Anthropogenic and natural sources of acidity and metals and their influence on the structure of stream food webs

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ABSTRACT

We compared food web structure in 20 streams with either anthropogenic or natural sources of acidity and metals or circumneutral water chemistry in New Zealand. Community and diet analysis indicated that mining streams receiving anthropogenic inputs of acidic and metal-rich drainage had much simpler food webs (fewer species, shorter food chains, less links) than those in naturally acidic, naturally high metal, and circumneutral streams. Food webs of naturally high metal streams were structurally similar to those in mining streams, lacking fish predators and having few species. Whereas, webs in naturally acidic streams differed very little from those in circumneutral streams due to strong similarities in community composition and diets of secondary and top consumers. The combined negative effects of acidity and metals on stream food webs are clear. However, elevated metal concentrations, regardless of source, appear to play a more important role than acidity in driving food web structure.

1. Introduction

Human activities, such as the combustion of fossil fuels and mining activities, have caused widespread acidification and metal contamination of freshwater ecosystems in many parts of the world. These anthropogenic activities accelerate the release of acidifying substances and increase leaching and mobility of metals that have resulted in substantial species loss and marked changes in ecosystem processes (Driscoll et al., 2001; Palmer et al., 2010). However, freshwater ecosystems with natural sources of acidity and metals also occur globally. Where acidity arises naturally in streams from the leaching of organic acids in soils or in poorly buffered catchments, the extent of species loss and changes in function are far less pronounced and in some places, biodiversity and ecosystem processes can be maintained (Collier et al., 1990; Petrin et al., 2008; Greig et al., 2010). Similarly, background metal levels can be also be naturally elevated in freshwaters as metals enter surface waters through natural weathering of bedrock or soils (Garrett, 2000; Kelley and Hudson, 2007). The dissolution of metals by weathering tends to occur at a slow rate and concentrations of dissolved metals in freshwaters vary depending on the underlying geology. Relatively few studies have examined the influence of naturally high metal concentrations on the structure and function of stream communities and it is not known if or how they differ

from communities in streams receiving anthropogenic inputs of metals. However, one study has shown that prior to mining, streams adjacent to a large lead-zinc ore deposit had few invertebrate taxa due to naturally elevated concentrations of metals in the water (see Scannell, 1996).

The greater negative effects of anthropogenic acidity on species diversity and some ecological processes is often attributed to the extent and source of acidity, increased mobility and bioavailability of metals (e.g. aluminium), and inability of organisms to adapt to rapid changes in pH, which extend beyond natural or historical ranges (Petrin et al., 2008). In contrast, strong similarities in community composition and ecosystem function are often reported between naturally acidic and circumneutral streams (Collier et al., 1990; Dangles et al., 2004). In regions with naturally low pH waters, many freshwater invertebrates and fish exhibit tolerance to a wide range of pH suggesting the species are pre-adapted to low pH (Collier et al., 1990; O'Halloran et al., 2008; Petrin et al., 2008).

Damage to freshwater ecosystems caused by anthropogenic acidification is most often associated with acidic precipitation caused by industrial emissions of sulphur dioxide and nitric oxides. However, acid mine drainage (AMD) is another major source of anthropogenic acidity worldwide. AMD is generated when sulphide minerals are exposed to weathering processes during mining activities (Kelly, 1988). Exposure to air and water generates sulphuric acid that is exported from mine sites and into nearby waterways. AMD impacted streams are characterized by extremely low pH (often < 3), high concentrations of metals (e.g. Al, Cu, Fe, Zn) and insoluble metal hydroxide deposits that coat stream substrata.

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Significant reductions in species richness and abundance of algae (Niyogi et al., 1999; Bray et al., 2008), invertebrates (Cherry et al., 2001; Battaglia et al., 2005), and fish (Sullivan and Gray, 1992; Greig et al., 2010) are typical of streams receiving mine drainage. These losses are often attributed to the substantial changes in pH and metal concentrations, which exceed the physiological tolerance limits of many species. For example, concentrations of dissolved metals typical of mining impacted streams are known to be directly toxic to fish via inhibition of ion exchange and respiratory stress (e.g. Baker and Schofield, 1982 and references therein). Species loss may also be due, in part, to the loss of habitat and refugia as substrata are covered by metal hydroxide precipitates in streams where pH > 3.5 and some metals become insoluble (e.g. Fe; McKnight and Feder, 1984).

To date, most studies of ecological change in streams associated with anthropogenic stress have focused on shifts in community composition and abundance rather than functional organization and interactions among species. But more recently, in order to further understand the wider effects of stress on streams, a food web approach has been taken (e.g. Culp et al., 2005; Woodward et al., 2010). Stressed food webs are expected to shorten and simplify owing to loss of sensitive species, removal of entire trophic levels (e.g. top predators), and decreases in interactions between species (Odum, 1985; McCann, 2000). Empirical evidence of modified food web structure has been reported in studies on freshwaters affected by acidification (Layer et al., 2010), warming (Woodward et al., 2010), and land use change (Thompson and Townsend, 2004). Changes in food web structure can be expected to have important implications for energy processing in these systems (Woodward, 2009).

Our objectives were to: 1) describe food web structure in streams receiving anthropogenic inputs of AMD; and 2) compare webs in mining streams to those in streams with natural sources of acidity and metals. We predicted that the extreme acidity and elevated metal concentrations of mining streams would generate a highly simplified food web structure compared to webs with natural sources. We expected that streams with natural sources of acidity and metals would have similar, intermediate-sized food webs including a more diverse consumer community comprised of acid and/or metal adapted species, and to be structurally more similar to webs in circumneutral streams.

2. Methods

2.1. Study sites

Food webs were sampled in 20 streams with either anthropogenic or natural sources of acidity and metals or circumneutral water chemistry on the South Island, New Zealand (see Supplementary material). We selected five streams from each of the following four types: mining (low pH, high metal); naturally acidic (low pH, low metal); naturally high metal (circumneutral pH, high metal); and circumneutral (circumneutral pH, low metal). Mining, naturally acidic, and circumneutral streams were all located in close proximity to each other in three areas (90–130 km apart). All naturally high metal streams were concentrated in the Red Hills range, further to the northeast (~80 km from nearest mining stream). Despite the physical distance, stream faunas in these areas are comparable given the cosmopolitan nature of New Zealand's freshwater biota (Harding et al., 1997). Mining streams received inputs of AMD from active or abandoned coal mines and were located in areas associated with the Brunner Coal Measures. Metal hydroxide precipitates were present on substrata in two mining streams. Natural acidity in streams in this area arises from the leaching of organic acids from soil and decomposing vegetation in surrounding forests (Collier et al., 1990). Streams with naturally high metal concentrations in our study contain nickel that is released from underlying ultramafic rocks and soils. All streams were selected to be as similar as possible with respect to other physicochemical factors and were in relatively isolated catchments dominated by native vegetation. Within each type, we selected streams across a gradient of elevation (20–550 m ASL) and vegetation cover (0–95%), except naturally high metal streams (see Results). Samples were collected on a single occasion in January–February 2009 (austral summer) at sites within a 20 m reach that included both pools and riffles.

2.2. Water chemistry & physical characteristics of streams

Stream water pH, specific conductivity, temperature, and dissolved oxygen were measured using standard meters (YSI 63 and YSI 550A, YSI Environmental Incorporated, Ohio, USA). Water samples (125 mL) collected for analysis of dissolved metals were filtered in the field through a 0.45 μm mixed cellulose ester filter, acidified with nitric acid, and kept cool until analysis by ICP-MS (Hill Laboratories, Hamilton, New Zealand). Wetted channel width, depth, and velocity were recorded along three randomly selected transects in each 20 m reach. Substrate size was estimated by measuring 30 randomly selected particles from the streambed. Vegetation cover in the middle of the reach was estimated visually using a densiometer (Robert E. Lemmon Forest Densiometer Model-A, Oklahoma, USA).

2.3. Basal resources – algae & detritus

Samples of algae and organic matter were collected to quantify basal food resources. Attached algae were removed from the surface of 15 randomly selected stones using a hard-bristled brush, rinsed with filtered stream water, and pooled into three 200 mL representative samples. The surface area of each stone was estimated from length measurements of the two main axes. In the field, a 50 mL subsample was filtered (0.7 μm-GF/F) and frozen for chlorophyll *a* analysis to determine algal biomass. In the laboratory, algal pigments were extracted in buffered ethanol (90%) and quantified using fluorometry (Trilogy Fluorometer, Turner Designs, California, USA). Benthic organic matter was collected in five Surber samples (0.06 m²; 250 μm mesh) and divided into two size fractions: FPOM (250–1000 μm) and CPOM (>1000 μm). Suspended organic matter (seston) was collected from 2 L of filtered (0.7 μm-GF/F) stream water. All FPOM, CPOM, and seston samples were dried, weighed, ashed (550 °C for 4 h) and re-weighed to determine ash-free dry mass (AFDM).

2.4. Consumer samples – benthic invertebrates & fish

Benthic invertebrates were collected in five Surber samples (0.06 m²; 250 μm mesh) from riffle and run habitats. They were fixed in ethanol (70%) and returned to the laboratory for processing. Taxa were identified and counted under a dissecting microscope to the lowest possible resolution according to Winterbourn et al. (2000a) and an unpublished key for hydrobiosid caddisflies (Brian Smith, NIWA, Hamilton, New Zealand). Following identification, molluscs and cased caddisflies were removed from their shells and cases, respectively. All invertebrates were classified into functional feeding groups, dried, weighed, ashed (550 °C for 4 h), and re-weighed together by group to determine AFDM. Kick net samples were collected at each stream to gain a more complete taxonomic list and collect individuals for gut contents analysis. Specimens for gut analysis were fixed in ethanol (70%) in the field. Fish and crayfish were sampled using quantitative electrofishing techniques in the 20 m reach. Stop nets were placed at the top and bottom of the reach and fish were removed during three successive passes. All fish were processed following Greig et al. (2010). Fish were returned to the stream except for a subset (up to 10 per species) that was retained for gut analysis. These fish were euthanized using 2-phenoxyethanol and preserved in ethanol (100%). Crayfish were collected for gut content analysis but were not included in invertebrate biomass estimates.

2.5. Food web structure & properties

Gut contents analysis was used to identify feeding links and construct food webs for each stream. Invertebrate guts were removed, mounted on slides in lactophenol-PVA stained with lignin pink, and examined under a microscope (400× magnification). Invertebrates found in gut contents were identified to the lowest possible taxon and counted. Otherwise, food was itemised as animal prey, filamentous algae, diatoms, other algae, plant detritus (CPOM), and amorphous detritus (FPOM). The relative abundance of food items was visually estimated by scanning the whole slide and categorised as: rare (<5%), common (5–20%), or abundant (>20%). Stomach contents of fish were examined under a dissecting microscope. Prey items were identified to the lowest taxonomic resolution possible and counted or estimated as described above. All terrestrial insects found in guts were grouped into a single basal resource category (i.e. terrestrial insect) and counted.

Because many species were present at low densities in our streams, particularly the mining streams, we were only able to collect a limited number of individuals of each species for gut analysis. Frequently, this was less than the minimum of 10 individuals per species recommended by Thompson et al. (2001). In order to standardise our effort and generate comparable food webs across the four stream groups, we identified gut contents from several different species in each functional feeding group in all streams to get dietary information on a wide range of species. The number of guts analysed for each species ranged from 2 to 47. We then compiled a cumulative binary matrix (Cohen et al., 1990) for predators and prey and included links found in all 20 streams. Based on this cumulative matrix, we constructed individual food webs for each stream and were able to infer links for species where gut content data was missing but the species was present in samples for a particular stream. This approach assumes the presence of a feeding interaction between two species in all streams in which they are found but does not allow for differences in

prey selection or the strength of interactions between streams (Havens, 1992). However, the procedure limited bias due to inadequate or unachievable sample size. We assessed invertebrates and fish in each stream for evidence of all six basal resources (algae, filamentous green algae, diatoms, FPOM, CPOM, terrestrial insects). If one or more was absent, all links with this resource were excluded for a particular stream. Links between predators and algal basal resources were also excluded to avoid links that were due to prey within prey (Thompson et al., 2001). However, detrital resource links were retained due to evidence of detritus in predator guts lacking prey. The constructed food webs did not incorporate meiofauna, bacteria, or fungi, and therefore provide a conservative estimate of overall food web structure.

The following food web properties were calculated for each stream: number of species, including basal resources (or web size, S), number of links (L); fraction of basal species (species with predators but no prey); fraction of intermediate species (species with predators and prey); fraction of top species (species with prey but no predators); maximum food chain length (number of links from a basal species to a top species, excluding feeding loops); predator—prey ratio (Cohen, 1977); linkage density (L/S; Pimm et al., 1991); and connectance (fraction of all possible links that are realised within a food web; L/S^2). This commonly used measure of connectance is less likely than other measures to be affected by differences in web size.

2.6. Statistical analysis

Principal components analysis (PCA) was conducted on chemical and physical variables. Conductivity and the concentrations of four metals were $\log_{10}$-transformed to meet assumptions of normality. Separation of streams along PCA axes was determined using multivariate analysis of variance (MANOVA) followed by univariate analysis of variance (ANOVA) on specific water chemistry variables. Differences in biomass of basal resources and consumers between stream groups were determined using ANOVA followed by Tukey's post-hoc tests where significant differences were found. CPOM, FPOM, algal, invertebrate and fish biomass data were square-root transformed prior to analysis.

Non-metric multidimensional scaling (NMDS), conducted on a Bray—Curtis similarity matrix, was used to describe differences in food web properties between streams. Food web property data were square-root transformed prior to analysis. Differences in food web properties between stream groups (i.e. mining, naturally acidic, naturally high metal, and circumneutral) were tested using analysis of similarities (ANOSIM). Next, similarity percentages (SIMPER) of food web properties were calculated to determine properties that contribute most to dissimilarity between stream groups. Finally, the BEST procedure was used to relate patterns in food web structure with physicochemical variables (Clarke and Warwick, 2001). In this procedure, the best matches are measured by Spearman rank correlation between the similarity matrices for food web properties (Bray—Curtis) and physicochemical variables (Euclidean distance).

ANOVA and MANOVA analyses were performed using SYSTAT 10 (SPSS, 2000). All other multivariate analyses described above were conducted using Primer 6.1.12 (Clarke and Gorley, 2006).

3. Results

3.1. Physicochemical variables

An ordination of water chemistry variables emphasized the separation of mining streams from all other streams (Fig. 1a). Separation occurred along a gradient of conductivity, concentrations of dissolved Al, Fe, Ni, Zn, and pH (Axis 1), but not temperature or dissolved oxygen (Axis 2) (MANOVA: Wilks $\lambda_{6,30} = 0.12$, $P < 0.001$. Univariate ANOVAs: Axis 1, $F_{3,16} = 29.03$, $P < 0.001$; Axis 2, $F_{3,16} = 1.78$, $P = 0.19$; Fig. 1a). pH differed significantly between all stream types, increasing from mining to naturally acidic, circumneutral, and naturally high metal streams (Table 1). Mining streams were twice as acidic as most naturally acidic streams and up to six times more acidic than all other streams in the study based on the concentration of H$^+$ ions. Conductivity and the concentrations of four dissolved metals (Al, Fe, Ni, Zn) also differed significantly between stream types and were one to three orders of magnitude higher in mining streams. In addition, the concentration of Ni and conductivity were one order of magnitude higher in naturally high metal than in naturally acidic and circumneutral streams and were in the range of those observed in mining streams (Table 1).

The streams had similar physical characteristics, including velocity (0.05—0.31 m s^{-1}), width (1.3—7.2 m), depth (0.07—0.23 m), and substrate size (7.5—13.7 cm). Streams in all groups were represented across the elevation and vegetation cover
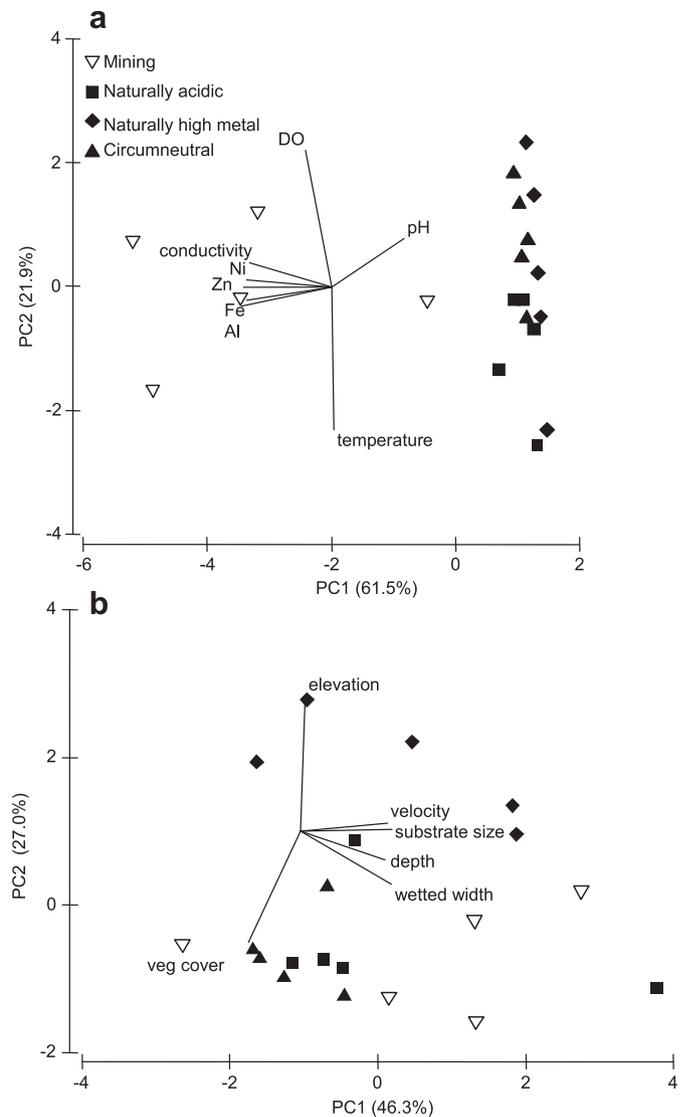

Fig. 1. Principal components analysis (PCA) of (a) water chemistry, and (b) physical habitat variables for mining, naturally acidic, naturally high metal, and circumneutral streams. Lines indicate correlation of variables with axes.

ranges, except for naturally high metal streams, which were only at higher elevations (791—1232 m ASL) and had 0% vegetation cover. Vegetation at these sites was predominately grasses and short shrubs, which did not provide any cover. Naturally high metal streams differed from all other streams based on elevation and vegetation cover but not other physical variables (MANOVA: Wilks $\lambda_{6,30} = 0.20$, $P < 0.001$. Univariate ANOVAs: Axis 1, $F_{3,16} = 1.08$, $P = 0.39$; Axis 2, $F_{3,16} = 15.32$, $P < 0.001$; Fig. 1b).

3.2. Food web components — basal resources & consumers

Basal resource biomass varied both within and between mining, naturally acidic, and circumneutral streams but was consistently lower in naturally high metal streams (Fig. 2a—c). Algal biomass was relatively low in all streams and differed among stream groups ($F_{3,56} = 5.24$, $P = 0.003$). This difference was driven by significantly lower algal biomass observed in naturally high metal streams (Fig. 2a). Across all streams, algal biomass was not related to vegetation cover ($R^2 = 0.15$, $P = 0.09$). Both CPOM and FPOM

Table 1
Physicochemical variables of the four stream types identified in Fig. 1. Values shown are group means ($\pm$SE) with ranges below. Results of one-way ANOVA tests for differences between stream groups for each variable are also shown. $N = 5$ streams per type.

Stream type		pH	Specific conductivity	Al	Fe	Ni	Zn	Elevation	Vegetation cover
			(μS_{25} cm^{-1})	(mg L^{-1})	(mg L^{-1})	(mg L^{-1})	(mg L^{-1})	(m ASL)	(%)
Mining	Mean $\pm$ SE	3.5 $\pm$ 0.4	689.2 $\pm$ 137.1	12.4 $\pm$ 5.2	10.21 $\pm$ 5.5	0.06 $\pm$ 0.02	0.3 $\pm$ 0.1	318.6 $\pm$ 90.6	58.0 $\pm$ 17.0
	Range	2.8–4.4	295.4–994.7	0.7–30.0	0.5–31.0	0.006–0.1	0.03–0.5	46.0–225.0	1.0–99.0
Naturally acidic	Mean $\pm$ SE	5.0 $\pm$ 0.3	34.4 $\pm$ 4.4	0.3 $\pm$ 0.1	0.3 $\pm$ 0.1	0.0006 $\pm$ 0.00007	0.007 $\pm$ 0.001	237.6 $\pm$ 96.5	40.0 $\pm$ 15.0
	Range	4.1–5.9	21.7–43.2	0.09–0.65	0.1–0.6	0.0005–0.0009	0.003–0.013	20.0–544.0	0–76.0
Naturally high metal	Mean $\pm$ SE	8.1 $\pm$ 0.1	112.9 $\pm$ 9.7	0.01 $\pm$ 0.01	0.03 $\pm$ 0.005	0.006 $\pm$ 0.003	0.003 $\pm$ 0.001	968.6 $\pm$ 100.1	2.0 $\pm$ 1.0
	Range	7.7–8.4	87.4–138.4	0.003–0.06	0.02–0.05	0.002–0.02	0.001–0.007	791.0–1232.0	0–12.5
Circumneutral	Mean $\pm$ SE	6.6 $\pm$ 0.1	79.4 $\pm$ 8.7	0.07 $\pm$ 0.02	0.09 $\pm$ 0.01	0.0005 $\pm$ 0.00001	0.007 $\pm$ 0.003	177.2 $\pm$ 36.2	60.0 $\pm$ 14.0
	Range	6.3–6.9	58.1–105.7	0.05–0.13	0.06–0.11	0.0005–0.00055	0.003–0.019	46.0–255.0	7.0–86.0
ANOVA	$F_{3,16}$	62.0	63.9	15.8	10.8	12.5	11.0	18.7	4.1
	P	<0.001	<0.001	<0.001	<0.001	<0.001	< 0.001	< 0.001	0.03

biomass differed significantly between stream groups ($F_{3,96} = 5.73$, $P = 0.001$ and $F_{3,96} = 4.51$, $P = 0.005$, respectively). Again, these detrital resources were significantly lower in naturally high metal streams (Fig. 2b and c) but biomass increased in streams with greater vegetation cover (CPOM: $R^2 = 0.34$, $P < 0.01$; FPOM: $R^2 = 0.28$, $P = 0.02$). Biomass of suspended seston was comparable across stream types ($F_{3,96} = 2.92$, $P = 0.07$; Fig. 2d).

Invertebrate consumer biomass was significantly lower in mining streams but similar among other stream groups ($F_{3,96} = 28.42$, $P < 0.001$; Fig. 3a). Species-poor communities in mining streams were comprised of only a few collector-browsers and predators including oligochaetes, orthoclad chironomids, and tanypod chironomids (Fig. 3c). Predatory dobsonflies (*Archichauliodes diversus*) and stoneflies (*Stenoperla maclellani*) as well as two collector-browsers (mayfly *Deleatidium* spp. and stonefly

Zelandoperla spp.) were common in naturally high metal streams (Fig. 3c). Species-rich communities in naturally acidic and circumneutral streams were very similar and contained a core group of filter-feeders (e.g. *Hydropsyche* spp., *Coloburiscus humeralis*) and collector-browsers (*Deleatidium* spp.; Fig. 3c). Fish were absent from all mining and naturally high metal streams. In contrast, fish biomass was comparable in naturally acidic and circumneutral streams (Fig. 3b). Communities in both these stream groups included longfin eels (*Anguilla dieffenbachii*), shortfin eels (*Anguilla australis*), brown trout (*Salmo trutta*), bullies (*Gobiomorphus* spp.), and galaxiids (*Galaxias* spp.). All fish were predators (Fig. 3d).

Fish and invertebrate consumer species used to construct food webs are listed in Table 2, as gut contents analysis was not conducted on some taxa (e.g. oligochaetes).
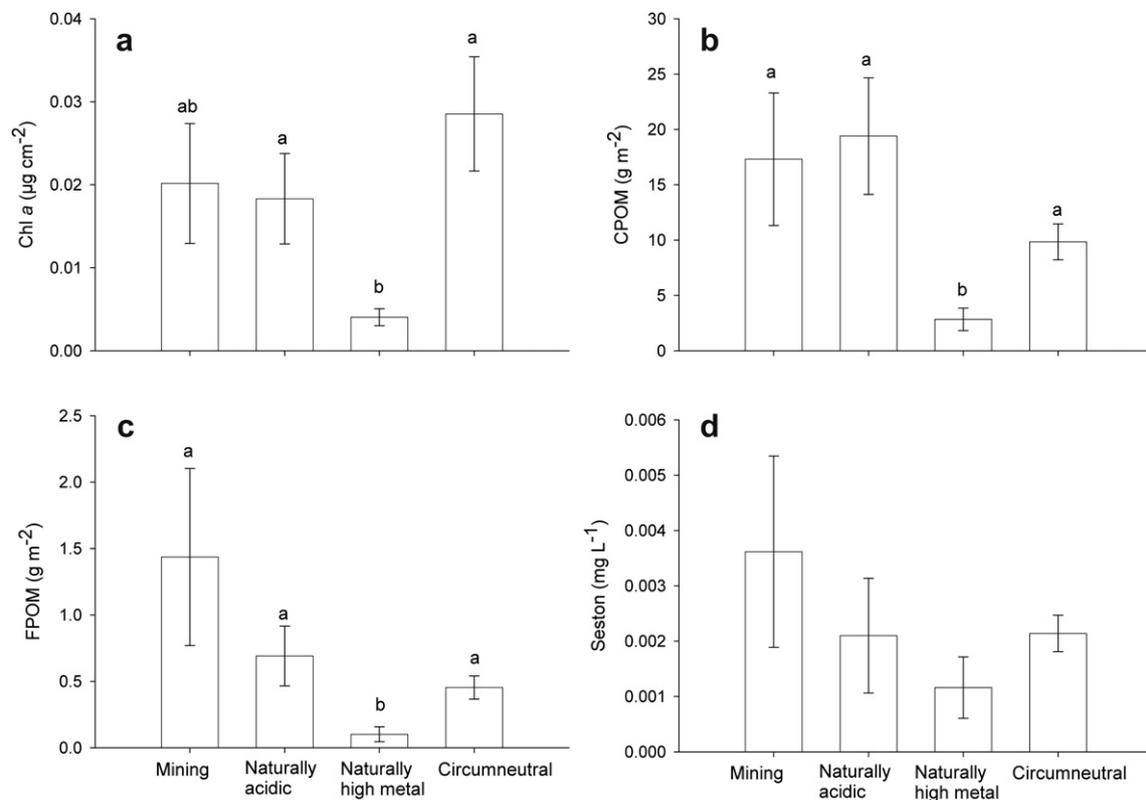

Fig. 2. Mean biomass of basal resources in mining, naturally acidic, naturally high metal, and circumneutral streams ($\pm$SE). a) algae (chlorophyll *a*), b) coarse particulate organic matter (CPOM), c) fine particulate organic matter (benthic FPOM), and d) seston. Significant post-hoc differences ($P < 0.05$) are indicated by different letters above each bar following significant one-way ANOVAs ($P < 0.05$). $N = 5$ stream per type.
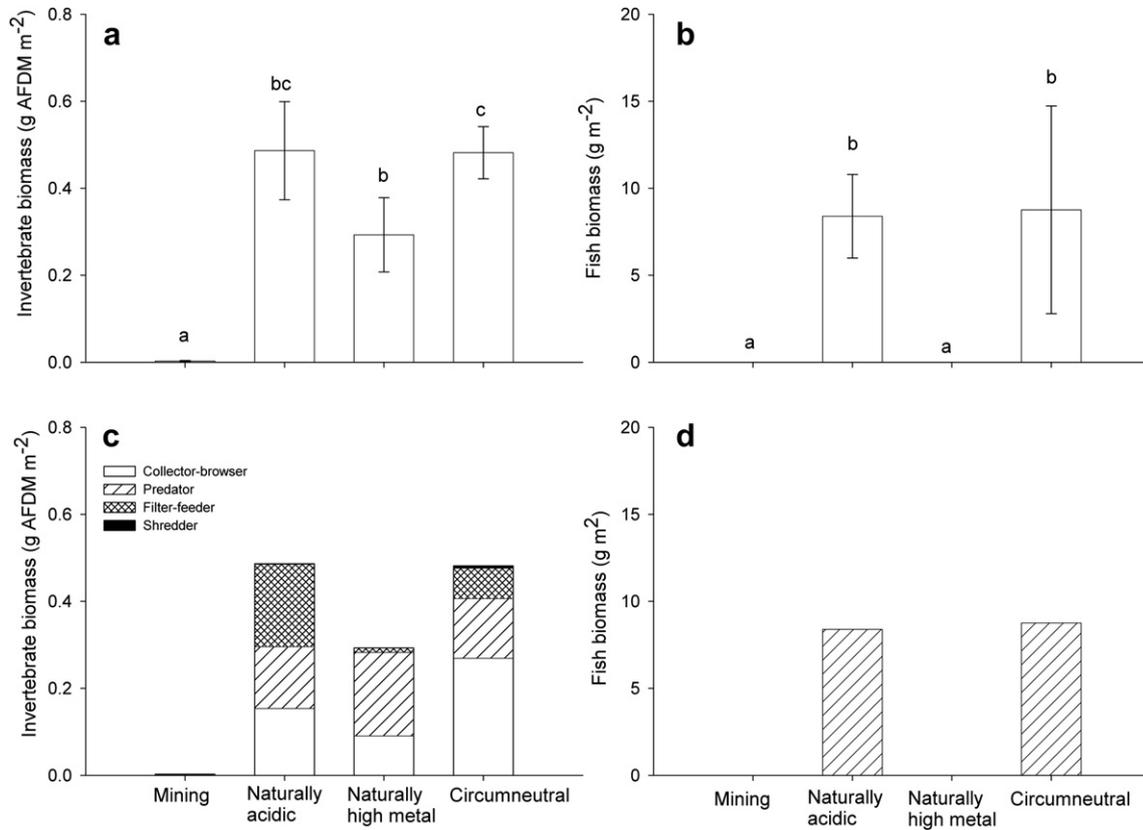
Fig. 3. Mean biomass of (a) invertebrate and (b) fish consumers in mining (low pH, high metal), naturally acidic (low pH, low metal), naturally high metal (circumneutral pH, high metal), and circumneutral (circumneutral pH, low metal) streams. (±SE). Significant post-hoc differences are indicated by different letters above each bar ($P < 0.05$). $N = 5$ streams per group. Mean biomass of (c) invertebrate functional feeding groups and (d) fish (all predatory).

Amorphous detritus (FPOM) was the main basal resource used by dominant primary consumers in mining and naturally acidic streams, while both detritus and algae were more commonly found in diets of primary consumers in circumneutral streams (Table 3). In contrast, green algae and diatoms formed the basis of diets for primary consumers in naturally high metal streams.

3.3. Food web structure

Food webs in mining streams were smaller, had fewer links per species and overall, and higher connectance than webs in all other streams types (Table 4). The structure of naturally high metal stream food webs was more similar to that observed in mining streams than naturally acidic or circumneutral streams, in terms of size (S), number of links, and maximum food chain length. Naturally acidic and circumneutral stream food webs were larger, had more links overall, and higher linkage density (Table 4). Connectance declined as web size increased from small mining webs to larger, more species-rich circumneutral and naturally acidic stream webs ($F_{1,18} = 37.83$, $P < 0.001$; Fig. 4).

Streams were separated into three clusters in the NMDS ordination of food web properties (Fig. 5) and significant differences were observed between food web properties of the stream groups (ANOSIM: Global $R = 0.70$, $P < 0.001$). Specifically, pairwise comparisons of mining and naturally high metal streams indicated that these groups differed significantly from each other and from the other two streams types ($P < 0.02$). In contrast, naturally acidic and circumneutral streams were very similar in terms of food web properties ($P = 0.52$). Average similarities (SIMPER) of food web properties within groups were high in mining, naturally acidic, naturally high metal, and circumneutral streams (average Bray–Curtis similarity = 92.3%, 89.3%, 90.5%, and 92.6%, respectively). Differences in numbers of links and web size made the greatest contributions to dissimilarity between food webs (Table 4). BEST analysis indicated that specific conductivity, dissolved nickel concentration, and elevation together provided the best explanation (62%) of the pattern in food web properties among stream groups (Global test $P < 0.001$). However, specific conductivity alone explained 49% of this pattern.

4. Discussion

Our findings confirm that anthropogenic acidity and metal contamination have a stronger negative effect on food web structure than natural sources. This effect is driven primarily by substantial changes in consumer communities and diet that resulted in differences in web size and number of links. Small, fishless mining stream food webs differed most from large, species-rich webs in naturally acidic and circumneutral streams that had many links overall (Fig. 6). However, we observed very little difference between the structures of naturally acidic and circumneutral webs due to comparable community composition and diet of consumers. Surprisingly, naturally high metal stream webs were more similar to mining than naturally acidic webs in terms of size, number of links, and the absence of fish as a top predator. Specific conductivity was identified as the most important water chemistry predictor distinguishing all streams based on food web properties. Together, these results highlight the potential importance of metals, regardless of source, as a driver of food web structure.

Table 2
Consumer taxa present in food webs and the number of streams in which they were found (− = absent).

Functional feeding group	Taxon	Stream type			
		Mining	Naturally acidic	Naturally high metal	Circumneutral
Vertebrate predator	Anguilla australis	−	1	−	1
	Anguilla dieffenbachii	−	4	−	4
	Galaxias brevipinnis	−	2	−	2
	Galaxias fasciatus	−	1	−	1
	Gobiomorphus hubbsi	−	−	−	1
	Gobiomorphus huttoni	−	1	−	2
	Salmo trutta	−	2	−	3
Invertebrate predator	Ameletopsis perscitus	−	2	−	−
	Aphrophila spp.	−	2	−	1
	Archichauliodes diversus	−	2	4	3
	Chironomidae (predatory)	1	4	−	5
	Costachorema spp.	−	4	3	4
	Hydrobiosella mixta	−	−	3	1
	Hydrobiosella spp.	−	3	−	3
	Hydrobiosis frater	−	2	1	1
	Hydrobiosis gollanis	−	2	−	1
	Hydrobiosis spp.	−	5	−	5
	Hydrochorema spp.	−	1	−	1
	Neurochorema spp.	−	2	−	−
	Plectrocnemia maclachlani	−	2	−	1
	Psilochorema spp.	1	3	1	4
	Stenoperla maclellani	−	1	2	1
	Stenoperla prasina	−	3	−	3
Collector browser	Chironomidae (non-predatory)	3	5	5	5
	Deleatidium spp.	1	5	4	5
	Helicopsyche spp.	−	−	−	3
	Homalaena sp.	−	4	−	3
	Hydora sp.	−	4	1	5
	Limonia nigrescens	−	−	−	1
	Nesameletus ornatus	−	−	4	4
	Oniscigaster distans	−	−	−	2
	Orthocladiinae	2	1	1	3
	Oxyethira albiceps	−	1	−	2
	Potamopyrgus antipodarum	−	−	−	1
	Pycnocentria spp.	−	3	−	4
	Rakiura vernale	−	−	−	1
	Zelandobius confusus	−	2	−	2
	Zelandobius spp.	−	3	−	5
	Zelandoperla sp.	−	2	−	3
	Zelolessica meizon	−	1	−	−
Shredder	Olinga feredayi	−	−	−	2
	Triplectides spp.	−	1	−	2
Filter feeder	Hydropsyche sp.	−	5	4	3
	Austrosimulium spp.	−	4	1	4
	Coloburiscus humeralis	−	3	−	4

Table 3
Basal resource use by numerically dominant primary consumers in each stream type (R = rare, <5%; C = common, 5–20%; A = abundant, >20%). * = non-predatory chironomids.

Stream type	Consumer taxon	Basal resources				
		CPOM	FPOM	Algae	Filamentous algae	Diatom
Mining	Chironomidae*	−	A	R	C	R
Naturally acidic	Deleatidium spp.	−	A	C	C	C
	Chironomidae*	R	C	C	C	C
	Austrosimulium	−	A	R	−	R
	Hydropsyche	R	A	−	C	−
	Coloburiscus humeralis	R	A	R	R	R
Circumneutral	Deleatidium spp.	R	C	R	R	−
	Chironomidae*	R	C	C	R	C
	Hydora spp.	−	C	C	−	C
Naturally high metal	Deleatidium spp.	−	C	A	−	A
	Chironomidae*	−	−	A	−	A
	Austrosimulium	−	A	R	−	R
	Nesameletus ornatus	−	C	A	−	A
	Hydropsyche	R	A	A	−	C

quality may limit invertebrate population sizes. For example, filamentous green algae can proliferate in mining impacted streams but may be inaccessible to many invertebrates as a food resource (Niyogi et al., 1999; Bray et al., 2008). However, we found that chironomids commonly consumed filamentous green algae, where present in mining streams in addition to amorphous detritus, which was their primary basal resource. Furthermore, metal hydroxide deposits, which can coat leaf litter and restrict decomposition (Schlief and Mutz, 2005) may negatively affect consumer feeding on detrital resources.

4.2. Comparison of food webs with anthropogenic vs. natural sources of acidity and metals

Our analysis revealed distinct differences in web size and number of links between mining and naturally acidic stream food webs. In particular, mining streams had smaller webs (i.e. five times fewer species) and 92% fewer links than those in naturally acidic streams. Notably, fish and crayfish commonly found in nearby naturally acidic waters were absent from mining streams. Many links were absent because fish were not found in mining streams due to the extreme water chemistry that exceeded the known pH and metal tolerance ranges of fish species in Westland (Greig et al., 2010). As larger species found higher in the food web, fish often add more links than invertebrates (Cohen et al., 2003). In New Zealand, almost all fish are predatory and feed generally on diverse invertebrate communities. Where present in naturally acidic streams, fish contributed 7–30 links per species whereas invertebrates contributed only 5–12 links on invertebrate prey. In mining streams, the number of links between invertebrate predators and prey items was further reduced to 1–2 per species. This represented a significant reduction and narrowing of energy pathways in these species-poor, sparsely populated mining streams. The abundance of large-bodied invertebrate predators often increases in the absence of fish in both acidic and heavy metal-contaminated waters (e.g. Hildrew, 1992; Rutherford and Mellow, 1994). However, this was not observed in our mining streams, where low abundances of small-bodied chironomids (Tanypodinae) and a free-living caddisfly (Psilochorema spp.) assumed the top food web position.

The absence of fish, smaller and less diverse invertebrate communities, and a reduced number of links resulted in naturally high metal streams sharing key structural properties with mining streams. Nickel is not highly mobile between the water and sediment at the pH levels observed in our naturally high metal streams (Table 1; Garrett, 2000). While the dissolved nickel concentrations

4.1. Short and simple mining food webs

Mining stream food webs were small, simple structures that were sparsely populated by low densities of tolerant invertebrates and lacked fish, which is typical of streams receiving AMD (e.g. Cherry et al., 2001; Greig et al., 2010). The combination of very few consumer species and the number of basal resource categories meant that only a small number of links were possible in our mining stream webs, because the proportion and position of species in different trophic levels limits the number of links (Schmid-Araya et al., 2002). Therefore, as a result of all consumers feeding on almost all available basal resources, mining webs had a high proportion of realised links and high connectance. Basal resource quantity was sufficient to support a small consumer community in mining streams. However, accessibility and food

Table 4
Food web properties for each stream group. S = web size, L = links, max FCL = maximum food chain length, basal sp., intermediate sp., and top species = proportions in web, predator:prey ratio (Cohen, 1977), C = connectance (L/S^2), L/S = links per species. Values shown are group means (±SE) and ranges. $N = 5$ streams per type.

Stream type	Mining		Naturally acidic		Naturally high metal		Circumneutral	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
S	6.4 ± 0.5	5–8	30.0 ± 3.5	17–37	11.6 ± 1.0	8–13	34.8 ± 4.2	28–51
L	8.8 ± 1.4	6–12	116.8 ± 21.4	37–165	26.8 ± 5.6	11–45	137.8 ± 27.8	96–247
Max FCL	2.0 ± 0	2–2	2.8 ± 0.2	2–3	2.0 ± 0	2–2	3.0 ± 0	3–3
Basal sp	0.53 ± 0.06	0.50–0.80	0.18 ± 0.02	0.11–0.24	0.29 ± 0.03	0.23–0.38	0.17 ± 0.02	0.12–0.21
Intermediate sp	0.07 ± 0.07	0–0.33	0.71 ± 0.04	0.53–0.84	0.47 ± 0.05	0.36–0.62	0.74 ± 0.02	0.64–0.77
Top sp	0.40 ± 0.03	0.33–0.50	0.11 ± 0.04	0.03–0.24	0.24 ± 0.03	0.15–0.31	0.09 ± 0.02	0.06–0.14
Predator:Prey	1.37 ± 0.19	1.00–2.00	1.07 ± 0.03	1.0–1.19	1.07 ± 0.05	0.90–1.20	1.10 ± 0.03	1.0–1.20
C	0.21 ± 0.02	0.17–0.24	0.13 ± 0.01	0.10–0.14	0.19 ± 0.02	0.15–0.27	0.11 ± 0.01	0.10–0.13
L/S	1.35 ± 0.12	1.00–1.71	3.73 ± 0.44	2.18–4.85	2.22 ± 0.36	1.38–3.46	3.85 ± 0.28	3.21–4.84

in these streams exceeded the known tolerance range of most New Zealand fish (Greig et al., 2010), they are not considered lethal for other fish taxa (Pyle et al., 2002; Pane et al., 2002). Nevertheless, some studies have shown that fish can be sensitive to chronic exposures (35 µg L^{-1}; Nebeker et al., 1985). Reduced prey availability may also contribute to the absence of fish in these naturally high metal streams. The less diverse and reduced invertebrate prey base may compromise fish feeding as reported in metal-contaminated lakes (Kövecses et al., 2005). This bottom-up energetic deficiency may stem from low levels of basal resources available to primary consumers in these streams. Our naturally high metal streams did occur at higher elevations than all other streams in this study and as many fish species are migratory, fish diversity does tend to decline with elevation in New Zealand. However, it seems unlikely that elevation limits fish distribution in this area, as brown trout, longfin eel, and several species of galaxiids are found in low metal streams at similar elevations (760–1150 m ASL) in nearby ranges (New Zealand Freshwater Fish Database, 2009).

4.3. Similarity between naturally acidic and circumneutral food webs

We observed no negative effect of natural acidity on food web structure. In fact, webs were highly comparable between naturally acidic and circumneutral streams. Both webs were species-rich, included fish as a top predator, and had many links overall. Consumer community-level patterns in our study were consistent with previous work that has shown similarities in invertebrate and fish community composition down to about pH 4.5 in New Zealand (Collier et al., 1990; Greig et al., 2010). It is likely that adaptation to

naturally low pH over evolutionary time partially accounts for these diverse communities in naturally acidic waters (Collier et al., 1990 Petrin et al., 2008). In addition, monomeric Al mobilized in naturally acidic streams is made biologically unavailable by dissolved organic carbon, so organisms are less likely to be metal-stressed (Collier et al., 1990). Our work builds on these earlier studies by identifying links between species and constructing food webs based on gut content analysis. Having many of the same predator and prey species resulted in similar patterns in connectance, number of links overall, and linkage density in these food webs.

Naturally acidic and circumneutral streams food webs have not been compared before, although one of the best described food webs in the ecological literature is for an acidic stream (Broadstone Stream; Hildrew, 2009). Food web properties in our naturally acidic streams were similar to those reported in early descriptions of Broadstone Stream (pH 4.5–6.6) in south-east England (Lancaster and Robertson, 1995; Woodward and Hildrew, 2001). Furthermore, these food web properties were comparable to properties reported in similar-sized circumneutral stream webs constructed with similar taxonomic resolution for basal species (e.g. Tavares-Cromar and Williams, 1996; Mantel et al., 2004). The structural similarities between naturally acidic and circumneutral stream food webs suggest that key ecosystem processes differ little between these stream types.

4.4. The importance of metals to stream food webs

Conductivity was identified as a key chemical variable explaining the differences in food web properties between stream types. As conductivity reflects in part the concentration of dissolved
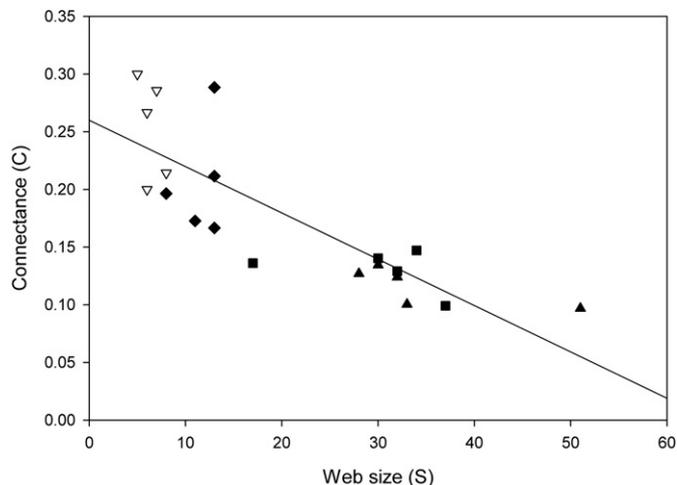

Fig. 4. Connectance (C) decreases as food web size (S) increases in all streams (open inverted triangles = mining, closed squares = naturally acidic, closed diamonds = naturally high metal, and closed triangles = circumneutral streams).
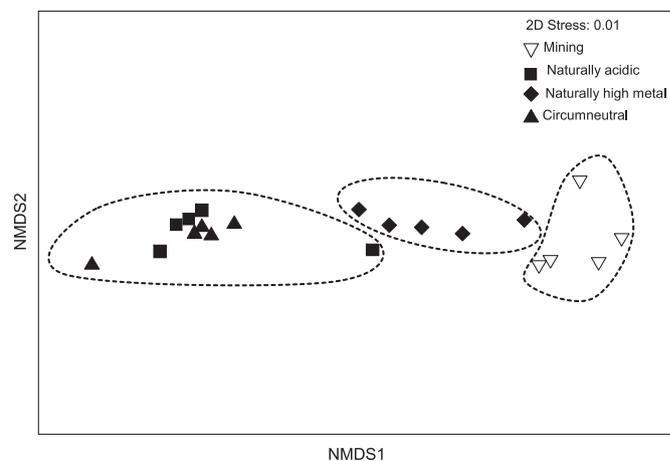

Fig. 5. NMDS ordination of streams using food web properties. Statistically different groups are identified by broken lines based on ANOSIM ($P < 0.01$).
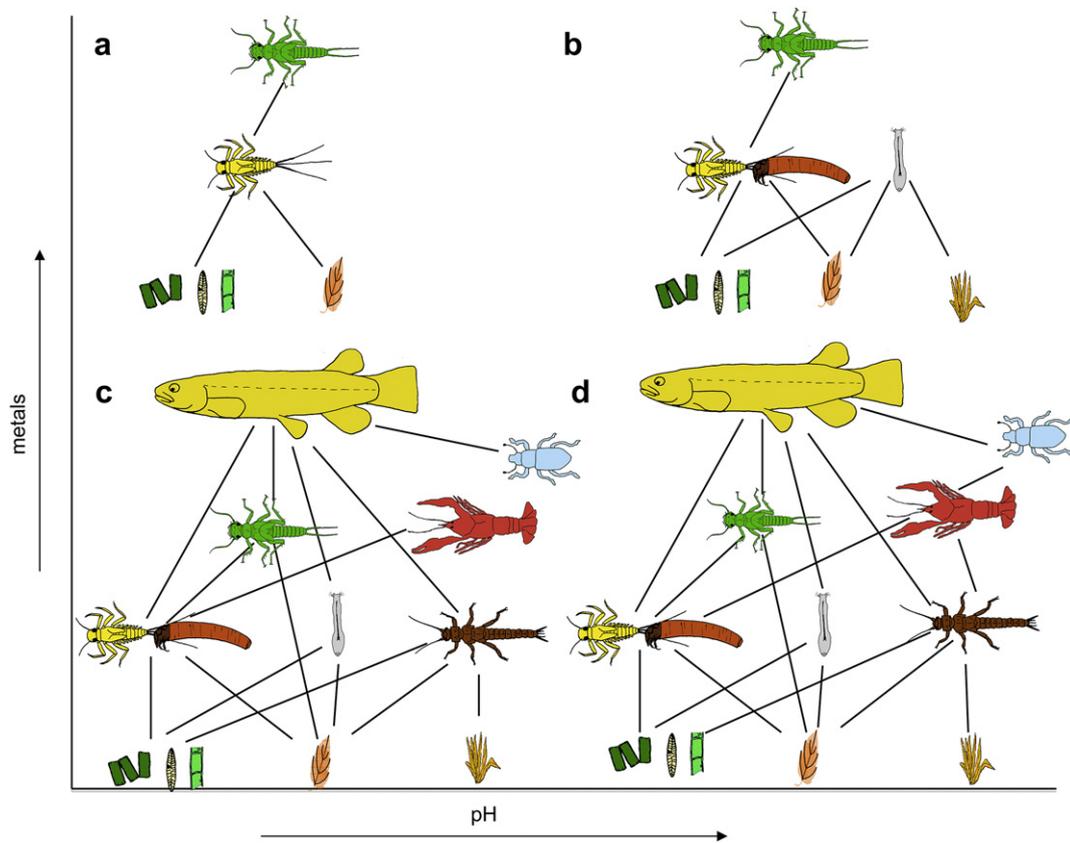
Fig. 6. Simplified food web diagrams in a) mining, b) naturally high metal, c) naturally acidic, and d) circumneutral streams. Links are based on gut contents analysis. Each node represents a combination of several species (e.g. stonefly represents multiple predatory invertebrate species).

metals, which is a function of pH, it can be considered a more effective indicator of mining contamination than pH alone (Winterbourn and McDiffett, 1996). The similarities between key food web properties of mining and naturally high metal streams highlight the potential importance of metals, regardless of source, as a driver of food web structure. This suggestion is consistent with that of Greig et al. (2010) who found that dissolved metal concentrations (Al, Zn, Mn, and Ni), rather than pH, explained fish diversity, density, and biomass in New Zealand streams with natural and mining-induced acidity. Limited information is available for metal tolerances of aquatic invertebrates in New Zealand (Hickey and Clements, 1998) but evidence from elsewhere indicates metals are an important force driving community structure and species interactions (e.g. Gower et al., 1994; Clements, 1999; Clements et al., 2000). More work is needed to understand the direct and indirect effects of metals in streams receiving either anthropogenic or natural inputs. In particular, very little research has been done to examine the effects of naturally elevated metal levels on aquatic biota. Understanding the role of metals in stream food webs is important because metals can bioaccumulate and transfer up the food chain, although this varies considerably between metals, species, and feeding pathways (e.g. Woodward et al., 1995; Beltman et al., 1999; Winterbourn et al., 2000b).

5. Conclusion

We found small and extremely simplified food webs in chronically stressed mining streams indicating that the combination of anthropogenic acidity and metals has serious implications for stream food webs. Stressors outside the natural range for a region clearly have negative impacts on food webs due to substantial changes at

each trophic level. Our comparison of stream food web structure revealed the importance of source (anthropogenic vs. natural) on food web size, food chain length, and interactions between species. Furthermore, the notable differences between mining and naturally acidic stream food web structure suggests that knowledge of food webs in naturally acidic streams is not necessarily useful for understanding and predicting food web patterns in streams acidified by mine drainage. It may be more useful to compare food web structure and function in mining impacted streams with those reported in other metal-stressed streams.

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.envpol.2011.10.024.

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