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Authors

Holmquist, Jeffrey G
Schmidt-Gengenbach, Jutta
Roche, James W

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STREAM MACROINVERTEBRATES AND HABITAT BELOW AND ABOVE TWO WILDERNESS FORDS USED BY MULES, HORSES, AND HIKERS IN YOSEMITE NATIONAL PARK

Jeffrey G. Holmquist^{1,3}, Jutta Schmidt-Gengenbach¹, and James W. Roche²

ABSTRACT.—Wilderness stream crossings used by mules, horses, and hikers are localized disturbances that may affect habitat immediately downstream, but the potential influence of fords on streams has received little investigation, particularly in terms of possible effects on fauna. Our overall null hypothesis was absence of below-above differences for either benthic macroinvertebrate assemblages or habitat characteristics at such fords. We further sought to determine (1) whether any such differences were present prior to annual use, suggesting longer-term effects, and (2) whether differences were present in late season, after annual use. We examined macroinvertebrates and habitat immediately below and above 2 fords crossing subalpine streams in Yosemite National Park in the Sierra Nevada (California, USA) in early and late season and over 2 years. There were both longer-term below-above differences, as well as differences that became apparent in late season, both of which were indicative of below-ford effects. Below fords there was evidence, either as main effects or interactions, of higher silt, sand, and gravel cover; a thicker periphyton layer; a greater Hilsenhoff biotic index; a higher proportion of tolerant taxa; higher chironomid midge and total densities; and greater species richness, largely a function of chironomid richness. There was also a lower expected number of species, a smaller proportion of sensitive taxa and predators, and lower densities of some sensitive Ephemeroptera (mayflies) and Plecoptera (stoneflies) below fords. Both hikers and stock may contribute to the apparent effects, but management interventions targeting stock may be particularly achievable. Among other approaches, simply halting stock strings briefly before reaching fords should reduce the volume of urine and feces directly entering streams, and handlers can expedite crossings if watering is not necessary.

RESUMEN.—Los senderos naturales utilizados por mulas, caballos y excursionistas para cruzar arroyos son perturbaciones localizadas que pueden afectar el hábitat río abajo inmediatamente, pero la posible influencia de los vados en arroyos ha sido objeto de escasa investigación, particularmente en lo que se refiere a posibles efectos sobre la fauna. Nuestra hipótesis nula general fue la ausencia de diferencias, entre la superficie y el interior, de grupos de macro-invertebrados bentónicos o en las características del hábitat en esos vados. Además, intentamos determinar si (1) cualquiera de dichas diferencias estuvieron presentes antes del uso anual, lo cual sugeriría efectos a largo plazo, y/o (2) si las diferencias estaban presentes al final de la temporada, tras su uso anual. Examinamos los macro-invertebrados y el hábitat inmediatamente por debajo y por encima de 2 vados que cruzan arroyos subalpinos en el Parque Nacional de Yosemite, en Sierra Nevada, (California, EE.UU.) en temporada temprana y tardía durante casi 2 años. Encontramos diferencias a largo plazo tanto por debajo como por encima, así como diferencias que se hacen evidentes al final de la temporada, las cuales son indicadores de un cierto nivel de efectos bajo los vados. Bajo los vados había evidencia, tanto en efectos directos como interacciones, de: mayor cantidad de obstrucciones de sedimentos, arena y grava; una capa más gruesa de perifiton; un índice biótico Hilsenhoff más elevado; una mayor proporción de taxa tolerantes; más quironómidos y densidades totales y una mayor riqueza de especies, esto último debido en gran medida a la función de la riqueza de quironómidos. También encontramos un número más reducido de especies de lo esperado, menor proporción de taxa sensibles y depredadores, y densidades más bajas de algunos Ephemeropteras sensibles y Plecoptera bajo los vados. Tanto los excursionistas como el ganado podrían contribuir a los efectos aparentes, pero la aplicación de acciones de manejo referentes al ganado puede ser un objetivo particularmente alcanzable. Entre otros enfoques, el hecho de contener, por medio de las ataduras del ganado brevemente antes de alcanzar las veredas, reduciría el volumen de orina y heces que entran directamente en los arroyos, y los responsables podrían agilizar los cruces si no fuera necesario beber agua.

The balancing of stream conservation with human and livestock access is an almost universal management concern (Mathooko 2001, Newsome et al. 2004, McIver and McInnis 2007). Most related work has focused on disturbance distributed along one or more stream

reaches (e.g., Braccia and Voshell 2007, Herbst et al. 2012). However, stream crossings on formal trails used by hikers and stock are localized disturbances focused at fords and habitat immediately downstream (Miller et al. 2010). Sedimentation can be higher at or below

¹White Mountain Research Center, Institute of the Environment and Sustainability, University of California Los Angeles, Bishop, CA 93514.

²Yosemite National Park, El Portal, CA 95318.

³E-mail: jholmquist@ucla.edu

fords relative to above-ford habitat (Fritz et al. 1999, but see Miller et al. 2010) which may, in combination with input of urine and feces (Miller et al. 2010), affect aquatic fauna (Kidd et al. 2014). Investigation of effects of fords on fauna has been limited (Kidd et al. 2014); Fritz et al. (1999) found that effects of bison crossings on benthic invertebrates were minor and concentrated in the area directly traversed by the animals, but effects of bison fords likely differ from those of the more frequent crossings made by domestic livestock and hikers at trail crossings. Mountain streams may be particularly sensitive to disturbance, especially if late-season flows are further lowered by drought or water withdrawals (Holmquist and Waddle 2013, Waddle and Holmquist 2013, see also Mathooko 2001).

Hiking and transport by horses and mules are the primary modes of travel along trails in fragile wilderness areas, and the consequences of such use is an important issue for managers (Olive and Marion 2009, Pickering et al. 2010). Strings of equine stock (pack stock) used for day tours and supplying remote locations, particularly in the western United States (McClaran 1989), travel along trails, and stock often urinate and defecate directly into streams while the pack strings are stopped mid-stream for watering at trail fords (Derlet and Carlson 2006). Horses and mules are heavy animals and are further laden with people and supplies. Their steel-shoed hooves have a high mass per unit substrate contact area (Newsome et al. 2004). Resuspension of fines and particulate organics is thus a possible result of stream fording. Equines are known to disrupt soil integrity on trails to a much greater extent than hikers (Wilson and Seney 1994, Deluca et al. 1998), thus increasing input of nutrients and sediments to streams via sloped trail approaches to fords (Olive and Marion 2009, Kidd et al. 2014). Although hikers create fewer effects on a per-individual basis, there are more hikers than stock along trails (Törn et al. 2009). Humans and equines (Cole 1995, Cole et al. 2004, Holmquist et al. 2014, Ostojka et al. 2014) have generally, though not exclusively, negative effects on wetland vegetation and fauna. Similarly, there may be negative effects on stream macrofauna immediately downstream of fords, but it is also possible that limited increases in particulate organics, periphyton, and habitat

heterogeneity could enhance diversity in these oligotrophic streams without negatively affecting sensitive taxa (Braccia and Voshell 2007).

Our overall null hypothesis was that there would be no below-above ford differences for benthic macroinvertebrate assemblages and habitat characteristics. We further sought to determine if there were interannual carryover effects that were present immediately below fords during early season (i.e., before new stock use or significant hiker use) in a given summer. Lastly, we wished to compare any such differences apparent during early season with conditions during late summer, after the majority of seasonal ford use. Such late-season sampling would capture both short-term annual effects as well as any interannual effects that might only become apparent later in the summer.

METHODS

Study Area, Design, and Sites

The trails of the Sierra Nevada of California have been traveled by foot, horse, and mule for well over a century, particularly since the 1940s (McClaran 1989), so there is potential for both current and legacy effects of fording disturbance. Tuolumne Meadows, in Yosemite National Park, is a primary staging area for stock and hiker use throughout the short sub-alpine summer.

This study focused on habitat immediately below and above fords (Below, Above) using above-ford reaches as reference habitat (Stoddard et al. 2006). We sampled in early summer ("Early"; <1 week before stock use began and before most hiker use; mean day of sampling: 10 June, SE 5 d) and again in late summer ("Late"; 11 August, SE 14 d), in 2 streams (Delaney and Ireland Creeks), and during 2 summers (2012, 2013); thus the design was a $2 \times 2 \times 2 \times 2$ balanced factorial design. The elements of greatest interest were (1) potential Treatment main effects across both early and late season, (2) Treatment \times Season interactions that might indicate increased below-above differences after most annual use, as well as (3) Treatment \times Stream interactions. We used stratified-random selection of sample locations from cobble-dominated riffle habitat that was no more than 80 m below or above a ford. There were 3 randomly selected sampling locations for each combination of factor levels,

thus a total of 48, and 3 new locations were selected below and above each ford on each visit (i.e., both early and late season in each of 2 years). The fords represent <4 m of stream length, so “under-foot” effects are spatially limited (Fritz et al. 1999), and we thus examined potential effects immediately downstream.

Delaney and Ireland Creeks are second-order, low-gradient (<0.2%), subalpine streams dominated by riffles and separated by 7 km (Delaney Creek ford: 37°53'06"N, 119°22'39"W, 2620 m; Ireland Creek ford: 37°49'32"N, 119°16'43"W, 2717 m). The use of only 2 streams is a limitation of this study; these streams were the only 2 in the funding-targeted study area with a combination of substantial stock usage, adequate wetted width, annual persistence, presence of riffles, and similar habitat below and above fords. The history of usage of these crossings is a strength of the study, which approximated a long-term experiment via sampling below and above the long-used fords. Both streams are bordered by lodgepole pine (*Pinus contorta* Douglas ex Loudon) forest and wet and dry meadow plant assemblages (Moore et al. 2013). Sierran subalpine streams have high spring flows and low discharge later in the summer (Waddle and Holmquist 2013). Mid-season discharges were similar for the 2 years at each stream: $0.035 \text{ m}^3 \cdot \text{s}^{-1}$ for Delaney (National Park Service [NPS] data) and $0.040 \text{ m}^3 \cdot \text{s}^{-1}$ for Ireland (personal observation). Submerged vascular plants were essentially absent from the streams. There were ~4600 Delaney crossings by individual mules or horses in 2012 and 4877 in 2013, as well as ~16,000 hiker crossings in both years (unpublished NPS data from permits and from images recorded with Reconyx PC800 motion-sensitive cameras). Ireland had ~400 stock and ~8000 hiker crossings in both 2012 and 2013, although stock traffic was greater (~1000 stock crossings) at this ford as recently as 2010. There were several pack string crossings per day at Delaney ($\bar{x} = 8.4$, SE 0.6, 2013 NPS data) and several per week at Ireland, whereas there were several hiker crossings per hour at both streams. Number of animals per stock crossing ranged from 1 to 15 ($\bar{x} = 6.5$, SE 0.10, 2013 NPS data for Delaney).

Sampling

We sampled macroinvertebrates with a standard 0.3×0.3 -m Surber sampler (Hauer and

Resh 2007) and recorded data on habitat characteristics that were likely to influence fauna; periphyton and coarse particulate organic matter (CPOM), for instance, provide both habitat and food resources for aquatic invertebrates (Allan and Castillo 2007). Prior to disturbing the substrate within the sampler, we determined depth (4 equidistant measurements) and percent cover by substrate particle size (modified Wentworth scale; Appendix), and we exposed larger particles in order to measure percent embeddedness, all within the area defined by the sampler. After completing each Surber sample, we measured velocity at 0.6 depth (General Oceanics meter, Miami, FL) and temperature and made a rapid periphyton assessment (see also Stevenson and Rollins 2007). Presence or absence of periphyton cover and thickness of the periphyton layer were recorded at 5 equidistant points along a transect running across the wetted width of the stream and located 0.25 m upstream of each Surber sample location (3 transects below and above each ford on each visit). Instead of subsampling, we sorted all fauna from each sample and identified each organism either to genus and species or, more frequently, genus and morphospecies. We separated all CPOM from each Surber sample into small (<1 cm²) and large (>1 cm²) categories. Each component was dried at 80 °C for 24 h and weighed.

The below- and above-ford physical environments were similar, as indicated by measures that were unlikely to be affected by crossings (Appendix). Gravel (2–16 mm), sand (0.1–2 mm), and silt (<0.1 mm) had the potential to be affected by crossings and are reported in the results.

Analysis

Analyses were via $2 \times 2 \times 2 \times 2$ general linear models that included Treatment, Season, Stream, and Year main effects, as well as all 6 two-way interactions (SYSTAT 2007). Habitat response variables included percent silt, sand, gravel, and embeddedness; small and large CPOM mass; and periphyton cover and thickness. Faunal metrics included total and population densities, species and family richness, percent dominance by the most abundant species in each sample, proportional composition by functional feeding groups, percent Ephemeroptera-Plecoptera-Trichoptera (%EPT),

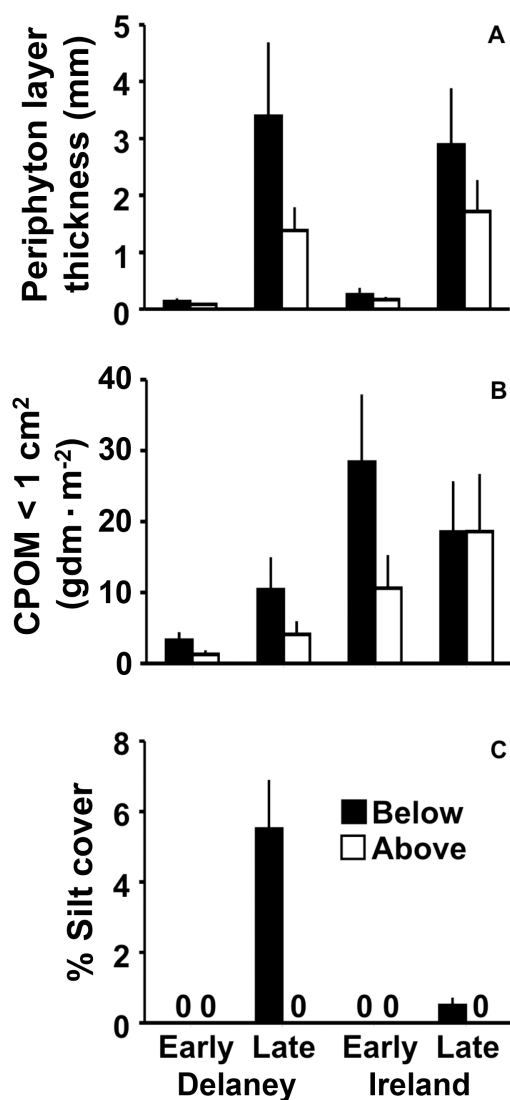


Fig. 1. Means (SE) for habitat response variables below and above 2 stream fords (Delaney, Ireland) during early and late season (years averaged): (A) Periphyton thickness on substrata; significant contrasts from general linear models: Treatment, Season (see also Table 1). (B) Gram dry mass per square meter ($\text{gdm} \cdot \text{m}^{-2}$) of coarse particulate organic matter (CPOM) smaller than 1 cm^2 ; significant contrasts: Treatment, Stream. (C) Percent cover by silt; significant contrasts: Treatment \times Season, Treatment \times Stream.

and expected number of taxa ($E(S)$), which adjusts richness as a function of abundance using rarefaction (Magurran 2004). We used the Hilsenhoff biotic index (HBI; Hilsenhoff 1987) to assess the relative importance of “tolerant” and “sensitive” taxa in the assemblage (i.e.,

those that can and cannot live, respectively, in degraded habitats). The Hilsenhoff biotic index (HBI) is $\sum(n_i a_i)/N$, where n_i = number of individuals in the i^{th} taxon, a_i = tolerance value (1–10) assigned to that taxon, and N = total number of individuals in the sample. We used the Southwest Association of Freshwater Invertebrate Taxonomists (2010) guide as our primary source of tolerance values and functional feeding group classification. We also evaluated the proportional abundance of sensitive taxa (tolerance 0–2) and tolerant taxa (tolerance 7–10; see also Herbst et al. 2012). Proportional variables were square-root transformed $[(y)^{0.5} + (y + 1)^{0.5}]$, and other variables were log transformed $[\log(y + 1)]$, although a small number of variables met the assumption of normality of residuals (Kolmogorov–Smirnov test) in an untransformed state and were therefore not modified. We estimated power *a priori* with G*Power (Erdfeilder et al. 1996). Because of the potential anthropogenic effects, we determined the alpha level necessary to allow equivalent beta error and adequate power (Mapstone 1995, Erdfeilder et al. 1996) (i.e., $\alpha = \beta = 0.064$, with an associated power of 0.936). We present both $\alpha = 0.05$ and $\alpha = 0.064$ as significance thresholds to offer additional perspective (additional discussion in Holmquist et al. 2010). Rank-abundance plots were constructed as a function of Treatment and Season to complement the general linear models.

RESULTS

Below-above ford differences were apparent for most habitat variables. There were Treatment main effects for small CPOM ($< 1 \text{ cm}^2$; $P = 0.0086$), periphyton layer thickness ($P = 0.040$), and percent gravel cover ($P = 0.017$); all were greater below fords (Fig. 1, Table 1). There were no Treatment \times Season interactions for these variables. There were Treatment \times Season interactions for both percent silt and sand cover, and both indicated greater below-above sediment cover differences (greater silt and sand below fords) in late season than were observed in early season (Fig. 1, Table 1). Indeed, we only detected silt in late season and below fords, and amounts were 10-fold greater in Delaney than in Ireland. There was also an accompanying Treatment main effect for silt, but it is generally

TABLE 1. Means (standard error in parentheses) for habitat metrics and results of general linear models (GLM); means by year are not included. T = Treatment (below ford, above ford); Se = Season (early, late); Y = Year (2012, 2013); St = Stream (Ireland, Delaney); CPOM = coarse particulate organic matter. Treatment-related interactions are bolded.

		Early		Late		GLM results				
		Below	Above	Below	Above	T	Se	Y	St	Significant interactions
Silt cover (%)	Ireland	0 (0)	0 (0)	0.500 (0.22)	0 (0)	**	**		**	T × Se**, T × St**, Se × St**
	Delaney	0 (0)	0 (0)	5.50 (1.4)	0 (0)					
Sand cover (%)	Ireland	2.83 (1.6)	5.83 (1.5)	3.00 (0.77)	0.833 (0.83)					T × Se**, Se × St**
	Delaney	0.833 (0.83)	1.00 (0.82)	5.67 (1.1)	2.33 (0.95)					
Gravel cover (%)	Ireland	8.00 (1.0)	9.17 (1.5)	9.67 (2.2)	6.67 (2.1)	**				Se × Y**, Se × St*
	Delaney	8.67 (2.6)	4.00 (0.82)	16.3 (4.9)	6.83 (1.1)					
Embeddedness (%)	Ireland	16.7 (1.7)	21.7 (1.7)	20.0 (2.2)	23.3 (2.8)					Se × Y**, Y × St*
	Delaney	24.2 (6.4)	28.3 (7.8)	25.0 (8.5)	14.2 (1.5)					
CPOM < 1 cm ² (gdm · m ⁻²)	Ireland	28.4 (9.5)	10.6 (4.7)	18.5 (7.2)	18.6 (8.1)	**			**	
	Delaney	3.31 (1.1)	1.29 (0.57)	10.4 (4.6)	4.09 (1.9)					
CPOM > 1 cm ² (gdm · m ⁻²)	Ireland	19.2 (17)	4.74 (4.7)	9.51 (5.6)	10.9 (10)					
	Delaney	1.03 (1.0)	0 (0)	13.9 (9.1)	10.9 (11)					
Periphyton cover (%)	Ireland	46.7 (16)	53.3 (12)	96.7 (3.3)	100 (0)		**	**		T × Y**, Se × Y**, Se × St*
	Delaney	36.7 (15)	33.3 (8.4)	100 (0)	100 (0)					
Periphyton thickness (mm)	Ireland	0.250 (0.13)	0.167 (0.05)	2.89 (1.0)	1.72 (0.55)	**	**	**		
	Delaney	0.133 (0.06)	0.083 (0.02)	3.39 (1.3)	1.38 (0.41)					

* $P < 0.064$ (see methods).

** $P < 0.05$.

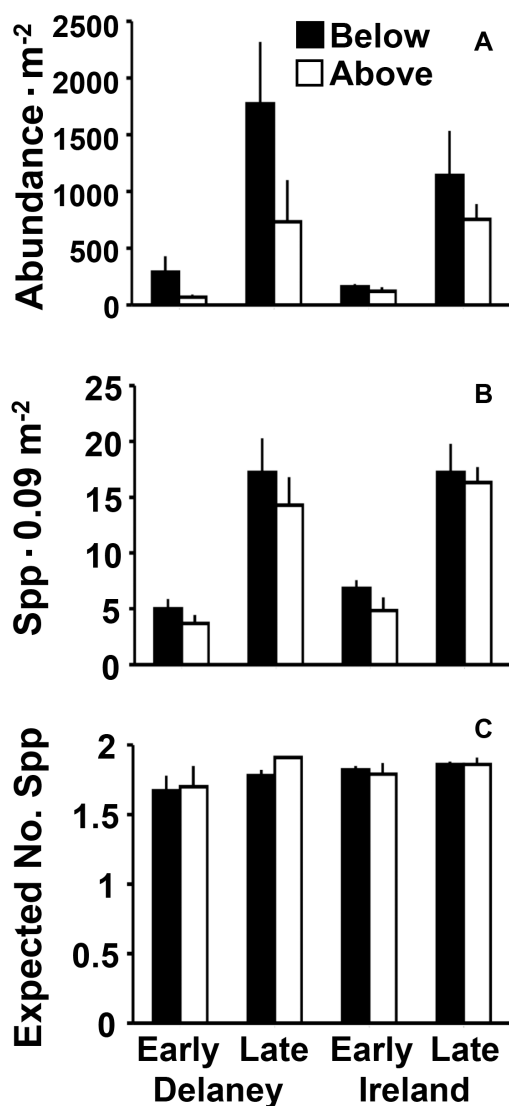


Fig. 2. Means (SE) for faunal assemblage metrics below and above 2 stream fords (Delaney, Ireland) during early and late season: (A) Total abundance · m⁻²; significant contrasts from general linear models: Treatment, Season (see also Table 2). (B) Species richness · 0.09 m⁻²; significant contrasts: Treatment, Season. (C) Expected number of species; significant contrasts: Season, Treatment × Stream.

not advisable to assess main effects in the presence of related interactions (Sokal and Rohlf 2012). Periphyton cover was greater below fords in 2012 but not 2013 (Treatment × Year). There were main effect differences for Season (more silt and periphyton cover and thickness in late season), as well as some

Year and Stream effects and related interactions (Table 1).

Below-above ford differences were also present for most faunal assemblage metrics. Mean abundance and species richness were greater below fords across both early and late season ($P = 0.0048$ and 0.028 , respectively); values were higher in late season (Fig. 2, Table 2). Conversely, $E(S)$ was lower below-ford than above (Delaney only). These trends for individual metrics are underscored by rank-abundance plots (Fig. 3). Higher abundance and richness were apparent below fords, but there was also high dominance below fords. The trends of higher abundance and richness during late season were clear in the rank-abundance plots as well. Percent tolerant fauna and HBI were significantly higher below fords in late season (Treatment × Season, $P = 0.047$ and 0.017 , respectively; Table 2, Fig. 4).

The highest densities across all study factors at the order level were observed for Diptera ($\bar{x} = 438$ m⁻², SE 101), Ephemeroptera ($\bar{x} = 83.1$ m⁻², SE 13), Plecoptera ($\bar{x} = 58.2$ m⁻², SE 11), Trichoptera ($\bar{x} = 37.2$ m⁻², SE 14), and tubificid oligochaetes ($\bar{x} = 12.5$ m⁻², SE 8.1; Table 3). The 2 most abundant families were dipterans and included a number of the most abundant genera: chironomid midges (*Microspectra*, *Eukiefferiella*, *Cricotopus*, *Orthocladus*) and simuliid black flies (*Prosimulium*). Other common families and genera included heptageniid (*Cinygmula*), baetid (*Baetis*), and ameletid mayflies, perlodid (*Rickera/Kogotus*) and nemourid stoneflies, hydroptilid (*Agraylea*) and limnephilid caddisflies, and naidid oligochaetes. Diptera and Plecoptera had the highest richness of families and genera.

There were a number of trends of either higher or lower population densities below fords; tolerant taxa generally had higher abundances below fords. The speciose, abundant, and tolerant chironomid midges were more common below fords than above fords during late season (Treatment × Season, $P = 0.029$), contributing to the trend of higher richness and abundance below fords (Fig. 4, Table 3). Two of the most abundant chironomid taxa also had Treatment-related trends: *Eukiefferiella* sp. 1 was similarly more abundant below fords than above fords in late season, and *Cricotopus* sp. was more abundant below fords at Delaney Creek only (Treatment × Stream). Baetidae (intermediate tolerance) were

TABLE 2. Means (standard error in parentheses) for faunal assemblage metrics and results of general linear models (GLM); means by year are not included. T = Treatment (below ford, above ford); Se = Season (early, late); Y = Year (2012, 2013); St = Stream (Ireland, Delaney); %EPT = percent of total abundance represented by Ephemeroptera, Plecoptera, and Trichoptera; HBI = Hilsenhoff biotic index. Treatment-related interactions are bolded.

		Early		Late		GLM results				
		Below	Above	Below	Above	T	Se	Y	St	Significant interactions
Total individuals · m ⁻²	Ireland	160 (26)	122 (37)	1143 (395)	754 (138)	**	**			Se × Y**
	Delaney	292 (140)	69.9 (21)	1774 (545)	735 (367)					
Species richness · 0.09 m ⁻²	Ireland	6.83 (0.75)	4.83 (1.2)	17.2 (2.6)	16.3 (1.4)	**	**			Se × Y**
	Delaney	5.00 (0.86)	3.67 (0.80)	17.2 (3.1)	14.3 (2.5)					
% Species dominance	Ireland	39.8 (4.7)	47.0 (6.6)	31.7 (3.8)	25.6 (6.8)		**			
	Delaney	59.4 (8.1)	50.1 (12)	36.7 (5.9)	21.0 (1.7)					
Expected no. of species	Ireland	1.82 (0.03)	1.79 (0.08)	1.86 (0.02)	1.86 (0.05)		**			T × St*
	Delaney	1.67 (0.11)	1.70 (0.15)	1.78 (0.04)	1.91 (0.01)					
% EPT	Ireland	45.4 (15)	30.4 (15)	41.5 (8.9)	47.9 (7.7)					St × Y**
	Delaney	37.9 (16)	46.2 (16)	17.0 (4.3)	41.3 (4.9)					
HBI	Ireland	3.87 (0.27)	4.93 (0.38)	5.17 (0.35)	4.84 (0.35)		**			T × Se** , T × St* , Se × St**
	Delaney	2.72 (0.28)	2.69 (0.62)	6.44 (0.32)	5.08 (0.48)					
% Tolerant individuals	Ireland	5.58 (4.3)	5.60 (4.7)	57.1 (4.6)	47.2 (6.2)		**			T × Se**
	Delaney	1.44 (0.93)	5.83 (4.2)	66.0 (9.1)	47.9 (5.8)					
% Sensitive individuals	Ireland	17.3 (4.0)	7.58 (4.0)	30.3 (6.5)	33.6 (6.9)				*	T × St** , Se × St** , St × Y**
	Delaney	34.6 (11)	44.5 (12)	11.5 (3.3)	31.1 (7.4)					

* $P < 0.064$ (see Methods).

** $P < 0.05$.

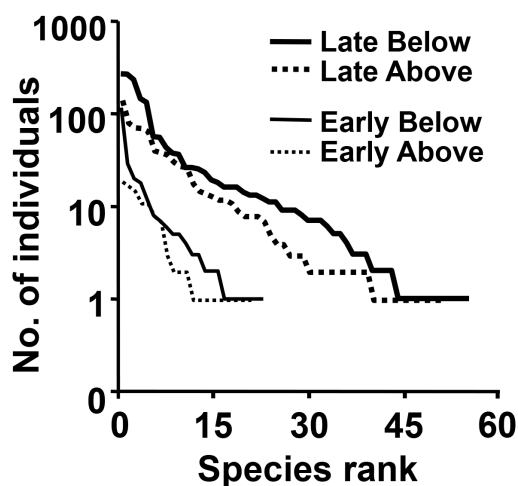


Fig. 3. Overall rank abundance plot by Treatment and Season using sample totals.

more abundant below fords than above at Delaney (Table 3). The comparatively sensitive heptageniid mayflies and nemourid stoneflies were both more abundant below fords than above fords during early season, but the inverse held during late season (Treatment \times Season). Hydroptilid microcaddisflies were less abundant below fords at Delaney. Nine of the top 10 families and 8 of the 10 most abundant taxa showed significant seasonal differences. Eight of these 9 families were more abundant overall in late season, as were all 8 of the species-level taxa that had a Season main effect.

Below-above ford differences were present among functional feeding groups. Collector-gatherers in combination with omnivores represented $\sim 90\%$ of the below-ford Delaney assemblage in late season (Treatment \times Season, $P = 0.0045$; Fig. 4, Table 4). Collector-gatherers were dominated by *Baetis* and the chironomids *Microspectra*, *Cricotopus*, and *Orthocladius*, as were omnivores by the chironomid *Eukiefferiella*. Percentage of predators, of which *Isoperla* and *Rickera/Kogotus* stoneflies were a dominant component, was higher below fords in early season, but was lower below the Delaney ford in late season (Table 4). Collector-filterers, mostly simuliid black flies, showed a strong seasonal effect (higher percentage in early season) but no treatment effect. Piercer-herbivores were, conversely, completely absent in early season; Season main effects were present for all groups except shredders.

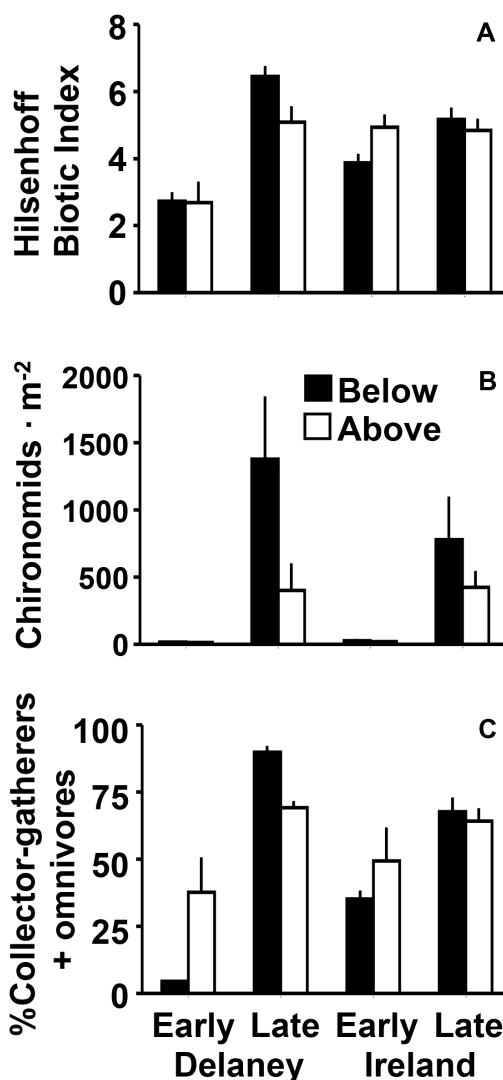


Fig. 4. Means (SE) for faunal metrics below and above 2 stream fords (Delaney, Ireland) during early and late season: (A) Hilsenhoff biotic index; higher numbers indicate greater tolerance to degraded conditions; significant contrasts from general linear models: Treatment \times Season, Treatment \times Stream (see also Table 2). (B) Chironomid midges $\cdot m^{-2}$; significant contrasts: Treatment \times Season (see also Table 3); (C) Percent collector-gatherers + omnivores; significant contrasts: Stream, Treatment \times Season (see also Table 4).

DISCUSSION

This study examined only 2 fords, thus requiring caution in interpretation, but results suggest some effects immediately downstream of crossings. Below-above differences that were

TABLE 3. Mean densities (individuals · m⁻²; standard error in parentheses) for orders and the 10 most abundant families and taxa, and results of general linear models (GLM); means by year not included. T = Treatment (below ford, above ford), Se = Season (early, late), Y = Year (2012, 2013), St = Stream (Ireland, Delaney). Treatment-related interactions are bolded.

		Early		Late		GLM results				
		Below	Above	Below	Above	T	Se	Y	St	Significant interactions
Ephemeroptera	Ireland	73.5 (33)	50.2 (28)	93.2 (34)	136 (28)					
	Delaney	37.6 (18)	12.5 (4.3)	168 (54)	93.2 (31)					
Ameletidae	Ireland	5.38 (5.4)	1.79 (1.8)	21.5 (9.2)	26.9 (9.1)		**			
	Delaney	1.79 (1.8)	1.79 (1.8)	43.0 (13)	43.0 (13)					
Baetidae	Ireland	14.3 (9.1)	19.7 (12)	19.7 (8.1)	26.9 (8.2)		**	**		T × St** , Se × St** , Se × Y**
	Delaney	1.79 (1.8)	0 (0)	95.0 (40)	25.1 (11)					
<i>Baetis</i> sp. 1	Ireland	0 (0)	0 (0)	7.17 (3.6)	25.1 (7.2)		**	**		T × St** , Se × Y**
	Delaney	0 (0)	0 (0)	93.2 (41)	25.1 (11)					
Heptageniidae	Ireland	50.2 (22)	26.9 (17)	34.0 (14)	60.9 (21)					T × Se** , Se × Y** , St × Y**
	Delaney	34.0 (16)	10.8 (4.8)	23.3 (18)	17.9 (8.6)					
<i>Cinygmula</i> sp.	Ireland	35.8 (17)	25.1 (16)	34.0 (14)	53.8 (22)				**	Se × St** , Se × Y**
	Delaney	16.1 (6.0)	8.96 (4.3)	0 (0)	1.79 (1.8)					
Plecoptera	Ireland	7.17 (3.6)	5.38 (3.7)	159 (44)	136 (21)					
	Delaney	12.5 (3.3)	3.58 (2.3)	64.5 (31)	77.0 (32)					
Nemouridae	Ireland	1.79 (1.8)	0 (0)	12.5 (8.1)	35.8 (17)		**			T × Se** , St × Y**
	Delaney	8.96 (1.8)	1.79 (1.8)	35.8 (28)	43.0 (23)					
Perlodidae	Ireland	0 (0)	0 (0)	136 (42)	100 (23)		**		**	Se × St**
	Delaney	0 (0)	0 (0)	8.96 (7.0)	3.58 (3.6)					
<i>Rickera/Kogotus</i>	Ireland	0 (0)	0 (0)	77.0 (22)	66.3 (17)		**	**	**	Se × St** , Se × Y** , St × Y**
	Delaney	0 (0)	0 (0)	0 (0)	0 (0)					
Trichoptera	Ireland	5.38 (3.7)	3.58 (3.6)	84.2 (27)	52.0 (39)					
	Delaney	0 (0)	1.79 (1.8)	34.0 (24)	116 (91)					
Hydroptilidae	Ireland	0 (0)	0 (0)	25.1 (13)	25.1 (25)		**			T × St** , St × Y**
	Delaney	0 (0)	0 (0)	3.58 (3.6)	108 (89)					
<i>Agraylea</i> sp.	Ireland	0 (0)	0 (0)	25.1 (13)	25.1 (25)		**			T × St** , St × Y**
	Delaney	0 (0)	0 (0)	3.58 (3.6)	108 (89)					
Limnephilidae	Ireland	0 (0)	1.79 (1.8)	52.0 (20)	25.1 (15)		**		**	Se × St**
	Delaney	0 (0)	0 (0)	8.96 (5.8)	1.79 (1.8)					
Coleoptera	Ireland	0 (0)	0 (0)	1.79 (1.8)	0 (0)					
	Delaney	0 (0)	1.79 (1.8)	1.79 (1.8)	1.79 (1.8)					
Diptera	Ireland	69.9 (16)	59.1 (20)	781 (325)	428 (125)					
	Delaney	242 (134)	50.2 (21)	1437 (507)	441 (220)					
Chironomidae	Ireland	26.9 (12)	19.7 (9.4)	778 (322)	423 (122)	**	**			T × Se**
	Delaney	16.1 (7.7)	14.3 (4.5)	1376 (469)	401 (202)					

**P* < 0.064 (see Methods).

***P* < 0.05.

TABLE 3. Continued.

		Early		Late		GLM results				
		Below	Above	Below	Above	T	Se	Y	St	Significant interactions
<i>Microspectra</i> sp. 1	Ireland	7.17 (7.2)	12.5 (11)	382 (190)	202 (101)		**		**	Se × Y**
	Delaney	1.79 (1.8)	1.79 (1.8)	91.4 (49)	55.5 (22)					
<i>Eukiefferiella</i> sp. 1	Ireland	0 (0)	0 (0)	35.8 (17)	7.17 (2.3)		**	**	**	T × Se**, Se × St**, Se × Y**
	Delaney	0 (0)	1.79 (1.8)	441 (188)	111 (72)					
<i>Eukiefferiella</i> sp. 2	Ireland	1.79 (1.8)	0 (0)	69.9 (50)	60.9 (21)		**			
	Delaney	3.58 (3.6)	0 (0)	344 (121)	86.0 (46)					
<i>Cricotopus</i> sp.	Ireland	0 (0)	0 (0)	93.2 (38)	84.2 (24)		**	**		T × St*, Se × Y**
	Delaney	0 (0)	0 (0)	165 (64)	46.6 (32)					
<i>Orthocladus</i> sp.	Ireland	8.96 (3.3)	3.58 (2.3)	3.58 (3.6)	26.9 (15)		**			Se × St**, Se × Y**
	Delaney	5.38 (5.4)	1.79 (1.8)	231 (206)	21.5 (12)					
Simuliidae	Ireland	32.3 (11)	37.6 (20)	1.79 (1.8)	0 (0)		**			Se × Y**
	Delaney	213 (124)	17.9 (11)	48.4 (44)	32.3 (20)					
<i>Prosimulium</i> sp.	Ireland	23.3 (7.0)	8.96 (3.3)	1.79 (1.8)	0 (0)	**				Se × Y**, St × Y**
	Delaney	186 (125)	17.9 (11)	7.17 (5.3)	0 (0)					
Trombidiformes (Acari)	Ireland	0 (0)	0 (0)	0 (0)	0 (0)					
	Delaney	0 (0)	0 (0)	1.79 (1.8)	1.79 (1.8)					
Veneroida (Bivalvia)	Ireland	0 (0)	0 (0)	0 (0)	0 (0)					
	Delaney	0 (0)	0 (0)	1.79 (1.8)	0 (0)					
Tubificida (Oligochaeta)	Ireland	3.58 (3.6)	1.79 (1.8)	23.3 (17)	0 (0)					
	Delaney	0 (0)	0 (0)	64.5 (62)	5.38 (2.4)					
Naididae	Ireland	3.58 (3.6)	1.79 (1.8)	23.3 (17)	0 (0)		**			
	Delaney	0 (0)	0 (0)	64.5 (62)	5.38 (2.4)					

* $P < 0.064$ (see methods).** $P < 0.05$.

TABLE 4. Means (standard error in parentheses) for percentages of total abundance by functional feeding group and results of general linear models (GLM); means by year are not included. T = Treatment (below ford, above ford), Se = Season (early, late), Y = Year (2012, 2013), St = Stream (Ireland, Delaney). Treatment-related interactions are bolded.

		Early		Late		GLM results				
		Below	Above	Below	Above	T	Se	Y	St	Significant interactions
% Predators	Ireland	8.88 (4.1)	3.25 (2.1)	18.0 (2.2)	16.9 (2.0)		**		**	T × Se**, T × Y**
	Delaney	3.76 (3.3)	2.38 (2.4)	4.46 (1.1)	13.9 (3.7)					
% Collector-gatherers	Ireland	34.0 (5.8)	48.6 (13)	57.0 (5.8)	53.7 (5.1)	**	**		**	T × Se*, Se × St**
	Delaney	3.67 (2.2)	33.4 (15)	40.8 (8.4)	47.1 (5.1)					
% Omnivores	Ireland	1.19 (1.2)	0.794 (0.79)	10.5 (2.7)	10.4 (1.1)		**		**	Se × St**
	Delaney	0.855 (0.85)	4.17 (4.2)	49.0 (10)	22.1 (3.9)					
% Collector-gatherers plus omnivores	Ireland	35.2 (5.4)	49.4 (12.5)	67.6 (7.2)	64.1 (4.9)	*	**		*	T × Se**, Se × St**
	Delaney	4.52 (2.3)	37.6 (13)	89.8 (3.2)	69.2 (2.4)					
% Collector-filterers	Ireland	26.5 (10)	33.3 (14)	0.062 (0.06)	0 (0)		**			St × Y**
	Delaney	47.1 (15)	16.0 (9.6)	1.52 (1.1)	2.22 (1.6)					
% Scrapers	Ireland	25.5 (11)	13.3 (7.5)	4.22 (2.2)	8.51 (2.5)		**			Se × St**, Se × Y**, St × Y**
	Delaney	32.4 (10)	36.3 (11)	1.19 (1.0)	2.10 (0.70)					
% Shredders	Ireland	3.90 (1.8)	0.794 (0.79)	4.70 (3.5)	7.48 (3.2)					T × Y*, Se × St**
	Delaney	12.2 (5.2)	7.74 (4.2)	2.83 (1.6)	5.59 (2.4)					
% Piercer-herbivores	Ireland	0 (0)	0 (0)	5.43 (2.7)	3.07 (3.1)		**			T × St**, T × Y*, St × Y**
	Delaney	0 (0)	0 (0)	0.240 (0.24)	6.98 (3.8)					

* $P < 0.064$ (see methods).

** $P < 0.05$.

already present before most annual use may indicate longer-lasting effects (see also Holmquist et al. 2010, 2013) that persist through winter and snowmelt flooding. Other below-above differences appeared only in late season. Summer use, perhaps compounded by low flows (Fritz et al. 1999), may have affected these measures, but lack of trail activity and periphyton dieback during winter, along with spring flushing flows, may have facilitated annual recovery (Fritz et al. 1999, Braccia and Voshell 2007, see also Gard 2002) such that early season differences were not present. Some late-season responses might also be indicative of longer-term impacts that only became detectable with population increases during late summer (see also Holmquist et al. 2013). The Delaney-only effects are consistent with the stream's more frequent crossings and shorter interdisturbance interval, although other unknown, interstream differences could have been influences as well.

Both stock and hikers probably contributed to the apparent habitat differences that were observed. Trail soil is loosened both by hikers and stock and transported downslope during rainfall along trail approaches to fords (Newsome et al. 2004, see also Kidd et al. 2014). Equine use promotes sediment yields that are 2–8 times greater than those produced by hikers (Kidd et al. 2014), but there were more hikers than stock, and total sediment yield from hikers could have equaled or surpassed yield from stock. Stock may have had a stronger influence on other apparent effects. We observed silt, sand, gravel, and small CPOM (see also Mathooko 2001) being directly mobilized at fords during stock crossings. In contrast, hiker mobilization of materials at fords was essentially absent because hikers were observed to always use logs or rocks to cross the streams. We observed deposits of hay fragments in pools below the Delaney ford that were identical in size and shape to those in local equine feces, suggesting direct feces input by stock and/or transport of pulverized feces from the trail approaches. Direct feces and urine input from hikers was likely low to absent, particularly because these sites are close enough to trailheads that there is little or no camping at these locations. Older stock fecal material settled at fords may be resuspended by subsequent crossings (Miller et al. 2010) and transported below fords. The

trends of increased sediment, CPOM, and periphyton immediately downstream of fords align with studies of more spatially extensive use of streams by livestock (Braccia and Voshell 2007, Herbst et al. 2012). Our observed below-above differences for fines were greater than Fritz et al. (1999) found at bison fords.

Below-above faunal differences may have been indirectly mediated by possible changes to the physical environment and trophic resources (Braccia and Voshell 2007, Herbst et al. 2012). Increases in fine sediment reduce interstitial volume and reduce habitat quality on upper substrate surfaces, leading to decreases in sensitive taxa and increases in abundance for oligochaetes and many chironomid taxa (Braccia and Voshell 2007, Kidd et al. 2014). Increased periphyton is often accompanied by increases in total faunal abundance, driven by increases in abundances of tolerant taxa (Tonkin et al. 2013). Faunal responses were similarly broadly consistent with responses to more extensive livestock use (Braccia and Voshell 2007, Herbst et al. 2012), and apparent faunal responses were also greater than those observed immediately below bison fords (Fritz et al. 1999). Below-above differences for fauna in our study tended to be greatest in late season, in concert with the greatest observed habitat differences.

We did not address how far downstream below-above differences may extend, as all of our sites were within 80 m of the fords. Manure can be carried 50 m downstream from the deposition point (Miller et al. 2010), and effects might be found further downstream.

Our results should be at least partially applicable to stock crossings that are not associated with formal fords where trails cross streams. Free-ranging domestic cattle focus crossings at specific points along streams, even when there is free access to an entire stream reach or segment (Clark 1998). Concentrated crossings and attendant effects may thus occur in other scenarios as well.

Bridges are physical interventions that prevent direct stream disturbance but may still allow drainage of sediment and feces into streams during rains (Newsome et al. 2004). Such structures are expensive and difficult to construct in remote wilderness areas. Minimization of trail slope angle near fords is less expensive and can reduce sedimentation from both hikers and stock (Marion and Leung

2004, Olive and Marion 2009, Kidd et al. 2014). Unlike free-ranging livestock, pack stock come with riders, and equine behavior may facilitate simple interventions that could reduce the effects attributable to stock. Equines can only urinate when stationary, and standing in water and urination by nearby animals are urination stimuli (pack stock handlers, personal communication). Briefly halting stock strings before reaching fords should reduce the volume of urine and feces directly entering streams (see also Billings 2005). Additionally, strings can be moved quickly across fords if watering is not needed. These approaches entail no expense and require only the cooperation of stock handlers.

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APPENDIX. Means (standard error in parentheses) for physical parameters above and below fords. Gravel, sand, and silt results are in Fig. 1 and Table 1.

Physical parameter	Below ford	Above ford
Distance from ford (m)	31.5 (13)	39.1 (14)
Wetted width (m)	4.6 (0.27)	4.4 (0.25)
Velocity (cm · s ⁻¹)	33.9 (4.3)	35.4 (4.7)
Water depth (cm)	12.7 (1.5)	14.1 (1.6)
Water temperature (°C)	10.6 (0.35)	11.5 (0.42)
pH	6.8 (0.07)	6.9 (0.05)
% Bedrock	1.3 (1.3)	0.0 (0.0)
% Boulder (>256 mm)	1.3 (1.3)	1.0 (0.85)
% Cobble (64–256 mm)	69.0 (3.7)	77.3 (2.8)
% Pebble (16–64 mm)	14.1 (1.8)	12.9 (2.0)