in the controlled experiment despite consistent

photoperiods for all temperature treatments, and photoperiod is considered secondary to temperature in governing development (Cabanita and Atkinson 2006, Newbold et al. 1994). Also, the density of predatory taxa such as trout and stoneflies has been shown to cause more rapid maturation and smaller body sizes of *Baetis* mayflies (Peckarsky et al. 2001), but the densities of fish and predatory invertebrate taxa did not influence emergence timing or adult body mass in our study.

Laboratory experiment

The results of the controlled experiment indicate that temperature has an effect on the emergence timing of *H. borealis*. However, this effect was not observed in the field due to the weekly sampling resolution, or was masked by environmental variables that were not measured. Growth has frequently been observed to respond directly to temperature in laboratory experiments, but multiple physical and biological factors may cloud this relationship for invertebrates observed in the field (Hawkins 1986). The 4.1 ⁰C difference in temperature between the coolest (17.8 ⁰C) and earlier-emerging middle (21.9 ⁰C) temperature treatment was similar to the 4.6 ⁰C range of average temperatures observed in the field. However, the 5.4 ⁰C difference between the middle and the warmest (27.3 ⁰C) treatments yielded no further effect on emergence timing. These results suggest that the emergence of *H. borealis* responds differentially to temperature changes within the tested range, with a strong response to increasing temperatures between approximately 18 and 22 ⁰C, and temperature increases above this reaching a physiological threshold and no longer triggering earlier emergence. If this is the case, it is curious that emergence timing did not vary in the field, where average site temperatures ranged from 18.6 to 23.2 ⁰C.

A notable difference in the temperature regimes between the laboratory experiment and field is the smaller diel variation in the laboratory. Aquatic insects and fish have been observed to both develop more rapidly (Hokanson et al. 1977, Sweeney 1978) and more slowly (Bradshaw 1980, Dickerson and Vinyard 1999) in daily fluctuating water temperatures compared to nearly constant temperatures of the same mean. However, this does not explain the differential response of *H. borealis* to temperature gradients in the laboratory and the Umatilla because the emergence timing at equivalent mean temperatures cannot be directly compared between the laboratory and the field.

The emergence pattern in the laboratory experiment may also result from the simplified results that are possible when comparing only 3 temperature treatments as opposed to a gradient of 8 temperatures from sites on the Umatilla. This is apparent when analyzing the cumulative emergence curves of field samples (Figure 2.4), in which differences in emergence timing exist between any 3 randomly selected field sites but are not related to the

temperature or discharge of that site. However, the variation in field emergence timing may be due to unmeasured site-specific attributes such as food resources, which should have been minimized by the standardized conditions and collection site of the experiment. The scope of inference for this experiment is limited, as the 17–25% survival rate is low enough to warrant caution when comparing the results to the large sample sizes collected in the field, even if this mortality rate is similar to controlled experiments in other studies in which conclusive results were obtained (e.g. Harper and Peckarsky 2006).

Adult body size

The expected relationship between adult body mass and water temperature was found for only one species in this study, the pyralid lepidopteran *Petrophila confusalis.* The average mass of female and male *P. confusalis* was 31% and 15% smaller, respectively, at the warmest site (U8) as compared to the coolest site (U1). This decrease in body size may influence the reproductive capacity of the population at the warmest site. Fecundity of female insects is positively correlated with body size (Hinton 1981) and larger males may be more successful at obtaining mates (Rantala et al. 2001), though the effect may not be universal for all species (Taylor et al. 1998). However, the emergence rate of *P. confusalis* at the impacted downstream sites is comparable to some of the less impacted upstream sites. This suggests that *P. confusalis* is capable of persisting at the impacted sites, and that the existing reproductive rate and downstream drift of insects during spring flows can mediate the loss of reproductive potential due to reduced body mass.

Our results do not fully conform to common theories of how temperature influences the size of aquatic invertebrates. The temperature-size rule states that warmer water temperatures are correlated with smaller body sizes in ectotherms (Atkinson 1994). The majority of studies on aquatic invertebrates support this concept (Atkinson 1995), and factors such as seasonal time constraints on larval development have not explained the observed exceptions (Cabanita and Atkinson 2006). The Thermal Equilibrium Hypothesis proposed by Vannote and Sweeney (1980) provides a mechanism for this temperature-size rule, proposing that increasing water temperatures may enlarge the energetic costs of respiration, thereby depressing growth rates and accelerating development. However, emergence timing remained unaltered for *P. confusalis* despite a reduction in adult body mass at the most downstream site, and neither emergence timing nor body mass were altered for *H. borealis* and *G. traviatum.* Confounding results were also found by Hogg and Williams (1996), who observed smaller adult body sizes for nemourid stoneflies in warmer water temperatures, but not for lepidostomatid caddisflies, despite earlier emergence. The holometabolous life history of the caddisflies was offered as an explanation for the discrepancy (Hogg and Williams

1996), but this is inconsistent with the markedly lower body size of the holometabolous *P. confusalis* at the site with the warmest temperatures in our study. Indeed, unlike the emergence timing results, adult body mass from our study cannot be explained by synchronized emergence through late instar or pupal diapause. While synchronized emergence will disrupt the temporal trend of decreasing body size throughout the flight season at a site, it cannot change any absolute differences in body sizes among sites (Hogue and Hawkins 1991).

The three species in this study are present along the study reaches of their respective river and thus appear adapted to tolerate broad ranges of temperature and discharge and have life histories that are highly resistant to alteration by these two factors. Notably, *H. borealis* is tolerant of temperatures up to 36 ⁰C (Resh et al. 1984) and low oxygen concentrations (Williams et al. 1983), and *P. confusalis* has been found in waters up to 28 ⁰C (Tuskes 1977). Changes in the life histories of these potentially resistant taxa may only be produced through changes in the temperature and discharge regimes more extreme than those observed in this study. Such a threshold may have been approached for *P. confusalis* at site U1, where a dramatic decrease in adult female body mass was observed.

CONCLUSIONS

These results are novel in that we found no evidence of altered emergence timing at a weekly sampling scale for the three tested species and reduced body mass for only a single species, despite large gradients in discharge and water temperature from successive agricultural water withdrawals. We suspect that our results may be due to the synchronization of emergence caused by a possible diapause, and by the known tolerance of high temperatures by two of these species. Comparatively few studies have examined the role of temperature and discharge on the life histories of holometabolous species, focusing instead on hemimetabolous Ephemeroptera and Plecoptera. Likewise, many studies have examined the effects of discharge and water temperature on relatively undisturbed stream systems or insects from such systems. Our results suggest that the three studied species are highly resistant to pronounced changes in discharge and temperature, and may be indicative of resistant invertebrate communities structured by decades of disturbance. It is important to note that the magnitude of discharge reduction and temperature elevation observed in our disturbed study rivers may have a much more pronounced impact on the life histories of invertebrates in small headwater streams or pristine rivers. We also submit that physiological differences between hemimetabolous and holometabolous species may prevent the relationship between emergence timing and temperature from occurring in the latter. Clearly

more research is needed to elucidate any differential responses to temperature between these two life history strategies.

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Figure 2.1. Delineated watersheds and relative location of study sites for the Umatilla River (A) and Walla Walla River (B). Lines perpendicular to river represent the location of diversion structures.
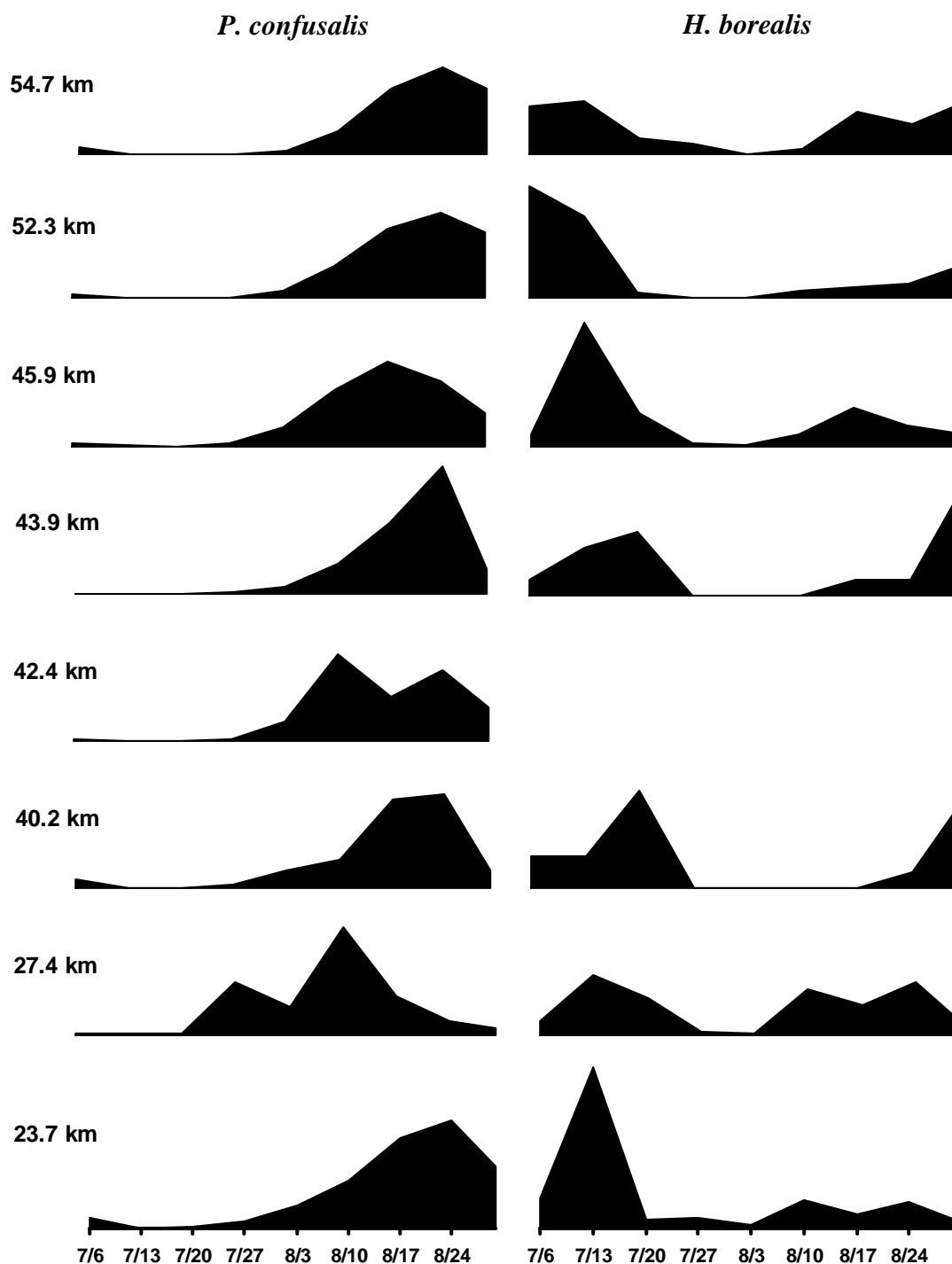
Figure 2.2. Emergence of *P. confusalis* and *H. borealis* from the Umatilla River sample sites (denoted by river kilometer) during the sample period. Vertical axes are standardized by the proportional emergence on each sample date. *H. borealis* at river kilometer 42.4 was excluded due to extremely low sample sizes.
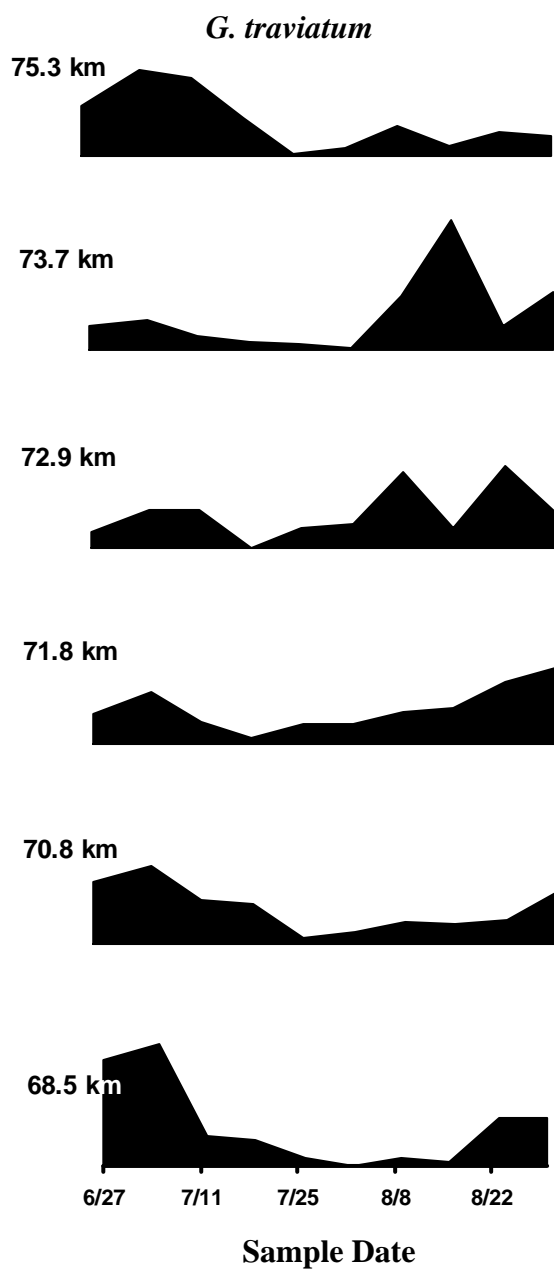
Figure 2.3. Emergence of *G. traviatum* from the Walla Walla River during the sample period. Vertical axes are standardized by the proportional emergence on each sample date.
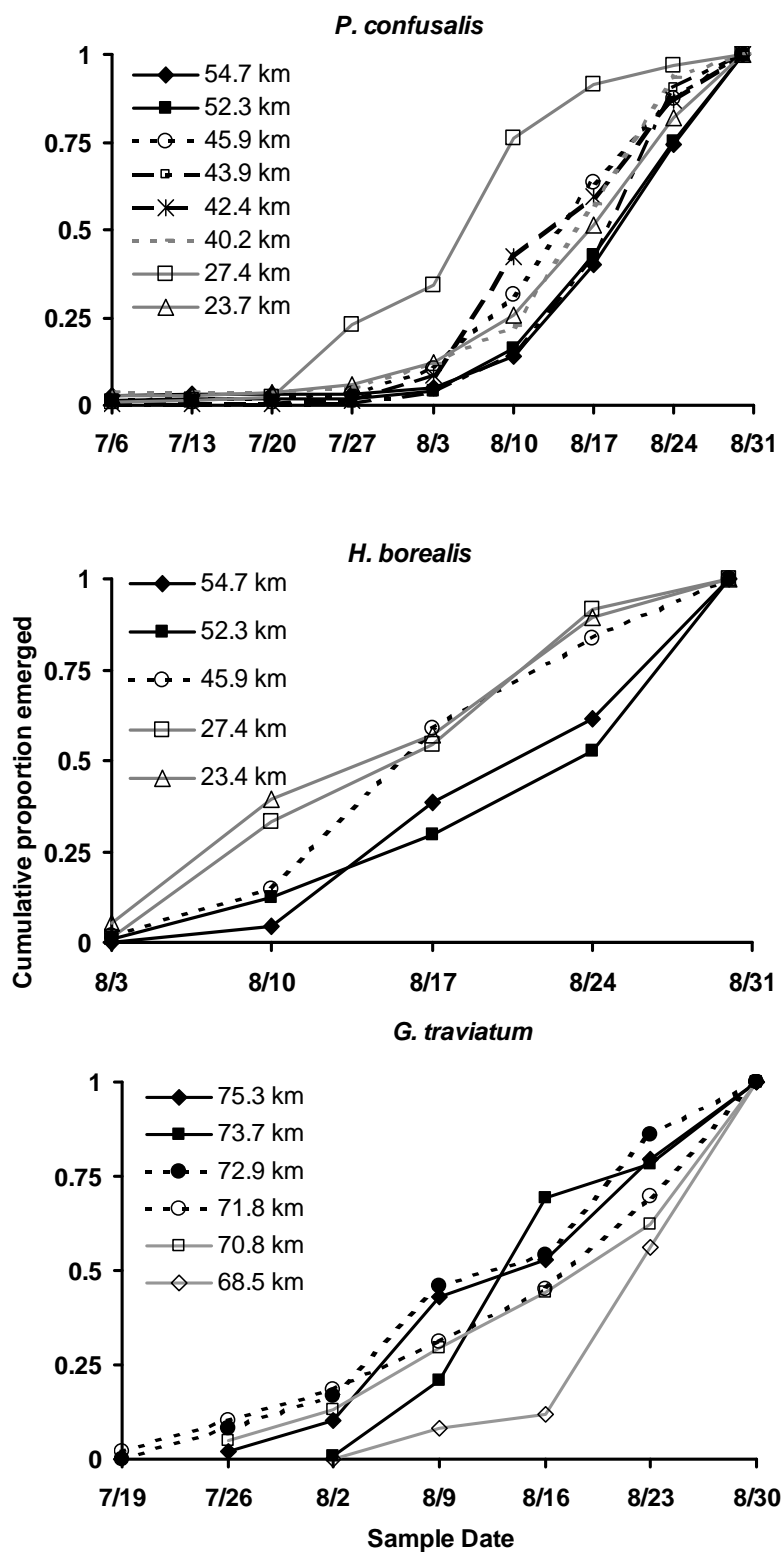
Figure 2.4. Cumulative proportional emergence of *P. confusalis* and the late summer peaks of *H. borealis* and *G. traviatum* at each sample site. *H. borealis* at river kilometer 42.4 was excluded due to low sample sizes.
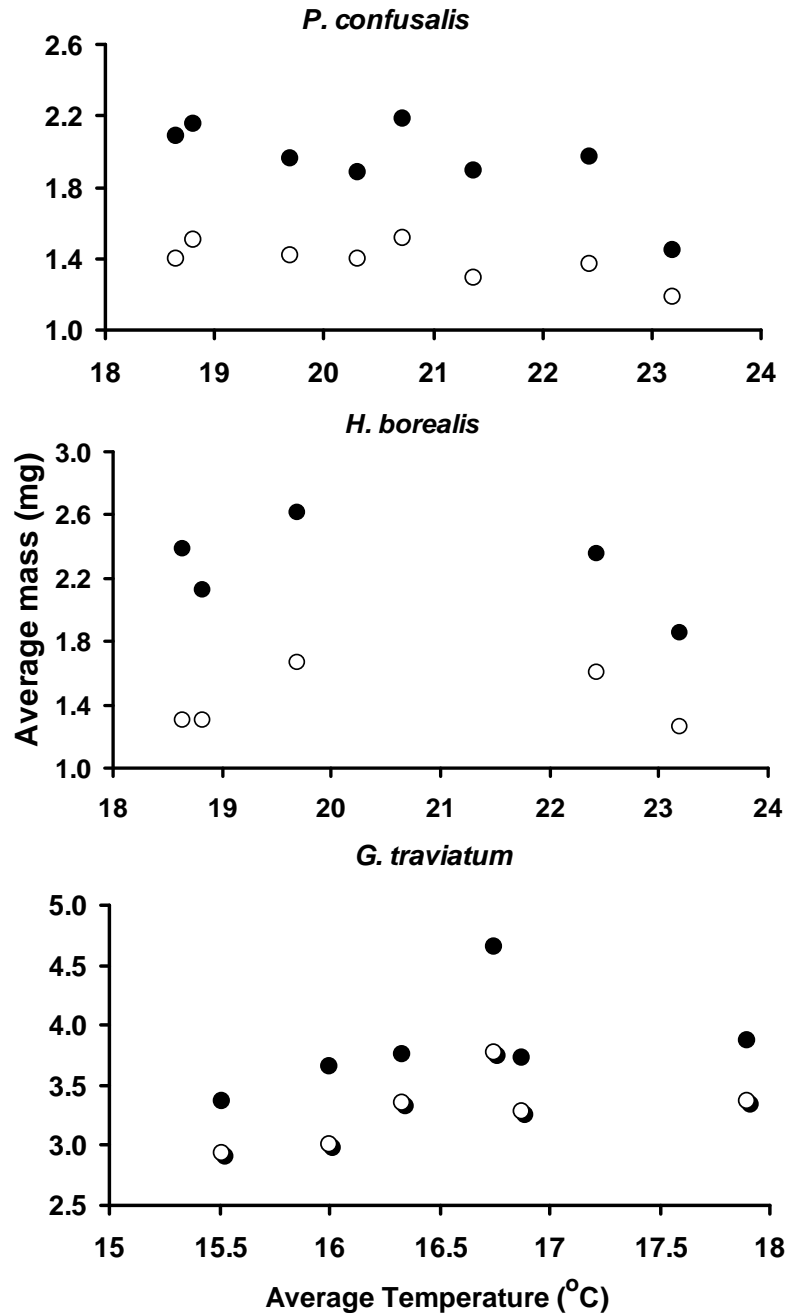
Figure 2.5. Average individual female (closed circles) and male (open circles) adult body mass at peak emergence at each sample site, denoted by the average water temperature of the site throughout the sampling period.
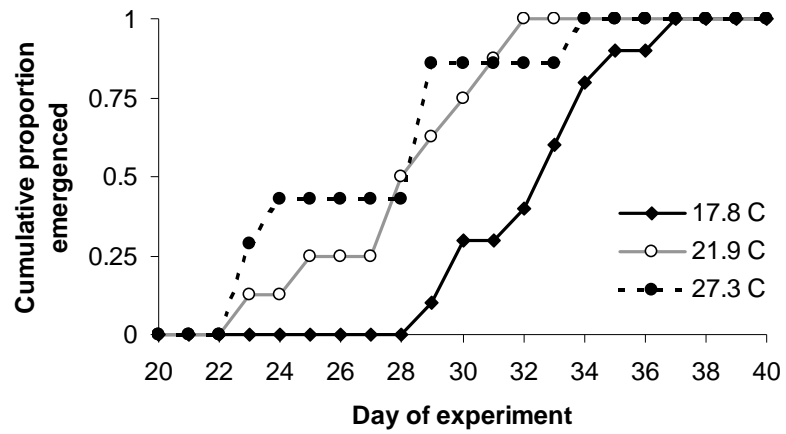
Figure 2.6. Cumulative proportional emergence of *H. borealis* from temperature treatments during the laboratory experiment.

Table 2.1. Location, discharge and water temperatures of each study site. Sites U8 and WW6 are the most upstream sites. [a]River kilometer is distance from confluence with the Columbia River. [b]Discharge and temperature are averaged throughout the summer sampling period. [c]Degree days are the total accumulated throughout the summer sampling period.

	Umatilla River				Walla Walla River			
Site name	River kilometer[a]	Average discharge (cms)[b]	Average temperature (degrees C)[b]	Total degree days[c]	Site name	River kilometer[a]	Average discharge (cms)[b]	Average temperature (degrees C)[b]	Total degree days[c]
U8	54.7	6.55	18.6	1167	WW6	75.3	3.23	15.5	1086
U7	52.3	6.24	18.8	1178	WW5	73.7	1.12	16.3	1143
U6	45.9	5.88	19.7	1233	WW4	72.9	1.09	16	1120
U5	43.9	0.63	20.7	1298	WW3	71.8	0.77	16.7	1172
U4	42.4	0.75	20.3	1275	WW2	70.8	0.74	16.9	1181
U3	40.2	0.64	21.4	1342	WW1	68.5	0.4	17.9	1253
U2	27.4	0.81	22.4	1408					
U1	23.7	0.48	23.2	1453					

Table 2.2. Best fit models from NPMR analysis of median emergence and average body mass. Predictor variables shown are those with the highest fit (xR^2).

Median Emergence

Response	Predictors	xR^2	Tolerance
P. confusalis	depth, substrate	-0.05	3.37, 2.83
H. borealis	depth	-0.29	3.37
G. traviatum	fish density	-0.04	9.38

Average Body Mass

Response	Predictors	xR^2	Tolerance
P. confusalis (female)	temperature	-0.13	2.27
P. confusalis (male)	temperature	-0.08	2.27
H. borealis (female)	discharge	0.04	117.9
H. borealis (male)	discharge	-0.08	117.9
G. traviatum (female)	canopy cover	-0.2	43.5
G. traviatum (male)	canopy cover	-0.22	43.5

Table 2.3. Total number of individuals collected during the entire sample period (*P. confusalis*) or the late season emergence period (*H. borealis* and *G. traviatum*), and number of males and females measured for adult body mass.

H. borealis (# individuals)			*P. confusalis* (# individuals)			*G. traviatum* (# individuals)			
Site	Total	Body mass		Total	Body mass		Site	Total	Body mass	
	Emerged	Female	Male	Emerged	Female	Male		Emerged	Female	Male
U8	91	20	56	586	89	127	WW6	48	23	5
U7	482	97	111	927	88	121	WW5	100	49	24
U6	60	14	23	208	75	90	WW4	100	31	20
U5	8	-	-	170	47	63	WW3	145	54	45
U4	7	-	-	148	55	54	WW2	58	21	17
U3	6	-	-	177	66	43	WW1	25	17	6
U2	624	115	71	294	60	87				
U1	684	85	86	140	43	52				

THE EFFECTS OF WATER WITHDRAWALS ON THE TIMING AND MAGNITUDE OF
AQUATIC INVERTEBRATE EMERGENCE FROM TWO ARID-LAND RIVERS

ABSTRACT

Small diversion dams are capable of removing much of a river's flow, often resulting in increased water temperatures and habitat loss. Warmer temperatures have been shown to accelerate aquatic invertebrate growth and development, and discharge reductions can reduce instream habitat, suggesting that water withdrawals may alter both the timing of emergence and the total emerging biomass from a river. To examine the influence of water withdrawals on the timing and magnitude of aquatic invertebrate emergence, the emergence and biomass of taxonomic families were monitored continuously during the summer of 2006 on the Umatilla and Walla Walla rivers in arid northeastern Oregon. Multiple sample sites were located along gradients of decreasing discharge and increasing water temperatures caused by successive diversions on each river. With the exception of Hydroptilidae, emergence timing was not correlated with discharge or water temperature for all taxonomic families, and the timing of total emergence remained similar among sites. However, total emerging biomass was reduced at sites subject to high water withdrawals, particularly on the more heavily diverted Umatilla River. These results suggest that the life histories of aquatic invertebrates in some rivers may be resistant to severe water withdrawals, but ecological effects may exist through the reduced export of emerging biomass into the riparian ecosystem.

INTRODUCTION

Water withdrawal is a widespread disturbance of lotic systems that can be expected to increase in severity as human populations expand (Oki and Kanae 2006, Malmqvist and Rundle 2002). Water withdrawals from low head diversion dams have a marked seasonal effect on discharge and temperature. Base flows are reduced during the summer irrigation season, which may increase water temperatures downstream of diversions (Cazaubon and Giudicelli 1999; Rader and Belish 1999), while the higher flows of spring and winter are allowed to proceed uninterrupted. Despite the vast number of water diversion points in temperate regions worldwide and the resulting reduction of in-stream flow during a critical hydrologic period for stream biota, our knowledge of the ecological consequences of water withdrawals is incomplete.

Aquatic invertebrate life histories are governed in part by temperatures which influence growth and development rates (Gallepp 1977; Sweeney and Vannote 1978; Giberson and Rosenberg 1992; Newbold et al. 1994) as well as high and low discharge events which can restrict the period of growth and the timing of life history events (Poff and Ward 1989; Lytle 2001; Lytle and Poff 2004) such as emergence. Water withdrawals may

therefore alter emergence timing of individual species by accelerating growth and development through increased water temperatures, or by reducing available development time by dewatering the stream.

Water withdrawals may also be capable of altering both the timing and magnitude of the peak aquatic invertebrate biomass emerging from a river. Earlier emergence of multiple taxa or a single dominant taxon may cause the peak of emerging biomass to shift in time. In studies that have examined the influence of temperature and discharge on aquatic invertebrate life histories, temperature has been found to be more important in driving phenotypic changes in life history than discharge (Delucchi and Peckarsky 1989; Huryn and Wallace 2000; Harper and Peckarsky 2006). However, it may be possible for discharge to influence the magnitude of peak emergence. Discharge reductions often shrink benthic habitat area (Cowx et al. 1984; Stanley et al. 1997; Brasher 2003; Miller et al. 2007; but see Rader and Belish 1999), depending on the severity of flow reduction and channel morphology. In addition to habitat loss, reductions in discharge from either water withdrawals or natural causes have been shown to both increase (Gore 1977; Extence 1981; Stanley et al. 1997; Miller et al. 2007) and decrease (Cowx et al. 1984; Englund and Malmqvist 1996) benthic invertebrate densities. Given that the magnitude of biomass emerging from a section of river depends largely on the emergence rate (an expression of benthic density) and the surface area from which emergence is occurring, reduced discharge may limit the emerging biomass that a river is capable of producing. Water withdrawals may thus have the capacity to modify the timing of peak energy export from the aquatic environment through altered water temperatures, and the magnitude of the export through reduced discharge.

The export of emerging aquatic insects can significantly influence food webs in the surrounding watershed, particularly in the riparian ecosystem. Jackson and Fisher (1986) observed that a scant 3% of emerged aquatic invertebrate biomass from a highly productive stream returned to the aquatic system, indicating a high terrestrial retention of aquatic-derived biomass. Aquatic insects provide significant energy sources for terrestrial organisms such as birds (Nakano and Murakami 2001; Sweeney and Vannote 1982), arthropods (Kato et al. 2003; Paetzold et al. 2006), lizards and bats (Power et al. 2004). Peak aquatic emergence may occur during periods of low terrestrial invertebrate production, increasing the importance of this source of prey for terrestrial consumers (Nakano and Murakami 2001). The importance of aquatically-derived organic matter in terrestrial food webs necessitates further research on the effects of human disturbances on energy flow between the stream and terrestrial systems (Baxter et al. 2005).

The objective of this study was to examine the effect of water withdrawals on the temporal occurrence and magnitude of aquatic invertebrate emergence. We monitored

emergence at multiple sites along a longitudinal gradient of decreasing discharge and increasing water temperatures resulting from multiple water diversion points on two arid-land rivers. We predicted that water withdrawals would cause earlier total emergence by modifying the emergence timing of individual taxonomic families. We also expected water withdrawals to depress the amount of emerging biomass through reduced habitat area relative to upstream sites unaffected by water withdrawal.

SITE DESCRIPTION

Study sites were located on the Umatilla and Walla Walla rivers of northeastern Oregon. The rivers are, respectively, 5th and 4th order tributaries to the Columbia River, originating in the coniferous forested Blue Mountains and flowing through the semi-arid plains of the Columbia Basin. Multiple low-head irrigation diversion dams (< 6 m) have been present on each river since the early 1900s, though no large impoundments are located on either mainstem. Land use along the study reaches of each river is dominated by irrigated agriculture, and the regional climate is warm and dry. Along the lower Umatilla River at Hermiston, Oregon, mean annual precipitation is 22.7 cm and mean maximum temperatures range from 30.1˚C in summer to -3.2˚C in winter (Western Regional Climate Center). Mean annual precipitation along the Walla Walla River at Milton-Freewater is 36.8 cm and mean maximum temperature is 29.4 ˚C and –3.4 ˚C in summer and winter, respectively (Western Regional Climate Center). The hydrology of each river is snowmelt dominated, with an average spring runoff (February-June) and baseflow (July-September) of 31.8 and 7.6 cubic meters per second (cms) for the Umatilla (United States Bureau of Reclamation) and 25.7 and 3.1 cms for the Walla Walla (United States Geological Survey).

A series of four irrigation diversion dams are present along the 31 km study reach of the lower Umatilla. Two diversion dams and a zone of high surface water loss to groundwater are located along the 7 km study reach of the Walla Walla. The diversion dams and losing reach on the Walla Walla created longitudinal gradients of decreasing discharge and increasing water temperatures during the summer months (Table 3.1). Concomitant decreases in wetted surface area of the river also occurred along the longitudinal gradient (Table 3.1). No tributaries enter either study reach.

METHODS
Field sampling

Emerging aquatic invertebrate adults were sampled at a single randomly selected riffle (sample site) above and below each diversion structure and the surface water loss zone during the summer of 2006, resulting in 8 sample sites on the Umatilla and 6 on the Walla Walla (Figure 2.1). Four floating pyramidal emergence traps (0.25 m^2 basal area, 1 mm mesh

size) were deployed randomly along a 50m transect at each sample site. Two of the traps were placed mid channel and two along the riverbank to capture taxa that crawl to shore to emerge (Paetzold and Tockner 2005).

Emergence traps were left in place continuously and sampled weekly for 9 weeks (6 July – 1 September) on the Umatilla and 10 weeks (27 June – 30 August) on the Walla Walla. During each sampling bout the water depth, velocity, substrate diameter, and percent canopy cover was measured at each emergence trap. Water temperature throughout the sample period was monitored continuously at 30 minute intervals at each sample site using Onset HOBO temperature loggers. Daily mean discharge data at the Umatilla sites was obtained from the United States Bureau of Reclamation with the exception of the lowest site, where instantaneous discharge measurements were taken. Walla Walla discharge was determined at each site from instantaneous measurements taken in mid June, July, and August. Discharge on the Walla Walla appeared to reach base flow and remain largely static among weekly sampling periods from 5 July to the end of the sampling season, based on the measured position of the water's edge relative to the shoreline emergence traps. All instantaneous discharge measurements were made by measuring depth and water velocity (at six-tenths of depth) using a Marsh-McBirney digital flow velocity meter at a minimum of 20 points across the river.

The wetted width for each site on a sample date was calculated with a width-discharge relationship built from three individual measurements of wetted width and instantaneous discharge in mid June, July, and August. Wetted area of the sample site was determined by multiplying the wetted width at each sample date by the 50 m length of the sample site.

Samples collected weekly from the emergence traps were preserved in 70% ethanol and brought to the laboratory where specimens were identified and counted at the family taxonomic level. Biomass of each taxonomic family in each sample was determined by drying a 50% subsample at 60 ºC for 24 hrs and weighing it to the nearest 0.1 mg. Exceptions include the families Helicopsychidae and Pyralidae on the Umatilla, and Glossosomatidae on the Walla Walla, for which nondestructive weighing techniques were desired because these taxa were used in a separate, related study. Biomass for these three families was determined by measuring body length from the front of the head to tip of the abdomen and applying the length-mass regression equations found in Sabo et al. (2002) for Pyralidae and Sample et al. (1993) for Helicopsychidae and Glossomatidae. For small sample sizes that included only a few individual insects and for which dry mass approached the detection limit of the balance, the average mass of individuals from that taxa were determined from the larger samples from that sample site. This average individual mass was then mulitiplied by the number of

individuals in the small sample to get an estimated mass. Taxonomic count and biomass data
from the four emergence trap samples at each site were composited for each sampling date
due to the patchy distribution of insects within sites.

Data analysis

The combined biomass of all taxonomic families on each sampling date was used to
describe the patterns of total emergence rate (mg m^{-2} wk^{-1}) across time and the longitudinal
gradient.   Total emerging biomass (g wk^{-1}) for each site each week was determined by
multiplying the total emergence rate by the wetted area of the sample site. The emergence
timing of individual taxonomic families was explored using count data to graph the cumulative
proportional emergence over time. The resulting cumulative emergence curve integrates
complex emergence patterns, allowing an intuitive visual display of emergence timing across
sites and the calculation of median emergence date (date at which 50% of individuals have
emerged) for each family. Taxonomic families with consistently small sample sizes or with
only the descending limb of the emergence peak occurring within the sampling period were
not included in emergence timing analysis.

We explored the strength of the relationships between median emergence date of
each family and discharge, temperature, physical habitat variables, and densities of predatory
benthic invertebrates and fish taxa (Wooster et al. unpubl.) from monthly surveys at each site
using nonparametric multiplicative regression (NPMR) (McCune 2006) run with HYPERNICHE
version 1.0 (McCune and Mefford 2004). We chose NPMR analysis to ensure that we could
detect nonlinear and complex relationships between variables. We selected a local mean
estimator and Gaussian weighting function for the local model, and specified a minimum of
three data points to be used in calculating the weighted estimate. Model fit was judged using a
cross-validated R^2 (xR^2), a more conservative method than the traditional R^2. For models with
two significant predictor variables, we used sensitivity analysis to determine the relative
importance of each variable (McCune 2006). Sensitivities are calculated by incrementally
adjusting values of the predictor variable and measuring the resulting change in the response
variable. A sensitivity of 1.0 indicates an equal change in the response variable for a given
change in the predictor, and therefore variables with higher sensitivities are more influential in
the model.

Because total emergent biomass at a site is the product of the emergence rate and
the wetted area of the river, we wished to determine the relative influence of each. It is also
likely that the mechanisms controlling these two factors differ, namely that wetted area is
primarily driven by discharge and channel morphology, while emergence rate may be the
product of a variety of factors such as temperature, density of predatory taxa, and habitat

variables. To determine whether weekly emerging biomass at a site was controlled more by emergence rate or wetted area, we used NPMR to examine the relationship between weekly emerging biomass and these two variables.

RESULTS

Timing of emergence

Timing of total emergence was similar among sites on each river, and while there was variation in emergence timing among sites (Figure 3.1), it did not differ along the longitudinal gradients of discharge or temperature. Total emergence at Umatilla River sites was higher in mid-July and late August, with a period of low emergence occurring midsummer between 27 Jul and 10 Aug (Figure 3.2). Emergence on the Walla Walla River peaked on 5 July at all sites, and declined to 8 – 26% of peak rates by the first week of August (Figure 3.3).

Similarly, the timing of emergence of most individual taxonomic families did not correspond to the gradients of discharge and temperature. Cumulative emergence curves indicate substantial variation in emergence timing among sites, yet date of median emergence for 7 out of 8 families on the Umatilla and all 8 families sampled on the Walla Walla was not significantly correlated to average discharge, average water temperature, predator densities, or other habitat variables (Table 3.2). A single exception was Hydroptilidae caddisflies on the Umatilla River, where median emergence occurred up to 17 days earlier at downstream sites (Figure 3.4) and was negatively correlated ($xR^2 = 0.28$) with average discharge (Table 3.2).

Magnitude of emergence

The maximum weekly emerging biomass and the average weekly emerging biomass throughout the season varied greatly among sites on each river, but declined from upstream to downstream for the Umatilla River only (Figure 3.5). Wetted area of the sample sites declined from upstream to downstream in both rivers, although the trend was more pronounced on the Umatilla (Table 3.1). Maximum weekly emerging biomass and average weekly emerging biomass at the lowermost site on the Umatilla River was 27% and 15%, respectively, of the uppermost. This difference was not as great on the Walla Walla River, at 69% and 62%, respectively. Emerging biomass from each weekly sampling on the Umatilla sites was correlated with both the wetted area and emergence rate for that week, though the emerging biomass was more sensitive to changes in wetted area than emergence rate (Table 3.3). Emergence rates at the two most downstream Umatilla sites (27.4 km and 23.7 km) were as high or higher than the two most upstream sites, but the reduced wetted areas of these sites depressed biomass emerging per week from the site (Figure 3.2). In contrast, biomass emerging per week from Walla Walla sites was associated much more strongly with

emergence rate than wetted area (Table 3.3). As a result, emerging biomass remained comparatively high at the downstream sites. NPMR analysis indicates that biomass emerging per week was not correlated with average weekly discharge or average temperature on either river. Wetted area of sample sites on both rivers is highly correlated with the average discharge during that sample week (simple linear regression, Umatilla: R^2 = 0.87; Walla Walla R^2 = 0.91).

DISCUSSION

Timing of emergence

The similarity in the timing of peak total emergence and timing of individual taxonomic families among sites on each river was unexpected. The life histories of aquatic invertebrates are expected to be shaped by discharge regimes (Poff and Allan 1997, Lytle 2001, Lytle and Poff 2004), and water temperatures have been shown to significantly alter growth and development rates in mayflies (Giberson and Rosenberg 1992, Harper et al. 1995, Harper and Peckarsky 2006), stoneflies (Nebeker 1971, Flannagan and Cobb 1991, Gregory et al. 2000), and a few caddisflies (Nebeker 1971, Hogg and Williams 1996). In contrast, out of the 12 families tested in this study, emergence timing was altered for only Hydroptilidae on the Umatilla River.

However, the relationship for Hydroptilidae was weak (Table 3.2), and this taxa contributed little to the total emerging biomass on the Umatilla (Table 3.4). The total emerging biomass on each river is dominated by a small number of abundant or comparatively massive taxa (Table 3.4), suggesting that the timing of total emergence is unlikely to be altered unless multiple or abundant taxa respond. Many studies addressing the alteration of larval growth or emergence timing due to changes in temperature or discharge have only examined a single (Sweeney 1978; Gregory et al. 2000; Chadwick and Feminella 2001; Cabanita and Atkinson 2006; Harper and Peckarsky 2006) or small handful (Giberson and Rosenberg 1992; Hogg and Williams 1996) of species (but see Nebeker 1971; Delucchi and Peckarsky 1989; Flannagan and Cobb 1991; Harper et al. 1995). It is important to note that examination of only a few taxa in a system can measure important consequences for individual species, but is too narrow to address potential effects on total emergence or energetic subsidies to the riparian ecosystem, particularly if those taxa are a small component of the total emerging biomass.

Species shifts within families may contribute to the similarity in family emergence timing. Several of the families observed (Hydropsychidae, Baetidae, and Chironomidae) are likely composed of several genera and multiple species. If the proportions of species within each family or the assemblage itself changes among sites, we may be unable to detect the responses of individual species to discharge and temperature alterations. However, three of

the families with unaltered emergence timing are composed of a single species, including Helicopsychidae (*Helicopsyche borealis*), Pyralidae (*Petrophila confusalis*), and Glossosomatidae (*Glossosoma traviatum*). Likewise, Leptohyphidae is composed almost entirely of the *Tricorythodes* genus, and the discreet unimodal emergence peak suggests it may be a single species.

Resistance of a disturbed system

The similarity in family emergence timing among sites may ultimately be the result of community shifts toward resistant taxa due to long term perturbations. Changes in community composition can occur over relatively short time periods when discharge or temperatures are altered. For example, Dewson et al. (2007a) observed reductions in the percent of EPT taxa on a pristine stream with experimentally reduced discharge after a single year. Similarly, functional feeding groups shifted within a single summer when 90% of the flow was experimentally removed from a small stream by Wills (2006). However, our study sites on the Umatilla and Walla Walla rivers (including the upstream U8 and WW6 sites) are not pristine and have been subjected to land use alterations, channel modifications, and impacted water quality in addition to water withdrawal on the downstream sites for nearly a century. Species intolerant of this artificial disturbance or unable to modify their life histories to avoid it (e.g. Delucchi and Peckarsky 1989, Lytle and Poff 2004) may have been removed from the system. As a result, the current invertebrate communities along the study reaches may have shifted to an alternate stable state, and the taxa that remain may be tolerant of greater reductions in flow and increases in temperature than were observed here. In anthropogenically disturbed environments, invertebrate assemblages have been shown to be resistant to floods (Rader et al. 2008) and severe water withdrawals (Miller et al. 2007), suggesting disturbance-tolerant species may also be resistant to alterations in emergence timing by discharge and temperature modifications.

Magnitude of emergence

The timing of emergence was largely unaffected by water withdrawals, but we detected a notable decline in the total biomass emerging from sample sites subject to progressively higher levels of water withdrawal. These results indicate that loss of wetted habitat area due to water withdrawals can greatly reduce the biomass emerging from a river, but this depends on site-specific emergence rates (a surrogate for benthic invertebrate densities) and the severity of discharge reductions. This effect was particularly strong on the Umatilla, where the weekly emergence rates were often (and sometime much) higher at the most downstream site than the most upstream site, suggesting high benthic invertebrate

numbers and secondary production per unit area.   However, the average estimated wetted habitat area of the downstream sample site was only 12% of the upstream site. As a result, total emerging biomass from the downstream sites was greatly reduced, despite the high emergence rates. In contrast, water withdrawals were not as intense on the Walla Walla (88% versus 93% of mean summer discharge), and wetted habitat area of the downstream site was 36% of the most upstream site. However, emergence rates at the downstream sites on the Walla Walla were still much higher than the upstream sites. Thus, emergence rate rather than wetted habitat area was the more dominant factor driving total emerging biomass on this river, and the difference in total biomass between the upper and lower sites was not nearly as large compared to the Umatilla.

The response of wetted habitat area itself to water withdrawals can be influenced by the channel morphology of individual sample sites (Stanley et al. 1997, Dewson et al. 2007b). Our observations are consistent with a number of studies that have found decreased wetted width from reductions in discharge (Gore 1977, Cowx et al. 1984, Stanley et al. 1997, Cazaubon and Giudicelli 1999). However, wetted width may decrease only modestly (Dewson et al. 2007a) or may remain static (Rader and Belish 1999, Wright and Symes 1999) with large decreases in discharge, depending on the width to depth ratio of the channel (Dewson et al. 2007a).

The large reduction in total emerging biomass at sites subject to water withdrawal, particularly on the Umatilla, may have ecological consequences for terrestrial consumers. Aquatic and riparian ecosystems provide reciprocal energetic subsidies through the emergence of aquatic invertebrates onto land and the falling of terrestrial invertebrates into the water (Malmqvist 2002, Baxter et al. 2005). The downstream decline in emerging biomass, particularly on the Umatilla, is likely to reduce prey availability for terrestrial consumers.

The loss of emerging biomass may be important to numerous terrestrial organisms. For example, birds (Nakano and Murakami 2001; Sweeney and Vannote 1982), arthropods (Kato et al. 2003; Paetzold et al. 2006), lizards and bats (Power et al. 2004) utilize emerged aquatic invertebrates to meet some portion of their energetic needs. Reliance on aquatic invertebrates may be high for some species such as the winter wren, which received 98% of its energy budget from this source over a 6 month period at a Japanese stream (Nakano and Murakami 2001), or spiders (Lycosidae) and beetles (Carabidae), which reduced the densities of emerged aquatic insects by 45% on a large Italian river (Paetzold and Tockner 2005). The impacts of aquatic invertebrates on the riparian system may extend beyond single predator-prey interactions, possibly influencing terrestrial vegetation, herbivorous insects, and predatory arthropods through trophic interactions (Henschel et al. 2001). However, the trophic effects of reduced emergent aquatic biomass may be limited to terrestrial environments very

near the river. Henschel et al. (2001) found the increase in terrestrial predators due to aquatic insects declined only 30 m from the bank of a German river much larger than either the Umatilla or Walla Walla. Similarly, Power et al. (2004) found that aquatic invertebrates declined exponentially with distance from river's edge, falling to 50% within 10 m.

CONCLUSIONS

The timing of aquatic invertebrate emergence was similar across broad gradients of temperature and discharge on our study rivers. However, the loss of instream habitat resulted in a significant decrease in the total emergent biomass at sites impacted by severe water withdrawals. Our study rivers have been subject to anthropogenic stressors for many years and may have invertebrate communities tolerant of high temperature and low discharges. However, water withdrawals from disturbed systems may still alter emergence dynamics and impact the surrounding riparian ecosystem by reducing the total biomass a river is able to export during the irrigation season. This potential impact to the riparian area may be amplified if the peak aquatic invertebrate emergence occurs during periods of low terrestrial invertebrate production (e.g. Nakano and Murakami 2001). Thus, for some rivers with resilient invertebrate communities, the riparian ecosystems may be affected more by water withdrawals than the aquatic invertebrates themselves. More research is needed to clarify and describe the impacts of severe water withdrawals on riparian foodwebs and the biotic energy flow between the terrestrial and aquatic environments.

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Walla Walla River
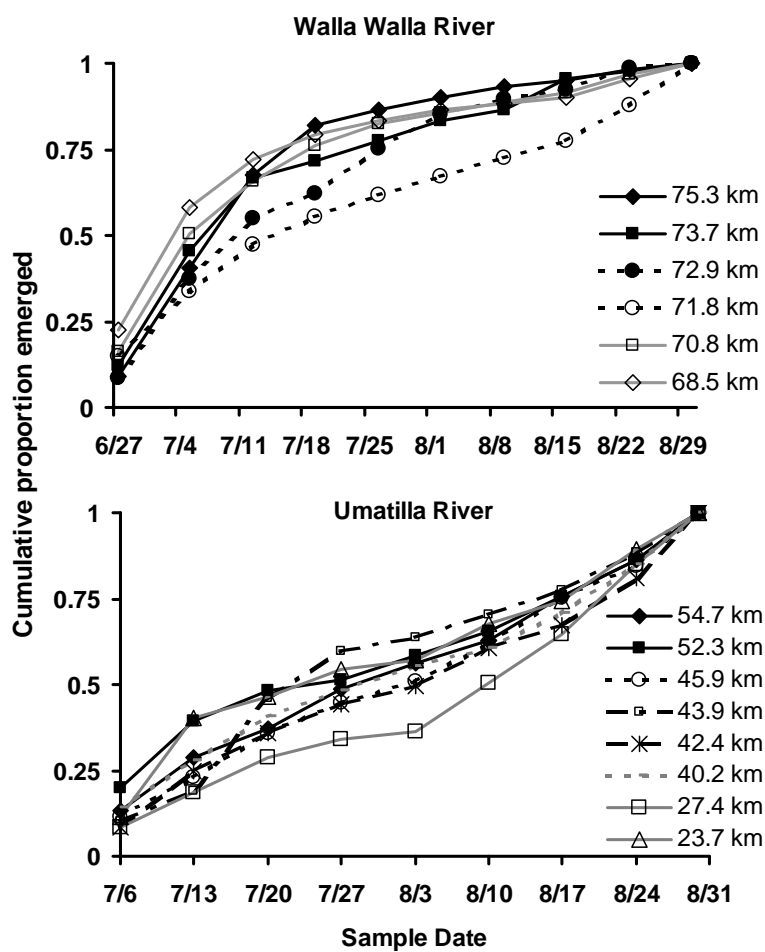
Umatilla River

Figure 3.1. Cumulative curves of total emergence on the Umatilla and Walla Walla rivers.

Figure 3.2. Total emergence rate (shaded area) and weekly biomass (solid black or white line) for each sample site on the Umatilla River through time.

Figure 3.3. Total emergence rate (shaded area) and weekly biomass (solid black or white line) for each sample site on the Walla Wala River through time.

Figure 3.4. Cumulative emergence curves of Hydroptilidae at each Umatilla River sample site.

Figure 3.5. Maximum weekly biomass (white) and sample season average biomass (black) emerging at each sample site

Table 3.1. Location, average discharge, average water temperature, and average wetted area during the sample period for each study site. Sites U8 and WW6 are the most upstream sites.

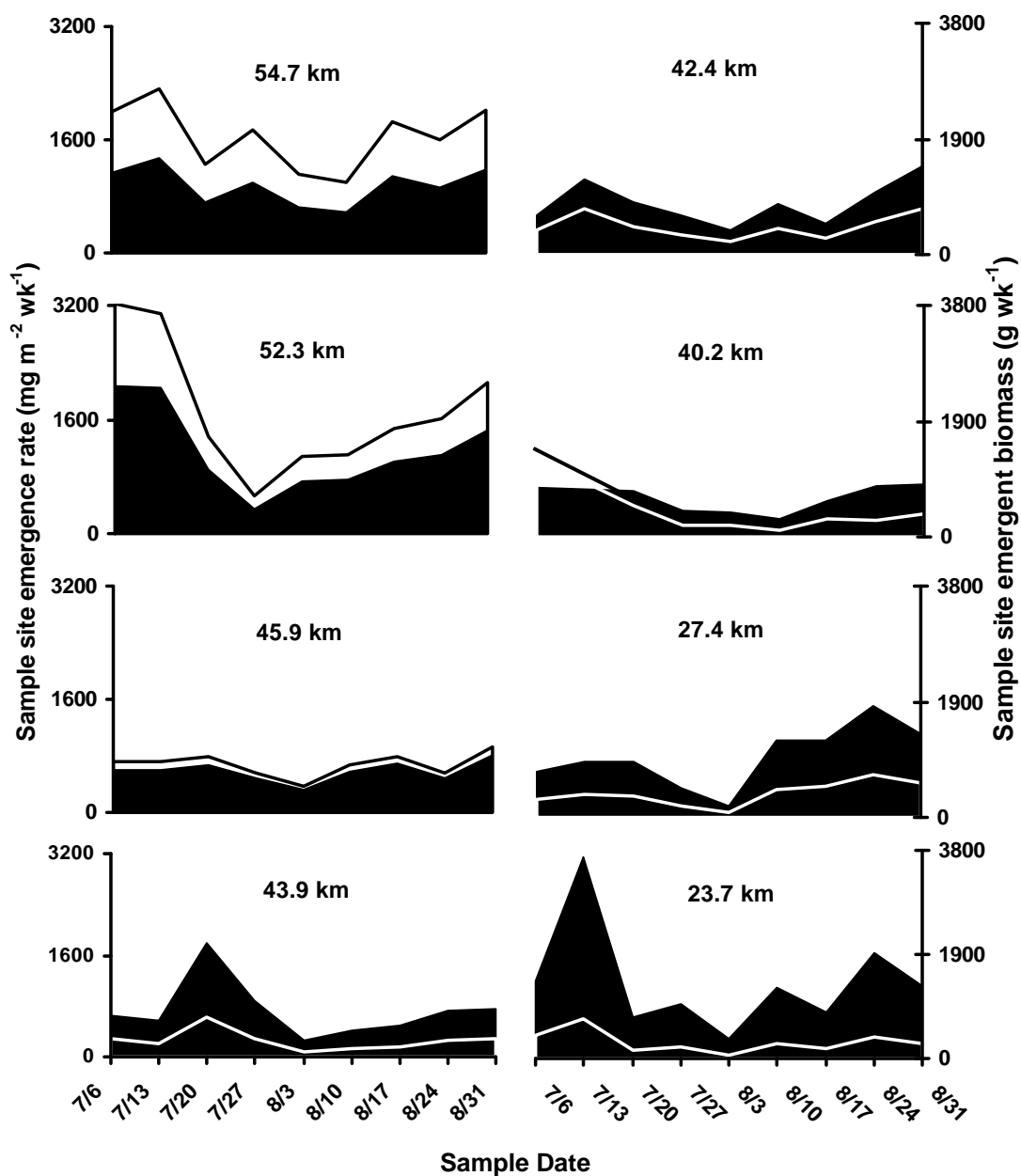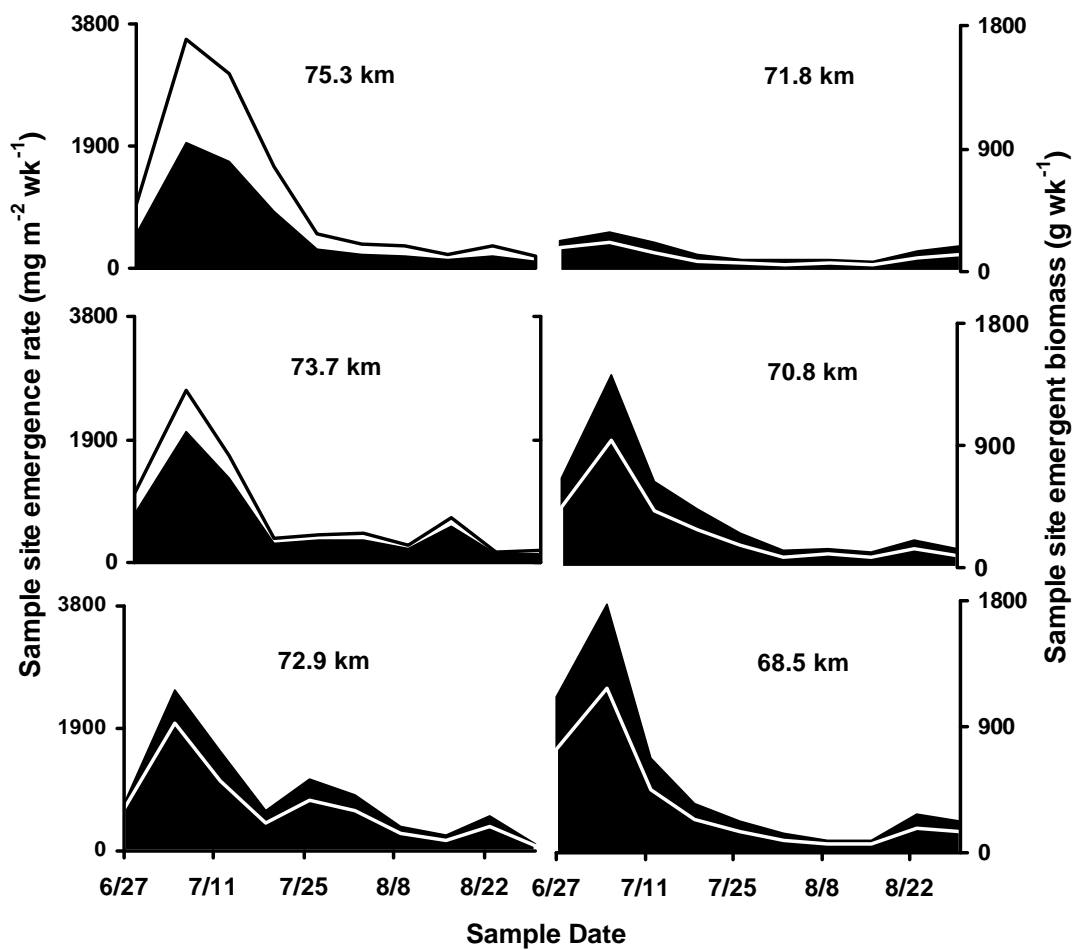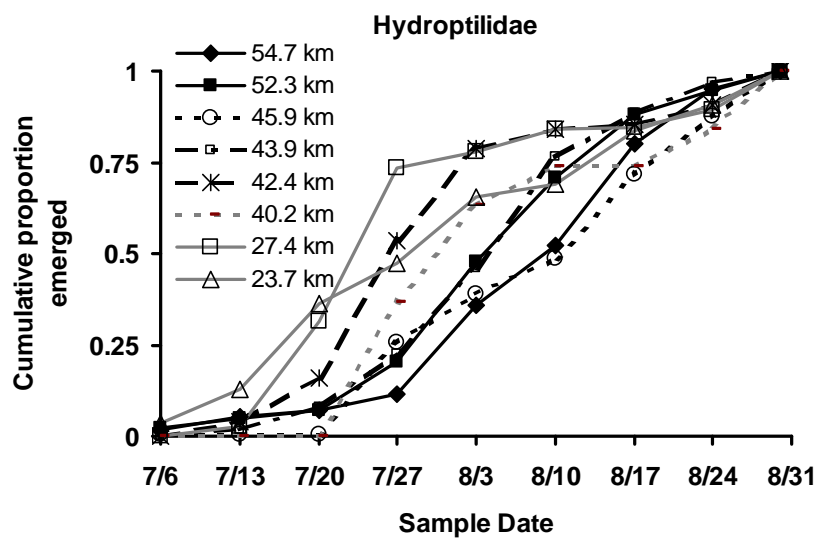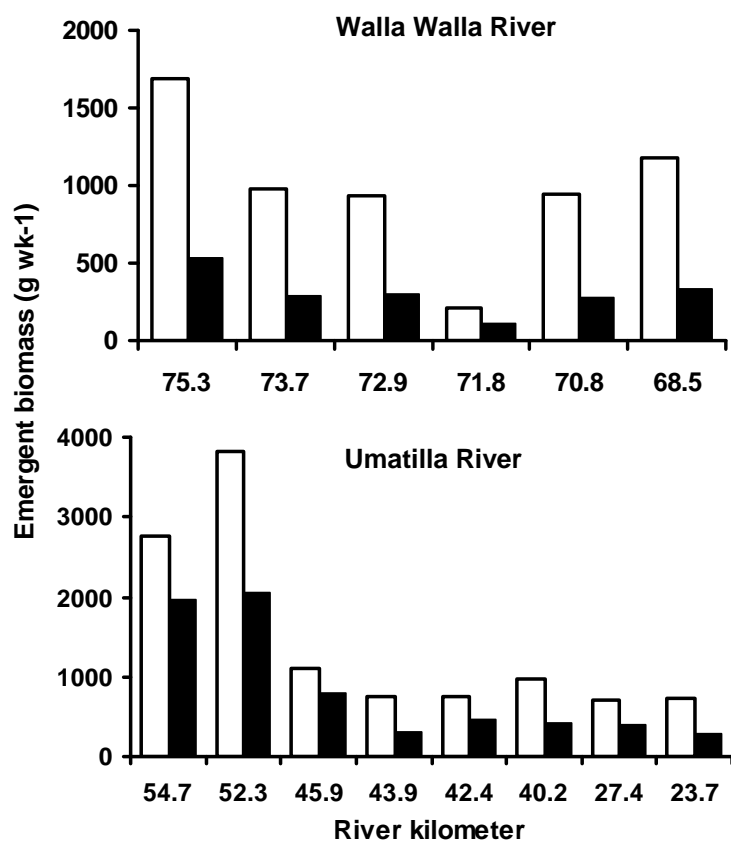|	Umatilla River				Walla Walla River				
Site name	River kilometer	Average discharge (cms)	Average temperature (degrees C)	Average wetted area (m^2)	Site name	River kilometer	Average discharge (cms)	Average temperature (degrees C)	Average wetted area (m^2)
U8	54.7	6.55	18.6	2049	WW6	75.3	3.23	15.5	861
U7	52.3	6.24	18.8	1764	WW5	73.7	1.12	16.3	469
U6	45.9	5.88	19.7	1381	WW4	72.9	1.09	16	346
U5	43.9	0.63	20.7	425	WW3	71.8	0.77	16.7	323
U4	42.4	0.75	20.3	641	WW2	70.8	0.74	16.9	315
U3	40.2	0.64	21.4	727	WW1	68.5	0.4	17.9	313
U2	27.4	0.81	22.4	465					
U1	23.7	0.48	23.2	250					

Table 3.2. NPMR model results for median emergence date of individual taxonomic families.

Umatilla River				Walla Walla River			
Response Taxa	Predictors	xR^2	Tolerance	Response Taxa	Predictors	xR^2	Tolerance
Hydropsychidae	Qavg, Substrate	-0.03	139.3, 3.0	Hydropsychidae	Canopy	-0.13	43.5
Helicopsychidae	Depth	-0.29	3.4	Glossosomatidae	Predfish	-0.04	9.4
Leptoceridae	Substrate	0.2	1.8	Brachycentridae	Predinv	-0.48	1.7
Hydroptilidae	Qavg	0.28	117.9	Hydroptilidae	Canopy	-0.02	43.5
Pyralidae	Depth, Substrate	-0.05	3.4, 2.8	Baetidae	Canopy	-0.43	43.5
Baetidae	Qavg, Predinv	-0.08	128.6, 824.5	Heptageniidae	Predinv	-0.38	137.5
Tricorythiidae	Qavg	0.03	117.9	Leptophlebiidae	Temperature	-0.51	1.91
Chironomidae	Predfish	-0.28	12	Chironomidae	Predinv	-0.24	137.5

Table 3.3. NPMR model results for correlating weekly emergent biomass with weekly emergence rate and site wetted area. Discharge and accumulated degree days did not contribute significantly to the fit (xR^2) of the models and are not displayed here.

Umatilla River

Response	Predictors	Sensitivity	xR^2
Weekly site biomass	Wetted area	0.59	0.69
	Emergence rate, wetted area	0.47, 0.58	0.89

Walla Walla River

Response	Predictors	Sensitivity	xR^2
Weekly site biomass	Emergence rate	1.03	0.82
	Emergence rate, wetted area	1.01, 0.08	0.94

Table 3.4. Relative contribution (in %) of each taxonomic family and order to the total site emergent biomass throughout the sampling period. [a] Consists primarily of Heptageniidae, Pyralidae, and Leptoceridae.

Umatilla River

	54.7 km	52.3 km	45.9 km	43.9 km	42.4 km	40.2 km	27.4 km	23.7 km
Trichoptera	**28**	**55**	**43**	**39**	**42**	**45**	**69**	**78**
Hydropsychidae	19	25	29	34	40	40	39	47
Helicopsychidae	3	23	6	<1	<1	<1	26	29
Hydroptilidae	5	6	3	1	<1	<1	1	<1
Leptoceridae	1	1	5	4	2	5	3	2
Ephemeroptera	**24**	**11**	**24**	**30**	**24**	**31**	**11**	**7**
Baetidae	6	4	13	17	16	17	7	3
Heptageniidae	16	1	10	12	7	11	1	1
Tricorythiidae	2	6	1	1	1	3	3	3
Lepidoptera	**11**	**17**	**7**	**6**	**3**	**6**	**3**	**1**
Pyralidae	11	17	7	6	3	6	3	1
Diptera	**26**	**9**	**14**	**17**	**23**	**11**	**16**	**10**
Chironomidae	24	8	12	14	21	10	12	10
Other	2	1	2	3	2	1	4	0
Plecoptera	**5**	**8**	**9**	**6**	**4**	**2**	**<1**	**0**
Perlidae	5	8	9	6	4	2	<1	0
Zygoptera	**6**	**1**	**3**	**2**	**2**	**4**	**1**	**2**

Walla Walla River

	75.3 km	73.7 km	72.9 km	71.8 km	70.8 km	68.5 km
Trichoptera	**74**	**48**	**52**	**57**	**50**	**62**
Hydropsychidae	37	15	33	20	38	58
Brachycentridae	21	9	7	2	2	1
Glossosomatidae	14	20	11	29	10	3
Ryacophilidae	1	3	1	4	<1	<1
Lepidostomatidae	1	1	<1	1	<1	<1
Hydroptilidae	<1	<1	<1	1	<1	<1
Ephemeroptera	**4**	**3**	**4**	**0**	**1**	**2**
Baetidae	2	1	3	<1	1	2
Leptophlebiidae	2	2	1	<1	<1	<1
Diptera	**21**	**25**	**29**	**43**	**31**	**22**
Chironomidae	18	23	23	35	25	18
Other	3	2	6	8	6	4
Plecoptera	**1**	**23**	**12**	**0**	**17**	**8**
Perlidae	1	23	12	0	17	8
Perlodidae	<1	<1	<1	<1	<1	<1
Miscellaneous[a]	**1**	**<1**	**1**	**<1**	**1**	**4**

CONTEXT AND IMPLICATIONS

Water temperature and discharge can be powerful drivers of aquatic invertebrate life histories, but they may not affect all invertebrate communities and river systems. There is an abundance of studies supporting the role of temperature in modifying growth, development, and emergence rates of aquatic insects, and theories predicting the constraints that discharge places on life history events. However, the emergence timing and adult body mass of the aquatic invertebrates in the Umatilla and Walla Walla rivers largely did not respond to discharge and temperature alterations from water withdrawals in this study. The results of this research are novel given the large gradients in discharge and water temperature. We suspect that our results may be due to the synchronization of emergence caused by a possible diapause in holometabolous species, and an invertebrate community composed of resilient taxa from decades of water withdrawals. The similarity in family emergence timing may also result from species shifts within each family across sites.

Many studies have examined the effects of discharge and water temperature on relatively undisturbed stream systems or insects from such systems. Additionally, comparatively few studies have examined the role of temperature and discharge on the life histories of holometabolous species, focusing instead on hemimetabolous Ephemeroptera and Plecoptera. Our study, in contrast, examined both holometabolous and hemimetabolous invertebrates from rivers with significant anthropogenic disturbance. Our results suggest that the aquatic invertebrates in the Umatilla and Walla Walla rivers are highly resistant to pronounced changes in discharge and temperature, and may be indicative of resistant invertebrate communities structured by decades of disturbance. As such, the magnitude of discharge reduction and temperature elevation observed in these study rivers may have a much more pronounced impact on the life histories of invertebrates in small headwater streams or pristine rivers. We also submit that physiological differences between hemimetabolous and holometabolous species may prevent the relationship between emergence timing and temperature from occurring in the latter.

Water withdrawals were not found to alter emergence timing in this study, but the loss of instream habitat resulted in a considerable decrease in the total emergent biomass at sites impacted by severe water withdrawals. Water withdrawals from disturbed systems may therefore alter emergence dynamics and impact the surrounding riparian ecosystem by reducing the total biomass a river is able to export during the irrigation season. The loss of emergent biomass may be particularly important if the peak aquatic invertebrate emergence occurs during periods of low terrestrial invertebrate production (e.g. Nakano and Murakami 2001). Thus, for some rivers with resilient invertebrate communities, water withdrawals may have a greater effect on the foodweb dynamics of the riparian community than on the ecology

of the aquatic invertebrates themselves. More research is needed to clarify the impacts of severe water withdrawals on riparian foodwebs and the connectivity between the terrestrial and aquatic environments.

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APPENDICES

# APPENDIX A: PHOTOGRAPH OF EMERGENCE TRAP

**APPENDIX B: DAILY MEAN DISCHARGE OF SELECT STUDY SITES
DURING THE SAMPLING PERIOD (DISCRETE INSTANTANEOUS
MEASUREMENTS OF UMATILLA 23.7 KM SITE AND WALLA WALLA
RIVER SITE DISCHARGES SHOWN AS POINTS)**
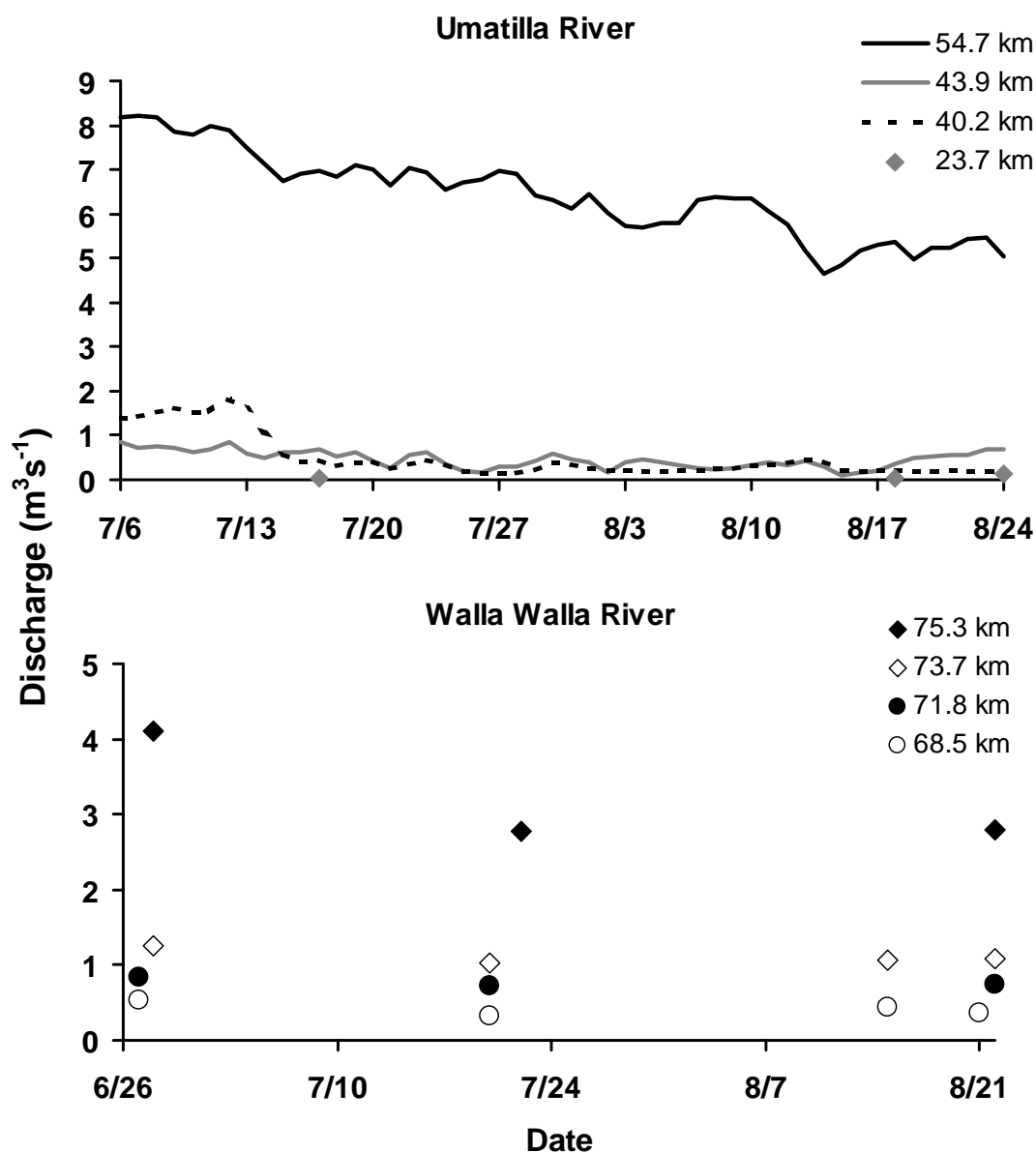
APPENDIX C: DAILY MEAN TEMPERATURE OF SELECT STUDY SITES ON THE UMATILLA AND WALLA WALLA RIVERS DURING THE SAMPLING PERIOD
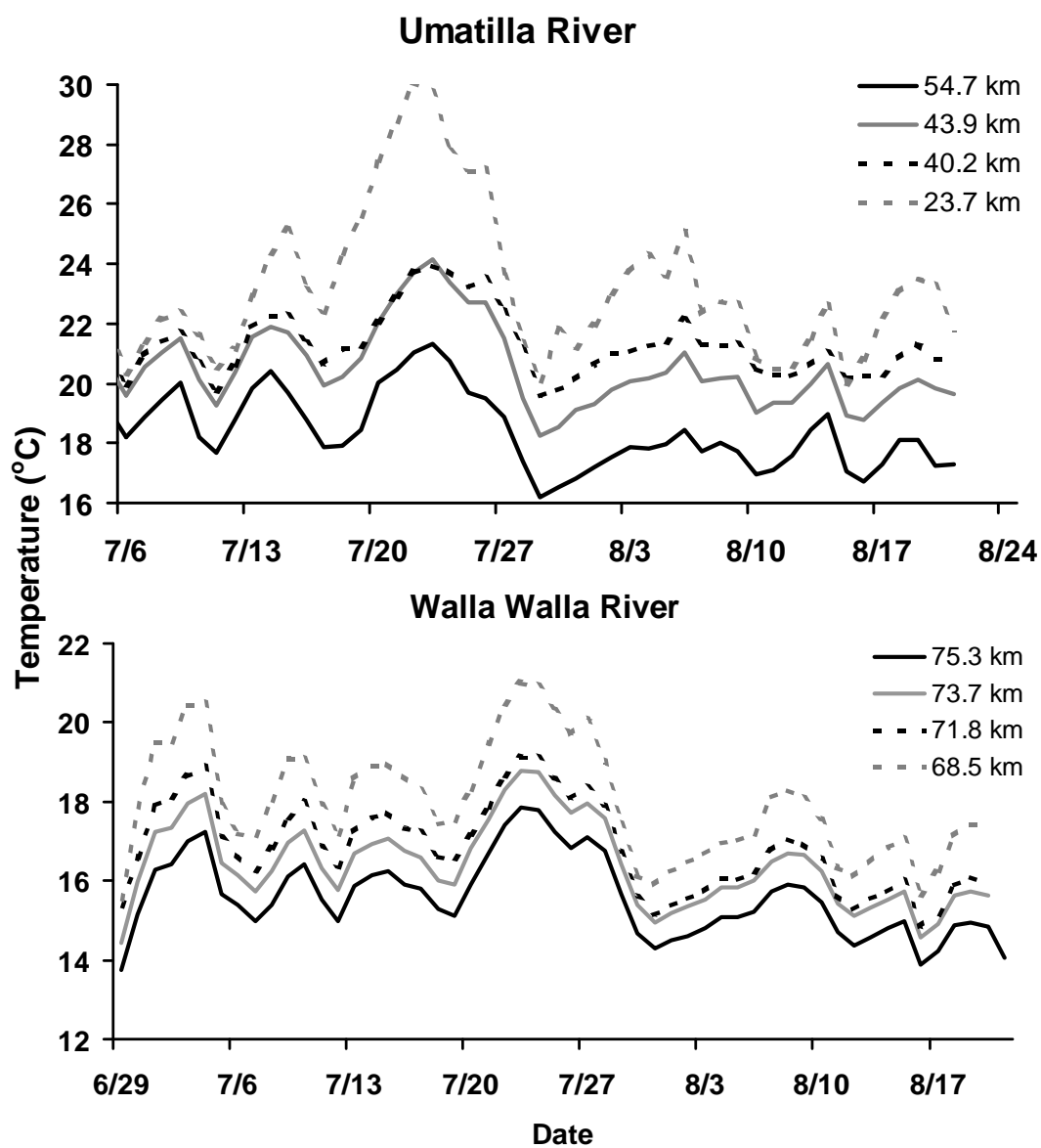
APPENDIX D: PHOTOGRAPHS OF UMATILLA RIVER SITES U8 (54.7 KM) AND U1 (23.7 KM), ILLUSTRATING THE EXTREME GRADIENT IN DISCHARGE

Site U8 (54.7 km)

Site U1 (23.7 km)
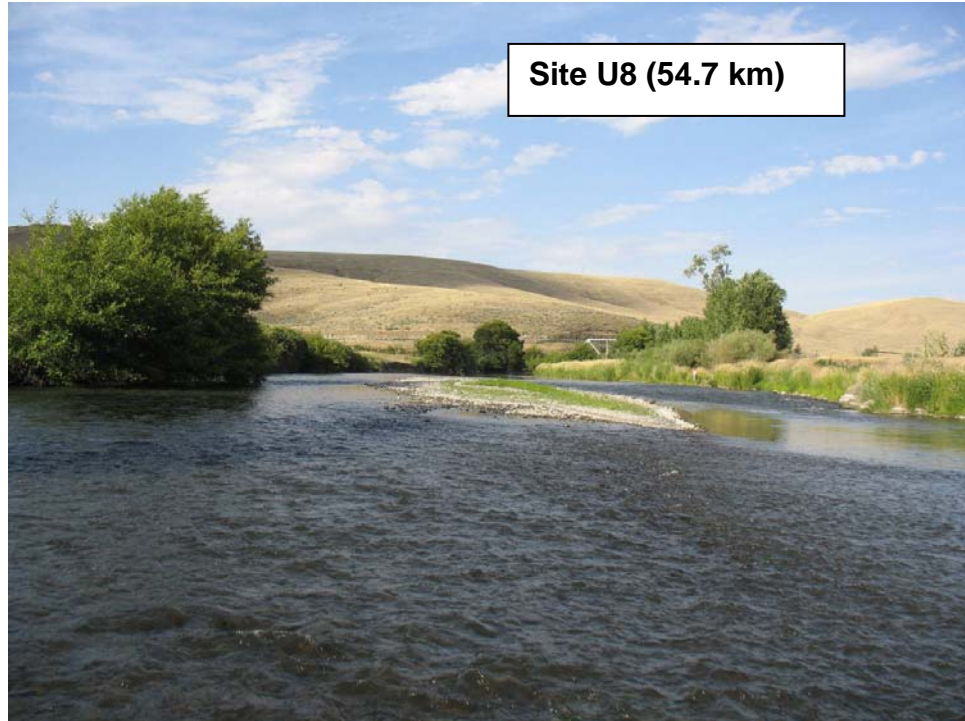
APPENDIX E: RELATIONSHIP BETWEEN BODY MASS AND ACCUMULATED DEGREE DAYS AT EMERGENCE FOR INDIVIDUAL INSECTS

P. confusalis

H. borealis

G. traviatum