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PERSPECTIVES

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Consequences of acid mine drainage for the structure and function of benthic stream communities: a review

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Abstract. Streams affected by acid mine drainage (AMD) are highly stressed ecosystems and occur worldwide. These streams typically have low pH, high concentrations of dissolved metals, and substrata coated with metal hydroxide precipitates. This combination of chemical and physical stressors creates a challenging environment for aquatic biota. We provide a synthesis of the effects of AMD on stream food webs to provide a holistic perspective of these highly stressed ecosystems. First, we reviewed the effects of AMD on the structure and function of algal, microbial, invertebrate, and fish communities. Then, we used this published information to propose generalized food webs and identify areas for future research. In general, AMD-affected streams have depauperate communities that are dominated by a few tolerant species, and ecosystem processes (e.g., decomposition) are often impaired. Biota respond differently to the individual stressors (e.g., pH compared to precipitates), which may complicate remediation efforts that focus primarily on neutralizing acidity and removing metals from mine discharges. Food webs in these streams are substantially altered because basal resources are less productive or inaccessible, microbial processing of organic matter is slow, many grazers and shredders are absent, and fish are replaced by invertebrates as top predators. Structurally, declines in species diversity and the loss of fish shorten and simplify food webs by decreasing the number of interactions among species. Functionally, most energy pathways are weakened by disrupted trophic links, and this problem should to be a key target of restoration efforts. We think research that focuses on species interactions in a foodweb context is needed to provide a better understanding of community organization and functioning in these highly stressed ecosystems.

Key words: AMD, stress, periphyton, microbial, invertebrate, fish, primary production, decomposition, ecosystem process, food web.

The global increase in mining activities raises increasing concern about effects on stream ecosystems, our lack of understanding of mining's complex ecological effects, and the need for effective mitigation and restoration techniques (Palmer et al. 2010). Acid mine drainage (AMD) is one of the most widely documented consequences of mining that affects freshwaters worldwide. AMD is often associated with coal, pyritic S, Cu, Zn, Ag, and Pb mining operations. AMD runs off active and abandoned mine sites into surface and groundwater systems and causes widespread contamination that is exported downstream (Gray 1997). Streams receiving mine drainage are highly acidic (often pH < 3) with elevated concentrations of dissolved metals (e.g., Al, Cu, Fe, Zn), and, in many cases, substrata are coated with metal hydroxide precipitates.

AMD exerts chemical and physical stresses on stream biota, but separating the effects of acidity, metal toxicity, and habitat degradation on biota in streams receiving AMD inputs is a significant challenge for freshwater scientists. Authors of a number of studies focused on patterns in community

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TABLE 1. Chemical and physical characteristics of streams affected by acid mine drainage (AMD). These streams were selected from the literature to demonstrate the wide variation in characteristics of AMD in streams from different sources and do not necessarily reflect the condition of all AMD-affected streams from a particular region. n/a = data not available.

Stream	Source	pH	Conductivity (μS/cm)	Metal concentration (mg/L)	Metal hydroxides (present/absent)	Reference
Peña del Hierro, Spain	Ag, Cu, various	1.5	20,500	3325.0 Fe[a], 82.1 Zn[a], 34.9 Cu[a], 1.8 Pb[a]	n/a	Sabater et al. 2003
St. Kevin's Gulch, USA	Ag	2.7	n/a	80.0 Zn[b]	Present	Niyogi et al. 2001
Miller Creek, New Zealand	Coal	2.9	944	16.5 Al[b], 5.2 Fe[b]	Absent	Winterbourn et al. 2000
Mosteirão, Portugal	Cupriferous pyrite	3.0	n/a	1.4 Cu[a], 2.3 Fe[a], 0.2 Pb[a]	n/a	Gerhardt et al. 2004
Gamble Gulch, USA	Ag	3.8	831	1.1 Zn[b]	Present	Niyogi et al. 2009
Neubecks Creek, Australia	Coal	5.1	787	~0.2 Ni[b], ~0.3 Zn[b]	Present	Battaglia et al. 2005
Burnett Stream, New Zealand	Coal	4.1	77	0.4 Al[b], 0.7 Fe[b]	Absent	Winterbourn et al. 2000
Slippery Rock Creek, USA	Coal	6.3	690	0.4 Fe[b], 0.1 Al[b], 0.07 Zn[b]	Present	DeNicola and Stapleton 2002
Zerbe Run, USA	Anthracite coal	6.3	524	7.1 Fe[b], 0.5 Al[b]	Present	MacCausland and McTammany 2007

[a] Total metals
[b] Dissolved metals

composition and relative abundance have demonstrated the negative effects of AMD on benthic communities. However, surprisingly few investigators have examined ecosystem processes in these streams. Focusing on the network of interactions among species by adopting a foodweb approach may be an effective way to understand stressed ecosystems and to complement existing research methods (Culp et al. 2005, Woodward 2009). This approach is useful because it focuses on the relationships between consumers and resources and may provide insights into direct and indirect effects of AMD on stream ecosystems. To our knowledge, a complete food web in an AMD-affected stream has not been published. To develop a perspective on food webs, we reviewed the published literature on the effects of AMD on the structure and function of microbial, algal, invertebrate, and fish communities in affected streams, and we present potential mechanisms responsible for these patterns. We then used this published information to assemble generalized food webs. In some cases, we also drew on insights provided in studies in similarly stressed (i.e., acidified or metal-contaminated) streams. We did not include macrophytes, bryophytes, and meiofauna in this review even though they are important components of stream food webs.

AMD: General Chemistry

AMD is formed when sulfide minerals and associated heavy metals are exposed to weathering processes during excavation of mineral deposits (Kelly 1988). Sulfuric acid is generated by the chemical oxidation of sulfides exposed to air (atmosphere) and water during excavation, reactions that are catalyzed by the activity of S-oxidizing bacteria. Metals are leached from the disturbed substrata under these highly oxidized and acidic conditions. The composition and concentration of metals found in AMD are related to the mineral deposits from which the drainage originated (Lottermoser 2003). The chemical and physical characteristics of streams affected by AMD can vary widely (Table 1), and the degree of impact depends primarily on the extent of dilution and buffering capacity of the receiving stream (Gray 1997). Thus, a large stream underlain by limestone would be less susceptible than a small headwater stream flowing over granitic bedrock or sandstone. The availability and speciation of metals is linked to pH. For example, when AMD enters a stream with a higher pH, the solubility of some metals may be exceeded (Table 2). Under these conditions of reduced acidity, metal hydroxides can precipitate out of solution and coat the streambed in the form of loose flocs or tight plaques. Precipitation of ferric iron as ferric hydroxide, frequently termed *yellow boy* is a visible sign of AMD that occurs when pH is $>\sim 3.5$ (Harding and Boothroyd 2004). In addition, streams associated with active mine sites may be turbid because of suspended metal precipitates or inorganic material (e.g., coal fines). On the

Table 2. Metal hydroxides precipitate at different pH levels (after Harding and Boothroyd 2004).

Metal	Minimum pH for precipitate formation
Sn	4.2
Fe^{3+}	3.5–4.3
Al	4.9–5.4
Pb^{2+}	6.3
Cu^{2+}	7.2
Zn	8.4
Ni	9.3
Fe^{2+}	9.5
Cd	9.7

other hand, streams downstream of abandoned mines or adits (underground mine entrances) often appear clear because metals remain dissolved under highly acidic conditions. Metals can cycle between particulate and dissolved forms many times as they move downstream. Defining criteria that identify the level of AMD impact (e.g., mild, moderate, severe) on streams may be difficult because of the complex nature of chemical and physical stress associated with different dissolved metals and metal hydroxide precipitates and variation in natural pH ranges between regions.

Effects of AMD on Benthic Communities

Periphyton

Periphyton is highly responsive to increased acidity and metal hydroxides that coat the streambed in AMD-affected streams (Douglas et al. 1998, Niyogi et al. 1999, Verb and Vis 2001, 2005, DeNicola and Stapleton 2002). Several investigators have shown that algal species richness and diversity are consistently lower in the presence of AMD than in unaffected streams (Fig. 1) because acid-sensitive species are replaced by a few species of tolerant diatoms (e.g., *Eunotia* spp.) or filamentous green algae (e.g., *Klebsormidium* spp.) (Douglas et al. 1998, Verb and Vis 2000, Bray et al. 2008). Verb and Vis (2005) modeled species data from 56 streams and showed that pH was a strong predictor of periphyton community composition. However, this predictability declines with decreasing stress along AMD impact gradients as other abiotic and biotic factors increasingly structure the community (Verb and Vis 2001, 2005, Bray et al. 2008). Species loss often is attributed to physiological sensitivity to low pH and high concentrations of dissolved metals. Tolerant species survive by reducing proton influx (H^+ ions), increasing proton pump

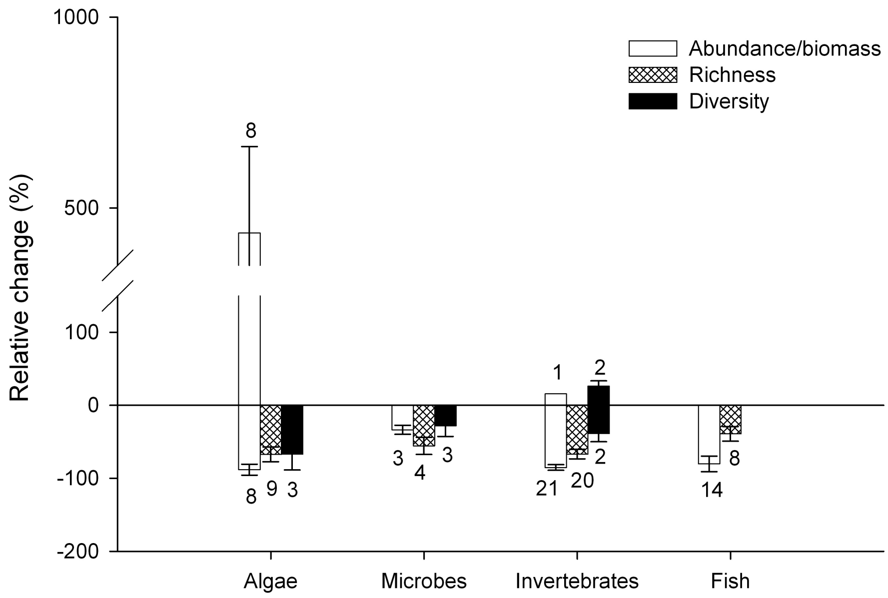

Fig. 1. Mean relative change (±1 SE) of community measures (abundance/biomass, species richness, species diversity) at sites affected by acid mine drainage (AMD) relative to nearby reference streams. The total number of sites in which relative change was positive or negative is given above or below each bar. Data sources: algae (Sode 1983, McKnight and Feder 1984, Douglas et al. 1998, Niyogi et al. 1999, 2002a, Verb and Vis 2000, 2005, Besser et al. 2001, Bray et al. 2008); microbes (Bermingham et al. 1996a, López-Archilla et al. 2001, Niyogi et al. 2002b, 2009, Schlief and Mutz 2005, Lear et al. 2009); invertebrates (Warner 1971, Letterman and Mitsch 1978, Sode 1983, McKnight and Feder 1984, Winterbourn and McDiffett 1996, Schultheis et al. 1997, Gray 1998, Soucek et al. 2000a, 2003, Winterbourn et al. 2000, Cherry et al. 2001, Gerhardt et al. 2004, Battaglia et al. 2005, MacCausland and McTammany 2007); and fish (Letterman and Mitsch 1978, Scullion and Edwards 1980, McCormick et al. 1994, Rutherford and Mellow 1994, Gray 1998, Besser et al. 2001, Schorr and Backer 2006, Greig et al. 2010).

efficiency, and forming metal complexes that prevent entry of metals into cells (Gross 2000, Novis and Harding 2007). Several authors have suggested that indirect effects of pH, which changes habitat quality through precipitation of metal hydroxides, may explain low species richness because deposits can coat streambed surfaces, smother algae, reduce light penetration, and decrease sites for colonization (McKnight and Feder 1984, Niyogi et al. 1999).

Algal biomass can vary substantially in AMD-affected streams. High biomass usually indicates dominance of large-celled filamentous green algae instead of diatoms (Verb and Vis 2000, Bray et al. 2008). Tolerant filamentous green algae, such as *Ulothrix*, can proliferate when metals remain dissolved in highly acidic waters (pH < 3) and adequate light creates ideal conditions for growth downstream of abandoned mine adits (Winterbourn et al. 2000) or under conditions of improved water and substrate quality after experimental diversion of AMD (Niyogi et al. 1999). On occasion, tolerant algal species may be abundant, possibly reflecting a preference for low pH or reduced interspecific competition for nutrients, light, or space (Sabater et al. 2003, Novis and Harding 2007). Some authors have speculated that reduced grazing pressure because of low density (or absence) of key grazers or the inability of tolerant grazers to consume dominant algae may lead to high algal biomass, but these interactions have not been tested in AMD-affected streams (Niyogi et al. 2002a, Bray et al. 2008). Low algal biomass has been reported commonly in the presence of metal hydroxides (McKnight and Feder 1984, Verb and Vis 2000, Bray et al. 2008) even when rates of deposition are low (Niyogi et al. 1999). Biomass was almost 50% lower at sites with ferric hydroxide deposition than at sites where it was absent (Sode 1983). Metal hydroxide deposits can suppress biomass by direct toxicity or by smothering the algae. Some metal deposits are more detrimental to algae than others (e.g., Al $>$ Fe; Niyogi et al. 1999), but the mechanism for this difference is not clear. In field studies, periphyton biomass was more negatively affected by physical stress from metal hydroxides than by pH or metals (McKnight and Feder 1984, Niyogi et al. 2002a). High variability in algal biomass that could not be traced to AMD has been observed in some studies. These findings highlight the importance of considering other factors that might influence algal communities (e.g., nutrients, grazing, interspecific competition; Verb and Vis 2000, Sabater et al. 2003) when evaluating the effects of AMD.

Metal hydroxide deposition has been implicated as a cause of reduced primary production, but this key ecosystem process has been investigated in only a limited number of studies. Sode (1983) and Niyogi et al. (2002a) observed marked declines in primary production at sites with high ferric iron and aluminum hydroxide precipitates, respectively. In 58 streams distributed along an AMD impact gradient, the rate of hydroxide deposition explained 50% of the variation in net primary productivity (<0.1–54 mg C m^{-2} h^{-1}) (Niyogi et al. 2002a). Moreover, along this AMD gradient, tolerant species were able to compensate to maintain function (and biomass) under chemical (pH, dissolved metals) but not physical (metal hydroxide deposits) stress. Production was low even at moderate levels of physical stress (Niyogi et al. 2002a). Primary production also may be limited by low HCO_3^- concentrations and by diffusion of CO_2 into the atmosphere that increases as acidity rises in the water column of streams receiving AMD (Allan and Castillo 2007). Breakdown of the HCO_3^- buffering system in acidified waters effectively reduces the amount of dissolved inorganic C (DIC) available for photosynthetic activity and benthic algal growth. For example, Fonyuy and Atekwana (2008) demonstrated the transformation of DIC to CO_2 gas in AMD streams and reported seasonal losses of 50 to 98% of DIC. However, species able to use DIC at low concentrations can thrive despite this loss, as shown by metaphytic blooms of filamentous green algae in an acidified lake with low DIC (82 μmol/L; Turner et al. 1987). Algal production also may be limited by other factors in AMD streams, including nutrient availability, light, flow, and grazing pressure. Some evidence suggests that AMD streams are nutrient poor (Hamsher et al. 2002, Novis and Harding 2007) because of low concentrations of inorganic N ($<$40 μg/L; P. M. Novis, Landcare Research, unpublished data) or precipitation of orthophosphates in acidic waters with high concentrations of Al (Gross 2000). However, high concentrations of dissolved inorganic N ($>$200 μg/L) and dissolved reactive P ($>$40 μg/L) have been recorded in some highly acidic AMD streams (D. K. Niyogi, University of Missouri, unpublished data). Clearly, significant gaps exist in our understanding of how primary production is affected by AMD and how nutrient availability and other controlling factors may influence the process in affected streams.

Bacteria and fungi

Microbial community structure and activity respond strongly to AMD. For the most part, microbial diversity, richness, and biomass are lower in streams receiving AMD relative to unaffected streams (Fig. 1). However, diverse and morphologically complex assemblages of bacteria, including Proteobacteria, Nitrospira, Firmicutes, and Acidobacteria, have been described on substrata in acidic, metal-rich AMD in both surface (López-Archilla et al. 2001, 2004) and subsurface waters (Baker and Banfield 2003). A diverse array of fungi, from yeasts to filamentous forms, also has been observed in AMD surface waters (Bridge Cooke 1976, López-Archilla et al. 2001, Amaral Zettler et al. 2002). However, fungal communities in AMD-affected and unaffected reaches or streams have been compared in only a few studies. In these experimental studies, fungal diversity estimated from conidia identification or production was lower on leaf litter conditioned in affected than in unaffected streams (Bermingham et al. 1996a, Niyogi et al. 2002b, 2009). Which factors drive community structure in these systems is unclear because information on bacterial and fungal communities is so scarce. However, some evidence suggests that pH may play a key role in determining microbial community composition. In a recent survey of 17 streams across an AMD gradient, bacterial communities in epilithic biofilm were less diverse in very acidic streams (pH < 3.5) and, based on analysis of deoxyribonucleic acid (DNA) sequences, differences in community structure were driven by low pH (Lear et al. 2009). Low pH can limit the growth of some microbes, but it stimulates the growth of certain Fe-oxidizing bacteria (e.g., *Gallionella*), which use available ferric iron for metabolism (Baker and Banfield 2003). Results of several studies suggest that high abundances of tolerant microbes in AMD streams may be caused by a physiological tolerance of acidic conditions; the absence of shredding invertebrates, which reduce leaf-litter surfaces for colonization or directly consume fungi; or the presence of filamentous green algae, which provides increased surface area for attachment and labile dissolved organic C (DOC) for bacterial growth (Niyogi et al. 2001, Sabater et al. 2003, Lear et al. 2009).

Microbial activity in AMD streams appears to be controlled primarily by the deposition of metal hydroxides, which accumulate as loose flocs or tight plaques on streambed substrata and limit colonization and respiration. Metal hydroxide deposits can reduce substrate availability and limit microbial colonization by coating leaf litter (Gray and Ward 1983, Siefert and Mutz 2001) or reducing periphyton biomass (Niyogi et. al 2002a). Thus, high microbial activity is restricted to periods before hydroxide deposits cover organic matter (Siefert and Mutz 2001, Schlief 2004, Schlief and Mutz 2005). In experimental studies of microbial respiration on leaf litter, breakdown rates consistently decline over time in the presence of metal hydroxide deposits (e.g., 20% in 7 wk, Schlief 2004; 60% in 8 mo, Schlief and Mutz 2005). Similar respiration rates have been reported for leaves coated with loose flocs (Niyogi et al. 2001, 2002b) and tight plaques (Schlief 2004), but the highest rates were always recorded at sites with low deposition. However, Niyogi et al. (2002b) found that respiration did not correspond to fungal biomass. This result was consistent with results obtained by Schlief and Mutz (2005), who observed that leaves from sites with high metal hydroxide deposits had low respiration and moderate fungal biomass. Schlief and Mutz (2005) suggested that hydroxide deposits negatively affect respiration, but also might serve as substrate for colonization by certain species of bacteria or fungi. In the absence of metal hydroxides, microbial activity varies in response to high concentrations of different dissolved metals. Respiration rates were high in an affected stream with high concentration of dissolved Zn (Niyogi et al. 2001). However, respiration rates were lower in the presence of elevated levels of Fe and Ni than at unaffected sites (Bermingham et al. 1996a). The role of reduced microbial activity in litter decomposition has been studied (see Synthesis – A Foodweb Perspective below), but consequences for organic matter retention and export to downstream communities have not yet been addressed.

Invertebrates

Invertebrate species richness, diversity, and abundance are frequently reduced in streams receiving AMD relative to unaffected streams (Fig. 1). Communities often are numerically dominated by acid-tolerant species of chironomids, beetles, and true bugs, whereas sensitive species of mayflies, caddisflies, and mollusks are excluded (e.g., Koryak et al. 1972, Gray 1998, Winterbourn 1998). In many severely affected streams, either only a few species remain (Winterbourn 1998, Cherry et al. 2001, Battaglia et al. 2005) or invertebrates are completely absent (Soucek et al. 2003). When AMD enters an unaffected waterway, changes in community structure usually are attributed to rapid and substantial shifts in pH and metal concentrations that exceed the physiological tolerance limits of many species. Stress and mortality are caused by impaired regulation of ions and metabolically active metals (Herrmann et al.1993, Rainbow 2002). These toxic effects can occur in streams receiving short-term episodic inputs (Soucek et al. 2000a, MacCausland and McTammany 2007) or in chronically affected streams (Letterman and Mitsch 1978, Schultheis et al. 1997, Battaglia et al. 2005). In streams with pH > 3.5 where some metals (e.g., Fe) are insoluble, low invertebrate richness and abundance may be caused, in part, by loss of habitat and refugia as substrata are covered by metal hydroxides (Warner 1971, Koryak et al. 1972, McKnight and Feder 1984, Gray 1998). Some evidence indicates that species richness may be limited more by loose, unstable flocs than by tight plaques (DeNicola and Stapleton 2002, MacCausland and McTammany 2007). Furthermore, metal hydroxides can be directly toxic to invertebrates by clogging gill surfaces (e.g., Soucek et al. 2000b). Results from experimental field studies suggest that water chemistry is a stronger predictor than metal precipitates on stream substrata (DeNicola and Stapleton 2002) or contaminated sediments (Cherry et al. 2001, Battaglia et al. 2005) of the distribution and colonization of invertebrates. However, invertebrate responses to metals in water and in substrate are complex and species-specific (Courtney and Clements 2002).

If the regional species pool contains acid- or metal-tolerant species, then total invertebrate species diversity can remain comparable to that in unaffected streams. For example, Gerhardt et al. (2004) reported compensatory replacement of crustaceans, mollusks, and mayflies by beetles and true bugs and increased species diversity downstream of an abandoned cupriferous pyrite mine relative to a nearby reference site. Results of other studies suggest that life-cycle stage, feeding strategy, or reduced competition or predation may be important in understanding the dynamics of tolerant species in AMD-affected streams. For example, acid-tolerant crayfish (*Cambarus* spp.) present in AMD-affected streams where pH was above established lethal limits had increased sensitivity to low pH and intermediate to high levels of dissolved metals during molting (Gallaway and Hummon 1991). Therefore, levels of AMD contamination that are otherwise tolerable can restrict molting success or be lethal during that period. Hünken and Mutz (2007) suggested that feeding on small particles retained in nets coated by metal hydroxides and reduced competition may have contributed to high abundances of a passive filter-feeding caddisfly (*Neureclipsis bimaculata*) in a mining-affected stream.

Results of several studies suggest that predators become numerically dominant in AMD-affected streams, whereas the abundances of other functional groups (filter feeders, collector-gatherers, scrapers, and shredders) tend to decrease (Schultheis et al. 1997, Gerhardt et al. 2004, Barnden and Harding 2005; but see Hünken and Mutz 2007). Similar shifts in functional feeding groups have been observed in acidic (Townsend et al. 1983, Mulholland et al. 1992) and metal-contaminated streams (Clements et al. 2000), except that the decline in shredders varies from the widely observed pattern of replacement of herbivores by detritivores in low-pH streams (e.g., Guerold et al. 1995). Tolerant invertebrate predators can dominate highly acidic (pH $\approx$ 3) stream communities (Gerhardt et al. 2004) or those with abundant Fe floc and precipitates (Barnden and Harding 2005). The absence of fish from AMD-affected streams may promote the dominance of tolerant invertebrate predators and suppress invertebrate prey, as occurs in acidic streams (Hildrew et al. 1984). Kiffney (1996) demonstrated increased predation intensity by stoneflies and increased prey vulnerability in experimental AMD stream channels. Alternatively, reduced interspecific competition subsequent to losses of sensitive predator species or an ability to feed on available prey may explain dominance of tolerant predators. The low abundance of most primary consumers may indicate that the quantity and quality of food resources available for invertebrates is altered in AMD-affected streams. Several investigators have suggested that low periphyton biomass associated with metal hydroxide deposits might reduce food availability or accessibility for grazers, collector-browsers, and scrapers (McKnight and Feder 1984, Niyogi et al. 2002a). Food quality may be affected by high concentrations of metals, which accumulate in periphyton, plant material, bacteria, and fungi (Bermingham et al. 1996b, Winterbourn et al. 2000). Uptake and accumulation of metals in invertebrates varies among metals and among taxa and can reflect differences in feeding habits (Beltman et al. 1999, Winterbourn et al. 2000, Besser et al. 2001). For example, Besser at al. (2001) found elevated concentrations of Zn, Cu, and Cd in a mayfly (*Rhithrogena*) that consumes periphyton, but the highest concentrations of Pb in a detritivorous stonefly (*Zapada*). Diet is clearly an important pathway for metal exposure in invertebrates, even when concentrations of dissolved metals are low in the water column (e.g., Fe; Winterbourn et al. 2000). However, whether metal concentration affects the palatability of these basal resources is not clear. A shredder (*Gammarus pulex*) consumed leaf litter coated with Fe hydroxides at the same rate as leaves conditioned in neutral stream waters in a laboratory feeding experiment, a result suggesting that palatability was not affected by the presence of metal hydroxides (Schlief and Mutz 2006). Fe adsorbed to organic material may have increased the palatability of these leaves (Schlief and Mutz 2006) or Fe-loving bacteria present on the hydroxide surface might be a suitable food resource for some consumers. The relative importance of resource quantity and quality in structuring invertebrate communities in AMD-affected streams requires further investigation.

Fish

Fish typically are absent from AMD-affected streams, particularly when pH < 5. However, if fish are present, their richness and abundance are always low relative to in unaffected streams (e.g., Sullivan and Gray 1992, Rutherford and Mellow 1994, Besser et al. 2001; Fig. 1). Eels (Gray 1998, Greig et al. 2010), centrarchids (Schorr and Backer 2006), and brown trout (Scullion and Edwards 1980, McCormick et al. 1994) have been recorded from AMD-affected streams. Schorr and Baker (2006) found that pH accounted for >70% of the variation in species richness and abundance, a result suggesting that acidity was the primary driver of fish communities in AMD-affected streams. However, if fish are locally adapted to tolerate low-pH waters, then the influence of metals might increase. Greig et al. (2010) showed that dissolved metals (including Fe, Al, Zn, Mn, and Ni) had the strongest negative effect on fish and that pH was a poor predictor of community structure in a survey of fish communities in AMD-affected (pH > 3.1), naturally acidic (pH = 4.3–6.0), and circumneutral (pH > 6.2) streams.

Direct toxicity of low pH and metals, accumulation of metal hydroxides on gill surfaces, streambed degradation, reduced egg viability, decreased food availability, or a metal-contaminated diet have been suggested as potential mechanisms for reduced or absent fish populations in AMD-affected streams (Letterman and Mitsch 1978, Scullion and Edwards 1980, Besser et al. 2001, Greig et al. 2010). Acidity and high concentrations of dissolved metals directly impair ion regulation and interfere with respiration in fish and lead to decreased fitness or death (Baker and Schofield 1982, Wendelaar Bonga 1997, Pane et al. 2004). Metal hydroxides, particularly Al, negatively affect respiration by adhering to and clogging gills (Rosseland et al. 1992). Rapid accumulation of Al precipitates on gills and increased mortality of bluegills (*Lepomis macrochirus*) was linked to freshly mixed AMD-contaminated and circumneutral stream water in experimental stream channels (Henry et al. 2001). These results highlight the potential for heightened toxicity to fish downstream of the confluence of AMD-affected with unaffected streams. Deposition of metal hydroxides and sediments associated with mine drainage also can reduce availability and quality of fish habitat by coating the streambed, which can negatively affect spawning and reproductive success. For example, accumulation of coal wastes and sediments accounted for a 30% reduction in spawning area and high mortality (>97%) of rainbow trout eggs (Scullion and Edwards 1980). Reduced fish density also has been attributed to low food availability and diversity rather than direct metal toxicity (Letterman and Mitsch 1978). Scullion and Edwards (1980) suggested that the change in fish density upstream ($0.18/m^2$) and downstream ($0.03/m^2$) of coal-mine discharge was linked to reduced availability of food because burrowing oligochaetes and chironomids buried in thick metal deposits dominated the downstream benthic invertebrate community. Fish in these polluted reaches fed almost exclusively on terrestrial insects (97% of stomach contents by volume), whereas fish in unpolluted reaches fed predominantly on aquatic invertebrates (86%). Even if food is not limited, accumulation of metals in invertebrates might be toxic to fish (Woodward et al. 1995, Besser et al. 2001). Last, fish may actively avoid waters with high metal concentrations (e.g., Åtland 1998) resulting in low densities or absence from contaminated waters.

Synthesis: A Foodweb Perspective

A foodweb analysis has the potential to provide novel insights into community dynamics and ecosystem function in stressed ecosystems by focusing attention on interactions among species and among trophic levels. This perspective is useful because populations are dependent on how their resources, prey, and predators respond to stress. To our knowledge, no studies have been published that describe a complete food web in an AMD-affected stream, although a highly resolved stream food web has been described for an acidic stream in the UK (Schmid-Araya et al. 2002). Therefore, we assembled 3 generalized food webs that represent likely scenarios in AMD-affected streams (Fig. 2A–C).

Food webs are expected to become shorter and simpler under stress because of loss of sensitive species, declines in community diversity, or removal of entire trophic levels (e.g., top predators) (Odum 1985, McCann 2000). Therefore, we truncated and simplified our proposed food webs in accordance with observed AMD-related changes in the abundance and composition of the algae, invertebrate, and fish communities. Short food chains are maintained by intense and frequent stress and reduced resource availability (Post 2002). The severe and usually chronic nature of AMD reduces algal and benthic invertebrate diversity and eliminates fish (Fig. 2A, B). Furthermore, filamentous green algae, which can dominate the periphyton (Fig. 2A), or detritus coated by metal hydroxide deposits (Fig. 2B) may be physically inaccessible for grazing invertebrate consumers able to tolerate AMD conditions. The reduced availability of these basal resources and low numbers

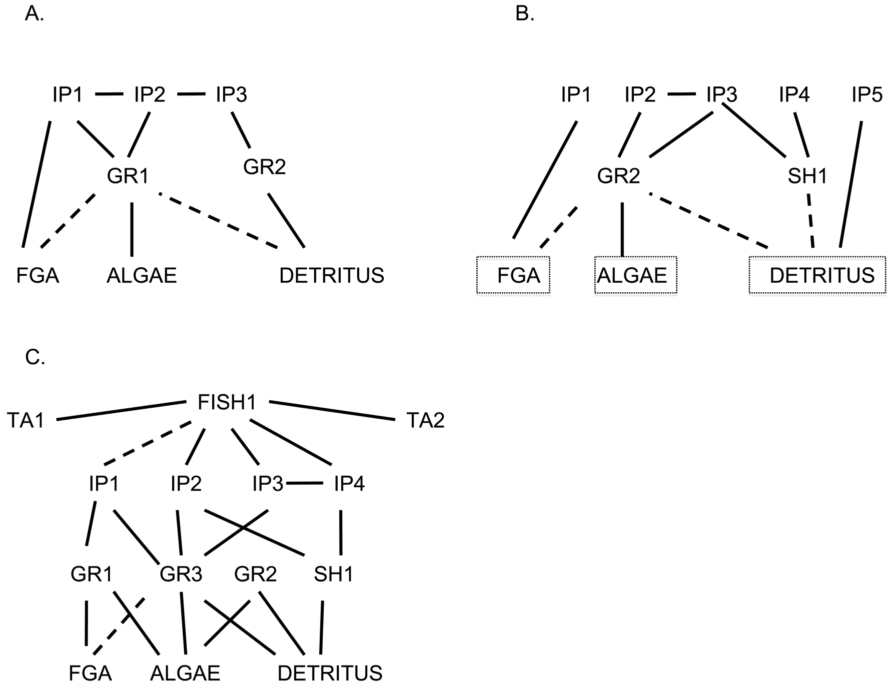

FIG. 2. Food webs in streams affected by acid mine drainage (AMD). A.—Severely affected stream with pH < 3 and high concentrations of dissolved metals. B.—Severely affected stream with metal hydroxide deposits present. C.—Mildly affected stream. Broken lines signify disrupted interactions. Basal resources have been simplified into functional groups. Boxes around basal resources in panel B indicate resources are covered by metal hydroxide deposits. FISH1 = fish species 1; IPx = invertebrate predator species x; GRx = grazer species x; SHx = shredder species x; TAx= terrestrial arthropod species x; FGA = filamentous green algae.

of invertebrate prey in AMD-affected streams places further restrictions on food-chain length by limiting the quantity and efficiency of energy transfer to higher trophic levels. In these food webs, fewer links connect species because fewer species are present (Fig. 2A, B). Reduced species diversity and a decreased number of connections among species results in simplified foodweb structure (Pimm 1982, Townsend et al. 1998, McCann 2000). In mildly affected streams (e.g., less acidic, low metal concentrations), food-chain length, foodweb size, and complexity should be higher relative to in strongly affected streams because of the presence of fish and increased invertebrate diversity (Fig. 2C). As a result, some energy pathways will be maintained (e.g., fish predation), but they might be inefficient. If invertebrate communities are impoverished or consist of species that can evade fish predation (e.g., burrowing chironomids or oligochaetes) then fish may rely increasingly on terrestrial arthropods as a food resource (Fig. 2C). We would expect energy-flow pathways between many consumers and their basal resources or prey to be weakened or disrupted in AMD-affected streams because of these substantial changes in foodweb structure.

Interpretation of these proposed food webs is limited by the lack of information on biotic interactions and ecosystem processes in these systems. Patterns observed in foodweb studies from other stressed ecosystems show different trends. For example, evidence from acid-stressed streams has shown that generalism and flexibility in feeding strategies can produce food webs with few species but many links (Hildrew 2009). Ledger and Hildrew (2001) reported that a predominantly detritivorous stonefly (*Nemurella pictetii*) grazed algae in an acidic stream lacking specialist grazers. In addition to shifts in feeding strategies, the presence of tolerant species and compensatory species replacements can maintain ecosystem processes despite the loss of certain species and truncation or simplification of the stream food web (Ledger and Hildrew 2005, Hildrew 2009). In contrast, if sensitive species are dominant contributors, then ecosystem processes may be substantially altered. For example, leaf-litter breakdown rates were significantly reduced in Zn-contaminated streams because of low production (or absence) of a metal-sensitive shredder (*Taenionema pallidum*), which plays a key role in this process (Carlisle and Clements 2005). Furthermore, under conditions of extreme stress so many species are lost that compensation by tolerant species is not possible and processes are completely disrupted.

By taking a foodweb perspective, we can recognize more clearly the importance of modified interactions among communities that affect ecosystem processes. For example, reduced rates of leaf-litter breakdown (up to 50%) have been observed in experimental studies in AMD-affected streams (Gray and Ward 1983, Schultheis et al. 1997, Niyogi et al. 2001, Siefert and Mutz 2001). Deposits of metal hydroxides inhibit microbial access to litter, but decreased microbial activity in these streams usually occurs in combination with a decline in shredding invertebrates (Schultheis et al. 1997, Niyogi et al. 2001). The interplay between microbes and invertebrates is critical in this process, and if significant amounts of litter remain undecomposed and accumulate in the stream, then energy transfer and nutrient cycling processes will be limited.

Conclusions

Mine drainage generated from current and historic mining activities radically alters receiving streams by introducing highly acidic waters with high concentrations of dissolved metals and metal hydroxides that are deposited and coat substrata. This complex combination of stressors causes substantial changes in the structure and function of benthic communities and food webs. Diversity, richness, and abundance of algal, microbial, invertebrate, and fish communities decrease consistently in response to AMD. Exceptions occur when abundances of tolerant taxa increase (e.g., filamentous chlorophytes). Primary production, microbial respiration, and decomposition also decrease consistently, but few studies of these ecosystem processes have been published for AMD-affected streams. Differential responses of biota to the individual stressors imposed by AMD (acidity, dissolved metals, and metal hydroxide deposits) are evident in measures of community structure (diversity, richness, abundance), whereas metal hydroxide deposits are always linked to reduced rates of ecosystem processes.

Few investigators have considered the mechanisms leading to the observed negative effects of AMD in stream ecosystems. In particular, altered biotic interactions have been suggested frequently but tested rarely. For example, under some circumstances, reductions in fish populations could be mediated by low resource availability rather than direct toxicity, or the accrual of filamentous green algae may be a result of release from grazing pressure instead of a direct response to high acidity (Scullion and Edwards 1980, Niyogi et al. 2002a). Tests of the strength, frequency, and relative importance of interactions between consumers and resources are needed (e.g., grazing and predation). Tests could be extended to include multiple trophic levels to reveal more information about interactions in the system as a whole (Woodward et al. 2009).

Tolerant species in every community in AMD-affected streams could be limited by the quantity, and in some cases the quality, of food resources. Little is known about the quality (e.g., C:N:P ratios, lipid content) of algal and detrital resources and assimilation of these resources by tolerant primary consumers. Invertebrates certainly are exposed to metals via consumption of metal-contaminated basal resources, but whether or how sequestration affects food quality and palatability is not known. The importance of resource subsidies to and from AMD-affected streams and adjacent habitats has not been investigated adequately. If in-stream food resources are limited in AMD-affected streams, then terrestrial subsidies (e.g., arthropods) may help support aquatic communities (Scullion and Edwards 1980). Conversely, loss of the reciprocal subsidy of adult insects from AMD-affected streams could negatively affect food webs in the surrounding terrestrial habitat (Burdon and Harding 2008). Similarly, the importance of connections with the hyporheic zone in AMD-affected streams has rarely been studied, despite the fact that this interface may provide a valuable source of organic C and nutrients. Limited evidence indicates that AMD contaminates the hyporheic zone in the same way it does surface waters (Nelson et al. 1993, Gray 1996, Anthony 1999). Further work is needed to understand the importance of the flow of nutrients, detritus, prey, and consumers within AMD-affected stream food webs and between food webs in AMD-affected streams and adjacent ecosystems and habitats. Factors that affect food quantity and quality translate directly into effects on energy flow and consumer production.

The strong negative effects of AMD on stream communities are well documented for some communities (e.g., invertebrates) but not for others. The paucity of studies of AMD effects on microbes, macrophytes, meiofauna, and tertiary consumers (small mammals, amphibians, birds) is a significant gap in our understanding of these systems, particularly from a foodweb perspective. Potentially toxic water chemistry and reduced food resources are likely to affect other top consumers severely. Such an effect has been manifested as poor breeding performance of a songbird (*Seiurus motacilla*) along acidic streams in the Appalachians (Mulvihill et al. 2008). Drastic community changes can occur in a stream food web when just one species is lost because of stress, and these effects propagate throughout the food web. In AMD-affected streams, many species are lost concurrently, and this simultaneous impact might be the cause of the rapid and almost complete collapse of foodweb structure in some streams (Gray 1997).

Our review brings together the effects of AMD on the structure and function of benthic communities, offers a foodweb perspective, and identifies biotic interactions and ecosystem processes as key areas for future research in AMD-affected streams. Our review also highlights the importance of considering the effects of metal hydroxides, which negatively affect each community but often are not considered in remediation efforts. We suggest that future investigators place a greater emphasis on a foodweb approach that incorporates both structural and functional attributes to assess the effects of AMD on stream ecosystems. This strategy should provide new and better insights into these stressed environments and how to restore them as functioning ecosystems, particularly as mining activities continue to increase worldwide.

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