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Periphyton communities in New Zealand streams impacted by acid mine drainage

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Abstract. Discharges from historic and current coal mines frequently generate waters low in pH (<3), high in heavy metals (e.g. Fe, Al) and cover streambeds in metal precipitates. The present study investigated periphyton communities at 52 stream sites on the West Coast, South Island, New Zealand, representing a range of impacts from acid mine drainage (AMD). Taxonomic richness was negatively related to acidity and metal oxides and biomass was negatively correlated with metal oxides, but positively related to acidity. Streams with low pH (<3.5) had low periphyton richness (14 taxa across all sites) and were dominated by *Klebsormidium acidophilum*, *Navicula cincta* and *Euglena mutabilis*. As pH increased, so did taxonomic richness while community dominance decreased and community composition became more variable. Canonical correspondence analyses of algal assemblages revealed patterns influenced by pH. These findings indicate that streams affected by AMD possess a predictable assemblage composition of algal species that can tolerate the extreme water chemistry and substrate conditions. The predictability of algal communities declines with decreasing stress, as other abiotic and biotic factors become increasingly more important.

Additional keywords: algal diversity, benthic algae, metal oxides, metals, pH.

Introduction

Periphyton assemblages can be spatially complex and temporally variable depending on a wide range of environmental and biological factors (Biggs and Kilroy 2004; Peterson 2007). In streams, light (DeNicola *et al.* 1992), nutrients (Biggs and Close 1989), temperature (DeNicola 1996), current velocity (Biggs and Close 1989), physical disturbance (Biggs and Close 1989), substrate type (Murdock and Dodds 2007), competition (Stevenson *et al.* 1991) and invertebrate grazing (Peterson *et al.* 2001) can all influence periphyton assemblages. However, in systems receiving acid mine drainage (AMD), the chemical characteristics of the receiving waters are of overriding importance and can strongly affect algal diversity and community structure (Verb and Vis 2000, 2001, 2005; Niyogi *et al.* 2002).

Acid mine drainage is often characterised by high acidity, high concentrations of dissolved metals (e.g. Fe, Al, Zn), and metal oxide deposition (Younger *et al.* 2002; Harding 2005). Metal oxides commonly precipitate from solution when acidic waters mix with waters of higher pH such that the solubility of the metals is exceeded. Highly turbid waters containing coal fines and suspended sediment can also be a major issue in active mine sites (Younger *et al.* 2002; Harding 2005).

Algal communities respond to these environmental stressors and may be structured by a combination of pH (Kinross *et al.* 1993), heavy metal contamination (Soldo and Behra 2000) and metal oxide deposition (Niyogi *et al.* 1999). Niyogi *et al.* (2002) found that even low levels of oxide deposition could decrease algal diversity, biomass and function. Similarly, Anthony (1999) found algal biomass was low in AMD-affected streams on the West Coast of the South Island, New Zealand, and suggested that metal oxides may have prevented attachment of algae or that precipitate deposition onto algal cells may have inhibited photosynthesis. Other authors have found increased algal biomass at low pH, but usually where metal oxide deposition was low or absent (Mulholland *et al.* 1986; Stokes 1986; Niyogi *et al.* 1999).

Many algal studies in AMD systems have concentrated on the most severely affected systems (e.g. Brake *et al.* 2001; Sabater *et al.* 2003), or have focussed on ecosystem functioning and biomass (Niyogi *et al.* 2002) rather than diversity and composition. Several studies have focussed on diatoms. For example, DeNicola (2000) produced a comprehensive review of diatoms in acidic habitats, such as sulfur ponds and AMD-impacted systems. He identified 124 taxa in habitats of pH ≤3.5 from 28 different studies. Species of *Eunotia*, *Pinnularia*, *Achnanthes*, *Nitzschia*, *Cymbella*, *Fragilaria* and *Synedra* have all been reported from AMD systems (DeNicola 2000; Hill *et al.* 2000; Verb and Vis 2000; Sabater *et al.* 2003). The euglenophyte *Euglena mutabilis* has also been commonly found at highly acidic sites (Verb and Vis 2000; Sabater *et al.* 2003). However, green algae (chlorophytes and streptophytes) often dominate algal communities in acidic waterways, and tolerant species of genera such as *Klebsormidium*, *Microspora*, *Mougeotia*, *Ulothrix*, *Stigeoclonium*, *Zygnema* and *Microthamnion* have been recorded in severely affected streams (Niyogi *et al.* 2002; Sabater *et al.* 2003; Verb and Vis 2005; Novis 2006; Novis and Harding 2007).

Periphyton assemblages in AMD streams in New Zealand have received little attention (Anthony 1999; Novis and Harding 2007). However, Winterbourn *et al.* (2000) identified

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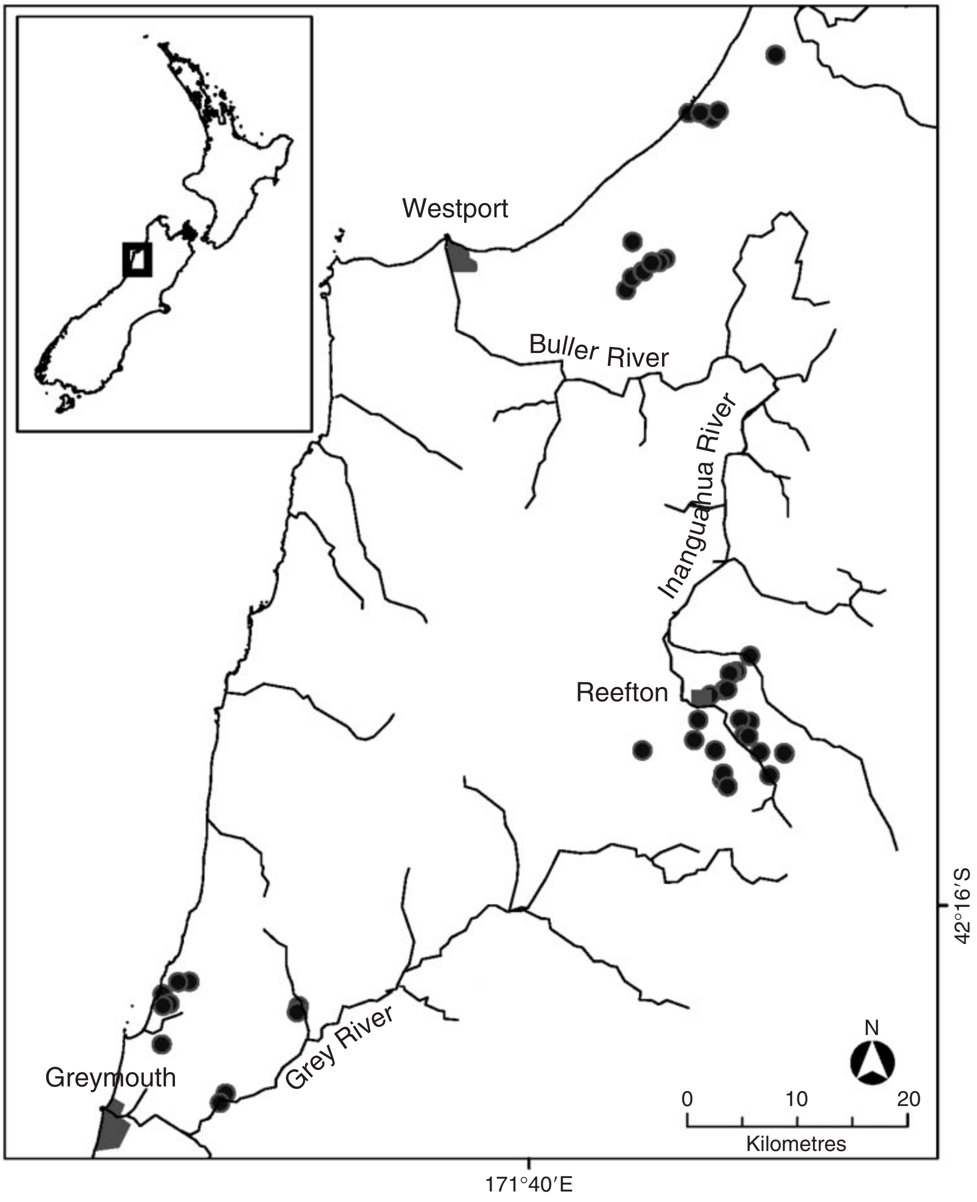

Fig. 1. Locations of 52 sites sampled on the West Coast of South Island, New Zealand.

Ulothrix sp. in acidic streams on the West Coast, and recent characterisation using morphological and molecular techniques has identified it as a new species, *Klebsormidium acidophilum* Novis (Novis 2006).

We investigated differences in periphyton communities across a gradient of streams of varying impact from AMD to determine if predictable algal assemblages occur in these systems associated with pH and other environmental characteristics. Based on international studies, we hypothesised that certain algal groups, including chlorophytes, streptophytes (formerly grouped within the chlorophytes), euglenophytes and some acid-tolerant diatoms would dominate the algal assemblages in the most acidic streams. We also hypothesised that pH would be the key factor related to AMD affecting algal assemblages.

Materials and methods

Study sites

We sampled 52 sites in 49 streams on the West Coast of the South Island, New Zealand (Fig. 1). Streams ranged from severely affected by AMD to unaffected reference streams. Each site was sampled on a single occasion between April 2006 and January 2007. This large sampling window was necessary to include the large number of sites, several of which were affected by severe weather. We discuss this limitation later in the discussion. Sites were selected from known mine-impacted systems and from mining regions listed on maps (1 : 50 000 260 series, Land Information New Zealand). Non-impacted reference sites were selected from maps based on their accessibility and physical and morphological similarities to AMD-impacted sites.

Sampling protocols

A 50-m reach was selected at each site. Physical measurements were made at each site, including an assessment of channel stability (Pfankuch 1975), mean surface water velocity, mean width and mean channel depth. Riparian canopy cover was visually estimated at the centre of the reach, and stream order and stream aspect were obtained from topographical maps. The reach location was recorded using GPS (Garmin eTrex LegendC 2004, www.garmin.com). A streambed substrate index (SI) (Jowett and Richardson 1990) was calculated; estimated percentages of each substrate category were multiplied by a weighted variable and summed giving a single continuous variable between 3 (sand-dominated bed) and 8 (bedrock-dominated bed):

$\mathrm{SI} = 0.08(\%\ \text{bedrock}) + 0.07(\%\ \text{boulder}) + 0.06(\%\ \text{cobble}) + 0.05(\%\ \text{gravel}) + 0.04(\%\ \text{fine gravel}) + 0.03(\%\ \text{sand})$. This index provides a simple composite variable from the percentage cover of the six sediment classes listed.

Measurements of pH, conductivity and temperature were recorded at each reach using an Oakton pH/CON 10 field meter (Oakton Instruments, Vernon Hills, IL). The degree of iron hydroxides present on the streambed was visually estimated over the reach using a precipitate index (PI) based on a 1–5 categorical scale (1 indicating no precipitates were present and 5 indicating 75–100% of the bed was covered in precipitates). This index is based on visual observations and is subject to observer bias; one individual (J. Bray) made all PI estimates in our study.

Two transects were randomly located within each reach and 10 estimates of algal cover (Verb and Vis 2001; Sabater *et al.* 2003) and algal matrix depth were recorded from each transect. Algal cover and matrix depth were estimated using a viewing tube. Similar to the method used by Entwisle (1989), a non-destructive biomass index (BI) was calculated by multiplying the percentage cover by the mean matrix depth and summing this for each visibly different type of periphyton:

$$\mathrm{BI} = \sum (\mathrm{C} \times \mathrm{D})$$

where C is the visual estimate of percentage cover for each different algal type and D is the matrix depth of each different type (mm). The BI method provides a quantitative estimate of algal biomass that generally works well for most algae in AMD environments, such as filamentous chlorophytes and streptophytes. It does have limitations for sites with thin biofilms, or sites that have limited algae because of severe effects of AMD or physical disturbances. Algal biomass would be underestimated in these cases, but the actual biomass at these sites, if measured as chlorophyll or biovolume, would also be very low compared with other AMD sites with abundant algae.

Each visually distinct type of periphyton present along the two transects in the sampling reach was collected for microscopic identification. Algal collection methods followed those of Biggs and Kilroy (2004) and involved scraping whole stones for cobbles and smaller substrata. Where it was necessary to sample boulders or bedrock, a modified bedrock sampler created a seal against the stream bottom and algae were scrubbed from the rock surface with a brush and withdrawn from the sampler with a large syringe. Periphyton samples were kept cool during transport to the laboratory for preservation and analysis. In the laboratory a sub-sample of each algal type was added to 100 mL of water, homogenised using a blender, and preserved in Lugol's iodine. Relative abundance counts were conducted on preserved samples by counting at least 300 algal 'units' on one to three slides of sample homogenate at 400–1000× magnification; algal units were individual algal cells or multicellular fragments of larger algae. To aid diatom identification, sub-samples were cleaned of organic material by oxidation in concentrated nitric acid and hydrogen peroxide, rinsed in distilled water and mounted (Kilroy *et al.* 2006). Identifications were made to the lowest taxonomic level, which was usually to genus and species. Assemblage composition data were compiled from taxa counts after weighting counts for each algal type by the proportion of total biomass of the reach for the algal type.

Data analyses

Correlation analysis was conducted to examine relationships among environmental variables, and regressions were used for relations between environmental variables and the biological data. Normality was tested using Kolmogorov–Smirnov and Lilliefors tests, and was visually assessed using histograms (STATISTICA Version 7.1, StatSoft Inc., www.statsoft.com). Data were transformed where necessary to conform to normality. Residual scatter plots were used to ensure the variances were not heteroscedastic. Where data were not normally distributed, non-parametric Spearman correlation analysis was used. Canonical correspondence analysis (CCA) was used to identify the environmental variables that most strongly influenced community composition (PC-ORD, Version 4.01, MjM Software, Glenedon Beach, OR). Relative abundance data were used, and axis scores were centred and standardised to unit variance. The significance of the ordination axes were tested by a Monte Carlo method using 99 runs.

Results

Physico-chemical conditions

Water chemistry varied markedly across the 52 stream reaches with pH ranging from 2.7 to 7.6 and specific conductivity ranging from 18 to 1220 $\mu\mathrm{S\,cm}^{-1}$. Metal oxides were visually absent at 23 of the sites (PI of 1) and covered most of the stream bed at seven sites (PI of 5).

Periphyton diversity and abundance

Taxonomic richness varied from 1 to 16 taxa per site and richness was significantly related to pH and the precipitate index (PI) (Fig. 2*a*, *b*). Multiple regression analysis indicated that pH and PI together accounted for 27% of the variation in richness (Table 1). The biomass index (BI) was significantly related to pH (Fig. 2*c*), with low pH sites having higher biomass. The pH and PI together explained 28% of the variation in BI among sites (Table 1); sites with low pH and low PI had higher BI values. No other measured variables, including depth, width, altitude, riparian canopy cover, channel stability index, velocity, substrate index and temperature, were significantly related to richness or the biomass index.

Total taxonomic richness within pH classes also varied markedly. Fourteen taxa were found at sites with pH less than 3.5 (Fig. 3). Greater numbers of taxa were found as pH increased, to a maximum of 56 taxa in all sites of circum-neutral pH (6.5 to 7.6).

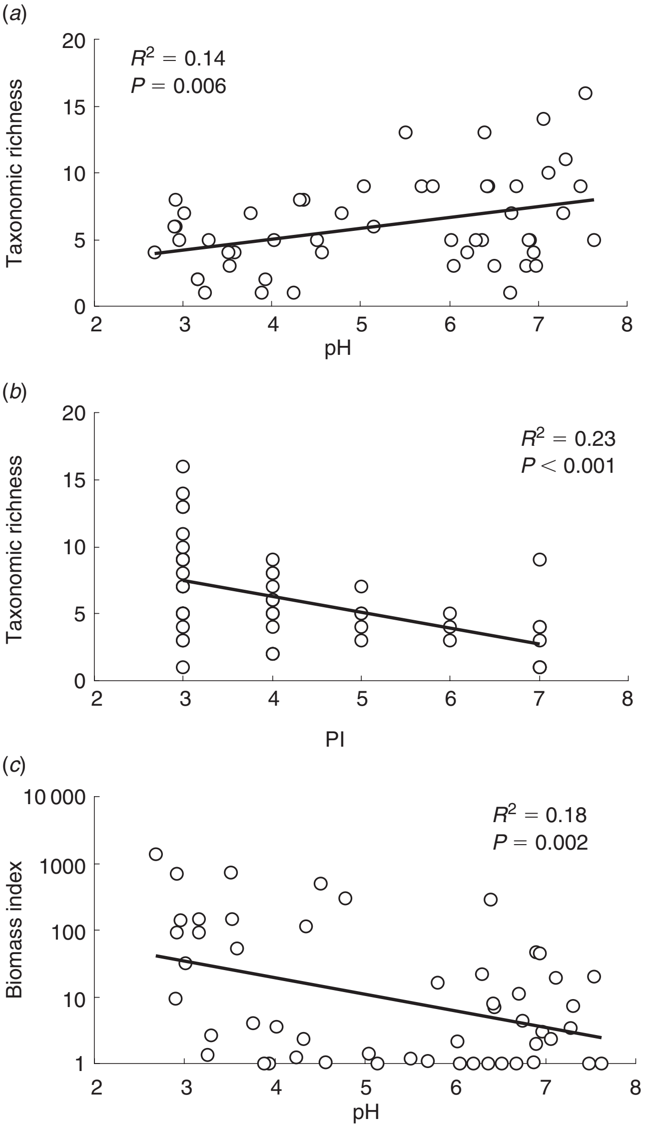

Fig. 2. Response of periphyton communities to acid mine drainage (AMD) stressors. Taxonomic richness of algal taxa against (*a*) pH and (*b*) precipitate index (PI). (*c*) Algal biomass index versus pH.

Table 1. Multiple regression results for effects of pH and precipitate index (PI) on taxonomic richness and biomass index of algal assemblages at 52 sites

Dependent variable	Overall r^2	Overall *P*-value	Independent variable	*P*-value
Taxonomic richness	0.27	<0.001	pH	0.095
			PI	0.005
Log (biomass index)	0.28	<0.001	pH	<0.001
			PI	0.013

Periphyton communities

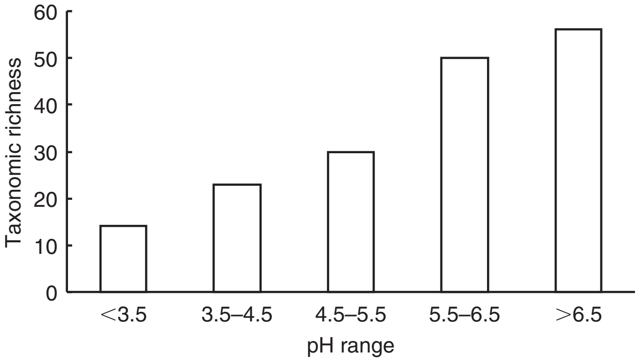

Fig. 3. Total number of algal taxa in all sites within pH classes.

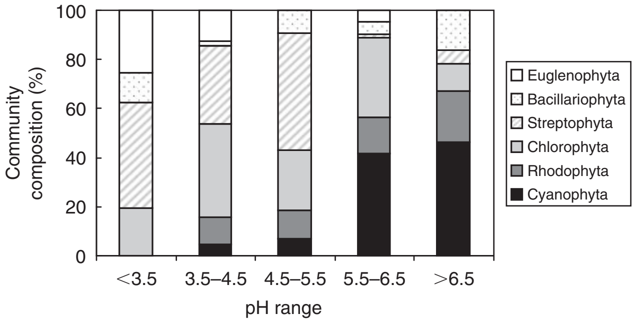

Fig. 4. Community composition (relative abundance) of algal phyla in sites within pH classes.

The relative abundance of algal phyla changed markedly among streams of differing pH (Fig. 4). At the most acidic sites (pH <3.5), streptophytes were dominant and euglenophytes, chlorophytes and bacillariophytes were also present. Between pH 3.5 and 4.5, chlorophytes and streptophytes were the main phyla represented and rhodophytes were represented by *Batrachospermum* at only two sites. As pH increased further, streptophytes and euglenophytes became less dominant and rhodophytes and cyanobacteria increased in relative abundance. Cyanobacteria were most common at the neutral sites (pH between 6.5 and 7.6). The one species of euglenophyte, *Euglena mutabilis*, was common at only one site with pH above 4.5 where heavy rains had created ponding. Chlorophytes were common (11–38% relative abundance) within all pH ranges, but the number of chlorophyte taxa increased with pH.

Ten sites were severely impacted by AMD and had pH <3.5. In total, 14 taxa were recorded from these sites, which were often dominated by the streptophyte *Klebsormidium acidophilum* (28% averaged relative abundance within this pH class), the euglenophyte *E. mutabilis* (25%), and the bacillariophyte *Navicula cincta* (12%). The streptophytes *Mougeotia depressa*, *Mougeotia* cf. *laevis* and less commonly *Zygnema* cf. *cylindrospermum* were also found within these low pH streams. Three other species of bacillariophytes and five chlorophytes made up the remainder of the species.

Ten sites had a pH ranging between 3.5 and 4.5 and supported a total of 23 taxa. AMD-tolerant species noted in the lowest pH class were present in many of these sites. Cyanobacteria, represented by two taxa, *Gloeocapsa* sp. and *Lyngbya* sp., were present at one of these sites (pH 4.3). At a site with pH 4.2, rhodophytes were also represented by *Batrachospermum atrum*.

Six sites occurred in the pH range 4.5–5.5 and had 30 algal taxa. The most dominant algal group was Streptophyta, which

Table 2. Spearman correlations of the relative abundance of common taxa (n = no. of sites) with pH, specific conductivity (SC), and the precipitate index (PI)

Significant relations ($P < 0.05$) are in bold

Phylum	Taxa	pH	SC	PI
Cyanophyta	*Chamaesiphon* cf. *incrustans* Grunow ($n = 5$)	**0.36**	**−0.33**	**−0.33**
	Heteroleibleinia purpurascens (Hansgirg ex Hansgirg) Anagnostidis and Komárek (9)	**0.43**	**−0.46**	**−0.47**
Rhodophyta	*Batrachospermum atrum* (Hudson) Harvey (7)	0.24	**−0.29**	**−0.33**
Euglenophyta	*Euglena mutabilis* Schmidtz (14)	**−0.58**	**0.55**	**0.34**
Chlorophyta	*Microspora quadrata* Hazen (17)	**−0.30**	0.19	0.07
	Microthamnion kuetzingianum Nägeli (14)	**−0.34**	**0.41**	**0.32**
	Oedogonium sp. (12)	**0.45**	−0.17	**−0.40**
Streptophyta	*Klebsormidium acidophilum* Novis (18)	**−0.70**	**0.62**	**0.52**
	Klebsormidium rivulare (Kützing) Morison and Sheath (12)	0.24	−0.26	**−0.36**
	Mougeotia cf. *laevis* (Kützing) Archer (13)	**−0.30**	0.02	−0.07
	Zygnema cf. *cylindrospermum* (West and G.S. West) Krieger (7)	−0.27	0.12	0.09
Bacillariophyta	*Cymbella kappi* Cholnoky (6)	**0.47**	**−0.29**	**−0.37**
	Frustulia rhomboides var. *crassinerva* (Brébisson) Ross. (5)	**0.28**	−0.08	0.03
	Gomphonema parvulum (Kütz) Grun. (5)	**0.39**	−0.27	−0.21
	Navicula cincta (Ehrenberg) Ralfs (7)	**−0.47**	**0.33**	0.15

was represented by five taxa, with *Zygnema* cf. *cylindrospermum* being dominant (17% averaged relative abundance). Bacillariophyte diversity increased, with eight taxa present, whereas chlorophyte and rhodophyte diversity remained low, with four and two taxa respectively. Cyanobacterial diversity increased and 10 taxa were observed between pH 4.5 and 5.5.

At 10 sites ranging from pH 5.5 to 6.5, algal diversity increased markedly, with 50 taxa present. Cyanobacteria were the most diverse group (18 taxa) and were numerically abundant. Bacillariophytes were also diverse (14 taxa) but were not abundant. Streptophytes (five taxa), chlorophytes (nine taxa), euglenophytes (one taxon) and three rhodophytes made up the remainder.

Above pH 6.5, 56 taxa were observed within 16 sites. These sites also had particularly high abundances and diversity of cyanobacteria (24 taxa). Both the rhodophytes, *B. atrum* and *Audouinella* sp., were present. Of the bacillariophytes, 15 taxa were identified and had generally low (<5%) relative abundances, except for *Diatoma vulgaris*, which made up ~50% of community composition at one site. Four streptophyte taxa were present, with the pollution-intolerant *Klebsormidium rivulare* being dominant. Eight chlorophyte taxa were present and the only xanthophycean (*Tribonema* sp.) of the study was found in this pH class.

AMD factors influencing algal assemblages

Several taxa showed distinct relationships with pH, conductivity and PI (Table 2). The relative abundances of *N. cincta*, *K. acidophilum*, *Microthamnion kuetzingianum* and *E. mutabilis* were significantly related to pH and conductivity. Additionally, these taxa were commonly found at sites with low pH, and rarely found at sites with higher pH (Fig. 5). In contrast, *Microspora* cf. *quadrata* occurred across a broad range in pH (2.9–6.9) and conductivity (24–1200 $\mu S\ cm^{-1}$). Although many algae showed no significant relationship with pH, conductivity or the estimated level of precipitates, some taxa were notably intolerant of AMD. For example, *Chamaesiphon* cf. *incrustans*, *Heteroleibleinia purpurascens* and *Cymbella kappi* were all negatively associated with increasing stress from each of the AMD variables (Table 2). *Oedogonium* sp. was similarly related to pH and the PI (Table 2, Fig. 5).

Canonical correspondence analysis (CCA) of periphyton community composition indicated that several environmental variables were closely correlated with the species matrix (Fig. 6). Sites were generally spread along Axis 1, which was positively correlated with pH (ter Braak correlation = 0.94), and negatively with conductivity (−0.61) and PI (−0.44). Axis 2 was positively correlated with PI (0.73). The lowest pH sites (pH <3.5) were generally clustered together with negative scores on Axis 1. Sites within the other pH categories were generally distributed along Axis 1 according to pH. The sites with pH >6.5, which were grouped to the right on Axis 1, were spread over a larger range along both axes compared with the sites in other pH ranges. The CCA had high species–environment Pearson correlations ($r = 0.94$ and $r = 0.92$ for Axes 1 and 2 respectively). Approximately 11% of the variation in the species matrix was explained by the environmental matrix. As expected from other analyses, the main taxa positioned negatively along Axis 1 (sites with low pH) were *N. cincta* (Axis 1 score of −1.5), *E. mutabilis* (−1.2), *K. acidophilum* (−1.4) and *M. kuetzingianum* (−1.2). *Chamaesiphon* cf. *incrustans* (1.1), *H. purpurascens* (1.4) and *C. kappi* (2.0) were common taxa (found at more than 5 sites) that were positioned positively on Axis 1.

Discussion

Periphyton diversity and biomass

Our findings show that low pH, high concentrations of dissolved metals (represented by high conductivity) and the high rates of metal oxide deposition (PI) are associated with reduced benthic algal diversity and altered community structure in streams. Reduced algal taxonomic richness has been reported in several studies of mine drainage (Verb and Vis 2000, 2001, 2005; Sabater *et al.* 2003). However, as in this study, numerous taxa have been

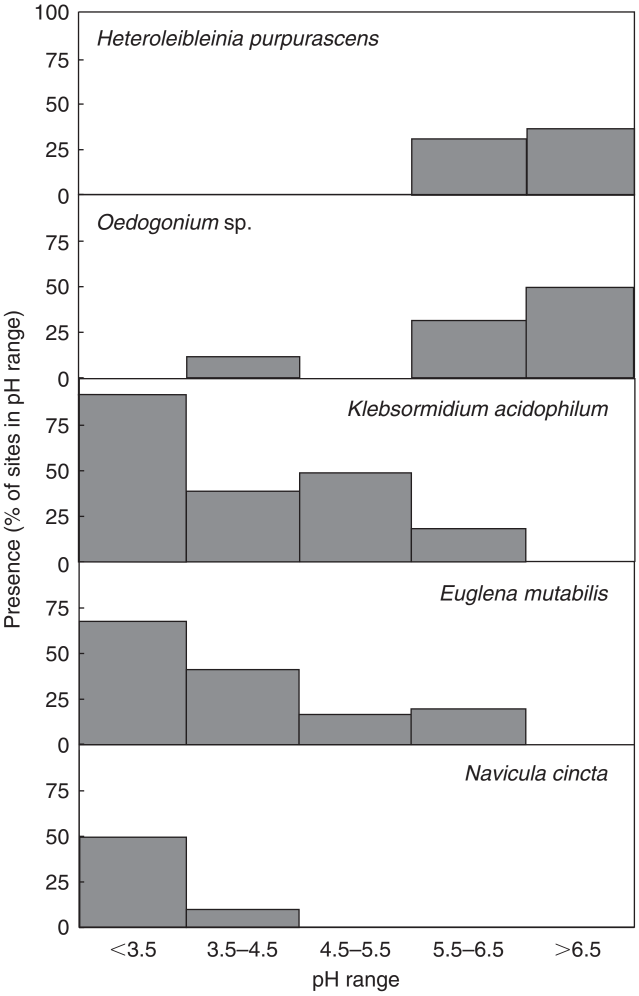

Fig. 5. Presence of main algal taxa at sites within pH classes.

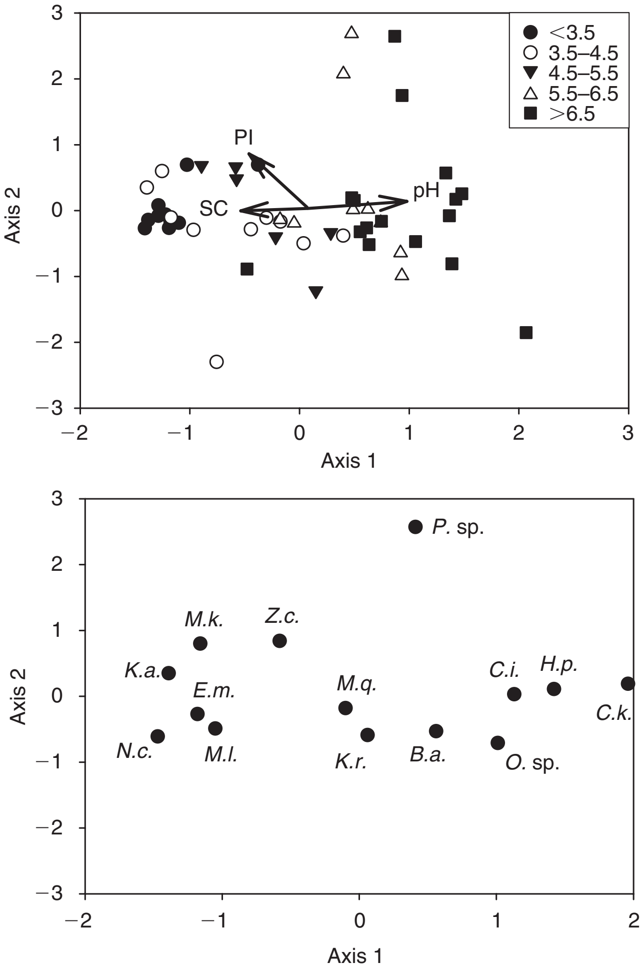

Fig. 6. Canonical correspondence analyses for algal assemblages and key algal taxa at each site. Arrows indicate main variables that were correlated with the two axes: SC is specific conductivity, T is temperature, and PI is the precipitation index. For algal taxa; *N.c.* = *Navicula cincta*, *K.a.* = *Klebsormidium acidophilum*, *E.m.* = *Euglena mutabilis*, *M.k.* = *Microthamnion kuetzingianum*, *M.l.* = *Mougeotia* cf. *laevis*, *Z.c.* = *Zygnema* cf. *cylindrospermum*, *M.q.* = *Microspora quadrata*, *K.r.* = *Klebsormidium rivulare*, *B.a.* = *Batrachospermum atrum*, *O.* sp. = *Oedogonium* sp., *P.* sp. = *Pseudanabaena* sp., *C.k.* = *Cymbella kappi*, *C.i.* = *Chamaesiphon incrustans*, *H.p.* = *Heteroleibleinia purpurascens*.

shown to be tolerant of conditions within AMD waterways, even at the most highly acidic sites (DeNicola 2000; Sabater *et al.* 2003; Novis and Harding 2007). *Klebsormidium acidophilum*, which has been reported as *Ulothrix* and *Hormidium* in other studies, was one commonly encountered alga in the most acidic sites (pH <3).

Algal biomass was significantly greater in the severely impacted, low pH streams, which is in accordance with several studies (Mulholland *et al.* 1986; Verb and Vis 2001; Sabater *et al.* 2003) but not others (Kinross *et al.* 1993; Anthony 1999; Hill *et al.* 2000; Verb and Vis 2005). Verb and Vis (2005) found an inverse relationship between biomass and dominance of diatom and macroalgal communities in AMD. They suggested that where diatoms dominate, low biomass may be expected, but where other algae dominate, high biomass may be expected. Although the mechanisms driving diatom dominance within AMD streams is unclear, guild competition or zonation may be important (e.g. Passy 2007). Niyogi *et al.* (1999, 2002) found that increases in algal biomass are limited by the rate of precipitate deposition, which varies according to pH and metal ion concentrations (Younger *et al.* 2002). Our findings are similar in that algal cover and biomass were very low or absent under high rates of oxide deposition. Oxide deposition may smother algae and inhibit photosynthesis, or colonisation may be limited if the entire substrate is covered with metal oxides (Anthony 1999). Certain species are adept at growth on these surfaces or are motile and are thus able to keep from being smothered (e.g. *N. cincta*, *E. mutabilis*). Certain filamentous species are also associated with iron oxide deposits (Niyogi *et al.* 2002) for unknown reasons. Such species (e.g. *K. acidophilum*, *M. kuetzingianum*) may be able to attach to metal oxides and have some means to keep from being smothered at moderate levels of deposition.

Several factors may account for high algal biomass in many low pH streams. Tolerant species may be stimulated where physicochemical conditions such as pH are optimised for that particular species (Novis 2006). Alternatively, other taxa may be limited by the extreme physicochemical conditions, releasing tolerant species from interspecific competition (Niyogi *et al.* 1999). Furthermore, physicochemical conditions often exclude grazers, thus releasing algae from any top-down control that might normally be occurring (Rosemond *et al.* 1993; Niyogi *et al.* 2002). Other factors such as light, physical disturbance, nutrient concentrations and substrate suitability are also important factors influencing biomass accrual and productivity (Biggs 1996; Murdock and Dodds 2007). Canopy cover was not related to biomass at our study sites, but many of our sites had limited canopy cover because of the mining disturbance. Thus, light was probably not limiting at most of our sites. Nutrient concentrations at some of our acidic sites can be very high, based on recent sampling (not concurrent with this study); dissolved reactive phosphorus can exceed 40 $\mu g\,L^{-1}$ at some acidic sites, and dissolved inorganic nitrogen (mainly ammonium-N) can reach over 200 $\mu g\,L^{-1}$ (D. K. Niyogi, unpubl. data). Thus, high nutrient concentrations, in conjunction with other factors such as stable flow and limited grazing, probably account for the high biomass at these acidic sites.

Factors related to AMD could account for a relatively small amount of the variation (less than 30%) in biomass and richness. Other factors at our study sites could account for additional variation in biomass, species composition and richness of the periphyton assemblages. Seasonal variation could be one factor, given the long sampling window of our study. However, the marine climate of this area of New Zealand has low variations in temperature compared with more continental streams. Additionally, a temporal analysis of algal assemblages in the same region showed that some sites, especially those with greater influence of mine drainage, did not have high variation in the algal richness or biomass (Bray 2007).

Periphyton community composition

Few studies have examined algal assemblages across a large gradient of AMD impact. Verb and Vis (2000, 2001) studied the diatom and macroalgal components of the AMD-impacted Hocking River drainage basin, Ohio, USA. They found that the macroalgal assemblage was a poor indicator of AMD stress (Verb and Vis 2001), but both the diatom (Verb and Vis 2000) and, in a spatially much broader study, the total algal assemblage (Verb and Vis 2005) may be predictable according to the level of AMD stress. Many studies suggest that green algae (including streptophytes) often dominate algal communities in AMD-affected streams (Verb and Vis 2001, 2005), a finding consistent with our study. Streptophytes had the highest relative abundance in all pH classes below 5.5. Cyanobacteria were more common at sites with higher pH, as other studies have found, but we did find them at pH as low as 4.3 as well.

Algal communities and the mechanisms driving structure

In the present study, the most significant factor that was related to community structure across the AMD gradient was pH. Other factors, including nutrients, were not measured at all sites and may have influenced periphyton composition and biomass. pH had the highest correlation with the species matrix in the CCA ordination analyses and explained much of the variation of the community data. Verb and Vis (2000, 2001, 2005) found that pH was the most influential variable affecting community composition in AMD habitats. In two of their studies, they also found distinct differences between AMD sites and sites they refer to as reclaimed and non-impacted sites. However, they did not sample across such a broad AMD gradient as this study. Tease and Coler (1984), in an experimental study, found that pH had the most severe effect on periphyton communities, far exceeding the effects of dissolved aluminium, other heavy metals and hydrocarbons.

Dissolved metals are known to be toxic to algae (Soldo and Behra 2000; Guasch *et al.* 2004) and have been shown to strongly influence their distributions across a watershed (Hill *et al.* 2000). In AMD streams, conductivities are often indicative of metal ion concentrations (Younger *et al.* 2002). In the present study, conductivity was highly correlated with the species matrix in each CCA. However, precipitate deposition was also important in explaining species composition at sites. As may be expected, the pH, dissolved metal concentrations and the deposition of metal oxides influence community composition individually and collectively (Hill *et al.* 2000; Griffith *et al.* 2002; Niyogi *et al.* 2002). Unfortunately, as other authors have found, the effects of heavy metal contamination (conductivity) and pH are hard to disentangle (Niyogi *et al.* 2002; Verb and Vis 2005).

Conclusions and implications

Our survey indicates that a predictable community of AMD-tolerant taxa often develops in streams that are severely affected by acidic mine drainage. Indeed, prolific growths of acid-tolerant taxa, including *K. acidophilum* and *E. mutabilis*, can be used as indicators of AMD-affected conditions in streams. In these environments, high biomass and primary production seem to occur in the absence of strong grazing pressure from invertebrates. However, the palatability of these acid-tolerant algal taxa to grazing animals warrants more investigation. With decreasing AMD stress, taxonomic richness increases and the community becomes less predictable; other factors such as flow, temperature and disturbance then become increasingly important in influencing the assemblage (Biggs 1996). The typical assemblage of our severely affected streams was similar in composition to AMD communities elsewhere (Novis and Harding 2007), and as elsewhere, algal biomass often increases with AMD impact, although this occurs within a template of metal oxide deposition and physical disturbance.

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