

ORIGINAL ARTICLE

Anthropogenic mining alters macroinvertebrate size spectra in streams

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Abstract

1. Food web properties can be used in bioassessment as indicators of ecosystem stress, although logistical constraints restrict their widespread use. Size spectra (body mass–abundance relationships) are easier to produce, still incorporate much of the variation in feeding interactions and indicate the strength of the energy transfer efficiency.
2. Here we examined the effect of acid mine drainage on the size spectra of stream macroinvertebrate communities in 25 New Zealand streams with a comparative survey. We predicted that the largest organisms would be most susceptible to acid mine drainage, leading to a reduction in their abundances and associated decrease in the range of body sizes present across the gradient, as well as a reduction in total community abundance.
3. The largest organisms were more sensitive to inputs of acid mine drainage and were absent at the most affected sites. Surprisingly, the smallest body sizes were also removed by acid mine drainage. This led to a reduction of up to two orders of magnitude in the range of body sizes present in mine impacted sites. Total community abundance decreased along the impact gradient.
4. The changes in size spectra were also associated with changes in the proportion of functional feeding groups, suggesting concomitant changes in food web structure. Specifically, communities became dominated by collector browsers and small bodied predators across the gradient. The simplification of the food web structure suggests that communities may be dominated by a few strong energy pathways, lowering their functionality and stability. However, the loss of large bodied predators also reduces top down pressure, probably increasing community stability. Further research is needed to elucidate the cumulative effects of these interacting processes.

KEYWORDS

abundance size spectra, bioassessment, body-size distribution, community response, ecological indicators, human impacts

1 | INTRODUCTION

The observation that the density of organisms is negatively related to their body size was noted nearly a century ago (Elton, 1927).

Since that time, this concept has proven empirically to be one of the most universal aspects of biological organisation (Petchey & Belgrano, 2010; White, Ernest, Kerkhoff, & Enquist, 2007), linking individual- and population-level traits with community structure

(O’Gorman et al., 2012), function (Dossena et al., 2012), energy transfer (Jennings & Blanchard, 2004; Trebilco, Baum, Salomon, & Dulvy, 2013) and stability (Sentis, Binzer, & Boukal, 2017; Tang, Pawar, & Allesina, 2014). Furthermore, size spectra relationship have strong theoretical grounding in the metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West, 2004). When all of the individuals from a given unit of area are measured, the relationship of their log density to their log body mass is generally negative, with a linear or slightly parabolic relationship (Martínez, Larrañaga, Miguélez, Yvon-Durocher, & Pozo, 2016; Sprules & Barth, 2015). The slope of this relationship is related to the efficiency of energy transfer from resources to consumers (e.g. from small, abundant individuals to rarer large individuals in predator–prey systems), while the intercept generally represents the overall community abundance (O’Gorman et al., 2012; Sprules & Barth, 2015). Therefore, the shape of the size spectra relationship at a site has important implications for food web structure and ecological functions. Changes in size spectra have been suggested as an important indicator of ecological health (Petchey & Belgrano, 2010; Reuman, Mulder, Raffaelli, & Cohen, 2008) and have been observed to respond to human impacts, including land use (Martínez et al., 2016), stream warming (e.g. climate change, O’Gorman et al., 2012), increased nutrients (Morin, Bourassa, & Cattaneo, 2001) and commercial exploitation (Jennings & Blanchard, 2004). Because size spectra are independent of taxa identity, they have potential utility as an assessment tool for novel stressors and impacts, particularly in systems that lack empirical data on taxon-specific sensitivities. In the face of contemporary challenges, including climate change, and the increasing presence of synthetic chemicals in the environment (Bernhardt, Rosi, & Gessner, 2017), understanding how size spectra respond to environmental impacts is a timely question for ecologists, and here we assess their use in acid mine drainage impacted streams.

Acid mine drainage (AMD) is a multi-factor stressor (Gray, 1997) affecting freshwater habitats globally (Hogsden & Harding, 2012a). Acid mine drainage is often associated with mining activities in geologic strata with high sulfur content and high levels of associated heavy metals, including Fe, Al, Zn, and Ni (Hogsden, Webster-Brown, & Harding, 2016). Excavated rock is exposed to air and water, resulting in sulfuric acid, which can significantly reduce the pH, and this increases the solubility of metal ions in the strata. Although receiving streams generally have higher pH and can neutralise the acidity in AMD, waters downstream of the source can remain very acidic ($\text{pH} < 3$) and have high levels of total dissolved metals (e.g. $>20 \text{ mg/L}$, Hogsden & Harding, 2012b). With the input of additional unimpacted tributaries, there is generally an increase in pH, which causes the solubility of the metals to decrease, resulting in metal precipitating onto the benthos causing the commonly observed *yellow boy* in AMD-impacted streams. AMD has been shown to strongly affect community composition (e.g. loss of sensitive species, Gangloff, Perkins, Blum, & Walker, 2015; Greig, Niyogi, Hogsden, Jellyman, & Harding, 2010; Underwood, Kruse, & Bowman, 2014; Winterbourn, 1998; reviewed in Hogsden & Harding, 2012b) and simplify food web structure (Hogsden & Harding, 2012a). However, to our knowledge,

no study on the distribution of individual body mass has been conducted in mining-impacted streams.

We assessed the impacts to size spectra in streams across an AMD gradient. We expected that the conditions of increasing AMD impact in streams would impact size spectra according to the following hypotheses: (1) The loss of individuals from environmental perturbations is rarely random, and the largest organisms in a system are generally more susceptible to local extinctions due to their increased energetic demands, larger home ranges, slower reproductive rates and lower densities (Brose et al., 2017; Brown et al., 2004; Woodward et al., 2012). Reduction in the density of the largest individuals should lead to steeper slopes of size spectra in response to the AMD gradient. (2) The intercept of size spectra represents the density of the average body size within the community and is dependent on total community abundance. Previous work has shown significant reductions in benthic community abundances in response to AMD. Therefore, we predict a reduction in the intercepts across the gradient. (3) Aquatic food webs are often size-structured, with larger individuals generally representing higher trophic levels. Additionally, because the largest taxa within a community generally occupy several body sizes and subsequent ontogenetic changes in both its predators and preys throughout its life history, these taxa are often the most well-connected (Brose et al., 2017). Thus, the range of body sizes present at a site has implications on food-web structure and trophic height. We expect that the magnitude of the reduction in the density of the largest sized individuals (hypothesis 1) will increase across the mining gradient and will result in the complete loss of the largest size classes at the most heavily impacted sites (e.g. reduced range of sizes present). Note that this differs from hypothesis 1 in that slopes are a proxy for transfer efficiency, while the range of body sizes present is a proxy for the presence of different trophic levels. If our hypotheses 1 and 2 are correct, this has strong implications in the structure and function of the food web present in these streams. As a coarse proxy for food web structure, we examined the proportion of individuals belonging to functional feeding groups (FFGs) across the AMD gradient. Different FFGs specialise on different food sources within the environment and represent different energy pathways within the community.

2 | METHODS

2.1 | Study site and stream characteristics

This study was conducted in the Buller–Grey region in the north-west of the South Island, New Zealand. The region has a long history of coalmining, and is part of the Westland Forest ecoregion, which has spatially consistent climatic conditions, geology and freshwater biota (Harding & Winterbourn, 1997; Harding, Winterbourn, & McDiffett, 1997). A total of 25 streams were sampled, 13 streams were sampled along an AMD gradient (which we refer to as *impacted* streams) based on known and relatively constant water chemistry (e.g. pH, conductivity, dissolved Al and Fe concentrations) over time (Greig et al., 2010; Hogsden & Harding, 2012a; Kitto, Gray, Greig,

Niyogi, & Harding, 2015; Winterbourn, McDiffett, Eppley, & Creek, 2000). In addition, we sampled 12 streams across a natural gradient of pH (~4–7) and low metal concentrations, to capture the range of natural variation. To our knowledge, these 12 streams are *unimpacted* by AMD inputs. All 25 streams were placed into a single gradient (see below) and analysed together. However, we occasionally discuss the differences between the AMD-impacted and unimpacted streams in order to place our results into context. No statistical analyses treated unimpacted and AMD-impacted streams as a categorical predictor. All streams were chosen to be as similar as possible with respect to other physical parameters and were in relatively isolated catchments dominated by native vegetation. All sampling occurred during January–February 2016 (Austral summer). Stream water pH, specific conductivity, dissolved oxygen and temperature were measured in the field using standard meters (YSI 550A & YSI 63; YSI Environmental Incorporated, Ohio, USA). Random water samples (50 ml) collected for analysis of dissolved metal concentrations were filtered in the field (0.45 µm mixed cellulose ester filter) and acidified (pH < 2) using ultrapure nitric acid. Samples were analysed for metals using inductively coupled plasma mass spectrometry (ICP-MS) at the University of Canterbury.

2.2 | Mining gradient

Water chemistry variables (Supporting Information Table S1) were combined into an AMD gradient using principal components analysis (PCA), using the R function *prcomp* in the stats package (R Development Core Team, 2017). Dissolved metal concentrations and conductivity were \log_{10} -transformed ($x + 1$) to satisfy assumptions of normality. All variables in the resemblance matrix were centred at 0 and scaled by their standard deviations before the PCA was conducted. The importance of the original variables to the PCA axes were determined using Pearson correlations. Site scores for PC axis 1 were extracted and used as a proxy for the AMD gradient in all further analyses.

2.3 | Community sampling and body mass estimation

Benthic macroinvertebrates were randomly collected in three Surber samples (0.06 m², 0.25 mm mesh) from riffle habitats at each site (Blakely & Harding, 2005). All samples were taken by the same person and with similar effort. Sample replication was a trade-off between the number of samples, the number of sites, and the processing and measurement of all individuals. Aquatic insect life histories in New Zealand are not characterised by strong seasonality (Winterbourn, Rounick, & Cowie, 1981). Emergence rates for some taxa are higher in summer, but numerous studies have shown a general lack of synchronised emergence, and a wide range of size classes and cohorts of a specific species are often observed together in New Zealand streams (Devonport & Winterbourn, 1976; Drummond, McIntosh, & Larned, 2015; Winterbourn et al., 1981). Therefore, we assume that there were no strong effects of

emergence or life history that could affect our findings. Samples were preserved with 100% ethanol in the field and returned to the laboratory for processing. Macroinvertebrates were separated and identified to the lowest practical taxonomic level (i.e. genus for mayflies, stoneflies and caddisflies, subfamily for Chironomidae larvae and family for other true flies and beetles, order for non-insect taxa) according to Winterbourn, Gregson, and Dolphin (2006), and unpublished keys (NIWA, Hamilton, New Zealand). Photos were taken of all individuals (~1–100 individuals per photo) using a Leica DFC295 digital camera mounted to a Leica model M125 microscope. All individuals were then measured to the nearest 0.1 mm using the software package Adobe Acrobat 9 Pro (San Jose, California, USA). Measurements were conducted according to the methods of Towers, Henderson, and Veltman (1994) and Stoffels, Karbe, and Paterson (2003). Briefly, individuals were generally measured from the anterior portion of the head to the last abdominal segment (not including cerci). Caddisflies with portable cases had the maximum length of the case recorded, except Helicopsychidae which were measured at the widest portion of the case. Finally, for the snail *Potamopyrgus antipodarum*, the shell height was measured. Because accurately sampling the smallest individuals is difficult, individuals ≤0.5 mm were removed from the data. Body lengths were converted to dry weight estimates (g) using published taxon-specific length-weight regressions for New Zealand invertebrate fauna (Stoffels et al., 2003; Towers et al., 1994).

2.4 | Size spectra

Body-mass–abundance relationships were assembled for all streams using the individual size distribution described by White et al. (2007). In each of the 25 streams, in order to get the best estimate of size spectra at each site, all individuals were combined and grouped into bins of equal logarithmic width (White, Enquist, & Green, 2008). We compare the use of the two most commonly used widths, \log_2 and \log_{10} (Jennings & Blanchard, 2004; Jennings, Warr, & Mackinson, 2002; White et al., 2008), in the Supporting Information Table S2, and compare the number of bins for each in Supporting Information Figures S1 and S2. Eighteen bins of \log_2 width were chosen in order to encompass the full range of body sizes present at all sites, while still allowing for robust regressions (Supporting Information). Abundances were normalised by dividing the frequency in a bin by the linear width of the bin (Sprules & Barth, 2015; White et al., 2007, 2008). Size spectra were plotted as $\log_{10} N \sim \log_{10} M$ where $\log_{10} M$ is the midpoint of the $\log_{10} M$ class, converted from \log_2 (Jennings & Blanchard, 2004).

The slope and y-intercept of size spectra have been shown to be correlated (Gómez-Canchong, Blanco, & Quiñones, 2013). Therefore, to make these response variables independent, the data from each stream were standardised to have the size range centred at $x = 0$, and report the y-intercept of the centred data as the community height (Blanchard et al., 2005; Sprules & Barth, 2015). This makes the slope and height parameters independent, with the former being more dependent on the relative abundance of small and

large individuals, and the latter on the total abundance within the community (Sprules & Barth, 2015). Each stream dataset was centred by subtracting the value of the mid-point bin from all bins within that stream, respectively.

Previous New Zealand studies have documented that fish are extremely sensitive to AMD inputs (Greig et al., 2010; Hogsden & Harding, 2012b) and in the present study were not found at any sites receiving AMD. Additionally, of the 12 streams that were unimpacted by AMD, six were naturally fishless. The presence of top predators can have impacts on biomass distributions of lower trophic levels, and can change the shape of the size spectra relationship (Brose et al., 2017). Since the present study is focused on the macroinvertebrate community size spectra response to AMD, we conducted preliminary analyses to test whether the presence of fish affected size spectra relationship of the macroinvertebrate community at the unimpacted sites. The presence of fish did not significantly impact either the slope or intercept of macroinvertebrate size spectra in unimpacted streams (Supporting Information Figure S3). Because fish are orders of magnitude larger than the majority of macroinvertebrates, and their absence is not wholly dependent on AMD inputs, their inclusion in the construction of size spectra represents a potential confounding factor. Thus, only the macroinvertebrates were used to construct size spectra for all sites, in all further analyses.

2.5 | Statistical analyses

Size spectra relationships are generally repeating negative parabolic domes, which only take on a linear relationship when sampling is performed across a large range of body sizes. Therefore, when focusing on a limited range of body sizes, as we do here, it is important to test both linear and quadratic models in order to maximise the

amount of variation explained (Sprules & Barth, 2015). We selected the best fitting model using Akaike's information criteria corrected for small sample sizes (AIC_c ; Burnham & Anderson, 2004). We found that the quadratic relationship best explained the variation among sites ($\Delta AIC_c \ll 2$). Furthermore, the conclusions reached using linear models were similar to those of the quadratic models (Supporting Information). The results of the quadratic models are presented throughout the rest of this paper.

To test for changes in size spectra across the mining gradient, we fitted linear regressions to the global dataset testing for significant effects of the predictors (independent variables) M , M^2 , PC1 and for interactions between M :PC1 and M^2 :PC1. The global model was in the form of:

$$\log_{10} N = \beta_0 + \beta_1 \log_{10} M + \beta_2 \log_{10} M^2 + \beta_3 \text{PC1} + \beta_4 \text{PC1} \log_{10} M + \beta_5 \text{PC1} \log_{10} M^2 + \epsilon$$

where N is the normalised abundance of individuals, M is the estimated body mass, PC1 (e.g. the mining gradient) are the site scores on the first axis determined by the PCA (see above), and ϵ is the residual error term. We then calculated the AIC_c of the global model as well as AIC_c for simplified models using the R function *dredge* in the package MuMIn (Bartoń, 2016). Simplified models were obtained by systematically testing all possible terms and interactions. Models were assessed and ranked according to ΔAIC_c , and only models with $\Delta AIC_c < 2$ were retained (Table 1; Burnham & Anderson, 2004). A significant coefficient for the PC1 variable (e.g. β_3 in the equation above) would indicate that the intercepts do respond to the mining gradient. Likewise, a significant coefficient for the M :PC1 and M^2 :PC1 interaction term (e.g. β_4 and β_5) would indicate that the slope and magnitude of curvature, respectively, vary in response to the mining gradient.

TABLE 1 AICc evidence table for model selection of quadratic size spectra relationship

Intercept	M	M^2	PC1	M :PC1	M^2 :PC1	R^2	K	logLik	AICc	ΔAIC_c	Weight
5.81	-0.9366	-0.3560	-0.0766	0.0551		0.85	6	-229.98	472.3	0.0	0.738
5.81	-0.9362	-0.3592	-0.0750	0.0554	-0.0018	0.85	7	-229.97	474.3	2.1	0.262
5.81	-1.0130	-0.3564	-0.0732			0.84	5	-241.43	493.1	20.8	0
5.81	-1.0130	-0.3466	-0.0779		0.0055	0.84	6	-241.32	494.9	22.7	0
5.80	-1.0220	-0.3111				0.82	4	-260.56	529.3	57.0	0
5.40	-1.0000		-0.0368	0.0557		0.75	5	-302.76	615.7	143.5	0
5.40	-1.0770		-0.0333			0.74	4	-309.93	628	155.7	0
5.42	-1.0780					0.74	3	-312.73	631.6	159.3	0
5.90		-0.5027	-0.0909			0.21	4	-471.85	951.8	479.6	0
5.91		-0.5146	-0.0852		-0.0068	0.21	5	-471.82	953.9	481.6	0
5.88		-0.4478				0.17	3	-478.14	962.4	490.1	0
5.33						0.00	2	-505.06	1014.2	541.9	0
5.31			-0.0348			0.01	3	-504.26	1014.6	542.4	0

The first six columns are the estimated parameter coefficients evaluated for a candidate model, with bold values indicating significance ($p < 0.05$). Blank entries indicate that that variable was not considered in that candidate model. K is the number of estimated parameters, including the residual error term. R^2 , coefficient of determination; logLik, log likelihood; AICc, Akaike's information criterion, corrected for small sample size; ΔAIC_c , difference in AICc for a candidate model from the lowest AICc value; last column is model weight. Models are ranked by ΔAIC_c values, where values < 2.00 indicate equivocal support. Only the first model has a $\Delta AIC_c < 2.00$ and was used in all further analyses.

To test hypothesis 3, we assessed the range of body sizes present within communities. The range of body size were calculated as $M_{\text{Range}} = \max(\log_{10} M) - \min(\log_{10} M)$ where M is the estimated individual dry weight, in g, within a site. Ranges were \log_{10} transformed, and a linear regression was performed, with the PC1 loadings (e.g. the mining gradient) as the independent variable. In order to investigate whether changes in M_{Range} were driven by changes in the presence of the smallest or largest sized organisms, we performed quantile regression ($\tau = 0.05$ and 0.95 , respectively) on the range of M present across the mining gradient. Confidence intervals (CIs) for quantile slope parameters were calculated by inverting a quantile rank-score test for the two values of τ (Dunham, Cade, & Terrell, 2002; Koenker & Machado, 1999).

Finally, as a coarse proxy for food web structure, we qualitatively assessed the proportion of individuals belonging to different FFGs across the AMD gradient. Changes in the presence or relative proportion of FFGs can represent changes in energy pathways and feeding links within a community. Functional feeding groups were assigned as in Winterbourn et al. (2006) and Hogsden and Harding (2012a). All statistical analyses were conducted in R version 3.3.3 (R Development Core Team, 2017). Annotated R scripts for the full analysis, including the creation of the figures, is available at <https://github.com/Jpomz/mining-size-spectra-Freshwater-Biology-accepted>. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v6g985s>.

3 | RESULTS

3.1 | Mining gradient

Streams varied markedly in pH (1.9–7.3), specific conductivity (15.2–2227 $\mu\text{S}/\text{cm}$), and concentrations of dissolved metals (Supporting Information Table S1). A PCA ordination of the chemical variables showed that PC axis 1 explained 78% of the variation and was highly correlated with pH, specific conductivity, and dissolved Fe, Al, Mg, Cd, Cu, Mn, Zn, Co and Ni (Pearson correlation > 0.85; Figure 1). These variables are known to vary in response to AMD, and the site scores on PC1 (Figure 1; hereafter referred to as the mining gradient)

were extracted and used as a measure of the mining related stress to which each community was exposed.

3.2 | Size spectra across the mining gradient

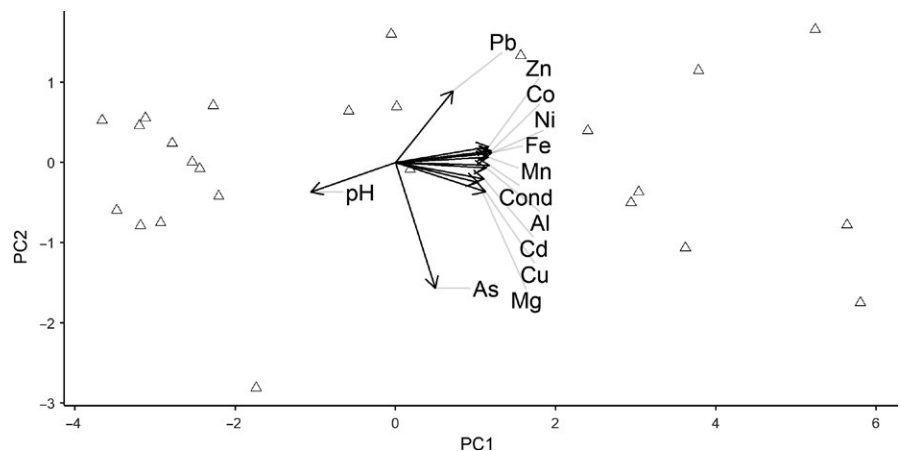
The best fitting model contained significant effects of M , M^2 , PC1 and an M :PC1 interaction (β_M , β_{M^2} , β_{PC1} , $\beta_{M:\text{PC1}}$, $p < 0.001$, Table 2). The full equation of this model is (site specific coefficient values in Supporting Information Table S3):

$$\begin{aligned} \log_{10} N = & -5.81 - 0.077\text{PC1} + (0.055\text{PC1} - 0.94) \\ & \log_{10} M - 0.36\log_{10} M^2 + \epsilon \end{aligned}$$

As expected, there was a strong, negative parabolic relationship to the number of individuals (N) within increasing body size bins (M) ($\beta_M = -0.937$, $p < 0.001$; $\beta_{M^2} = -0.356$, $p < 0.001$; adjusted $R^2 = 0.85$; $F_{4,284} = 405.5$; $p < 0.001$, Figure 2). The magnitude of this curvature was not affected by the mining gradient (no $\beta_{M^2:\text{PC1}}$ interaction term in the best fitting model, Table 1). Because size spectra analyses are generally not performed using quadratic equations, we compare the results of both linear and quadratic equations in the Supplementary Material, and show the coefficient estimates in Supporting Information Table S4. The overall conclusions reached are generally similar, regardless of which model was used.

The community height (y-intercept of the centred data) did vary significantly across the mining gradient ($\beta_{\text{PC1}} = -0.077$, $p < 0.001$), indicating a decrease in overall community abundance. To put this in context, we compared this with density estimates calculated directly from our Surber samples and found general agreement in the conclusions reached (Supporting Information). Additionally, there was an increase in the slope of the relationship across the mining gradient ($\beta_{M:\text{PC1}} = 0.055$, $p < 0.001$, Figure 3), leading to higher relative abundances of larger individuals in impacted streams. The M_{range} decreased significantly across the mining gradient ($p < 0.001$, adjusted $R^2 = 0.58$, $F_{1,23} = 34.11$, intercept = 3.23, slope = -0.19 , Figure 4A), and this was driven by the asymmetric loss of the largest individuals (Figure 4B). The size of the smallest organisms increases across the mining gradient (e.g. the smallest size classes were removed at impacted sites), although

FIGURE 1 Principal components analysis ordination of chemical variables. The first axis, PC1, explains 78% of the variation, and is strongly correlated with pH, conductivity, and concentrations of Fe, Al, Mg, Cd, Cu, Mn, Co and Ni, and can be interpreted as a mining gradient, with mining stress increasing from left to right. PC2 explains 8.2% of the variation and was not used in further analyses. The site-specific scores for PC axis 1 were extracted and used to represent the mining gradient in all further analyses



this is not statistically significant, as the CI for the quantile regression ($\tau = 0.05$) slope estimate includes 0 (coefficient estimate = 0.03, CI = [−0.85, 0.05]). However, the size of the largest organisms

TABLE 2 Results of the top least squares regression model for size spectra across the mining gradient

Coefficient	Estimate	SE	p
Intercept	5.80572	0.04427	<0.001
M	−0.93663	0.03316	<0.001
M ²	−0.35596	0.0261	<0.001
PC1	−0.07657	0.01111	<0.001
M:PC1	0.05514	0.01139	<0.001

Estimate, estimated coefficient value as determined by the multiple linear regression; SE, standard error of the coefficient estimate.

significantly decreases across the mining gradient (quantile regression $\tau = 0.95$ coefficient estimate = −0.14, CI = [−0.15, −0.11]), and this was due to the removal of the largest size classes. Communities at unimpacted streams had body sizes ranging up to 4.5 orders of magnitude, while highly impacted streams had body sizes ranging by <3 orders of magnitude. These changes in body mass range resulted from a loss of both the smallest and largest size classes, although the larger size classes were more greatly affected. Impacted streams lost one to four of the smallest size bins, but five to eight of the largest size bins.

3.3 | Functional feeding groups

The proportion of FFGs in the unimpacted streams was remarkably similar (Figure 5). Across the gradient, from less- to more-impacted streams, collector-browsers became the dominant group, which

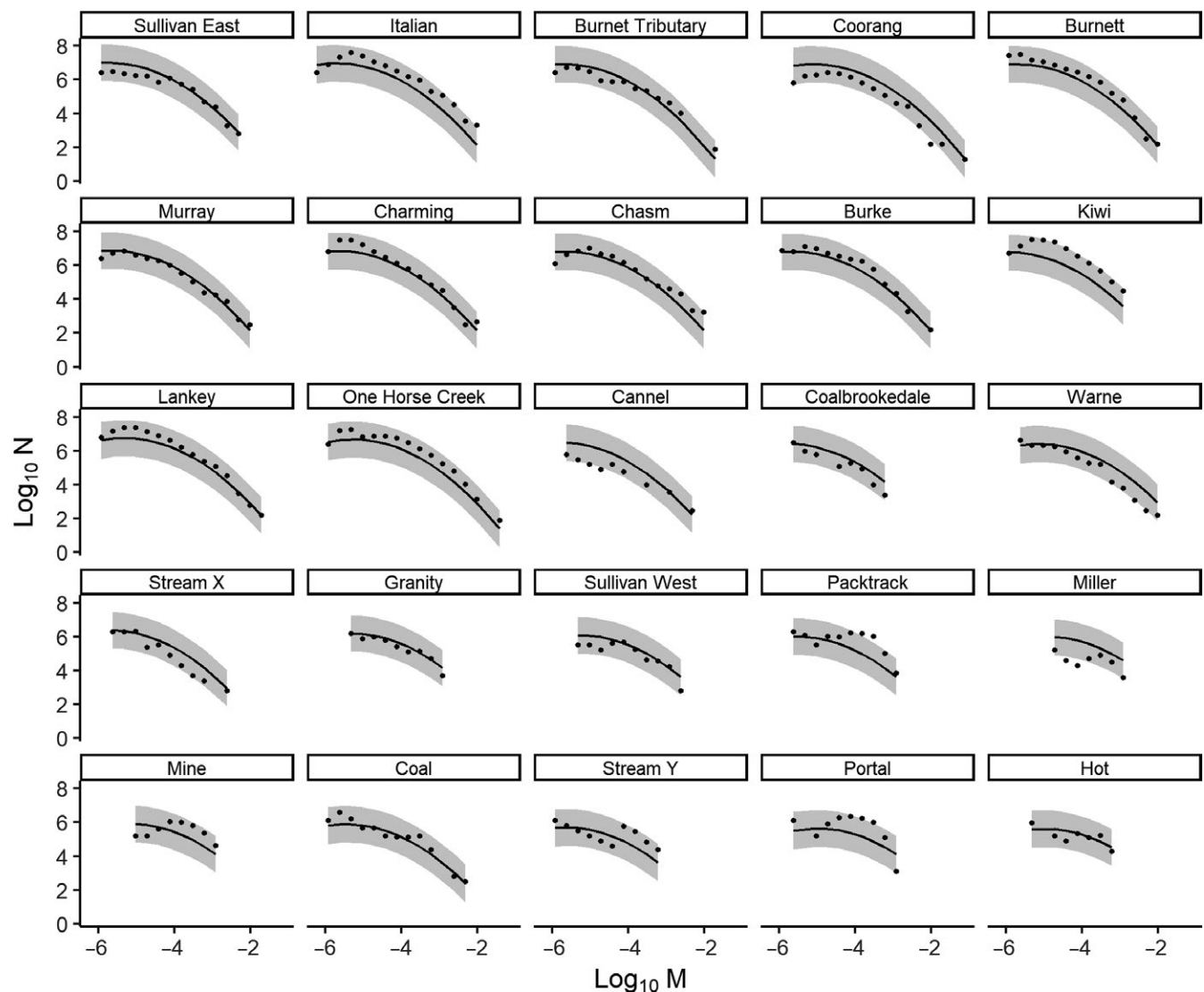


FIGURE 2 Body mass–abundance relationships for 25 sites across a mining gradient (impact increasing from top left to bottom right). Points are the summed abundances within each size bin from empirical data with fitted values (line) for highest ranked model (see results for specifics) with its 95% prediction interval (grey shading). Regression formula: $\text{Log}_{10} N = 5.81 - 0.94 \text{Log}_{10} M - 0.36 \text{Log}_{10} M^2 - 0.077 \text{PC1} + 0.055 \text{Log}_{10} M : \text{PC1}$ where N is the normalised abundance, M is the estimated dry mass in g and PC1 is the specific site score on PC axis 1 representing the acid mine drainage gradient (see methods)

is entirely explained by the communities becoming dominated by the Chironomidae subfamilies Diamesinae and Orthoclaadiinae. Grazers were generally absent from the AMD-impacted streams, which was mainly due to the loss of the New Zealand mud snail, *Potamopyrgus antipodarum*, whose shells are extremely sensitive to reduced pH. The grazers present in moderately impacted streams were dominated by the cased caddisfly *Oxyethira* spp. Although shredding taxa are generally poorly represented in New Zealand streams (Winterbourn et al., 1981), they were present in nearly all of the unimpacted sites, and completely absent in AMD-impacted

streams. The single exception to this was the presence of two individual Scirtidae beetles in a single stream, which is heavily impacted by AMD. Omnivores (predominantly the caddisfly *Aoteapsyche* spp.) accounted for a high proportion of the community in moderately AMD-impacted streams but were mostly excluded from the most heavily impacted sites. Filter feeders (dominated by the mayfly *Coloburiscus humeralis* and the blackfly *Austrosimulium* spp.) were present in all unimpacted streams, and generally absent in the AMD-impacted sites. Predators in the unimpacted streams were dominated by the large-bodied dobsonfly *Archichauliodes diversus*, and members of the caddisfly family Hydrobiosidae. The large stonefly *Stenoperla prasina*, was also present in eight of the 12 unimpacted sites, although they were generally found in low densities. All of the large predators were absent from the impacted streams (although a single small *S. prasina* instar was found in a moderately impacted site). Predators were completely removed in about half of the impacted streams but when they were present, their proportions were relatively high compared to the unimpacted sites. Predators in the AMD-impacted streams were mostly small individuals belonging to the Empididae and Ceratopogonidae families. Although both of these families are generally classified as predators, they are most likely consuming smaller Meiofauna (or very small instars of macroinvertebrates) due to their body sizes. The dominant taxa (relative proportion ≥ 0.05) by site, their relative proportions and FFG are presented in Supporting Information Table S5.

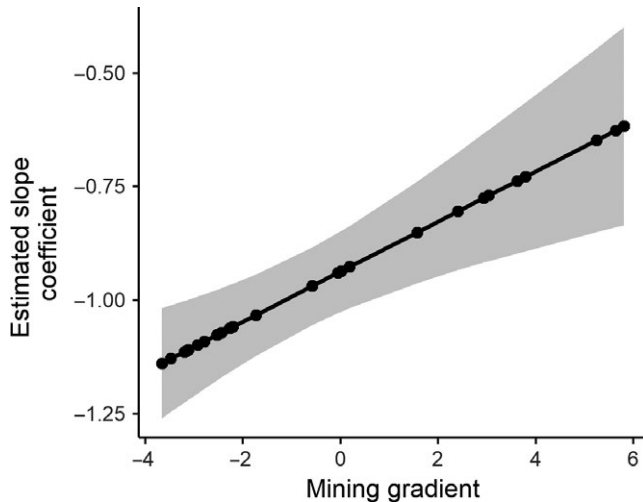


FIGURE 3 Estimated slope scaling coefficient for size spectra. Points are the site-specific estimated slope coefficient for the best fitting model. The solid line and grey shading are the predicted slope coefficient and 95% prediction interval, respectively, across the mining gradient. Mining impacts increase left to right

4 | DISCUSSION

The decreasing abundance of larger organisms in communities is one of the most well documented allometric scaling relationships

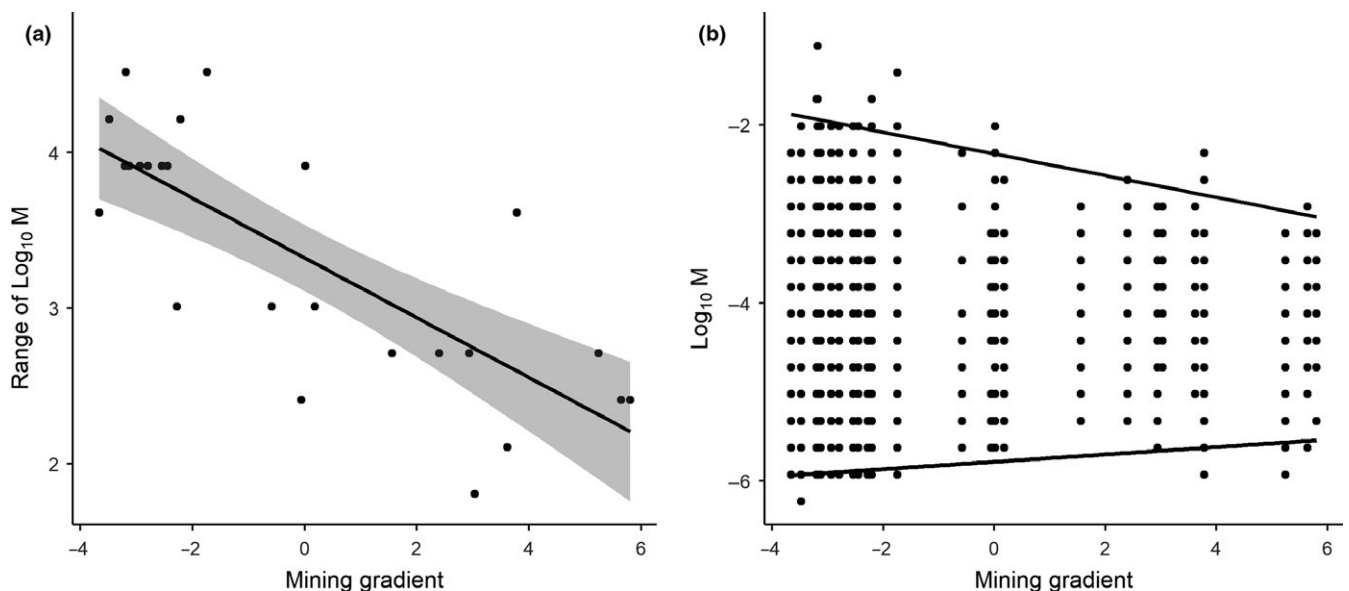


FIGURE 4 (a) Range of body size, $\log_{10} [\max(M) - \min(M)]$, in g. The range of M significantly decreases in response to the mining gradient, (black solid line, grey shading is 95% prediction interval). (b) Quantile regressions of the 95th and 5th percentile (top and bottom solid lines, respectively) of body size ($\log_{10} M$, in g) present across the mining gradient (mine impacts increase from left to right)

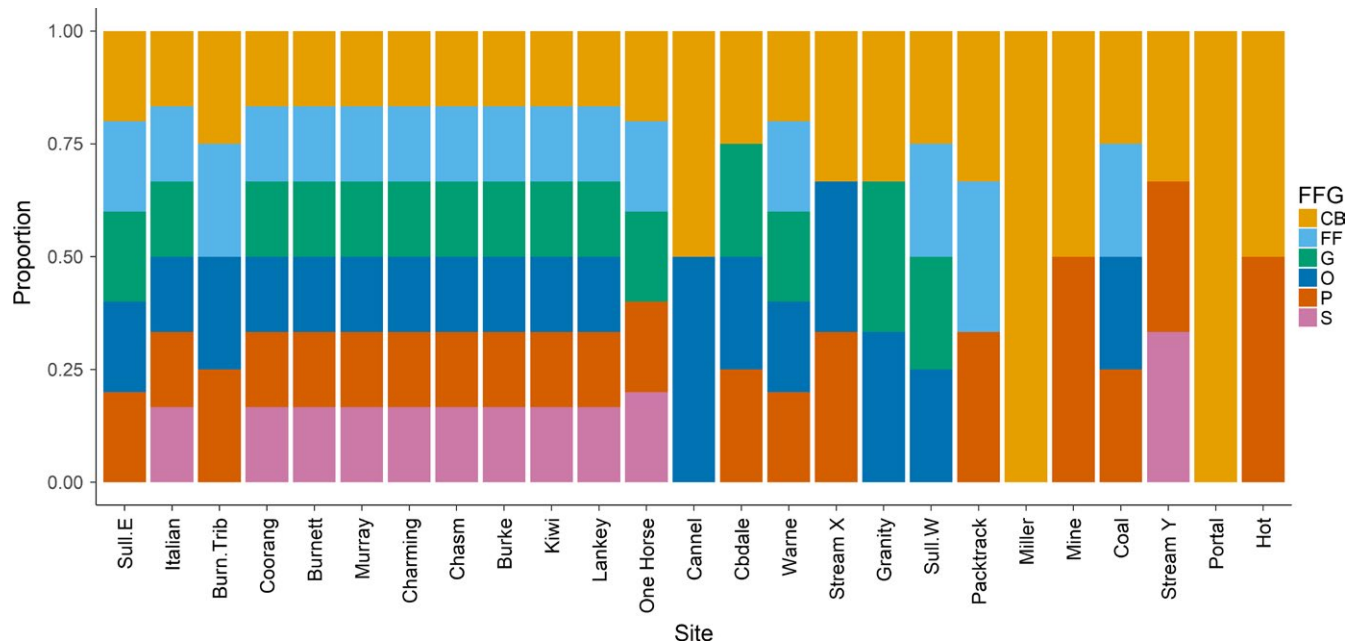


FIGURE 5 Proportion of individuals belonging to different functional feeding groups (FFG) at sites along an impact gradient of acid mine drainage. Site names are abbreviated where necessary for visualisation and are ordered by increasing impacts from left to right. All streams left of Cannel Creek are unimpacted by acid mine drainage. CB, collector-browser; FF, filter feeder; G, grazer; O, omnivore; P, predator; S, shredder [Colour figure can be viewed at wileyonlinelibrary.com]

in ecology (Petchey & Belgrano, 2010; Trebilco et al., 2013; White et al., 2007). Deviations from this relationship have been attributed to human impacts (e.g. commercial fishing, Jennings & Blanchard, 2004), environmental stress (e.g. drought, Woodward et al., 2012; warming, Dossena et al., 2012; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011), and ecosystem size (Warburton, 2015), and have been suggested as a potential metric for assessing ecological status (Gray et al., 2014; Petchey & Belgrano, 2010). In the present study, we found systematic responses of benthic macroinvertebrate size spectra relationships to a gradient of AMD impacts. Previous research in AMD streams has noted a marked decline in taxonomic richness and subsequent change in community dominance and composition where acid and metal tolerant invertebrates survive (Clements, Carlisle, Lazorchak, & Johnson, 2000; Hogsden & Harding, 2012a; Winterbourn, 1998; Winterbourn & McDiffett, 1996). In addition to these well-documented community changes in response to AMD, our study shows changes in the distribution of biomass and size structure within the communities.

There was a significant reduction in the intercept of the centred data along the AMD gradient, which reflects an overall decrease in community abundance (e.g. mean [min; max] individuals/m² across all unimpacted sites were 4,669 [1,500; 10,122], compared with 1,021 [94; 3,344] at all AMD-impacted sites). This is consistent with previous studies that have shown marked declines in macroinvertebrates densities in response to AMD inputs. The reduction in community abundance could be due to an increase in metabolic demands. Low pH and elevated trace metal concentrations can both impact respiration and osmoregulation efficiencies, leading to increased respiration rates. This in turn leads to higher

energy demands, potentially at the cost of secondary growth, emergence success (for taxa with an adult aerial phase), and reproductive output (Adams et al., 2011; Havas & Hutchinson, 1983; Herrmann, 1987; Herrmann & Andersson, 1986). Predators may be at a greater risk of local extirpations due to their higher total energetic demands (due to larger body size; Brown et al., 2004) and the increased metabolic costs associated with an active foraging nature (e.g. searching, capturing and handling prey). The higher cost of living in AMD-impacted environments removes sensitive species but is also likely to lower the number of individuals of tolerant taxa that can survive. An alternative explanation for the reduction in community abundance could be lower primary production or lower quantity or quality of basal resources, which cannot support large communities. However, Hogsden, Winterbourn, and Harding (2013) showed that both the quantity and quality of basal resources was not a likely limiting factor for primary consumers across an AMD gradient, lending support to our metabolic cost hypothesis.

There was also a significant increase in the estimated slope coefficient in response to the AMD gradient. Differences in slopes indicate changes to the trophic transfer efficiency within communities. Shallow slopes, in combination with a lower y-intercept, have been attributed to a reduction in trophic transfer efficiency. However, this assumes a fixed body mass of the largest and smallest organisms within a community, respectively (O'Gorman et al., 2012). In the current study, the situation is more complex, due to the complete removal of the largest sized organisms. Generally speaking, with a few notable exceptions (e.g. parasitoids are often similar in size to their hosts, Brose et al., 2007), niche space and trophic level are highly size dependent, particularly in aquatic systems (Brose et al., 2006;

Stouffer, Rezende, & Amaral, 2011), the reduction in the range of body sizes present has strong implications for the structure of the food web, number of trophic levels, and the number of energy pathways available to the community. This is consistent with the changes to the proportion of individuals within each FFG across the gradient. Although predator FFGs are present in some of the most heavily impacted sites, they are entirely composed of small bodied predators that are likely to be preying upon meiofauna or extremely small macroinvertebrate instars, which are likely below the size range sampled in the present study.

Predators can also directly influence the shape of the size spectrum of their prey (Blanchard et al., 2009; Brose et al., 2017; Hartvig, Andersen, & Beyer, 2011). Predator–prey interactions are largely size-structured, where a large predator generally consumes smaller individuals, which transfers energy from abundant small individuals, to fewer, larger, ones. This, in turn, causes a reduction in the abundance of the smaller individuals, leading to the theoretical and empirically observed slopes of about -1 (Brown et al., 2004; Jennings & Blanchard, 2004; Trebilco et al., 2013). However, in communities feeding on non-size structured resources (e.g. detritus), size spectrum slopes are shallower (e.g. -0.56 to -0.87 , Blanchard et al., 2009) than in predator prey communities. In the present study, the estimated slope coefficients for the AMD-impacted streams ranged from -0.97 to -0.62 , and the most heavily impacted sites had a slope coefficient shallower than -0.80 . The complete removal of large predators at the most heavily impacted sites likely causes a release from top-down control on the smaller prey (Daan, Gislason, Pope, & Rice, 2005), explaining the resemblance of slopes of size spectra at impacted sites to the size spectra slopes observed in detritivore communities (Blanchard et al., 2009).

The loss of predators, coupled with changes in proportions of FFGs represents a simplification of the food web, with fewer links and energy pathways possible, and this has implications for food web stability. Food webs with many weak interactions are generally considered to be more stable compared with food webs dominated by a few strong links (Wootton & Stouffer, 2015). The

strength of predator–prey feeding links are often considered to be proportional to the predator–prey body size ratios (Berlow et al., 2009; Emmerson & Raffaelli, 2004; Tang et al., 2014), with stronger interactions occurring between large predators and small prey. Likewise, Tang et al. (2014) found that stability is directly influenced by the correlation of interaction strengths between predators and their prey, and that these strengths can be largely determined by body size. Our findings suggest conflicting interpretations regarding the stability of AMD-impacted food webs. On the one hand, the reduction and absence of large predators means that the links present are likely to be weaker than in unimpacted streams, and therefore the food web should be more stable. On the other, the simplification of the food web and the loss of FFGs and alternative energy pathways means that there are fewer potential links, and that the links present will have stronger interaction strengths relative to unimpacted streams. This suggests that the food webs in impacted streams would be less stable than unimpacted streams. Further research is needed to tease these interacting mechanisms apart and determine if AMD-impacted food webs are more or less stable.

Changes in food web structure also have implications for the restoration of sites impacted by environmental perturbations. Biotic responses in systems that are recovering from physical or chemical impacts can be delayed or patchy in nature, are modulated by the species and interactions present, and do not follow a reverse trajectory of the response to the original impact (Scheffer, Carpenter, Foley, Folke, & Walker, 2001), thereby causing the community to appear to be impacted for long after the stressor has been removed (Gray et al., 2014, 2016; Layer et al., 2011). One explanation for this is that impacted communities have found an alternative stable state, and that this state has internal ecological inertia (Layer et al., 2011), or *negative resilience* (Lake, 2013), which impedes the community returning to a non-impacted state. Studies of food web stability across productivity gradients suggest that food webs alternate between stable and unstable conditions. Simple food webs in low productivity sites can be organised into stable configurations. As productivity increases, the community can support

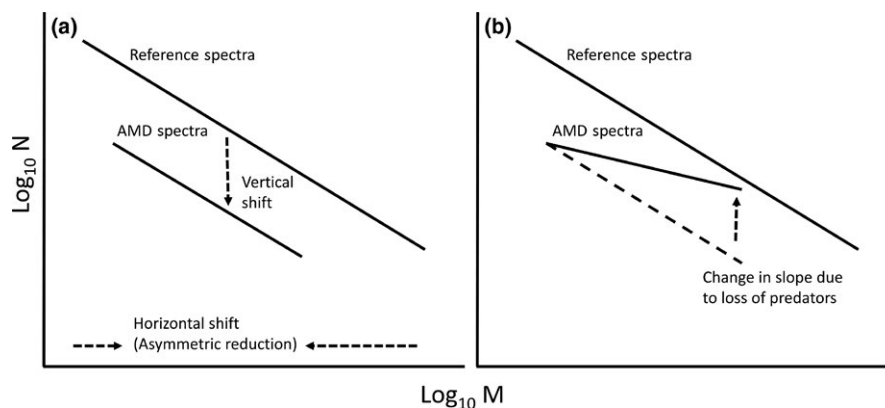


FIGURE 6 Conceptual figure of impacts of acid mine drainage to stream macroinvertebrate size spectra. Inputs of acid mine drainage (AMD) cause consistent changes to reference spectra. (a) Spectra impacted by acid mine drainage resulted from a vertical shift (reduced community abundance) and asymmetric horizontal shift (large body sizes are more impacted). (b) The loss of large predators also resulted in a reduction in top-down control of prey abundances, causing an increase in the slope (dashed arrow) of spectra impacted by AMD

more biomass at the top of the food chain, which in turn causes stronger, destabilising top-down interactions. When larger individuals or taxa colonise these communities, they primarily predate upon the larger species present, which decreases their abundance (and hence indirectly reducing the top-down control on smaller individuals), and ultimately rearranges the organization and strength of feeding links, leading to more stable food web configurations (Neutel et al., 2007). A similar mechanism was found in Broadstone Stream in the UK, where biotic recovery lagged chemical remediation by several years, and was characterized by the successive re-invasion of consistently larger bodied predators (Layer et al., 2011). Therefore, if the goal of a restoration project is to return the community to an unimpacted state, in addition to remediating the chemical or physical stressor, it may be necessary to assist in biotic recovery with species reintroductions, particularly when large predators have been removed.

In addition to the strong response of the communities to AMD inputs, we found a remarkable agreement in the communities at the unimpacted streams, despite covering a wide range of natural conditions (e.g. pH 4.8–7.3). For example, the shape of the size spectrum, and the proportion of individuals in the different FFGs were both very similar in the unimpacted sites. This adds to the growing body of literature showing that size spectra relationships are a good proxy variable for ecological status (Martínez et al., 2016; Petchey & Belgrano, 2010; Trebilco et al., 2013; Warburton, 2015). This result is encouraging, because it indicates that community-level responses avoid some of the challenges that traditional, taxonomic based bio-monitoring programmes have faced e.g. variable species distributions, biogeographical constraints, context and pollutant specific sensitivities (Gray et al., 2014).

We found that AMD affected stream macroinvertebrate size spectra in consistent ways, represented conceptually in Figure 6. Specifically, we found that community abundance and overall body size decreased in AMD streams, resulting in smaller communities, with more homogenous distributions of biomass. The harsh environment caused by heavy AMD inputs probably increased the energetic demands on macroinvertebrates, lowering the overall community abundance (lowered y-intercept). These impacts were greater on larger individuals (asymmetric reduction in range of body sizes present). Since most predators are generally larger bodied, their removal causes a release from predation pressure, allowing the abundance of smaller individuals to decline less significantly than would be expected otherwise (shallower size spectrum slope). These findings have implications for the structure, function and stability of food webs in impacted streams, and should be taken into account when designing remediation efforts.

These findings add a new perspective to the impact of AMD which to our knowledge has not been previously reported, and which would not be captured by using traditional biomonitoring methods. For example, if taxonomic or functional groups were aggregated and their biomass measured directly, the relationships would be skewed as the individual-level information would be lost. Likewise, construction of food webs across a large number of streams (e.g. 25 in the present study) via visual identification of gut contents would require

much greater allocations of effort. Food webs could be constructed using stable isotope methods, but again the individual level data would be lost. However, size spectra incorporate information from the individual-, population- and community-level regarding energy transfer efficiency, and the partitioning of nutrients and biomass within an ecosystem (Martínez et al., 2016; Woodward et al., 2005). Likewise, with the individual-level data retained it is easy to aggregate and to different organisational levels and analyses them separately, as needed. Therefore, we feel that the information gained from size spectra analyses far outweighs the additional labour required. Further work is needed to assess the sensitivity of size spectra across other environmental gradients, to further our understanding of their potential use as an indicator of ecological status.

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AUTHOR CONTRIBUTION

J.P. and J.H. designed the study. J.P. and H.W. analysed the data. J.P. wrote the first draft of the manuscript, and all authors contributed to revisions.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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