Resistance of aquatic insects to a low-flow disturbance: exploring a trait-based approach

Annika W. Walters[1]

Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, Connecticut 06520-8106 USA

Abstract. Low-flow disturbances are predicted to increase in frequency and intensity because of climate change and extensive human water withdrawal, but the effect of decreased flow on aquatic insect communities is not well understood. I explored the resistance of aquatic insects to reduced flow by creating an experimental low-flow disturbance that diverted ~40 to 80% of the water in 3 replicate streams for 2 summers. I sampled the aquatic insect community in control and treatment reaches before and during the 3-mo water diversions. I used a trait-based approach to analyze the data because traits have the potential to increase mechanistic understanding and predictive capabilities. The analysis focused on 6 traits: desiccation resistance, maximum crawling rate, armoring, size at maturity, rheophily, and habit. Community trait composition underwent strong seasonal shifts, but few consistent responses to reduced flow were observed. The 2 trait states that did appear to confer increased resistance were high crawling rate and armoring. These trait states can provide protection from predators. Thus, biotic interactions might be important during low-flow disturbance.

Key words: water diversion, drought, biological traits, macroinvertebrates.

Stream ecosystems frequently experience natural hydrological disturbance from droughts and floods, and climate change is expected to increase the frequency of these events (Arnell et al. 1996). Streams also are undergoing anthropogenic disturbance as a result of dam construction, water withdrawal, and stream channelization (Rosenberg et al. 2000). Predicting the susceptibility of stream communities to these disturbances is a major challenge. Trait-based approaches are advocated as a way to increase predictive capabilities because their use allows generalization across sites with disparate taxonomic composition (Poff 1997, McGill et al. 2006, Violle et al. 2007). The habitat templet hypothesis (Southwood 1977, 1988, Townsend et al. 1997) predicts that the biological traits of an organism will match environmental conditions. As the environment becomes more extreme, the species traits should become more similar and should be those that confer resistance to the disturbance (Poff 1997, Statzner et al. 2001).

Traits usually are measured at the individual level and are used comparatively across taxonomic group-

ings (McGill et al. 2006). A trait can have multiple states or modalities. For example, the trait, size at maturity, can have 3 states: small, medium, and large. Commonly used traits include morphological, physiological, and life-history characteristics. Aquatic insects differ substantially in body size, mobility, habitat preferences, and life histories, and are an ideal group with which to test the utility of a trait-based approach because their traits are strongly related to local environmental variables (Richards et al. 1997, Horrigan and Baird 2008).

Trait-based approaches are not new to stream ecology. For example, aquatic insect functional feeding groups are widely used and have been influential in stream theory (Vannote et al. 1980). Applications of trait-based approaches are increasing as investigators use traits to explore variation in aquatic insect distribution along longitudinal gradients (Finn and Poff 2005, Ilg and Castella 2006) and across varying climatic and disturbance regimes (Townsend et al. 1997, Bonada et al. 2007b, Díaz et al. 2008). Most studies compare across spatial scales, but a few have addressed temporal responses to disturbances (Vieira et al. 2004, Griswold et al. 2008). I examined the temporal response of individual trait states to low-flow disturbance. Potential advantages of a trait-

[1] Present address: Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Blvd. E., Seattle, Washington 98112 USA. E-mail: annika.walters@gmail.com

based approach are increased predictive and explanatory capabilities, improved mechanistic understanding, and insight into functional and ecosystem responses (McGill et al. 2006).

Trait-based approaches have been tested for biomonitoring applications (Charvet et al. 2000, Dolédec and Statzner 2008, Tullos et al. 2009) but are relatively unexplored in the context of environmental-flow management. Minimum environmental-flow requirements are being developed for streams worldwide in response to increased water demand and climate change (Postel et al. 1996, Richter et al. 2006). Effective environmental-flow requirements require detailed knowledge of the relationship between flow regimes and stream community structure, and a trait-based approach may generate relationships with greater transferability across sites than a taxonomy-based approach.

Shifts in the magnitude of flow should affect a variety of aquatic insect traits. A number of mechanisms, including shifts in habitat availability, physiological tolerances, and behavioral responses of the insects, may drive trait-state responses to reduced flow. Horrigan and Baird (2008) found several traits, including crawling rate, rheophily, and thermal tolerance, that were sensitive to flow at a large biogeographic scale. Reduced flow often leads to decreases in overall habitat availability and an increased proportion of pool habitat. These changes would favor insects with the ability to move as habitat contracts, e.g., insects with a high crawling or swimming rate or burrowers, and insects adapted to the warmer temperatures and lower O_2 levels of pools. In contrast, aquatic insects associated with riffle habitats decline during low-flow disturbances (Castella et al. 1995, Boulton 2003). Flow reduction also changes the importance of biotic interactions. Protection from predators is likely to be especially important in low-flow conditions because the relative abundance of predators increases as flow decreases (Miller et al. 2007, Walters and Post, in press). For some trait states, the expected response to low flow is unclear. Statzner and Bêche (2010) predicted that the frequency of larger insects would increase because of release from high flow, but Townsend et al. (1997) argued that smaller insects are generally more resistant to disturbance and better able to use interstitial refugia.

I used a trait-based approach to evaluate the resistance of aquatic insects to reduced flow. I experimentally diverted water from streams to create a low-flow disturbance and measured traits (desiccation resistance, maximum crawling rate, armoring, size at maturity, rheophily, and habit). I developed predictions of the expected response or each trait state

TABLE 1. Hypothesized effects of reduced flow on the 6 focal traits.

Trait	Hypothesis
Desiccation resistance	↑ insects with ability to survive desiccation
Maximum crawling rate	↑ insects with high crawling rate (>100 cm/h)
Armoring	↑ armored insects (heavily sclerotized or cased)
Size at maturity	↑ small insects (<9 mm)
Rheophily	↑ insects preferring depositional-only habitat
Habit	↑ burrowing insects

to low-flow disturbance (Table 1). My objective was to determine which traits might be useful for predicting the effects of water withdrawal on stream communities.

Methods

Study sites

The study streams were in Yale-Myers Forest, a 3213-ha mixed-hardwood forest in Windham and Tolland counties, Connecticut. I used 3 stream sites: the outlet to Paine Pond (lat 41°55′37″N, long −72°08′59″W), the east branch of Lead Mine Brook (lat 41°57′44″N, long −72°10′09″W), and the west branch of Lead Mine Brook (lat 41°57′18″N, long −72°09′52″W). All streams were 2nd-order perennial streams with watershed areas ranging from 1 to 5 km². In each stream, I identified and marked a representative 200-m section that was 1 to 3 m wide and 5 to 15 cm deep, with a pebble–cobble substrate and a pool–riffle morphology.

Water diversion

Water diversion took place during 2 summers (12 June–3 October 2006, 20 June–19 September 2007). In each stream, I split the study section into 2 adjacent 100-m-long reaches. I used wooden weirs to direct flow into pipes and diverted water around the lower (treatment) 100-m reach. I left the upper (control) 100-m reach undisturbed.

I obtained continuous records of stream discharge from water-level loggers that recorded stream stage at 30-min intervals throughout the course of the experiment. I used Hobo water-level loggers (U20-001-01; Onset Computer Corporation, Bourne, Massachusetts), which also logged water temperature, in most streams, but I used Global Water WL16 water-level loggers (Global Water Instrumentation, Gold River, California) in 1 stream in 2006. In this stream, I

measured water temperature twice a month at midday at 2 points in each 100-m reach.

I measured discharge throughout the summer at 2 transects/reach. At each transect, I measured width, depth (5 measurements), and water velocity (4 measurements; Global Water flow probe FP101; Global Water Instrumentation). I multiplied water velocity by transect area to obtain discharge (m^3/s). I constructed stage–discharge curves for each reach ($y = ax^b$; R^2 range 2006: 0.90–0.97, 2007: 0.90–0.98) and used them to convert water-level data to discharge.

Insect community composition

I sampled insect community composition in control and treatment reaches in May (before water diversion started) and in August (after water diversion had been occurring for 2 mo). I placed a WaterMark Surber sampler (0.09-m^2, mesh size = 0.5 mm; Aquatic Research Instruments, Hope, Idaho) at 3 sites each in riffle and pool habitat in each reach. I used a random number table to choose sites with the constraint that the distance between same-habitat sites was ≥20 m. I disturbed all substrate within the sampler to a depth of 5 to 8 cm to dislodge insects into the net and placed each sample in a plastic bag with 70% ethanol. I sorted insects within 24 h and identified them using keys in Peckarsky et al. (1990) and in Merritt and Cummins (1996). I used family-level identifications because some insects were too small or damaged for reliable genus-level identification. When possible, specimens also were identified to the genus level.

I assigned trait states to each family using data published by Poff et al. (2006). I assigned trait states to families on the basis of the most common genus in each sample. Family-level taxonomic resolution provides comparable metrics of community structure to species- and genus-level resolution for freshwater benthic macroinvertebrates (Bowman and Bailey 1997, Gayraud et al. 2003). When trait information for a family was not available, I excluded the family from the analysis. This practice led to the exclusion of 10 families (630 individuals of >45,000 collected).

I used the results of previous studies of traits and hydrologic disturbance (e.g., Townsend et al. 1997, Griswold et al. 2008, Horrigan and Baird 2008) to decide which traits to use. I chose 6 traits that were not highly phylogenetically correlated and that covered life history, mobility, morphology, and ecological characteristics (Vieira et al. 2006): desiccation resistance, maximum crawling rate, armoring, size at maturity, rheophily, and habit. Habit refers to an aquatic insect's mode of existence and includes

skaters, swimmers, clingers, sprawlers, climbers, and burrowers (Merritt and Cummins 1996).

Data analysis

In each 100-m reach, I scaled pool and riffle insect samples by the availability of pool and riffle habitat. I determined the area of riffle and pool habitat based on the mean values from the 2 habitat surveys that were conducted closest to the time of insect sampling. I conducted habitat surveys at 10-m intervals along the 100-m stream reach by measuring the width and depth of the stream reach and making a visual estimate of % pool and % riffle habitat. For each habitat type, I multiplied the density of each family with a given trait state by the mean area of available habitat. I summed the values for pool and riffle habitats to obtain the total abundance of insects with that trait state for the 100-m stream reach. I used the relative abundance of each insect trait-state grouping for all data analysis.

I did all statistical analyses in R (version 2.10.1; R Development Core Team, Vienna, Austria) and judged statistical significance at $p \leq 0.05$. For each trait state, I used a linear mixed-effect model to test for differences in relative abundances of trait states among diversion (treatment vs control reaches), month (May [before diversion] vs August [during diversion]), and month × diversion effects. I included stream identity as a random factor. The effect of interest was the month × diversion interaction because it tested whether the treatment reaches responded differently than the control.

I used discharge records for Mt. Hope River, a nearby stream gauged by the US Geological Survey (USGS) since 1940, to put the discharge values into an historical context (USGS National Water Information System database). The relationship between Mt. Hope River summer flow and flow in the control reaches was a power relationship, $y = ax^b$, for all 3 streams (R^2 = 0.96, R^2 = 0.93, and R^2 = 0.96). I used these relationships to estimate historical discharge and low-flow indices for the study streams. I used summer Q values (% time that a discharge was equaled or exceeded from June to September) as a low-flow index (Gordon et al. 2004).

The 2 years differed greatly in terms of stream flow. August 2006 was the 10th-wettest and August 2007 was the 3rd-driest August on record for Mt. Hope River (67-y record). I used a linear mixed-effect model to test for differences in relative abundances of trait states among year (2006 vs 2007), month (May vs August), and year × month effects to assess the effects of natural variation between years. I included stream

TABLE 2. Mean daily discharge, standard deviation in daily discharge, and mean water temperature for each stream reach and the % difference between the control and treatment reaches as a result of water diversion. The calculations exclude the 1st mo of diversion when the diversion levels were still increasing and the last 2 to 3 d when preparations for take down were occurring. In 2006, the data covers 12 July to 30 September and in 2007, it covers 20 July to 16 September.

		2006			2007		
Variable	Stream	Control	Treatment	% change	Control	Treatment	% change
Mean daily	1	0.0194	0.0034	−82%	0.0053	0.0023	−57%
discharge (m³/s)	2	0.0267	0.0141	−47%	0.0035	0.0019	−46%
	3	0.0319	0.0183	−43%	0.0055	0.0023	−58%
Standard deviation	1	0.0087	0.0053	−39%	0.0056	0.0026	−54%
of daily discharge	2	0.0130	0.0109	−16%	0.0040	0.0015	−63%
	3	0.0214	0.0171	−20%	0.0057	0.0035	−39%
Mean water	1	19.8	18.3	−7%	18.7	17.2	−8%
temperature (°C)	2	19.3	18.8	−3%	18.5	16.8	−9%
	3	19.2	18.9	−2%	17.5	17.3	−1%

identity as a random factor. The year × month interaction was the effect of interest because it tested whether responses differed between a high-flow (2006) and a low-flow (2007) year.

Results

Water diversion

My goal was to divert as much water as possible without dewatering the stream completely. The weirs diverted ~40 to 80% of the water in each stream (Table 2). The standard deviation in discharge was reduced in all streams, with greater reductions in 2007 than in 2006 (Table 2). 2007 was a very dry year so water was diverted to the point at which the stream was a series of disconnected pools. In 2006, summer Q values for mean daily flow (12 July–30 September) in the control reaches were 21.4 to 25.9, whereas in the treatment reaches they were 43.8 to 90.0. In 2007, summer Q values for mean daily flow (20 July–16 September) in the control reaches were 75 to 97.9, and in the treatment reaches they were 96.8 to 99.8. The difference in Q values between years reflected the fact that 2006 was a wet year, so despite an equivalent amount of diversion, flow levels were greater in 2006 than in 2007. Water diversion was accompanied by a 1 to 9% decrease in water temperature (Table 2), probably because diversion increased the proportion of groundwater in the stream.

Trait states

In the diversion experiment, none of the traits analyzed showed a significant month × diversion effect, but some traits differed between months (Table 3, Fig. 1A–L). The relative abundance of insects with a high crawling rate increased and the relative

abundance of insects with a small size at maturity decreased between May and August in 2006 and 2007 (Fig. 1C, D, G, H). In 2007, the relative abundance of desiccation resistant and armored insects increased between May and August (Fig. 1B, F). In 2006, the relative abundance of armored insects was significantly higher in treatment than in control reaches (Fig. 1E).

In the interannual comparison, the relative abundances of insects with desiccation resistance, high crawling rate, and armoring were affected by year, month, and the year × month interaction (Table 4, Fig. 2A–C). The relative abundances of aquatic insects with these trait states increased between May and August and the increase was greater in 2007 (the low-flow year) than in 2006. In all 3 cases, the direction of the response matched expectations (Table 1). The relative abundance of insects with small body size decreased between May and August (Fig. 2D). Rheophily and habit were not affected by year, month, or their interaction (Fig. 2E, F).

Discussion

Trait-based approaches have intuitive appeal because they can provide a mechanistic link between pattern and process (Verberk et al. 2008). They may offer insight into behaviors that enable individuals to resist low-flow disturbance, and they provide the generality required to make comparisons and predictions across differing sites.

I used an experimental approach to test for causal links between relative abundances of trait states and flow. Water diversion reduced flow by ~40 to 80% in 2 summers, but the month × diversion interaction did not significantly affect the relative abundance of any trait state. Month did significantly affect trait compo-

TABLE 3. Analysis of trait-state response to experimental flow reduction in 2006 and 2007. The F-values and p-values for the mixed-effect linear model are shown for month (May [before diversion] vs August [during diversion]), diversion (control vs treatment reach), and the month $\times$ diversion interaction. The month $\times$ diversion interaction tested for the effects of flow reductions. Values significant at the $p = 0.05$ level are indicated in bold.

Variable	2006			2007		
	Month	Diversion	Month $\times$ diversion	Month	Diversion	Month $\times$ diversion
Desiccation resistant	$F_{1,6} = 0.35, p = 0.58$	$F_{1,6} = 4.60, p = 0.08$	$F_{1,6} = 0.30, p = 0.60$	$F_{1,6} = 5.66, p = 0.05$	$F_{1,6} = 3.98, p = 0.09$	$F_{1,6} = 0.21, p = 0.66$
High crawling rate	$F_{1,6} = 7.08, p = 0.04$	$F_{1,6} = 1.25, p = 0.31$	$F_{1,6} = 2.25, p = 0.18$	$F_{1,6} = 57.36, p < 0.01$	$F_{1,6} = 0.05, p = 0.82$	$F_{1,6} = 0.12, p = 0.74$
Armored	$F_{1,6} = 4.98, p = 0.07$	$F_{1,6} = 6.73, p = 0.04$	$F_{1,6} = 0.08, p = 0.79$	$F_{1,6} = 22.65, p < 0.01$	$F_{1,6} = 3.79, p = 0.10$	$F_{1,6} = 1.11, p = 0.33$
Small size at maturity	$F_{1,6} = 50.89, p < 0.01$	$F_{1,6} = 2.13, p = 0.19$	$F_{1,6} = 0.51, p = 0.50$	$F_{1,6} = 50.26, p < 0.01$	$F_{1,6} = 0.00, p = 0.96$	$F_{1,6} = 0.71, p = 0.43$
Depositional only	$F_{1,6} = 0.57, p = 0.48$	$F_{1,6} = 0.49, p = 0.51$	$F_{1,6} = 0.02, p = 0.91$	$F_{1,6} = 0.73, p = 0.43$	$F_{1,6} = 0.02, p = 0.90$	$F_{1,6} = 0.26, p = 0.63$
Burrowing habit	$F_{1,6} = 0.66, p = 0.45$	$F_{1,6} = 0.61, p = 0.46$	$F_{1,6} = 0.03, p = 0.87$	$F_{1,6} = 1.53, p = 0.26$	$F_{1,6} = 0.10, p = 0.76$	$F_{1,6} = 0.10, p = 0.76$

sition, a result suggesting that strong seasonal shifts in trait composition may have obscured responses to flow. Alternatively, measureable responses to flow might not occur until some threshold is passed. If conditions in both control and treatment reaches were above (or below) the flow threshold in a given year, then relative abundances of traits might not differ between them. For example, in August 2006, the relative abundance of insects with a high crawling rate was higher, but more variable, in treatment than in control reaches (Fig. 1C), but in August 2007, a low-flow year, the relative abundance of crawlers was high in both treatment and control reaches (Fig. 1D). This pattern could have occurred if flow was so low in 2007 that both reaches were affected. In contrast, in August 2006, the relative abundance of armored insects did not differ between treatment and control reaches (Fig. 1E), but in August 2007, the relative abundance of armored insects was higher in treatment than in control reaches (Fig. 1F), suggesting a shift at very low flow levels. These subtle patterns were apparent because of the natural difference in flow between the 2 years.

The analysis of the experimental water diversion data was based on the assumption that the diversion did not have effects beyond the annual scale. The treatment reaches were connected to undisturbed stretches of stream, so dispersal probably allowed the community to recover during the winter between the 2 diversion periods. I also controlled for lagging experimental effects by comparing trait composition between years and by focusing on differences between control reaches. In control reaches, the relative abundances of insects that were resistant to desiccation, had a high crawling rate, or were armored increased more from May to August in 2007 (low-flow year) than in 2006 (high-flow year) (Fig. 2A–C). These changes in control reaches suggest that the responses probably occurred over a spatial scale larger than the study reaches. In all cases, the direction of the response matched the hypothesized effect of low flow on trait composition. In contrast to predictions, the relative abundance of small insects, insects preferring depositional habitat, and burrowing insects did not differ between years in control reaches (Fig. 2D–F).

Overall, the significant effects observed in control reaches between low- and high-flow years combined with the subtle patterns in the data from the diversion experiment suggest that high crawling rate and armoring confer some resistance to reduced flow. However, the response of the desiccation-resistant trait state is less clear. The relative abundance of desiccation resistance was higher in control reaches in
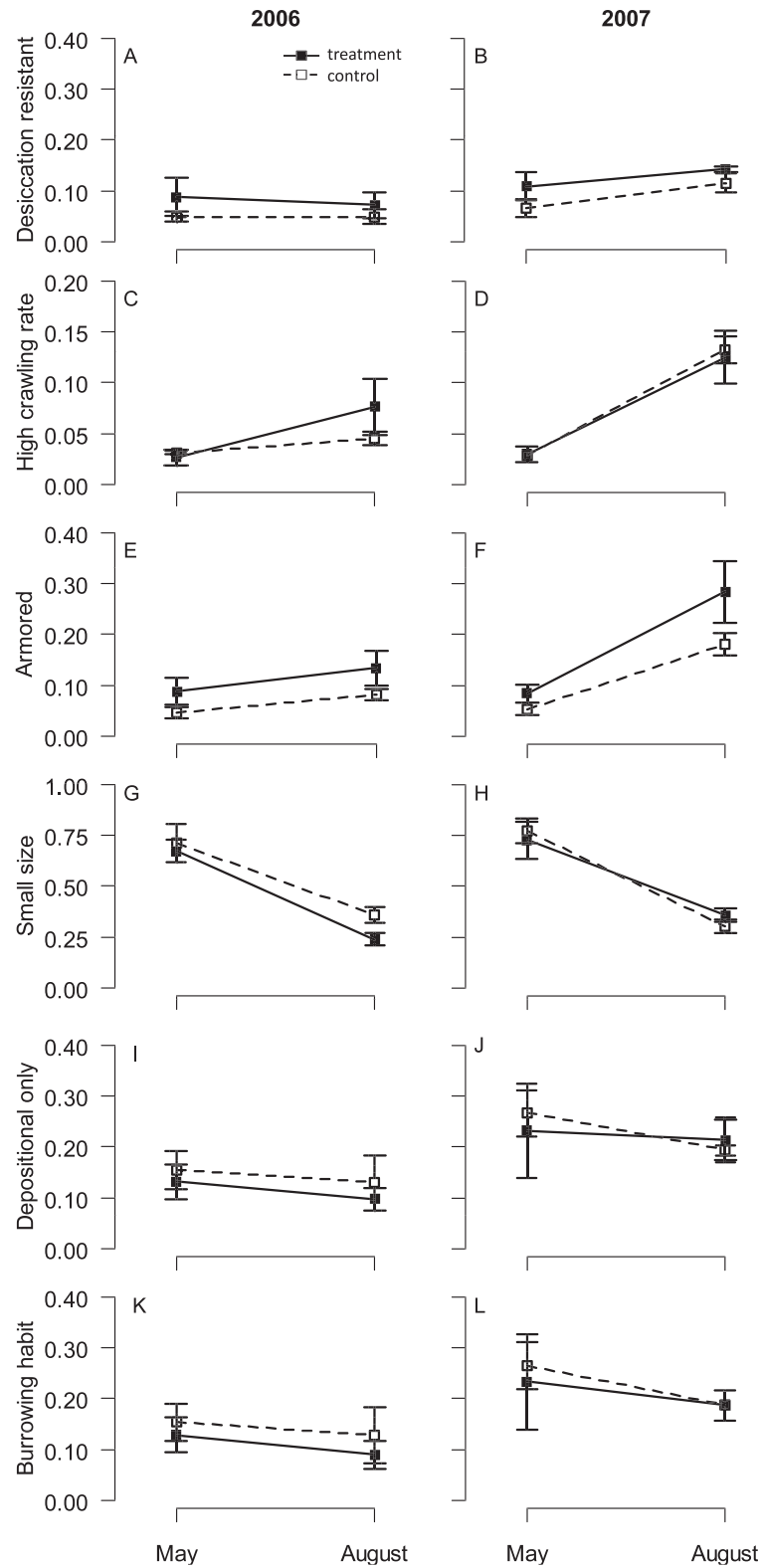
FIG. 1.   Mean (±1 SE) proportion of aquatic insect community that was desiccation resistant (A, B), had a high crawling rate (C, D), was armored (E, F), had small size at maturity (G, H), had a depositional-only habitat preference (I, J), and had a burrowing habit (K, L) before water diversion started (May) and while water diversion was ongoing (August) in 2006 (A, C, E, G, I, K) and 2007 (B, D, F, H, J, L).

TABLE 4.   Analysis of trait-state response to years with differing flow regimes. The F-values and p-values for the mixed-effect linear model are shown for month (May vs August), year (2006 vs 2007), and the month × year interaction. The month × year interaction tested for different responses between high- and low-flow years. Values significant at the $p = 0.05$ level are indicated in bold.

	Month	Year	Month × year
Desiccation resistant	**$F_{1,6} = 12.63, p = 0.01$**	**$F_{1,6} = 35.65, p < 0.01$**	**$F_{1,6} = 13.26, p = 0.01$**
High crawling rate	**$F_{1,6} = 94.61, p < 0.01$**	**$F_{1,6} = 48.90, p < 0.01$**	**$F_{1,6} = 55.48, p < 0.01$**
Armored	**$F_{1,6} = 28.30, p < 0.01$**	**$F_{1,6} = 12.28, p = 0.01$**	**$F_{1,6} = 8.90, p = 0.02$**
Small size at maturity	**$F_{1,6} = 43.92, p < 0.01$**	$F_{1,6} = 0.00, p = 0.97$	$F_{1,6} = 0.84, p = 0.39$
Depositional only	$F_{1,6} = 1.43, p = 0.28$	$F_{1,6} = 4.76, p = 0.07$	$F_{1,6} = 0.35, p = 0.58$
Burrowing habit	$F_{1,6} = 1.63, p = 0.25$	$F_{1,6} = 4.41, p = 0.08$	$F_{1,6} = 0.42, p = 0.54$

the low-flow than in the high-flow year, but the increase was small and no response was observed during the diversion experiment. The study streams are perennial, and the trait state might have been too uncommon among the insects found in these streams to detect a measurable response.

The increased relative abundance of insects with a high crawling rate suggests a behavioral mechanism by which individuals may respond to reduced flow. The dominant behavioral response to reduced flow is drift (Corrarino and Brusven 1983, James et al. 2009), but organisms capable of crawling can follow the
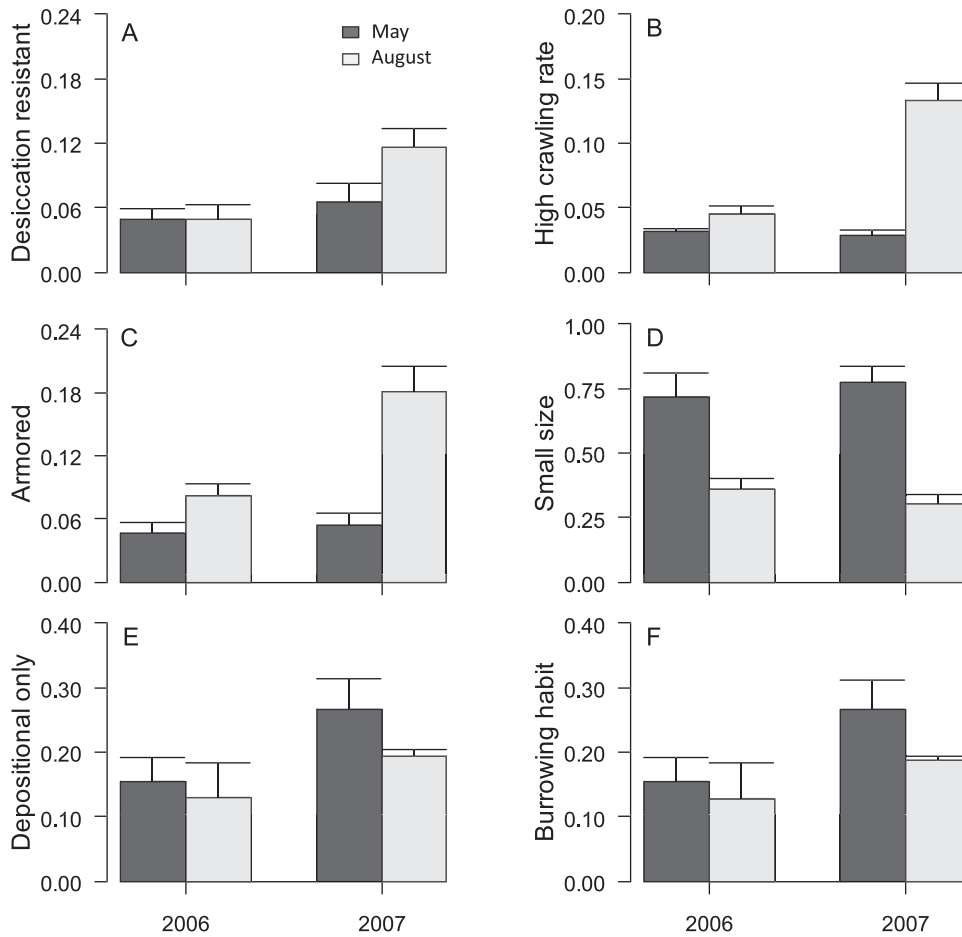

FIG. 2.   Mean (+1 SE) proportion of aquatic insect community in control reaches (no water diversion) that was desiccation resistant (A), had a high crawling rate (B), was armored (C), had a small size at maturity (D), had a depositional-only habitat preference (E), and had a burrowing habit (F) in 2006 and 2007.

retreating water to avoid stranding (Stanley et al. 1994). Burrowing also enables organisms to avoid desiccation, but I found no evidence that the relative abundance of burrowers shifted. I did not sample the hyporheic zone, but in a study similar to mine, James et al. (2008) sampled the hyporheic zone and did not see shifts in the abundance, vertical distribution, or community composition of hyporheic macroinvertebrates. Dewson et al. (2007) did an extensive literature review and found no studies in which use of the hyporheic zone changed when flow decreased. The ability to burrow has been linked to desiccation resistance for crayfish and aquatic insects in intermittent streams (Boulton and Stanley 1995, Acosta and Perry 2001), but this trait does not appear to be important for aquatic insects in perennial streams.

The increase in relative abundance of armored insects during low flow suggests that the importance of biotic interactions might increase as flow decreases. Armored organisms, such as cased caddisflies, experience high mortality during floods because their heavy cases increase the probability of being washed away (Wootton et al. 1996). However, during low flow, armoring can be advantageous because it provides protection from predators. Aquatic insects with moderate-to-strong armoring predominated in a study of dry-season communities in California streams (Bêche et al. 2006). Biomass of predatory insects increased in my study streams when flow was reduced (Walters and Post, in press), and density of predators increased in response to low-flow disturbance in other studies (Extence 1981, Miller et al. 2007). The increased relative abundance of insects with a high crawling rate also might have been a response to increased predation, because a high crawling rate increases the ability of organisms to escape predation.

In contrast to predictions, I found no evidence that the relative abundance of insects with depositional-habitat preference changed in response to low flow. This result was surprising because the proportion of depositional habitat in a stream increases as flow decreases (Stanley et al. 1997, Bunn and Arthington 2002), and aquatic insects that prefer riffle habitats often decline during low-flow disturbance (Castella et al. 1995, Boulton 2003). Insects that prefer depositional habitats probably are adapted to the lower water velocities and decreased O_2 levels of depositional habitats and, as a result, are more resistant to low-flow disturbance. James et al. (2008) also found that flow reduction did not affect the abundance of common pool macroinvertebrates. Their study was similar to mine in that flow reduction was not accompanied by an increase in water temperature.

Perhaps warmer water temperatures and lower O_2 availability rather than reduced flow, per se, are the factors that determine how insects with depositional-habitat preference respond to low flow (Miller et al. 2007). Physiological tolerances, e.g., O_2 demand, are assumed to be the drivers of responses to reduced flow, but in cases where flow is altered without substantial alteration of water temperature or O_2 availability, other factors, such as predation, may be more important.

The relative abundance of insects with small body size decreased sharply between May and August, but did not respond to flow reduction. In the context of my study, size referred to average size at maturity for the insect family and was not related to insect growth during the summer. However, measurement of individual insects suggested that, for some families, average size within a family did decrease when flow was reduced (Walters and Post, in press). Size probably is a more important trait for resilience than for resistance of communities to low-flow disturbance because small size and the ability to reproduce quickly would allow organisms to recolonize disturbed habitats rapidly (Townsend et al. 1997, Rapport and Whitford 1999). Size also may be important for resistance to other types of disturbance, such as floods.

Some investigators advocate a trait-based approach to understanding disturbance and steam communities (Bonada et al. 2007a), whereas others conclude that traits and taxonomy have equal explanatory power (Finn and Poff 2005, Heino et al. 2007). In my study, a trait-based approach did not appear to offer more insight or predictive capability than a more-traditional taxonomic analysis of the same streams (Walters and Post, in press). The utility of a trait-based approach should be greatest when taxonomic groups vary greatly among sites or in situations when the available data are insufficient to make predictions regarding specific taxa. The lack of strong support for a trait-based approach in my study could be a consequence of its small geographic scale or consideration of the wrong suite of traits. Variation in taxonomic composition was limited, and many of the focal trait states made up only a small proportion of the community.

The trait-based approach also will be less effective if assumptions underlying the approach are not met. Trait-based approaches are based on the habitat templet hypothesis, which suggests that harsh conditions associated with low-flow disturbance will lead to high similarity among communities (Southwood 1988). In contrast, in a few studies (mine included) of low-flow disturbance in streams, greater taxonomic

similarity has been found among high-flow than among low-flow communities (Griswold et al. 2008, Walters and Post, in press). Higher (nonflood) flow levels also constitute environmentally challenging conditions and distinct suites of traits or taxa are associated with these conditions (Statzner and Bêche 2010). Trait composition of low-flow communities could differ because as a stream reach dries, the community becomes fragmented and isolated in separate pools with differing environmental conditions and community trajectories (Stanley et al. 1997). This results in increased habitat heterogeneity, decreased habitat connectivity, and stochasticity in community assembly.

Trait-based approaches are a promising direction for biomonitoring efforts (Dolédec and Statzner 2010). My results do not indicate a suite of traits that will be useful in environmental flow management, but they do eliminate a few obvious choices, such as small body size and preference for depositional habitat. My results suggest that the most promising traits are those that are linked to predator resistance (high crawling rate and armoring). Linking species traits to environmental drivers has the potential to increase understanding of the resistance and resilience of communities to disturbance, but seasonal shifts in trait-state composition, indirect effects (e.g., increased predation), high variability in community responses, and the potential for flow thresholds make a priori prediction of appropriate traits challenging.

Acknowledgements

Literature Cited

ACOSTA, C. A., AND S. A. PERRY. 2001. Impact of hydropattern disturbance on crayfish population dynamics in seasonal wetlands of Everglades National Park, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 11: 45–57.

ARNELL, N., B. BATES, H. LANG, J. MAGNUSON, AND P. MULHOLLAND. 1996. Hydrology and freshwater ecology. Pages 325–363 in R. T. Watson, M. C. Zinyowera, and R. H. Moss (editors). Climate change 1995: impacts, adaptations and mitigation of climate change: scientific-technical analyses. Cambridge University Press, Cambridge, UK.

BÊCHE, L. A., E. P. MCELRAVY, AND V. H. RESH. 2006. Long-term seasonal variation in the biological traits of benthic macroinvertebrates in two Mediterranean-climate streams in California, USA. Freshwater Biology 51:56–75.

BONADA, N., S. DOLÉDEC, AND B. STATZNER. 2007a. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. Global Change Biology 13:1658–1671.

BONADA, N., M. RIERADEVALL, AND N. PRAT. 2007b. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. Hydrobiologia 589:91–106.

BOULTON, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48:1173–1185.

BOULTON, A. J., AND E. H. STANLEY. 1995. Hyporheic processes during flooding and drying in a Sonoran desert stream 2: faunal dynamics. Archiv für Hydrobiologie 134:27–52.

BOWMAN, M. F., AND R. C. BAILEY. 1997. Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? Canadian Journal of Fisheries and Aquatic Sciences 54:1802–1807.

BUNN, S. E., AND A. H. ARTHINGTON. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

CASTELLA, E., M. BICKERTON, P. D. ARMITAGE, AND G. E. PETTS. 1995. The effects of water abstractions on invertebrate communities in U.K. streams. Hydrobiologia 308: 167–182.

CHARVET, S., B. STATZNER, P. USSEGLIO-POLATERA, AND B. DUMONT. 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. Freshwater Biology 43: 277–296.

CORRARINO, C. A., AND M. A. BRUSVEN. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. Freshwater Invertebrate Biology 2: 88–98.

DEWSON, Z. S., A. B. W. JAMES, AND R. G. DEATH. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. Journal of the North American Benthological Society 26:401–415.

DÍAZ, A. M., M. L. S. ALONSO, AND M. GUTIÉRREZ. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. Freshwater Biology 53:1–21.

DOLÉDEC, S., AND B. STATZNER. 2008. Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. Freshwater Biology 53:617–634.

DOLÉDEC, S., AND B. STATZNER. 2010. Reponses of freshwater biota to human disturbances: contribution of J-NABS to developments in ecological integrity assessments. Journal of the North American Benthological Society 29: 286–311.

EXTENCE, C. A. 1981. The effect of drought on benthic invertebrate communities in a lowland river. Hydrobiologia 83:217–224.

FINN, D. S., AND N. L. POFF. 2005. Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. Freshwater Biology 50:243–261.

GAYRAUD, S., B. STATZNER, P. BADY, A. HAYBACHP, F. SCHOLL, P. USSEGLIO-POLATERA, AND M. BACCHI. 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. Freshwater Biology 48:2045–2064.

GORDON, N. D., T. A. MCMAHON, B. L. FINLAYSON, C. J. GIPPEL, AND R. J. NATHAN. 2004. Stream hydrology: an introduction for ecologists. 2nd edition. John Wiley and Sons, West Sussex, UK.

GRISWOLD, M. W., R. W. BERZINIS, T. L. CRISMAN, AND S. W. GOLLADAY. 2008. Impacts of climatic stability on the structural and functional aspects of macroinvertebrate communities after severe drought. Freshwater Biology 53:2465–2483.

HEINO, J., H. MYKRÄ, J. KOTANEN, AND T. MUOTKA. 2007. Ecological filters and variability in stream macroinvertebrate communities: do taxonomic and functional structure follow the same path? Ecography 30:217–230.

HORRIGAN, N., AND D. J. BAIRD. 2008. Trait patterns of aquatic insects across gradients of flow-related factors: a multivariate analysis of Canadian national data. Canadian Journal of Fisheries and Aquatic Sciences 65:670–680.

ILG, C., AND E. CASTELLA. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. Freshwater Biology 51:840–853.

JAMES, A. B. W., Z. S. DEWSON, AND R. G. DEATH. 2008. Do stream invertebrates use instream refugia in response to severe short-term flow reduction in New Zealand streams? Freshwater Biology 53:1316–1334.

JAMES, A. B. W., Z. S. DEWSON, AND R. G. DEATH. 2009. The influence of flow reduction on macroinvertebrate drift density and distance in three New Zealand streams. Journal of the North American Benthological Society 28:220–232.

MCGILL, B. J., B. J. ENQUIST, E. WEIHER, AND M. WESTOBY. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.

MILLER, S. W., D. WOOSTER, AND J. LI. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. Freshwater Biology 52:2494–2510.

PECKARSKY, B. L., P. R. FRAISSINET, M. A. PENTON, AND D. J. CONKLIN. 1990. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithaca, New York.

POFF, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391–409.

POFF, N. L., J. D. OLDEN, N. K. M. VIEIRA, D. S. FINN, M. P. SIMONS, AND B. C. KONDRATIEFF. 2006. Functional traits niches of North American lotic insects: trait-based ecological application in light of phylogenetic relationships. Journal of the North American Benthological Society 25:730–755.

POSTEL, S. L., G. C. DAILY, AND P. R. EHRLICH. 1996. Human appropriation of renewable fresh water. Science 271:785–788.

RAPPORT, D. J., AND W. G. WHITFORD. 1999. How ecosystems respond to stress: common properties of arid and aquatic systems. BioScience 49:193–203.

RICHARDS, C., R. J. HARO, L. B. JOHNSON, AND G. E. HOST. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37:219–231.

RICHTER, B. D., A. T. WARNER, J. L. MEYER, AND K. LUTZ. 2006. A collaborative and adaptive process for developing environmental flow recommendations. River Research and Applications 22:297–318.

ROSENBERG, D. M., P. MCCULLY, AND C. M. PRINGLE. 2000. Global-scale environmental effects of hydrological alterations: introduction. BioScience 50:746–751.

SOUTHWOOD, T. R. E. 1977. Habitat, the template for ecological strategies? Journal of Animal Ecology 46:337–365.

SOUTHWOOD, T. R. E. 1988. Tactics, strategies and templets. Oikos 52:3–18.

STANLEY, E. H., D. L. BUSCHMAN, A. J. BOULTON, N. B. GRIMM, AND S. G. FISHER. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. American Midland Naturalist 131:288–300.

STANLEY, E. H., S. G. FISHER, AND N. B. GRIMM. 1997. Ecosystem expansion and contraction in streams. BioScience 47:427–435.

STATZNER, B., AND L. A. BÊCHE. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshwater Biology 55:80–119.

STATZNER, B., A. G. HILDREW, AND V. H. RESH. 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. Annual Review of Entomology 46:291–316.

TOWNSEND, C. R., S. DOLÉDEC, AND M. R. SCARSBROOK. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. Freshwater Biology 37:367–387.

TULLOS, D. D., D. L. PENROSE, G. D. JENNINGS, AND W. G. COPE. 2009. Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration. Journal of the North American Benthological Society 28:80–92.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

VERBERK, W., H. SIEPEL, AND H. ESSELINK. 2008. Life-history strategies in freshwater macroinvertebrates. Freshwater Biology 53:1722–1738.

VIEIRA, N. K. M., W. H. CLEMENTS, L. S. GUEVARA, AND B. F. JACOBS. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. Freshwater Biology 49:1243–1259.

VIEIRA, N. K. M., N. L. POFF, D. M. CARLISLE, S. R. MOULTON, M. L. KOSKI, AND B. C. KONDRATIEFF. 2006. A database of lotic invertebrate traits for North America. U.S. Geological Survey Data Series 187. US Geological Survey, Reston, Virginia.

VIOLLE, C., M. L. NAVAS, D. VILE, E. KAZAKOU, C. FORTUNEL, I. HUMMEL, AND E. GARNIER. 2007. Let the concept of trait be functional! Oikos 116:882–892.

WALTERS, A. W., AND D. M. POST. How low can you go? Impacts of a low flow disturbance on aquatic insect communities. Ecological Applications (in press).

WOOTTON, J. T., M. S. PARKER, AND M. E. POWER. 1996. Effects of disturbance on river food webs. Science 273: 1558–1561.