

Behavioral Responses of *Drunella coloradensis* (Ephemeroptera) Nymphs to Short-Term pH Reductions

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Behavioral responses of *Drunella coloradensis* nymphs were examined in outdoor experimental stream channels after pH reductions of 1 and 2 pH units below ambient. The severity of pH decline below the ambient of 7.8 influenced the behavior patterns displayed by nymphs. At pH 7.01 (an intermediate pH decline) nymphs sat less frequently and burrowed more than controls. Burrowing behavior frequency returned to control levels and drifting and crawling behaviors increased relative to controls at pH 6.02. Ventilatory behaviors increased with pH decline, but were independent of the severity of acidity increases. These results suggest that individual behaviors may offer a more sensitive indicator of sub-acute stress in aquatic insect communities than population or community monitoring. Behaviors leading to increased activity levels in stream insects may have community-level effects via changes in predator-prey encounter rates or increased susceptibility to passive drift. These potential changes are discussed in reference to monitoring for acidification effects.

On a étudié les comportements de nymphes de *Drunella coloradensis* dans des tronçons de cours d'eau expérimentaux après une réduction de 1 et 2 unités de pH par rapport au pH ambiant. La gravité de la baisse de pH par rapport au pH ambiant de 7,8, a influencé les comportements manifestés par les nymphes. À pH 7,01 (soit une baisse intermédiaire du pH), les nymphes se posaient moins fréquemment et s'enfouissaient davantage que les témoins. La fréquence du comportement d'enfouissement retrouvait celle des groupes-témoins et les comportements de dérive et de rampe se faisaient plus fréquents par rapport aux témoins, à pH 6,02. Les comportements ventilatoires se sont accrus à mesure que le pH baissait, mais ils étaient indépendants de la gravité de l'acidification. Ces résultats donnent à penser que les comportements individuels peuvent constituer un indicateur plus sensible du stress subaigu dans des communautés d'insectes aquatiques que ne l'est la surveillance des populations ou des communautés. Des comportements qui conduisent à une activité accrue chez les insectes lotiques peuvent avoir des effets au niveau de la communauté dans la mesure où sont modifiés les taux de rencontre entre prédateurs et proies ou encore est accrue la susceptibilité à une dérive passive. Il est question de ces changements en termes de surveillance des effets de l'acidification.

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Aquatic ecologists have demonstrated that reduced pH may have negative effects on individuals, populations, and communities of aquatic insects. To assess the potential impacts of acidification in lotic systems, researchers have monitored community level effects on benthic density, diversity, or functional group abundance (Friberg et al. 1980; Hall et al. 1980; Hildrew et al. 1984; Allard and Moreau 1987; Hopkins et al. 1989; Hall 1990). Studies concerning individual responses to acidification have focused on physiology, body mass changes, and survival or emergence (Bell 1971; Fiance 1978; Havas and Hutchinson 1983; Allard and Moreau 1986; Correa et al. 1986; Herrmann and Andersson 1986; Rowe et al. 1988, 1989; Mackie 1989; Chmielewski and Hall 1992). Drift rates are probably the most widely examined response to acidification (Hall et al. 1980; Pratt and Hall 1981; Oimerod et al. 1987; Hopkins et al. 1989; Bernard et al. 1990): generally drift increases in most taxa. Grazing mayflies (e.g., baetids and siphonurids), and small chironomid midges (Orthcladiinae) appear to be the most sensitive insects to reduced pH. Although increased drift rates have been documented with experimental acid additions, it is unknown whether this drift response is active, passive, or a combination of these. Other factors (both genetic

and environmental) might also act to increase or decrease the likelihood of drift and no research demonstrates whether other behaviors in insects are altered under acid stress (but McCahon et al. (1989) have addressed changes in feeding rates of amphipods and snails in relation to increased acidity). The importance of insect behaviors in response to acidification and the implications of behavioral alterations in determining the outcome of higher level interactions has not yet been addressed.

Aquatic insects might use behaviors such as drifting or burrowing to evade exposure to short-term increases in acidity. One might expect some behaviors to predominate depending on the severity of the disturbance (Resh et al. 1988) and the energetic trade-offs between behavior and physiology (Dill 1987). In particular, regulatory behaviors (e.g., Wiley and Kohler 1984) often involve conflicts with other behaviors and are likely to be the most sensitive indicators of stress. For example, under low oxygen conditions metabolic carbon dioxide must be counteracted before tissue acidosis occurs (Nation 1985). Mayflies might increase gill ventilation rates to overcome a minimal oxygen debt or drift if the oxygen stress is severe (Eriksen 1963; Wiley and Kohler 1980). Drifting, however, may pose added predation risks from visually feeding fish (Waters

1972; Allan 1978, 1984; Stewart and Szczytko 1983; Skinner 1985). Thus, a conflict would arise if predation risk was high and oxygen stress was greater than could be overcome by increases in ventilation rate.

As with a low oxygen stress, increased acidity may lead to a physiological disruption that requires rectification. In mayflies, metabolic ion concentrations are disrupted with increasing acidity (Rowe et al. 1988, 1989; but see Berrill et al. 1991), and depending on the costs, certain behavioral responses might be expected as counter measures. For example, behaviors which ensure adequate evasion of the stress, yet do not increase predation risks, might be favored. If behavioral responses to stress maximize regulatory efficiency based on energetic trade-offs, drift (a physiologically inexpensive, direct escape) should increase under stressful conditions (i.e., reduced pH) if there are no other associated costs. If there are costs to drifting, behaviors other than drifting may be even more sensitive indicators of acid stress in aquatic insects. At low-level pH stress, trade-offs may exist between risks associated with physiological intolerance and predation such that drifting is avoided until physiologically necessary.

Here we report the results of a replicated experimental stream study in which we reduced ambient pH and observed *Drunella coloradensis* nymphs for behavioral changes. We predicted that: (1) nymphal behavior would be influenced by low-level, short-term pH reductions and (2) drifting (a potentially expensive behavior in terms of predation, but energetically inexpensive) would occur more often at the lowest pH levels examined compared to lesser pH declines. Our results suggest that nymphal behavior is influenced by acidity increases, but to different degrees depending on the severity of pH reductions. We discuss these results in reference to monitoring for acidification effects and the implications of behavioral alterations in response to stress.

Study Site and Methods

Site Description

Two montane streams in the Rocky Mountains of southeast Wyoming were used; Little Brooklyn Lake inlet (LB) and Mullen Creek (MC). LB is a second order stream at 3158 m elevation in a remote location of the Medicine Bow National Forest in southeast Wyoming (41°22'W, 106°15'N). MC is a first order stream at 2572 m elevation located adjacent to the United States Forest Service (USFS) research station 1 km west of Centennial, WY (41°18'W, 106°09'N). Substrate, flow and water chemistry, especially pH and alkalinity, are similar between the LB and MC sites, which are approximately 10 km apart (Table 1). Water chemistry in LB is monitored routinely by USFS personnel as part of their Glacier Lakes Ecosystem Experiments Site (GLEES).

Both sites occur within forest habitat dominated by lodgepole pine (*Pinus contorta*), Ponderosa pine (*Pinus ponderosa*), and scattered stands of quaking aspen (*Populus tremuloides*). Both sites are fed primarily by snowmelt, but LB has a lake approximately 2 km upstream while MC has no upstream lake. MC and LB both contain brook trout populations (*Salmo fontinalis*).

Study Organism

The mayfly *Drunella coloradensis* (Dodds) (Ephemeroptera) is widely distributed and generally occurs at elevations greater

TABLE 1. Water chemistry for the Mullen Creek (MC) study site and Little Brooklyn Lake inlet (LB) nymph collection site on 8 August 1991. All measurements are in $\mu\text{eq/L}$ unless stated otherwise.

Variable	Site	
	MC	LB
pH	7.80	7.49
Temperature ($^{\circ}\text{C}$)	11.0	12.0
Conductivity ($\mu\text{S}/\text{cm}^2$)	111.87	69.91
Alkalinity	1127.58	1156.38
Ca^{2+}	871.66	807.63
Mg^{2+}	203.57	251.64
Na^+	201.92	18.40
K^+	22.20	6.30
NH_4^+	1.45	3.06
Cl^-	10.92	2.02
NO_3^-	0.06	1.86
SO_4^{2-}	92.03	18.61

than 1700 m (Jensen 1966; Ward 1985). Like most ephemeroptera, *D. coloradensis* is a poor swimmer, generally slow-moving, and exhibits a clinging/sprawling life style (Edmunds 1984). Primary food items include diatoms at early instars and animal matter during later instars. In Oregon this species exhibits a univoltine life history and shows very synchronous nymphal growth (Hawkins 1990). Adults emerge in late summer and early autumn (Jensen 1966; personal observation). This species occurs in both LB and MC, but in low numbers in MC.

Experimental Procedures

Drunella coloradensis nymphs were collected from LB on 31 July and 6 August 1991. Nymphs were picked from stones using a fine brush or forceps, placed in a cooler with LB stream water, and transported to the study reach on MC, nymphs were placed in in-stream enclosures for at least 48 h prior to use in experiments. In-stream enclosures were weighted sieving buckets and contained MC substrate with attached periphyton. Only insects that responded to stimulation with a brush were used for experiments. Nymphs were identified using keys of Edmunds (1984) and Ward (1985).

Experimental stream chambers were constructed of clear Plexiglas. The chambers measured $57.0 \times 33.5 \times 20$ cm with a 10-cm collecting basin at each end (Fig. 1). Five panels divided each chamber into six, 5×34.5 -cm stream channels. A 1-mm mesh plastic screen served as a barrier on the upper and lower channel ends. In each experimental chamber, stream water was recirculated with a magnetic, centrifugal pump (Little Giant, Model 3-MD-SC) and transferred through a series of Teflon tubes such that channel velocity was within 2 cm/s of the velocity at the LB collection site.

Three experimental chambers were imbedded 2–5 cm within the substrate of MC to maintain slope and contact with surrounding water. Thus the stream served as a bath to maintain the water temperature within the chambers. Each chamber represents one of three pH treatments: an ambient control (pH approx. 8.0), 1 pH unit below ambient, and 2 pH units below ambient. Treatments are referred to as C, -1, and -2, respectively. The six channels in each chamber received 2–3 cm of stream substrate (a sand and gravel mixture) that had been sifted to remove any organisms. Chambers were filled with 12 L of MC

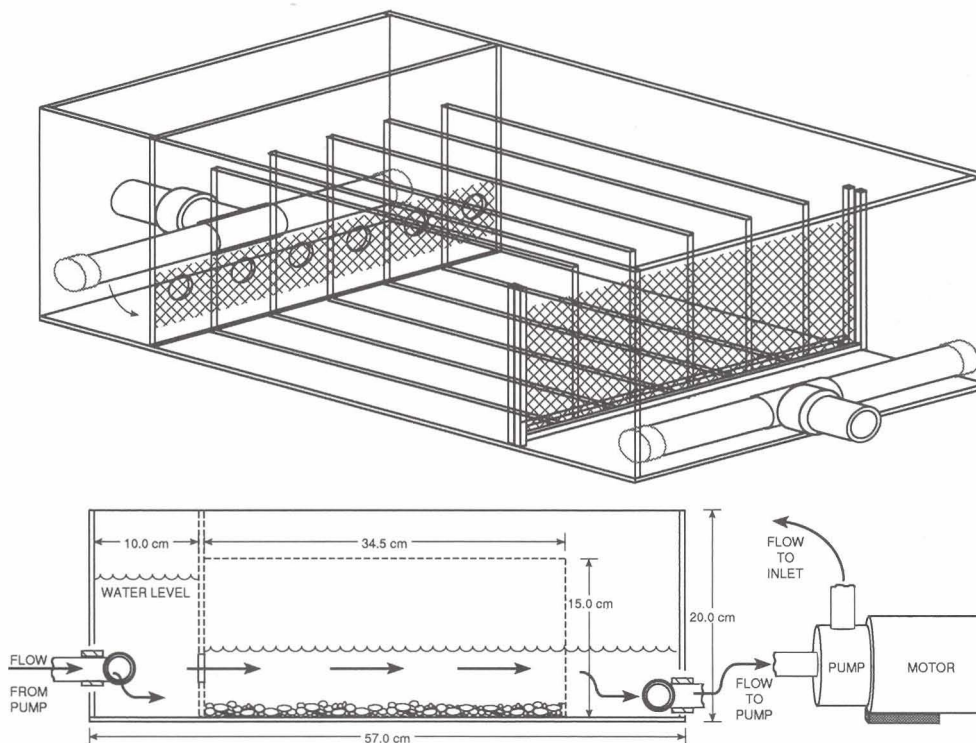


FIG. 1. Diagram of experimental stream chambers used for examining behavioral responses to acidification. Chambers are self-contained, recirculating units powered by magnetic, centrifugal pumps. Chamber measurements (length, width, and height) are $57.0 \times 33.5 \times 20.0$ cm. Each chamber is subdivided into 6 channels measuring $34.5 \times 5.0 \times 15.0$ cm (l,w,h, respectively). There is a 10-cm wide collecting basin at each end of a chamber. The units are placed in-stream for temperature regulation.

stream water and the water was circulated in the chambers for 24 h prior to insect and acid additions.

Each channel received one *D. coloradensis* nymph (six nymphs per treatment per day). Nymphs were acclimated to channels for 24 h prior to acid additions. At 09:00 on 2 and 8 August enough $0.01 M H_2SO_4$ was added to reduce pH levels in two chambers -1 and -2 pH units below ambient (control pH = 7.79, -1 pH = 7.01, -2 pH = 6.02). Continuous recording pH meters (Photovolt Aquacord Model 130) monitored pH levels and manual acid additions were used to maintain pH levels. Water samples for chemical analyses were collected from each chamber at the start and the conclusion of each experiment. Samples were analyzed for major anions and cations by the USFS Water Chemistry Lab in Ft. Collins, CO.

Scan sampling of behaviors was performed at 5-min intervals during the first 2 h following acid additions. Scan sampling requires an observation of each individual after a fixed amount of time (Martin and Bateson 1986). Because each channel contains only one nymph, an observer could scan each of the 18 channels (six per treatment) for a nymph, record its behavior, and continue through the remaining channels. A "scan" was completed within 5 min and the procedure was repeated 25 times. The behaviors of sitting (*s*), ventilating (*v*), burrowing (*b*), drifting (*d*), crawling (*c*), and ventilating while crawling (*vc*) were recorded. "Sitting" represented a nymph sitting on an exposed substrate surface without movement of the gills or body. "Ventilating" represented a nymph with visible gill movement sitting on an exposed substrate surface. "Burrowing" was recorded for a nymph not visible drifting or visible on the surface of any substrate. "Drifting" represented a nymph in the water

column. "Crawling" was recorded for a nymph moving across the substrate without visible gill movement. "Ventilating while crawling" was recorded for nymphs moving across the substrate while having visible gill fluttering.

The total frequency of behavioral responses was tested for independence of pH treatment using a Kruskal-Wallis one-way ANOVA. A posteriori multiple comparisons within behaviors were based on a modified Mann-Whitney *U*-test (Sokal and Rohlf 1981). The frequency of behaviors was not significantly different between trial days for 16 of 18 comparisons. Because there were only two significant differences, we pooled all behaviors from the two trial days. We feel pooling caused statistical analyses to be more conservative (i.e., less likely to show a significant treatment effect if one did not occur) because of the additional variance within comparison treatments and was appropriate in this study.

Results

Water chemistry changed as expected after acid additions. Alkalinity and pH levels declined while conductivity and SO_4^{2-} levels increased (Table 2). Changes in the major cations (Ca^{2+} , Mg^{2+} , Na^+ , and K^+) were somewhat erratic, but all generally increased with acid additions; anions also tended to increase.

Acid treatment influenced the frequency of behaviors displayed by *D. coloradensis* nymphs, but did not prevent or change any behavior (i.e., nymphs exhibited all behaviors under all treatments, but at varying frequencies). Kruskal-Wallis ANOVA results suggest that all behavioral frequencies were altered by at least one treatment (Table 3).

TABLE 2. Water chemistry in experimental chambers before acid additions and after 2-h experiments. The pH was reduced using 0.01 M H₂SO₄. Ions are in µeq/L unless stated otherwise.

Variable	Before			After		
	Control	-1	-2	Control	-1	-2
pH	7.79	7.81	7.81	7.92	7.01	6.02
Temperature (°C)	10.2	10.5	10.1	11.0	11.1	10.9
Conduct. (µS/cm ²)	112.2	110.2	113.0	111.7	127.6	143.3
Alkalinity	1194.8	1148.3	1126.1	1184.2	446.7	56.2
Ca ²⁺	953.3	825.7	815.9	828.1	836.1	873.0
Mg ²⁺	210.4	202.8	197.5	202.4	195.9	212.5
Na ⁺	200.6	201.4	203.7	201.1	203.8	208.9
K ⁺	20.9	20.8	23.4	21.8	22.9	27.3
NH ₄ ⁺	1.3	1.7	1.4	1.6	1.3	1.2
Cl ⁻	10.2	10.2	12.3	10.9	12.6	15.9
NO ₃ ⁻	0.0	0.0	0.0	0.0	0.0	0.0
SO ₄ ²⁻	94.8	110.8	144.9	97.0	768.6	1105.7

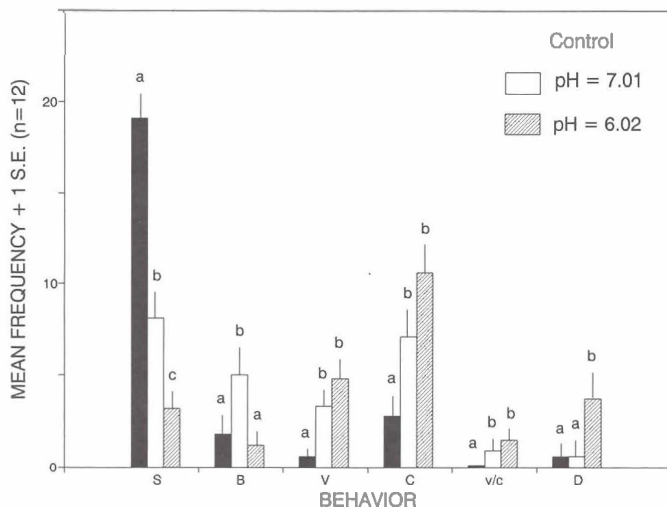


FIG. 2. Within behavior comparisons for larval responses to acid additions. Multiple comparisons within behaviors were tested using a modified Mann-Whitney *U*-test. Three comparisons were made for each behavior (C vs. -1, C vs. -2, and -1 vs. -2). Same letters within a behavior indicate the treatments were not different at $P < 0.05$. See text for P values of significant differences. On behavior axis, S = sitting; B = burrowing; V = ventilating; C = crawling; v/c = ventilating while crawling; and D = drifting.

The frequency of sitting declined with increasing acidity (Fig. 2). The control nymphs sat more frequently than any other behavior. Control nymphs sat approximately 75% of observations and this was more than both -1 and -2 nymphs (Mann-Whitney *U*-test, $P < 0.001$, and $P < 0.001$ respectively). The -1 treatment nymphs also sat more than -2 nymphs ($P < 0.05$; Fig. 2) and sitting was the most frequent behavior recorded for the -1 nymphs (about 32% of observations).

Burrowing behavior increased at intermediate acidity levels and then declined back to control frequencies at higher acid treatment levels (Fig. 2). Burrowing of -1 nymphs was greater than both control and -2 nymphs (Mann-Whitney *U*-test, $P < 0.01$ and $P < 0.05$), but was never the most frequent behavior recorded. Burrowing behavior was recorded for 20% of observations at intermediate pH levels, but less than 10% of control and -2 observations.

Crawling (c), ventilating (v), and ventilating while crawling

TABLE 3. Mean frequency (± 1 SE) of observed behaviors for *D. coloradensis* nymphs after acid addition experiments ($n = 12$ nymphs/treatment). Nymphs were observed at 5-min intervals during the 2-h experiments. Control: pH = 7.81, -1: pH = 7.01, -2: pH = 6.02. See text for explanation of behaviors. H = Kruskal-Wallis statistic examining treatment effects on behaviors. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Behavior	Treatment			H
	Control	-1	-2	
Sit	19.1 (1.25)	8.1 (1.20)	3.2 (0.76)	24.777***
Burrow	1.8 (0.80)	5.0 (1.45)	1.2 (0.64)	8.238*
Drift	0.6 (0.22)	0.6 (0.48)	3.7 (1.06)	10.308**
Ventilate	0.6 (0.27)	3.3 (0.63)	4.8 (0.80)	18.158***
vc	0.1 (0.08)	0.9 (0.32)	1.5 (0.34)	13.399**
Crawl	2.8 (0.81)	7.1 (1.26)	10.6 (0.82)	15.689***

(vc) showed a similar trend with pH. The -1 and -2 treatment nymphs were not significantly different from each other in these three behaviors, but were different from the controls for these behaviors (C vs. -1c, C vs. -2c, Cv vs. -1v, Cv vs. -2v, Cvc vs. -1vc, Cvc vs. -2vc; $U = 112.0^*$, 137.5^{***} , 130.5^{***} , 134.5^{***} , 109.0^* , 128.0^{**} , respectively). Crawling was the most frequent behavior recorded for the -2 nymphs, occurring 42.4% of observations. Behaviors of v and vc were never the most frequently recorded behaviors, but were more frequent for -2 nymphs relative to other treatments (19.2 and 6% respectively).

Drifting behavior occurred more frequently in -2 nymphs than control and -1 treatments (Mann-Whitney *U*-test, $P < 0.05$). Drift rates showed an approximately 6-fold increase in the -2 treatment compared to both -1 and control treatments. Drifting was the third most frequent behavior observed in -2 nymphs, but the least frequent behavior in control nymphs (Fig. 2). Drifting behavior showed no significant increase at intermediate pH levels. Drifting was not correlated with crawling for the control, -1 or -2 treatments (Spearman's rho, all $P > 0.05$).

Discussion

The frequencies of behaviors displayed by *D. coloradensis* nymphs were influenced by acidity in our experiment and depended on the severity of pH reduction. In general, as acidity

levels increased, activity levels also increased (e.g., crawling was more frequent in the treatment chambers than in the controls). Early toxicity research suggested that increased activity, including crawling, loss of equilibrium, and drifting, might be a generalized, first response mechanism to physiological stress (Jensen and Gaufin 1964a, 1964b; Muirhead-Thomson 1978). It is also interesting that endoparasitic infections also cause increased activity levels in some mayfly species (Benton and Pritchard 1990). Increased movement patterns might alter interactions between stream insects by increasing encounter rates with predators (Soluk and Collins 1988) or by increasing the probability of abrasion by water currents (Poff et al. 1991).

Peckarsky (1980, 1982, 1991) and Peckarsky and Dodson (1980) showed that behavioral interactions (especially predator/prey) are important in structuring lotic insect communities under natural conditions. Behavioral responses to environmental stress (especially involving physiological adjustments) may have grave implications to these interactions if the species within a community exhibit some tolerance differences to the stress. For example, Warner et al. (1993) showed that pH tolerance differences in anuran tadpoles, when combined with population density differences, may alter the outcome of inter- and intraspecific competition even at pH levels not resulting in death. Likewise, Clements et al. (1989) showed that sublethal copper exposure increased the ability of predatory stoneflies to capture net-spinning caddis flies because the stoneflies were more tolerant of copper than were the caddis larvae. In our experiment, the increased crawling behavior displayed by mayfly nymphs might result in increased encounter rates with predators, reduced ability to detect predators, or an increased likelihood of passive drift due to abrasion by currents. If mayfly nymphs are less tolerant of pH stress than are their stonefly predators, and if a general response to stress is evasion, stonefly predators might experience higher prey capture rates either because of increased prey encounters or because prey are less capable of detecting predators.

As with crawling, increases in drifting rates may influence encounter frequency between species. Drifting frequency increased at the lowest pH level examined in our experiment, but not dramatically. Drift responses might have been dampened because the pH reductions in this experiment were not very severe, *D. coloradensis* might be very tolerant of acidity, or drifting may be phylogenetically or morphologically constrained in this species. Also, scan sampling probably gave conservative measurements of drifting behavior because drifting bouts of shorter duration than scan intervals would be missed. Depending on natural drift distances, short channel length might have led to an over- or under-estimate of drifting frequency because drifters encountered the retaining net. If drift was an active evasion tactic, nymphs would be expected to remain on the downstream end of the channels attempting to reenter the water column (i.e., drifting to avoid stress). Nymphs did not remain on the screen, but generally crawled back to the substrate.

Another active behavior, burrowing, may negate the consequences of increased crawling and drifting due to acid stress. At intermediate pH, burrowing may be a pH-stress avoidance behavior that is risk-free in terms of predation if predators are less able to burrow than are prey. Also, ion-exchange dynamics within the substrate (or any material where an insect can hide) may be different enough that pH levels are more stable (Likens 1989), offering a potential refuge from

pH stress. Weatherley et al. (1989) showed that pH levels were positively related to increasing depth within the substrate and that pH was up to 2 units higher in the substrate than in the overlying water. This relationship must ultimately depend on the nature of the substrate. The value of burrowing as an evasion tactic will depend on this and a combination of biotic and abiotic factors and their relative costs. Body morphology, nature of the substrate, cost of drifting, and predation risks within the substrate are examples of potential factors determining the likelihood of burrowing as an escape strategy. In general, small-bodied nymphs should burrow better than large-bodied nymphs because of access to interstitial spaces. Examination of size distributions of drift and benthos between pre- and post-acid additions under experimental conditions might address this possibility. Likewise, nymphs with fusiform bodies might be expected to burrow better than dorso-ventrally flattened nymphs (i.e., baetids vs. heptageniids). Swimming ability and propensity to drift would require attention when interpreting such data.

The use of inadequate endpoints might lessen our ability to interpret results when monitoring for acidification effects. This study suggests that current sampling protocols may, in fact, under represent potential impacts and that behaviors may provide an earlier indication of acid stress in insect communities. Routine monitoring of insect communities for acidification effects generally include drift, benthic, and emergence estimates (e.g., Hall et al. 1980). Our results suggest there are lower thresholds of stress (i.e., intermediate pH declines influencing behavior) that would not be detected with drift estimates. Benthic estimates using Surber-type samplers give no indication whether insects are hiding in the substratum or normally reside there. Possibly, examinations of lateral fringe or within-leafpack communities would be better methods to estimate refuge seeking behavior. Behaviors might also offer useful tools in toxicological research and field testing for potential hazards by yielding more realistic estimates of first-effects concentrations of stressors. Here, using a simple, replicated observation method we have demonstrated that behavioral responses of a common, lotic mayfly are altered dramatically by a low-level, pH disturbance. Regardless of how monitoring protocols are devised in the future, it is clear that behaviors will have to be incorporated into sampling designs.

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References

- ALLAN, J.D. 1978. Trout predation and the size composition of stream drift. *Limnol. Oceanogr.* 23: 1231-1237.
- ALLAN, J.D. 1984. The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos* 42: 68-76.
- ALLARD, M., AND G. MOREAU. 1986. Influence of acidification and aluminum on the density and biomass of lotic benthic invertebrates. *Water Air Soil Pollut.* 30: 673-679.
- ALLARD, M., AND G. MOREAU. 1987. Effects of experimental acidification on a lotic macroinvertebrate community. *Hydrobiologia* 144: 37-49.
- BELL, H. 1971. Effect of pH on the survival and emergence of aquatic insects. *Water Res.* 5: 313-339.

- BENTON, M.J., AND G. PRITCHARD. 1990. Mayfly locomotory responses to endoparasitic infection and predator presence: the effects on encounter rate. *Freshwater Biol.* 23: 363-371.
- BERNARD, D.P., W.E. NEILL, AND L. ROWE. 1990. Impact of mild experimental acidification on short term invertebrate drift in a sensitive British Columbia stream. *Hydrobiologia* 203: 63-72.
- BERRILL, M., G. TAYLOR, AND H. SAVARD. 1991. Are chloride cells involved in low pH tolerance and sensitivity? The mayfly possibility. *Can. J. Fish. Aquat. Sci.* 48: 1220-1225.
- CHMIELEWSKI, C.M., AND R.J. HALL. 1992. Responses of immature blackflies (Diptera: Simuliidae) to experimental pulses of acidity. *Can. J. Fish. Aquat. Sci.* 49: 833-840.
- CLEMENTS, W.H., D.S. CHERRY, AND J. CAIRNS, JR. 1989. The influence of copper exposure on predator-prey interactions in aquatic insect communities. *Freshwater Biol.* 21: 483-488.
- CORREA, M., R. COLER, C.M. YIN, AND E. KAUFMAN. 1986. Oxygen consumption and ammonia excretion in the detritivore caddisfly *Limnephilus* sp. exposed to low pH and aluminum. *Hydrobiologia* 140: 237-241.
- DILL, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. *Can. J. Zool.* 65: 803-811.
- EDMONDS, G.F., JR. 1984. Ephemeroptera, p. 94-125. In R.W. Merritt and K.W. Cummins [ed.] An introduction to the aquatic insects of North America, 2nd ed. Kendall/Hunt Publishing, Dubuque IA.
- ERIKSEN, C.H. 1963. Respiratory regulation in *Ephemera simulans* (Walker) and *Hexagenia limbata* (Serville) (Ephemeroptera). *J. Exp. Biol.* 40: 455-468.
- FIANCE, S.B. 1978. Effects of pH on the biology and distribution of *Ephemera fulvipes* (Ephemeroptera). *Oikos* 31: 332-339.
- FRIBERG, F., C. OTTO, AND B.S. SVENSSON. 1980. Effects of acidification on the dynamics of allochthonous leaf material and benthic invertebrate communities in running waters, p. 304-305. In Drablos and Tollan [ed.] Proceedings of the International Conference on the Ecological Impacts of Acid Precipitation, SNSF Project, Norway.
- HALL, R.J. 1990. Relative importance of seasonal, short-term pH disturbances during discharge variation on a stream ecosystem. *Can. J. Fish. Aquat. Sci.* 47: 2261-2274.
- HALL, R.J., G.E. LIKENS, S.B. FIANCE, AND G.R. HENDREY. 1980. Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* 61: 976-989.
- HAVAS, M., AND T.C. HUTCHINSON. 1983. Effects of low pH on the chemical composition of aquatic invertebrates from tundra ponds at the Smoking Hills, N.W.T., Canada. *Can. J. Zool.* 61: 241-249.
- HAWKINS, C.P. 1990. Relationships between habitat dynamics, food availability, and growth patterns of Ephemeroptera mayflies from Western North America, p. 35-42. In I.C. Campbell [ed.] Mayflies and stoneflies. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- HERRMANN, J., AND K.G. ANDERSSON. 1986. Aluminum impact on respiration of lotic mayflies at low pH. *Water Air Soil Pollut.* 30: 703-709.
- HILDREW, A.G., C.R. TOWNSEND, AND J. FRANCIS. 1984. Cellulolytic decomposition in streams of contrasting pH and its relationship with invertebrate community structure. *Freshwater Biol.* 14: 323-328.
- HOPKINS, P.S., K.W. KRATZ, AND S.D. COOPER. 1989. Effects of an experimental acid pulse on invertebrates in a high altitude Sierra Nevada stream. *Hydrobiologia* 171: 45-58.
- JENSEN, S.L. 1966. Mayflies of Idaho. M.S. thesis, University of Utah, Salt Lake City, UT. 366 p.
- JENSEN, L.D., AND A.R. GAUFIN. 1964a. Effects of ten organic insecticides on two species of stonefly naiads. *Trans. Am. Fish. Soc.* 93: 27-34.
- JENSEN, L.D., AND A.R. GAUFIN. 1964b. Long-term effects of organic insecticides on two species of stonefly naiads. *Trans. Am. Fish. Soc.* 93: 357-364.
- LIKENS, G.E. 1989. Acid rain and its effects on sediments in lakes and streams. *Hydrobiologia* 176/177: 331-348.
- MACKIE, G.L. 1989. Tolerances of five benthic invertebrates to hydrogen and metals (Cd, Pb, Al). *Arch. Environ. Contam. Toxicol.* 18: 215-223.
- MARTIN, P., AND P. BATESON. 1986. Measuring behavior: an introductory guide. Cambridge University Press, Cambridge.
- MCCAHOON, C.P., A.F. BROWN, M.J. POULTON, AND D. PASCOE. 1989. Effects of acid, aluminum, and lime additions on fish and invertebrates in a chronically acidic Welsh stream. *Water Air Soil Pollut.* 45: 345-359.
- MUIRHEAD-THOMSON, R.C. 1978. Lethal and behavioral impact of permethrin (NRDC 143) on selected stream macroinvertebrates. *Mosquito News* 38: 185-190.
- NATION, J.L. 1985. Respiratory systems, p. 185-225. In M.S. Blum [ed.] Fundamentals of insect physiology. John Wiley and Sons, Incorporated, New York, NY.
- ORMEROD, S.J., P. BOOLE, C.P. MCCAHOON, N.S. WEATHERLEY, D. PASCOE, R.W. EDWARDS. 1987. Short-term experimental acidification of a Welsh stream: comparing the biological effects of hydrogen ions and aluminum. *Freshwater Biol.* 17: 341-356.
- PECKARSKY, B.L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61: 932-943.
- PECKARSKY, B.L. 1982. Aquatic insect predator-prey relations. *BioScience* 32: 261-266.
- PECKARSKY, B.L. 1991. A field test of resource depression by predatory stonefly larvae. *Oikos* 61: 3-10.
- PECKARSKY, B.L., AND S.I. DODSON. 1980. Do stonefly predators influence benthic distributions in streams? *Ecology* 61: 1275-1282.
- POFF, N.L., R.D. DECINO, AND J.V. WARD. 1991. Size-dependent drift responses of mayflies to experimental hydrologic variation: active predator avoidance or passive hydrodynamic displacement? *Oecologia* 88: 577-586.
- PRATT, J.M., AND R.J. HALL. 1981. Acute effects of stream acidification on the diversity of macroinvertebrate drift, p. 77-95. In R. Singer [ed.] Effects of acid precipitation on benthos. North American Benthological Society.
- RESH, V.H., A.V. BROWN, A.P. COVICH, M.E. GURTZ, H.W. LI, G.W. MINSHALL, S.R. REICE, A.L. SHELDON, J.B. WALLACE, R.C. WISSMAR. 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* 7: 433-455.
- ROWE, L., M. BERRILL, AND L. HOLLETT. 1988. The influence of season and pH on mortality, molting, and whole-body ion concentrations in nymphs of the mayfly *Stenonema femoratum*. *Comp. Biochem. Physiol.* 90A: 405-408.
- ROWE, L., M. BERRILL, L. HOLLETT, AND R.J. HALL. 1989. The effects of short-term laboratory pH depressions on molting, mortality, and major ion concentrations in the mayflies *Stenonema femoratum* and *Leptophlebia cupida*. *Hydrobiologia* 184: 89-97.
- SKINNER, W.D. 1985. Night-day drift patterns and the size of larvae of two aquatic insects. *Hydrobiologia* 124: 283-285.
- SOKAL, R.R., AND F.J. ROHLF. 1981. Biometry, 2nd ed. W.H. Freeman and Company, New York, NY.
- SOLUK, D.A. AND N.C. COLLINS. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52: 94-100.
- STEWART, K.W., AND S.W. SZCYTKO. 1983. Drift of Ephemeroptera and Plecoptera in two Colorado rivers. *Freshw. Invert. Biol.* 2: 117-131.
- WARD, J.V. 1985. An illustrated guide to the mountain stream insects of Colorado. Professor Publishing, Boulder, CO.
- WARNER, S.C., J. TRAVIS, AND W.A. DUNSON. 1993. Effect of pH variation on interspecific competition between two species of hyliid tadpoles. *Ecology* 74: 183-194.
- WATERS, T.F. 1972. The drift of stream insects. *Ann. Rev. Entomol.* 17: 253-272.
- WEATHERLEY, N.S., S.P. THOMAS, AND S.J. ORMEROD. 1989. Chemical and biological effects of acid, aluminum, and lime additions to a Welsh Hill-stream. *Environ. Pollut.* 56: 283-297.
- WILEY, M.J., AND S.L. KOHLER. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. *Can. J. Zool.* 58: 618-622.
- WILEY, M., AND S.L. KOHLER. 1984. Behavioral adaptations of aquatic insects, p. 101-133. In V.H. Resh, and D.M. Rosenberg [ed.] The ecology of aquatic insects. Praeger Publishers, New York, NY.