

The influence of sediment mobility and channel geomorphology on periphyton abundance

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SUMMARY

1. River managers currently have difficulty predicting the combined effects of changes in flow regime and nutrients on periphyton biomass. Biomass accumulation is known to be promoted by increasing nutrients, light and temperature, and its loss has been related to invertebrate grazing and hydrological disturbance. However, biomass predictors that are reliable across a range of rivers have proven elusive. One possible contributing reason is that disturbance thresholds used in predictive models are typically linked to flow metrics, whereas the mechanisms for periphyton removal (current drag, abrasion and molar action by mobile sediment) relate more directly to hydraulic and geomorphic conditions.

2. We explored this possibility by relating periphyton removal events to hydraulic thresholds for sediment entrainment in 18 gravel- to boulder-bed river reaches at which periphyton cover and nutrient concentrations had been regularly monitored. We converted observed threshold discharges for periphyton removal into shear stress thresholds using hydraulic models.

3. Our results demonstrate that: (i) abrasion by finer fractions of the bed material (2–16 mm) was the dominant physical mechanism removing periphyton; (ii) the frequency of mobility of this fine bed material was the dominant control on periphyton abundance and (iii) growth-promoting variables, such as nutrient concentrations, tended to only become important to periphyton abundance when the frequency of sediment movement was low.

4. These findings highlight the importance of geomorphic differences between sites and explain why a single flow metric may be a poor predictor of periphyton abundance across geomorphically different rivers. Our analysis suggests that partitioning sites based on frequency of sediment mobility (either sand or the D_{50}) could improve predictability of sites at which there is potential for nuisance levels of periphyton to develop.

Keywords: abrasion, disturbance flow, benthic algae, periphyton, threshold

Introduction

Periphyton (benthic algae) is an essential component of healthy stream ecosystems, providing important basal resources for food webs (Lamberti, 1996; Hillebrand, de Montpelier & Liess, 2004). However, in high abundance, periphyton can have negative effects on habitat, water quality and instream biodiversity, and degrade the recreational and aesthetic values of rivers and streams (Biggs, 2000a; Suplee *et al.*, 2009; Smith, Duffy & Novak, 2015). The risk of undesirable levels of periphyton may increase through both eutrophication of waterways and

alteration of flow regimes, both of which are frequent outcomes of catchment land-use intensification (Foley *et al.*, 2005). There is a global need to manage both river flow regimes and nutrient inputs into waterways to prevent or mitigate the undesirable effects of excess periphyton. Such management would be facilitated by the use of reliable quantitative relationships between periphyton abundance and key driver variables.

A wide range of environmental variables influences periphyton abundance including light, water temperature, nutrient loading, grazing and river flow (Biggs, Stevenson & Lowe, 1998). Where light is not limiting,

the key drivers are generally agreed to be nutrient supply (Borchardt, 1996; Dodds, Smith & Zander, 1997; Biggs, 2000b), which promotes algal growth, and hydrological disturbance (Biggs *et al.*, 1998), which leads to periphyton removal.

Efforts to develop periphyton–environmental variable relationships have often focused on linking periphyton biomass (measured as mean annual or seasonal chlorophyll *a*) to nutrient concentrations, measured as total nitrogen and total phosphorus (TN, TP), or soluble inorganic nitrogen (SIN) and soluble reactive phosphorus (SRP). Unexplained variance in the relationships is generally high (e.g. at least 60%) (Dodds, Smith & Lohman, 2002; Stevenson *et al.*, 2008; but see Lohman, Jones & Perkins 1992). Inclusion of variables describing either flood disturbance or its corollary, accrual period (the time available for periphyton to accrue between flood events) can improve the predictive power of relationships. In New Zealand, the average annual frequency of flow events exceeding three times the median flow (FRE3) was identified as the best of a wide range of flow metrics for explaining variance in stream biota (including periphyton) (Clausen & Biggs, 1997). The explanatory power of FRE3 alone was low (R^2 of 0.18, Clausen & Biggs, 1998) but, using a combination of accrual period (derived from FRE3) and mean SIN or SRP concentration, Biggs (2000b) explained over 70% of the variation in maximum monthly chlorophyll *a* (over at least 12 months) across 31 unshaded sites in hill-fed, gravel-bed rivers. However, models developed from a wider range of river types, and using a more comprehensive selection of potential predictor variables including several flow metrics, had much lower predictive power (Snelder *et al.*, 2013).

In general, existing relationships linking periphyton to environmental variables currently either lack precision or lack the resolution to separate rivers that are unlikely to experience nuisance levels of periphyton from those in which periphyton will be more sensitive to changes in nutrient concentrations. One potential issue is that variables representing flood disturbance frequencies are generally derived directly from discharge data (Lohman *et al.* 1993, Biggs, 2000b). Use of discharge data has appeal because these are often readily obtained from river monitoring agencies, and flow metrics are relatively easy to derive. However, simple flow metrics are unlikely to accurately represent the stream-bed processes that directly affect periphyton during floods (Biggs, Smith & Duncan, 1999), which are driven by local shear stress and interactions with bed sediment movement, rather than flow magnitude. Periphyton

removal by flood disturbance occurs as a result of three mechanisms:

- Drag: elevated shear stress caused by increased water velocity causes sloughing (detachment) of periphyton mats or filament breakage (e.g. Biggs & Thomsen, 1995). In drag removal, detachment or sloughing occurs when the forces applied to the periphyton are sufficient to remove all or part of the biomass. The degree of biomass loss increases as shear stress increases, but not necessarily in a linear relationship (Biggs & Thomsen, 1995). Biomass loss at a given shear stress also depends on the age and health of the periphyton and the type of periphyton community (Biggs & Thomsen, 1995; Cullis, Crimaldi & McKnight, 2013).

- Abrasion: periphyton is worn-off substrata by mobilised sediment in suspension or saltation (e.g. Horner & Welch 1981; Luce, Cattaneo & Lapointe, 2010a; Luce, Steele & Lapointe, 2010b; Luce *et al.*, 2013). Laboratory studies have indicated that abrasion likely accounts for a significant proportion of periphyton removal during floods (Francoeur & Biggs, 2006). These findings have been confirmed in field experiments, which also demonstrated a threshold response in periphyton removal to sand abrasion, and that saltating coarse sand abraded surfaces more effectively than fine sand moving in suspension (Luce *et al.*, 2013).

- Molar action: periphyton is scoured from surfaces by the tumbling of the gravel/cobble substrata upon which it grows (e.g. Biggs & Close, 1989; Biggs *et al.*, 1999). Movement of large proportions of particles on the channel bed can remove most periphyton biomass (Peterson, 1996; Townsend, Scarsbrook & Doledec, 1997; Biggs *et al.*, 1999).

Incorporating variables directly describing sediment stability into relationships predicting periphyton abundance across rivers has already been shown to increase explanatory power (e.g. Clausen & Biggs, 1998; Biggs *et al.*, 1999). However, these relationships have generally been applied to a relatively narrow range of environments (e.g. Parker & Huryn, 2011; Bona, La Morgia & Falasco, 2012). Rivers differ in sediment supply (which controls the availability of fine bed material fractions on the bed surface) and substrate stability (Mueller & Pitlick, 2013), and these differences have been used as a basis for classing rivers into different geomorphic types (e.g. Schumm, 1985; Church, 1992).

In this study we aimed to explain variability in averaged periphyton abundance across sites by comparing observed periphyton removal with sediment entrainment thresholds. The study was founded on the idea that understanding geomorphic differences in rivers,

particularly in terms of their bed sediment stability, may improve understanding of which rivers are most vulnerable to changes in flow or nutrients with respect to developing high levels of periphyton.

In this context, we aimed to answer three questions:

1. Is a particular physical mechanism (i.e. drag, abrasion or molar action) responsible for keeping periphyton within a healthy range at each site, and is there a consistent mechanism across sites?

2. Does frequency of sediment movement help explain differences in periphyton abundance across a range of sites taking into account other growth-promoting variables?

3. Do periphyton removal flows have a stronger relationship with sediment-related flow metrics than direct flow metrics, in particular three times the median flow?

Methods

Site selection

Our approach in this study was to select sites that cover a spectrum of periphyton abundance, flow, nutrient concentration and geomorphic characteristics. The study was conducted in the Manawatu-Wanganui region of south-central North Island, New Zealand (Fig. 1). Periphyton has been monitored monthly at sites throughout

the region since 2008 and, for this study, we used a 5-year dataset (2009–2013) of monthly periphyton biomass (as chlorophyll *a*), and SIN and SRP concentrations (Table 1) from 18 sites. Each monitoring site had a flow gauge and all were either wadeable or accessible by kayak for a sufficient distance upstream and downstream of the periphyton survey area for the geomorphic surveys (see below). The selected sites covered a wide range of periphyton abundance and potential driver variables (nutrients, flow regime, bed sediment). Mean and maximum monthly chlorophyll *a* and mean SIN and SRP concentrations were calculated for each site. Daily mean and daily maximum flow data were extracted for the period between 2000 and 2013. Median flow for that period was calculated from mean daily flow data.

Periphyton and nutrient sample collection and analysis

Periphyton samples for analysis of chlorophyll *a* were collected monthly at each site, except during periods of high flow when the survey area was inaccessible. These occasions were reported as missing data. All samples were collected in defined, wadeable runs (i.e. river reaches with more or less smooth unbroken water surface, up to 0.6 m deep). Ten rocks were collected equally spaced along one or more transects to represent a reach

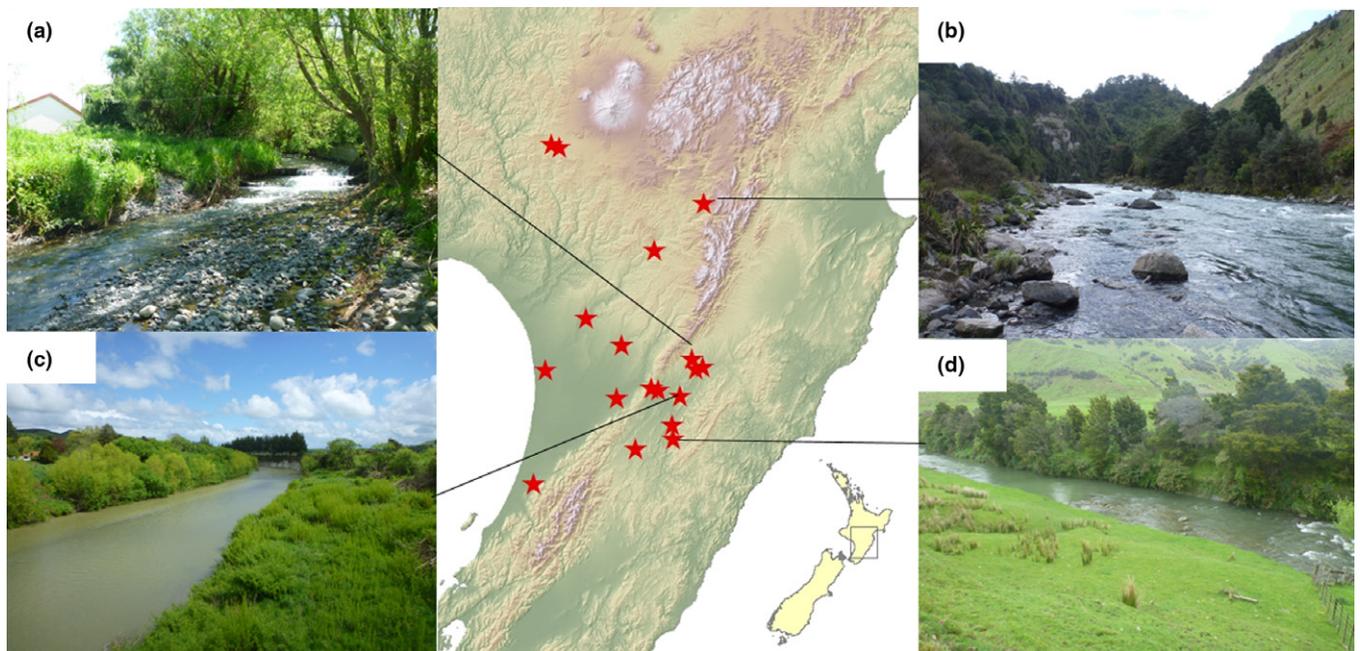


Fig. 1 Map showing the location of the study sites in the Manawatu-Wanganui Region of New Zealand, and photographs of four example sites (a) Kumeti at Te Rehunga, (b) Rangitikei at Pukeokahu, (c) Manawatu at Hopelands and (d) Makuri at Tuscan Hills, covering a spectrum of periphyton abundance, discharge and bed sediment size.

Table 1 Study site characteristics. Sites are in alphabetic order. The study sites were selected to cover a gradient of periphyton abundance (mean and maximum chlorophyll *a*), nutrient concentrations (SIN and SRP), flow regime (median and maximum flow) and bed sediment size distribution (D_{50} and D_{90}).

Site	Monthly periphyton data				Dominant taxa, summer 2012		Monthly nutrient data		Shade	Water temp (°C)	Flow data		Sediment data			
	Mean Chl <i>a</i> (mg m ⁻²)	Max Chl <i>a</i> (mg m ⁻²)	Films (%)	Mats (%)	Fils (%)	Dominant, subdominant (% biovolume)	Mean SIN (mg L ⁻¹)	Mean SRP (mg L ⁻¹)			Median flow, Q ₅₀ (m ³ s ⁻¹)	Max flow (m ³ s ⁻¹)	D ₅₀ (mm)	D ₉₀ (mm)	Sand (%)	
Kumeti at Te Rehunga	5.0	37	42.6	0.3	0.3	0.3	<i>Audouinella</i> (54%), <i>Gomphonema</i> (30%)	0.53	0.011	High	13.3	0.31	22	25.1	80.1	2.9
Makakahi at Hamua	45.7	220	64.5	14.9	10.9	10.9	<i>Melosira</i> (99%), <i>Cymbella</i> (1%)	0.48	0.007	Low	12.7	3.14	483	56.0	96.4	1.7
Makotuku at Raetihi	42.4	215	45.3	10.9	8.8	8.8	<i>Rossthidium</i> (29%), <i>Oedogonium</i> (28%)	0.36	0.006	Low	10.7	0.73	225	89.2	275.4	5.5
Makuri at Tuscan Hills	81.3	300	52.0	18.3	6.5	6.5	<i>Diatoma</i> (45%), <i>Melosira</i> (38%)	0.88	0.007	Low	12.4	3.49	270	59.5	375.8	7.7
Manawatu at Hopelands	56.6	355	41.6	9.9	9.8	9.8	<i>Stigeoclonium</i> (81%), <i>Melosira</i> (11%)	0.66	0.024	Low	15.0	15.05	1670	16.9	53.5	2.9
Manawatu at Teachers College	9.2	145	41.8	2.3	3.3	3.3	<i>Stigeoclonium</i> (46%), <i>Melosira</i> (24%)	0.42	0.012	Low	14.9	65.76	3515	22.5	78.9	4.0
Manawatu at Upper Gorge	14.9	90	46.5	3.9	5.6	5.6	<i>Melosira</i> (82%), <i>Stigeoclonium</i> (11%)	0.54	0.012	Mod	14.0	51.11	2731	29.2	80.6	8.9
Mangapapa at Troup Rd	5.7	44	57.4	0.5	1.0	1.0	<i>Melosira</i> (97%), <i>Navicula</i> (2%)	0.40	0.016	Low	15.0	0.33	94	25.1	61.2	10.1
Mangawhero at Pakihi Rd Bridge	23.5	80	61.3	11.8	5.0	5.0	<i>Audouinella</i> (49%), <i>Melosira</i> (23%)	0.27	0.013	High	10.3	3.30	164	37.9	147.0	10.4
Oroua at Almadale	4.3	35	50.0	0.8	1.8	1.8	<i>Rossthidium</i> (28%), <i>Navicula</i> (26%)	0.14	0.009	Low	12.6	6.06	475	23.0	78.9	7.0
Oruakeretaki at SH2	14.5	170	46.8	3.9	1.7	1.7	<i>Melosira</i> (82%), <i>Stigeoclonium</i> (8%)	0.76	0.014	Low	14.7	1.39	48	27.6	106.0	5.4
Rangitikei at Mangaweka	9.7	41	55.6	4.5	11.0	11.0	<i>Cladophora</i> (32%), <i>Diatoma</i> (32%)	0.07	0.007	Low	12.7	45.25	1756	30.5	81.0	3.8
Rangitikei at McKelvies	17.0	120	39.2	8.1	11.8	11.8	<i>Melosira</i> (44%), <i>Stigeoclonium</i> (32%)	0.14	0.013	Low	14.8	46.41	1115	24.1	50.3	4.4
Rangitikei at Onepuhi	5.6	65	42.8	1.4	4.8	4.8	<i>Melosira</i> (59%), <i>Diatoma</i> (8%)	0.09	0.009	Low	13.6	48.57	2009	38.8	99.3	5.5
Rangitikei at Pukeokahu	4.1	42	56.3	3.6	4.1	4.1	<i>Epithemia</i> (22%), <i>Gomphonopsis</i> (21%)	0.03	0.006	Low	11.3	16.73	954	122.1	479.7	7.3
Tamaki at Stephensons	10.8	175	50.1	3.5	0.7	0.7	<i>Gomphonema</i> (45%), <i>Melosira</i> (34%)	0.45	0.009	Mod	14.4	2.25	93	26.6	62.9	3.7
Tiraumea at Ngaturi	74.5	270	50.0	18.2	11.2	11.2	<i>Diatoma</i> (35%), <i>Melosira</i> (25%)	0.61	0.011	Low	12.9	7.13	748	45.7	93.5	4.2
Waikawa at Nth Manakau	4.2	22	57.7	1.4	4.8	4.8	<i>Melosira</i> (58%), <i>Cymbella</i> (22%)	0.07	0.010	Low	13.1	0.88	50	37.7	107.2	11.0

of up to 40 m long. Periphyton was scrubbed from a defined area (0.002 m²) on each rock and pooled into a single composite sample at each site. Samples were stored frozen until analysis. In the laboratory, chlorophyll *a* was determined by extraction in boiling 90% ethanol following by spectrophotometric determination of chlorophyll *a* concentration, with acid correction (Biggs & Kilroy, 2000). During monthly sampling visual estimates of percentage cover of broad classes of periphyton (bare, films, mats and filaments; e.g. Snelder *et al.*, 2013) were also recorded (Table 1). Periphyton taxa present at each site were determined on one occasion in summer 2012, when chlorophyll *a* was relatively high at most sites. At least 300 cells were identified to genus level using an inverted microscope at 400×. Larger cells, including large filamentous algae, were enumerated at 100× in at least 10 fields of view per sample. All cell counts were converted into biovolumes using cell dimensions measured with an ocular micrometre. The dominant and subdominant taxa were identified, based on % biovolume (Table 1).

A water sample for determination of dissolved nutrient concentrations was collected at each site at the time of periphyton sample collection. Samples were kept cool and filtered through 0.45 µm cellulose acetate filters within 24 h of collection. SRP and SIN (the sum of nitrate-nitrogen, nitrite-nitrogen and ammoniacal nitrogen) were determined using standard colorimetric methods (APHA 2005) or ion chromatography (EPA 1993).

Other growth-promoting variables

Water temperature was recorded at each site during each monitoring visit (Table 1). Sites were typically visited in the same order each visit, which means that differences in temperatures between sites may be biased by the time of day when monitoring typically took place.

The degree of shading at each site was assessed in three categories (low, moderate and high) based on the height and proximity of riparian tree cover, and the aspect of the channel (i.e. north–south vs east–west).

Geomorphic data collection

Estimating sediment entrainment discharges required data on bed-surface material grain size as well as channel topographic and hydraulic data from which to build 1D hydraulic models. We measured the bed-surface grain size distribution using the Wolman method (Wolman 1954), measuring between 200 and 350 clasts at each site and calculating the median grain size (D_{50}) and

the size of which is 90% finer (D_{90}) (Table 1). The proportion of sand was calculated as the mean of monthly visual estimates of % sand cover in the reach where periphyton was collected (Table 1). We surveyed at least seven cross sections and a thalweg profile at each site to represent the channel topography. At the smaller sites this surveying was conducted by foot using real-time kinematic (RTK) GPS. At the larger and deeper sites dry parts of the channel were surveyed by foot and the wetted part of the channel was surveyed using a kayak equipped with a depth sounder coupled with RTK GPS. The length of the surveyed reaches was set so that at least one pool and riffle upstream and downstream of the periphyton monitoring area were captured, providing good hydraulic control over the periphyton monitoring area. The cross-section profiles captured the bankfull channel. Long profiles of the water surface were surveyed with RTK GPS to enable model hydraulic calibration. Discharge during the surveys was extracted from the current stage-discharge rating.

Identifying periphyton removal mechanisms

Our approach to answering this question was (i) establish the 'periphyton removal flow', i.e. the flow that typically reduces periphyton abundance to a low level at each site; (ii) calculate the flows required for sediment mobility (for 2 mm sand up to the bed-surface median size, D_{50}) at each site; (iii) establish the key removal mechanism at each site based on the mobility of sediment at periphyton removal flows and (iv) determine whether a common mechanism applies across sites.

Establishing periphyton removal flows. To remove any potential bias in our selection of periphyton removal discharges (which we term Q_{pr}), our aim was to use an objective and consistent approach that could be applied to all sites, acknowledging that the approach taken might not best suit every site and that there is uncertainty in establishing the Q_{pr} at a given site when comparing continuous-flow data with monthly periphyton data.

Biggs & Close (1989) identified threshold relationships between periphyton biomass and flow on the day of periphyton biomass sampling. However, because periphyton biomass on the day of sampling reflects hydraulic disturbance and/or growth in the days preceding sampling, our approach was to relate chlorophyll *a* to peak discharge in a given window of time prior to periphyton sampling. There is uncertainty in selecting the appropriate time window because too long a window

may capture both flood removal of periphyton and subsequent periphyton regrowth and may overestimate Q_{pr} , whereas too short a window may miss a flood that effectively removed periphyton and thereby underestimate Q_{pr} . We plotted chlorophyll a versus peak instantaneous flow in the previous 1, 7, 14 and 30 days. Visual assessment of these plots showed clear flow thresholds at most sites using either a 7-day or 14-day window (e.g. Fig. 2a). Results presented in this study are based on using the 7-day window data to identify Q_{pr} as these data produced the clearest thresholds overall. Supporting this, periphyton has been reported to recover to pre-scouring biomass within 10 days (Stevenson, 1990; Fuller *et al.*, 2008), although recovery was sometimes to low levels (Davie *et al.* 2012). Moreover, observations of periphyton in New Zealand rivers following floods of at least three times the median flow indicate that the time required for biomass recovery generally exceeds 7 days (Suren *et al.*, 2003; C. Kilroy, pers. obs.). As a sensitivity analysis we also calculated Q_{pr} values based on the 14-day flow window and consider the effect of using these alternative Q_{pr} values (see Discussion).

The 7-day window threshold plots showed that chlorophyll a values typically dropped to 10 mg m^{-2} or lower when the flow exceeded a given threshold (e.g. Fig. 2a). A biomass of 10 mg m^{-2} of chlorophyll a approximately corresponds to 100% cover by 'thin films' of periphyton (Kilroy *et al.*, 2013). This biomass is also well below the mean chlorophyll a threshold considered as the maximum for maintenance of 'clean-water' benthic invertebrate biodiversity (15 mg m^{-2} , Biggs, 2000a). Therefore, we deemed periphyton removal to have occurred when the chlorophyll a concentration fell to $<10 \text{ mg m}^{-2}$.

We defined Q_{pr} for each site by first ranking all peak 7-day antecedent flows for which chlorophyll a

$>10 \text{ mg m}^{-2}$, and then taking 95th percentile of this flow distribution as the Q_{pr} (Fig. 2b), thereby removing the occasional outlier point. As a sensitivity analysis we also calculated Q_{pr} based on dropping chlorophyll a to 15 or 20 mg m^{-2} . The resulting Q_{pr} values corresponded poorly to the observed thresholds, particularly at oligotrophic sites, so these results were not considered further.

Establishing flows required to move sediment. We calculated the flows required to entrain bed sediment at each site in a two-step process. First, we calculated the entrainment shear stress for various sediment sizes, then we transformed this stress into a flow rate using output from a 1D hydraulic model.

The stress for general entrainment of the bed surface, represented by its median (D_{50}) size, was calculated using Shield's equation:

$$\tau_{crD_{50}} = \tau_{cr}^* (\rho_s - \rho) g D_{50}$$

where τ_{cr}^* is the Shields number (or the critical value of the dimensionless shear stress), ρ_s is the sediment density, ρ is water density (taken as 1000 kg m^{-3}) and g is the gravitational acceleration (9.81 m s^{-2}). For a closely packed population of grains of similar size, τ_{cr}^* is *c.* 0.06 (Shields, 1936), but for usual mixtures of sediments on stream beds τ_{cr}^* has been found by observation to vary between 0.030 and 0.073 (Buffington & Montgomery, 1997), when D is the D_{50} of the bed-surface material. We assumed a Shields number of 0.035 (e.g. Parker & Klingeman, 1982) for all sites. While this is towards the low end of the 0.030–0.073 mobility envelope shown by Buffington & Montgomery (1997), we wanted to assess the lowest flow at which sediment could start to become mobile (i.e. a threshold for potential abrasion). As a sensitivity exercise, we also assessed sediment mobility

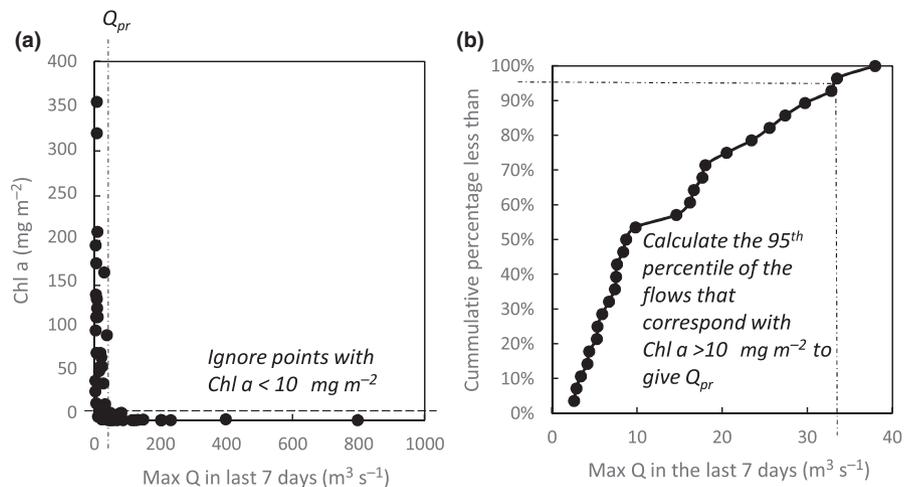


Fig. 2 (a) Example of the relationship between chlorophyll a (Chl a) and peak 7-day antecedent flow (for Manawatu at Hopelands). The horizontal dashed line marks the 10 mg m^{-2} Chl a threshold. (b) Cumulative distribution of flows for data with Chl $a > 10 \text{ mg m}^{-2}$. The periphyton removal flow (Q_{pr}) is taken as the 95th percentile ($33 \text{ m}^3 \text{ s}^{-1}$). Note that this aligns visually with the flow where the scatter of Chl a values reduces in (a).

using a Shields number of 0.052 (which is the mid-range value of Buffington & Montgomery, 1997) (see Discussion).

To calculate the critical shear stress required to mobilise finer fractions in the bed (such as those causing abrasion) we needed to account for hiding, whereby smaller clasts become relatively less mobile due to the shelter of larger clasts (e.g. Parker, 2008). The equation used to calculate the critical shear stress to mobilise a given size fraction (τ_{crD_i}) was as follows:

$$\tau_{crD_i} = \tau_{crD_{50}} \times \left(\frac{D_i}{D_{50}} \right)^{(1-\gamma)}$$

where D_i is the grain size of interest and γ is the hiding coefficient, which takes a value between 1 (for equal mobility) and 0 (for no hiding). Gravel beds with small fines content tend towards equal mobility (e.g. Parker, Klingeman & McLean, 1982), whereas sites with sandy gravels tend towards limited hiding (e.g. Wilcock, 1993). We used a hiding coefficient of 0.81 for all sites. This γ value is the average of those compiled by Parker (2008) from field studies that observed the mobility of bed surfaces composed of grain-size mixtures. γ ranged from 0.65 to 0.9 in Parker's (2008) compilation, so we also undertook a sensitivity analysis using these values (see Discussion).

There is some uncertainty around the key grain size when considering the process of abrasion. Therefore, we calculated the flows required to initiate the motion of sand 2, 4, 8 and 16 mm grains.

We transformed entrainment stress at the periphyton monitoring locations to flow rate using output from the GRATE (Gravel Routing And Textural Evolution) 1D hydraulic model (Walsh 2015 GRATE V3.61 Technical Reference Manual, J. Walsh unpubl. data), which solves the governing equations for one-dimensional open-channel flow with a quasi-steady flow approximation. The models were calibrated by adjusting cross-section Manning n values until the modelled and surveyed water surface profiles at the calibration flow aligned. The model was then run for a range of flows between base flow and bankfull. The model time step was always 1 min. The calibration flow ranged among sites between 0.5 and 3.5 times the median flow (averaging 1.5 times median flow). Review of model calibrations at higher flows was not considered necessary since the shear stress partition exercise described below effectively discards all contributions to total Mannings n other than the contribution from grain roughness.

In cases where the periphyton monitoring area covered much of the channel width, we extracted the cross-section averaged total shear stress (τ) from the model.

At sites where periphyton sampling was precluded by deep water on a portion of the cross section, the shear stress was distributed over the cross section by depth (making the results quasi-2D) and the shear stress was then averaged across the area where periphyton monitoring was actually carried out.

The total shear stress over the channel boundary is developed from both grain roughness and form roughness (due to bedforms and bankside vegetation), but only the grain stress component (τ') is available to entrain bed sediment. We calculated the grain stress as:

$$\tau' = \rho g h' S_f$$

where h' is flow depth due to grain drag and S_f is the friction slope. We determined h' by iterative solution of the Einstein/Keulegan resistance formulation (Wilcock & Kenworthy, 2002):

$$u/(gh'S_f)^{0.5} = 2.5 \ln(11h'/k_s)$$

where u is the mean velocity and k_s is the equivalent sand grain roughness (taken as 2.8 times the 84th percentile size of the bed-surface material, D_{84}). We applied this approach using hydraulic data extracted from the model at the periphyton monitoring sites.

By running each model over a range of flows, we compiled flow versus grain stress 'ratings' for the periphyton monitoring sites. These were then interpolated to derive the flows associated with the entrainment stresses for each grain size of interest.

Exploring whether there is a common periphyton removal mechanism. Our approach was to assess whether drag, abrasion or molar action was typically responsible for reducing periphyton to $<10 \text{ mg m}^{-2}$ at each site by comparing the estimated periphyton removal threshold flow (Q_{pr}) with the ranges of discharge that caused drag, abrasion and molar action. We infer that if Q_{pr} occurs during flows less than that required to move sand, then the only mechanism available is drag. If Q_{pr} occurs during flows greater than that required to mobilise the D_{50} , then we assume that molar action is the dominant mechanism. Previous research relating to periphyton removal has focused on mobility of the D_{84} when considering broad-scale bed molar action (e.g. Duncan & Biggs, 1998; Biggs *et al.*, 1999). However, geomorphic literature (e.g. Parker *et al.*, 1982; Montgomery *et al.*, 1996) suggests that general mobility is initiated once the D_{50} size becomes mobile, so we have taken this approach. If Q_{pr} occurs during flows between sand mobility and D_{50} mobility, then we assume that abrasion is the dominant mechanism.

To further explore relationships between periphyton removal and sediment mobility, we investigated whether a common grain size was required to be mobile for effective periphyton removal across sites (rather than a common mechanism). To assess this we calculated the grain stress at the periphyton removal threshold flow (τ'_{pr}) for comparison with the critical stress for various grain sizes (τ_{cri}). This enabled a graphical comparison across all sites of grain stress (standardised to τ'_{pr}). The sites were then sorted by τ'_{pr}/τ_{cri} and grouped to show the dominant mechanism.

Relating periphyton abundance to frequency of sediment movement and growth-promoting variables

The record of daily maximum flows (extracted from 15-min flow records) at each site was used to calculate the percentage of days on which the instantaneous flow was greater than that required to mobilise sand (i.e. periphyton removal by abrasion) or the D_{50} (i.e. removal by molar action).

We then plotted time-averaged chlorophyll *a* against a range of growth-promoting variables, including time-averaged SIN, SRP, water temperature and degree of shading. We visually inspected the plots to determine whether sediment mobility influenced the relationships.

Comparing flow and sediment-related metrics as predictors of periphyton removal

The most commonly used metrics for defining the periphyton disturbance flow in New Zealand are those based on multiples of the median flow (Clausen & Biggs, 1997; Booker, 2013), in particular three times the median flow ($3Q_{50}$). We compared the relationships between Q_{pr} (the 'observed' periphyton removal flow) and various predictors of the periphyton removal flow (Q_{sand} , $Q_{16\text{ mm}}$, $Q_{D_{50}}$ and $3Q_{50}$).

Results

Periphyton removal mechanisms

At most sites the periphyton removal flow aligned with a visually distinct threshold reduction in periphyton abundance (Fig. 3a, c). At some sites there was a less distinct drop in periphyton abundance. However, the range of flows that cause abrasion was also wider at these sites (Fig. 3b, d).

At most sites the grain stress at the flow that removes periphyton (τ'_{pr}) was less than the critical grain stress to

mobilise sand (τ_{sand}) and greater than the critical grain stress that moves 16 mm sediment ($\tau_{16\text{ mm}}$) (Fig. 4). In other words, abrasion was the most common mechanism of removal and the sediment size required for effective abrasion ranged between 2 mm (sand) and 16 mm. At two sites (Rangitikei at Onepuhi and Tiraumea at Ngaturu) drag was clearly sufficient to remove periphyton ($\tau'_{pr} \ll \tau_{sand}$). At three sites τ'_{pr}/τ_{sand} was very close to 1, so it remains uncertain whether the key mechanism of removal at these sites was drag or abrasion. Molar action ($\tau'_{pr} > \tau_{D_{50}}$) operated at the periphyton removal threshold at two sites (Mangapapa at Troup Road and Oroua at Almadale), but was also very close to occurring at Waikawa at Manakau Road. The calculated flows required to move sand ranged between 0.5 and 14.8 times the median flow, and flows required to remove periphyton ranged between 1.7 and 14.5 times the median flow (Table 2).

Periphyton abundance related to frequency of sediment movement and growth-promoting variables

Flows competent to mobilise sand occurred between 2 and 79% of days, and flows competent to mobilise the D_{50} occurred between 0 and 25% of days (Table 2). When mean chlorophyll *a* was plotted against various growth-promoting variables (mean SRP, SIN and water temperature), and sites were classified based on both degree of shading and frequency of sediment mobility, some clear trends emerged (Fig. 5). Sites that maintained low mean chlorophyll *a* ($<20\text{ mg m}^{-2}$) covered a spectrum of nutrient availability, water temperature and light availability, but were all highly mobile ($>10\%$ of days with abrasion) with two exceptions. Rangitikei at Pukeokahu and Rangitikei at Mangaweka (R@P and R@M on Fig. 5) both had low mobility ($<10\%$ of days with abrasion) and were not light limited but maintained a low mean chlorophyll *a* (4.1 and 9.7 mg m^{-2} , respectively). However, these two sites also had low mean SRP, SIN and water temperature. The only highly mobile site that achieved a high mean chlorophyll *a* (of 56.6 mg m^{-2}) was Manawatu at Hopelands (M@H on Fig. 5) and this site had all growth-promoting variables in its favour with relatively high SIN, high SRP, low shade and high mean water temperature.

Comparing predictors of periphyton removal flows

As measured by linear regression coefficients (R^2), all tested sediment mobility metrics performed better as predictors of Q_{pr} than did the $3Q_{50}$ flow metric (Fig. 6).

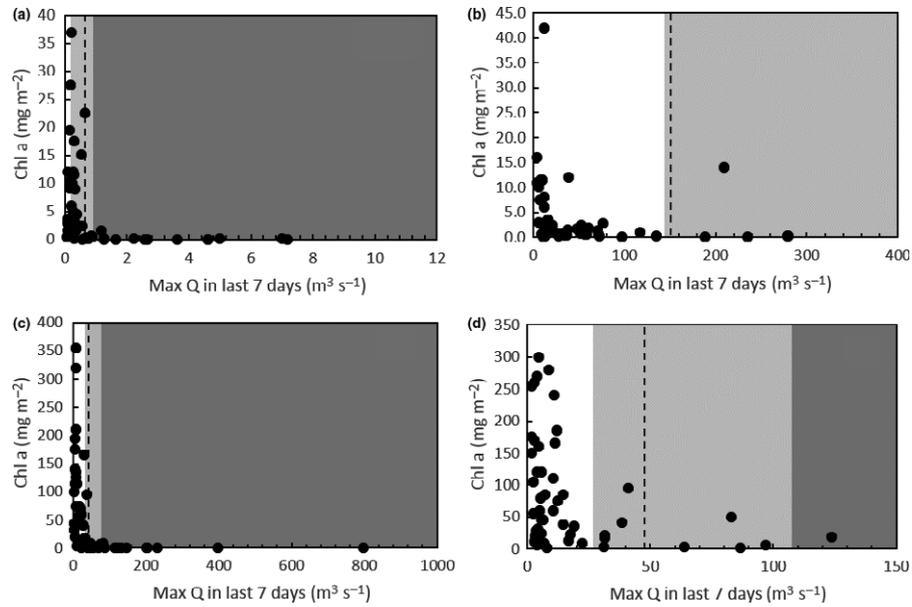


Fig. 3 Example plots of chlorophyll *a* versus peak 7-day antecedent flow overlaid on flow ranges for different removal mechanisms (drag, abrasion, molar action). White area indicates the flows at which no sediment is mobile and drag is the only mechanism available to remove periphyton, light grey area indicates range of flows at which abrasion may occur, and dark grey area shows flows at which molar action may occur. Dashed line is the estimated Q_{pr} , which in each of these cases falls within the abrasion range of flows. These sites are the same as shown in Fig. 1 (i.e. they represent the spectrum of sites in terms of periphyton abundance, mean discharge and bed sediment size).

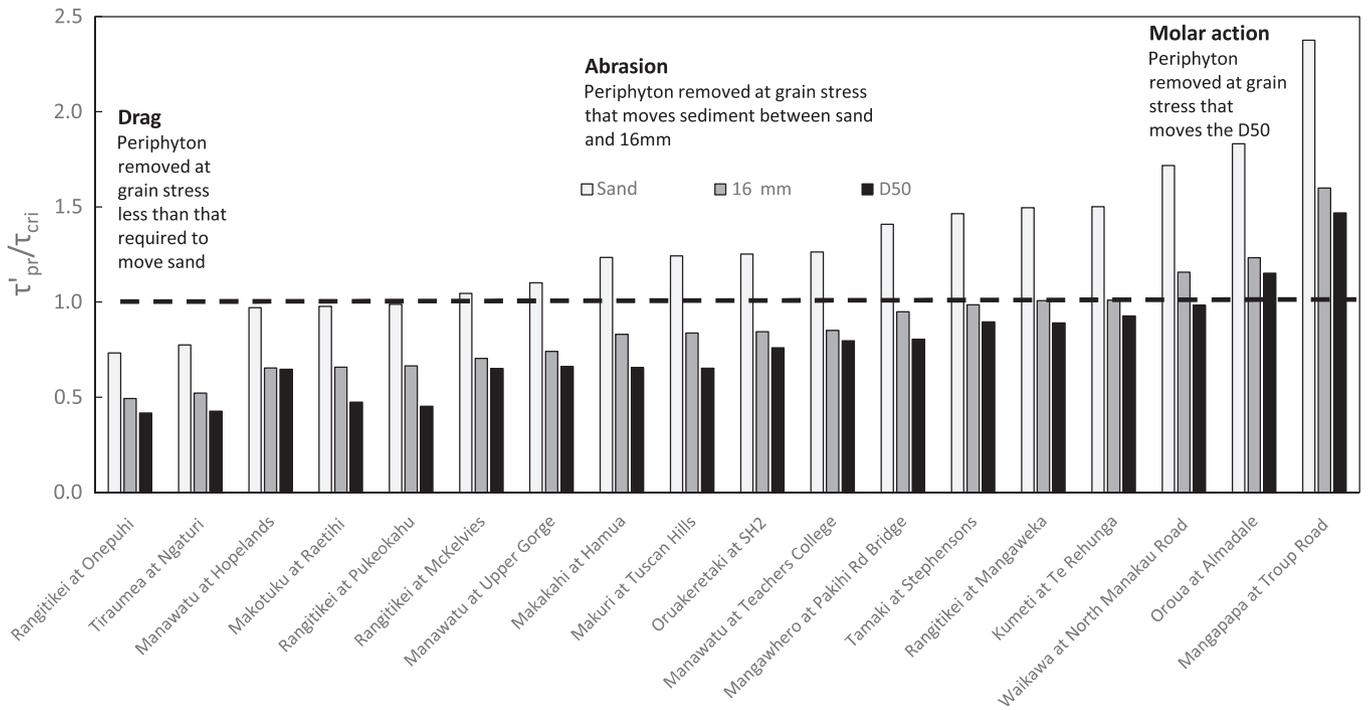


Fig. 4 Grain stress at periphyton removal flows relative to the critical stress for sand, 16 mm gravel and the D_{50} at each study site. Sites are sorted from left to right by increasing periphyton removal grain stress relative to sand-mobilising grain stress. This sorts the sites by the proposed mechanism of periphyton removal: drag, abrasion or molar action. Bars that extend above 1, marked with a dashed line, indicate sediment sizes that are mobile at the estimated Q_{pr} .

Table 2 Summary of flows required to initiate key mechanisms of periphyton removal, along with the estimated threshold flows for periphyton removal (Q_{pr}) and the median flow (Q_{50}). The frequency of sand mobility and D_{50} mobility is presented as the percentage of days over the study period that flows were greater than flows required to initiate mobility. Sites with a $Q_{D_{50}}$ of 'none' are those where bankfull flow is not competent to mobilise the D_{50} .

Site	Q_{sand} ($m^3 s^{-1}$)	$Q_{D_{50}}$ ($m^3 s^{-1}$)	Q_{pr} ($m^3 s^{-1}$)	Q_{50} ($m^3 s^{-1}$)	Q_{pr}/Q_{50}	Q_{sand}/Q_{50}	% days > Q_{sand}	% days > $Q_{D_{50}}$
Kumeti at Te Rehunga	0.2	0.9	0.6	0.31	1.9	0.5	79.0%	13.0%
Makakahi at Hamua	26.4	70.2	38.1	3.14	12.1	8.4	6.5%	1.6%
Makotuku at Raetihi	10.7	61.0	10.5	0.73	14.5	14.8	3.9%	0.3%
Makuri at Tuscan Hills	27.1	107.8	40.8	3.49	11.7	7.8	5.4%	0.0%
Manawatu at Hopelands	35.1	78.3	33.2	15.05	2.2	2.3	25.6%	10.5%
Manawatu at Teachers College	102.7	161.3	129.2	65.76	2.0	1.6	40.6%	24.2%
Manawatu at Upper Gorge	147.9	378.1	155.8	51.11	3.0	2.9	20.7%	5.0%
Mangapapa at Troup Rd	1.1	2.5	4.0	0.33	12.2	3.2	24.7%	10.0%
Mangawhero at Pakihi Rd Br	9.0	22.3	15.7	3.3	4.8	2.7	14.2%	3.0%
Oroua at Almadale	6.2	13.7	17.9	6.06	3.0	1.0	55.7%	25.2%
Oruakeretaki at SH2	1.1	3.0	2.3	1.39	1.7	0.8	65.9%	22.5%
Rangitikei at Mangaweka	251.7	344.9	318.6	45.25	7.0	5.6	4.4%	2.3%
Rangitikei at McKelvies	95.3	130.3	98.2	46.41	2.1	2.1	29.0%	19.3%
Rangitikei at Onepuhi	140.7	224.9	101.7	48.57	2.1	2.9	16.5%	7.7%
Rangitikei at Pukeokahu	187.8	none	158.5	16.73	9.5	11.2	1.9%	0.0%
Tamaki at Stephensons	2.4	5.6	4.5	2.25	2.0	1.0	52.6%	20.1%
Tiraumea at Ngaturi	82.3	none	46.6	7.13	6.5	11.5	5.1%	0.0%
Waikawa at North Manakau	3.2	6.5	6.4	0.88	7.3	3.6	15.5%	6.1%

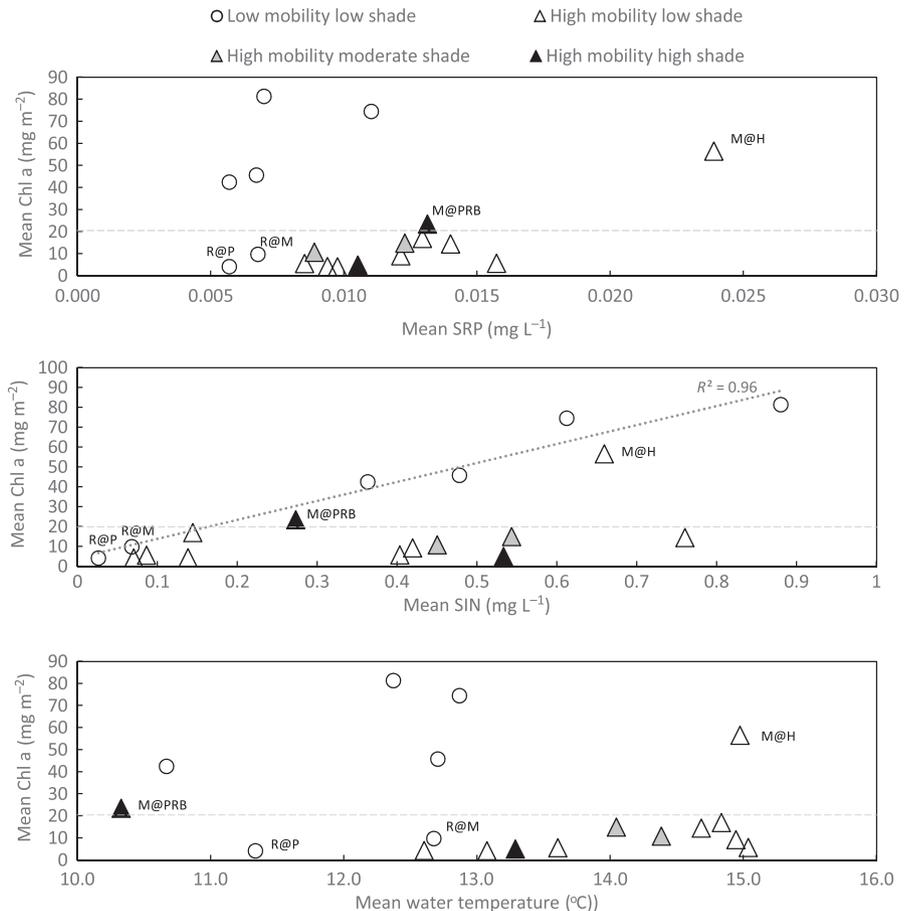


Fig. 5 Mean chlorophyll *a* versus mean soluble reactive phosphorous (SRP, top), mean soluble inorganic nitrogen (SIN, middle) and mean water temperature (bottom), with sites coded by frequency of mobility (symbol shape) and degree of shade (symbol shade). High mobility sites have sand mobile >10% of days. Low mobility sites have sand mobile <10% of days. Shade was classified based on height and proximity of tree cover and aspect of the channel (north-south vs east-west) (Table 1).

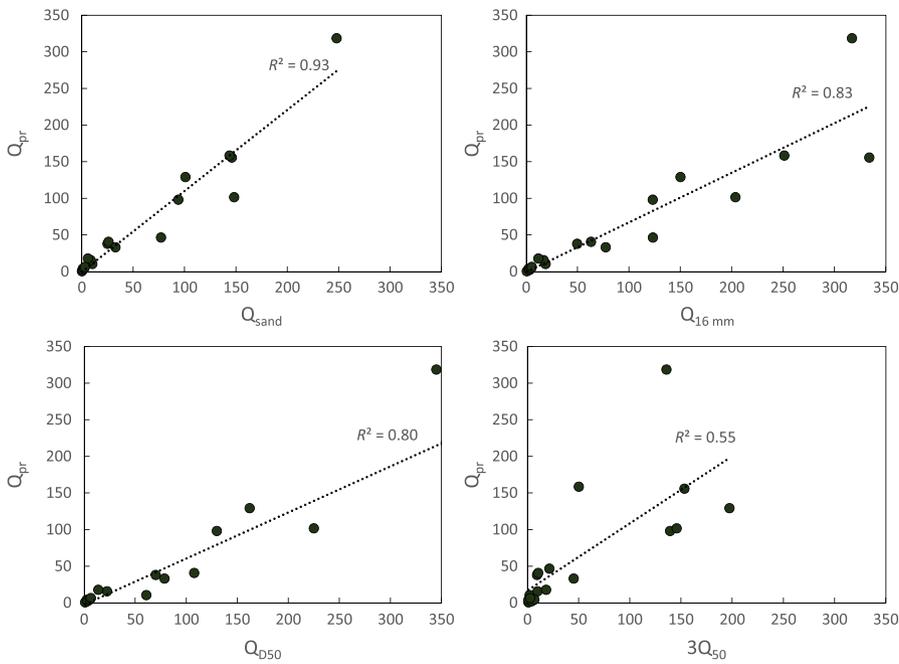


Fig. 6 Predicting the periphyton removal flow (Q_{pr} , $m^3 s^{-1}$) using various metrics (Q_{sand} , $Q_{16 mm}$, Q_{D50} and $3Q_{50}$). All sediment mobility metrics show a stronger relationship with Q_{pr} than does $3Q_{50}$.

The strongest Q_{pr} predictor was Q_{sand} with an R^2 of 0.93.

Discussion

How do periphyton removal flows relate to sediment mobility?

Our first question was whether a particular physical mechanism (i.e. drag, abrasion or molar action) was responsible for removing periphyton down to low levels ($<10 mg m^{-2}$) at each site, and whether the mechanism was consistent across sites. Our results demonstrated that periphyton removal flows were related to sediment mobility. Abrasion appeared to be the dominant physical mechanism that removed periphyton at most sites, although the size of sediment required to be mobile was less clear.

Some periphyton communities are more loosely attached than other communities and, therefore, we might expect correspondence between the key mechanism of removal and the typical periphyton community at that site. Comparing the results in Fig. 4 with the dominant taxa data in Table 1 shows that the two sites where drag was the clear mechanism of removal (Rangitikei at Onepuhi and Tiraumea at Ngaturi) were both dominated by *Melosira* and *Diotoma*. These diatom taxa are both known to attach only loosely to substrates and, therefore, drag seems a reasonable mechanism of removal. However, the two sites at the other end of

Fig. 4, where the key mechanism of removal has been identified as molar action (Mangapapa at Troup Road and Oroua at Almadale), were also dominated by loosely attached diatoms (*Melosira*, *Rossithidium* and *Navicula*). Sites with taxa that adhere more tightly to the bed were distributed within the group of sites with abrasion identified as the mechanism of removal. For example, the tightly adhering red alga *Audouinella* dominated at Kumeti at Te Rehunga, possibly reflecting the fact that this site had the highest frequency of sand mobility of all the sites. However, the site with next highest frequency (Oruakeretaki at SH2) was dominated by loosely attached *Melosira*. In summary, our results showed no clear relationship between the mechanism of removal and the periphyton community present. The fact that taxa data were available for only one time during the study period limits data interpretation. However, the monthly data on percentage cover of films, mats and filaments covered the full study period. There was also no pattern between these broad classes and the mechanisms of removal.

There are various potential reasons for the lack of relationship between periphyton community type and identified removal mechanism. Firstly, our identification of removal mechanism does not take account of the frequency of this mechanism or how rate of sediment transport influences efficiency of periphyton removal, but we note that this should vary between sites due to varying availability of the finer bed material fractions (see % sand in Table 1). The reality of whether a flow

actually causes sediment mobility will be inherently spatially and temporally variable due to temporally variable sediment supply and spatially variable bed composition. Taking abrasion as an example, even if sand is theoretically mobile, its effectiveness at removing periphyton will be spatially and temporally variable due to sand supply and the age, health and type of periphyton community (Biggs & Thomsen, 1995; Cullis *et al.*, 2013). Abrasion is likely to be least effective in channels where part of the bed is rarely mobilised and periphyton can find refuge in the lee of large immobile clasts.

Secondly, there remains uncertainty in both the identification of Q_{pr} and in the calculation of flows required to entrain bed sediment. Some uncertainty in the identification of a periphyton removal threshold discharge (Q_{pr}) for each site is inevitable, as the removal threshold at a site can be expected to vary since the proportion of periphyton lost during floods of similar magnitude can vary depending on pre-flood biomass, age, health, species or the antecedent conditions under which the periphyton grew (Biggs & Close, 1989; Biggs & Thomsen, 1995). Also, we assumed a set antecedent flow window of 7 days in our criteria for identifying Q_{pr} . We acknowledge that a 7-day window may not be the best choice for every site, but our aim was to apply a consistent, objective approach across all sites. As a sensitivity analysis we also calculated Q_{pr} values based on the 14-day flow window. The effect of choosing this larger window is to generally identify a larger removal discharge. This made a significant difference to Q_{pr} at six sites (altering the identified mechanism of removal), however, it made little to no difference at most sites and did not alter the key finding that abrasion is the most common mechanism of removal (12/18 sites vs 11/18 sites using the 7-day window).

We also acknowledge uncertainty in the calculated thresholds of sediment mobility as these are based on modelled results. To model the flows required to initiate mobility of different fractions of the bed, we carried out a shear stress partition and assumed a hiding coefficient (Parker *et al.*, 1982; Wilcock, 1993; Parker, 2008). Carrying out a shear stress partition is important as the proportion of the total shear stress that is exerted on the bed (grain stress) varies between reaches depending on the size of the bed material. Reaches with very large bed material (i.e. a rougher bed) will have a higher grain stress relative to the total shear stress. We kept the hiding coefficient consistent across sites to avoid any bias. In reality, the degree of hiding will vary between sites due to variability in bed sediment size distribution. The key point is that it is important to allow for hiding,

particularly at sites with very large bed material. If hiding is ignored (i.e. a hiding coefficient of 0), then the mobility of the finer fractions of the bed will be overestimated. For our sites using a hiding coefficient of 0 resulted in sand mobilisation 100% of the time at 13 of 18 sites. We also assumed a Shield's number of 0.035. We carried out a sensitivity analysis varying the hiding coefficient between 0.65 and 0.9 and varying the Shield's number between 0.035 and 0.052. With a hiding coefficient of 0.65 and a Shield's number of 0.035 (the maximum mobility scenario), abrasion becomes the mechanism of removal at all sites other than Mangapapa at Troup Road and Oroua at Almadale, where molar action remains the mechanism of removal. With a hiding coefficient of 0.9 and a Shield's number of 0.052 (low mobility scenario) drag becomes the key mechanism of removal at all sites except Manawatu at Teachers College (abrasion) and Mangapapa at Troup Road (molar action).

Does frequency of sediment movement help explain differences in periphyton abundance across a range of sites?

Our results show that understanding differences in the frequency of sediment mobility between sites may improve the prediction of sites with the potential to develop nuisance levels of periphyton based on other factors such as nutrient levels, water temperature and light availability. The general pattern shown in Fig. 5 is that sites that experience frequent bed mobility have limited potential to develop high levels of chlorophyll *a* regardless of nutrient availability, whereas sites with low sediment mobility do have potential to develop high levels of chlorophyll *a* under non-limiting light conditions. Our data also indicates that there is a strong relationship between mean chlorophyll *a* and mean SIN at the low mobility sites (R^2 of 0.96). The key point from Fig. 5 is that by understanding the relative mobility of sediment we can understand some of the noise in the relationships when all sites are grouped together. These results may help explain why some previous studies reported weak relationships between nutrient concentrations and periphyton abundance (e.g. Welch *et al.*, 1988; Lewis & McCutchan, 2010), whereas others have found strong links (Lohman, Jones & Perkins, 1992; Biggs, 2000b).

The sites identified as low mobility in Fig. 5 all had <10% of days when sand could be mobilised and <3% of days when the D_{50} could be mobile. The split between what is considered low mobility and high mobility is arbitrary. Mangawhero at Pakihi Road Bridge (noted on

Fig. 5 as M@PRB) could potentially be considered to have low mobility as the D_{50} is mobile on 3% of days, but sand is mobile on 15% of days so we classified this site as high mobility. Altering the Shield's number and hiding coefficient in our sensitivity analysis only reduced the mobility of the D_{50} at each site but resulted in a range of potential frequencies of sand mobility at each site. Therefore, the actual frequency of abrasion at our sites remains uncertain, but we can be confident that sites identified as low mobility in Fig. 5 have D_{50} mobility <3% of days.

If these frequencies are described in terms of days per year, the sites we have identified as low mobility in Fig. 5 all have D_{50} mobile <10 days year⁻¹. Biggs *et al.* (1999) found that chlorophyll *a* was 2–10× higher where bed sediments moved <15× year⁻¹. If we were to classify our sites as low mobility based on D_{50} mobility occurring <15× year⁻¹, then Mangawhero at Pakihi Road Bridge would be classed as low mobility. The results from the two studies are not directly comparable as Biggs *et al.* (1999) focused on mobility of the D_{84} and their calculation of frequency above threshold was defined in terms of events per year, where consecutive days above the disturbance threshold are part of the same event. This alternative definition of frequency of disturbance may perform better for some sites. When we analysed the data for our sites we found that number of events above threshold performed less well as a predictor than number or percentage of days above threshold. This is because for highly mobile sites, a very high number of days above threshold (e.g. many consecutive days with sand mobile) gives a low frequency of events which is misleading.

We also note that our calculations of flow frequencies (days above threshold flow) are based on the instantaneous flow record for each site rather than a mean daily flow record (as used by Biggs *et al.*, 1999, when calculating FRE₃ and FRE_{D84}). We argue that using an instantaneous flow record is important when predicting frequency of disturbance, since flows can rise and fall rapidly, particularly in small catchments, and calculations based on mean daily flows will damp peak flows and thereby miss some sediment entrainment and periphyton removal events.

There remains considerable work to do around predicting periphyton abundance at any point in time within a site, both with regard to understanding space-time variability in removal processes and antecedent periphyton cover, and capturing this understanding within simple but reliable indicators/rules of thumb for application to river management.

Do sediment-related metrics provide improved prediction of periphyton removal flows?

Our third question was whether sediment entrainment-related metrics show a stronger relationship with periphyton removal flows than do multiples of the median flow (e.g. 3Q₅₀). The latter have been shown to perform reasonably well (e.g. Clausen & Biggs, 1997) and on this basis 3Q₅₀ has been used as a 'rule of thumb' to define the flood size that removes periphyton (e.g. Heath *et al.*, 2015). However, we found in this study that all tested sediment-related metrics performed better than the 3Q₅₀ as predictors of Q_{pr}. We, therefore, conclude that prediction of the periphyton disturbance flows can be improved by using flow metrics that relate to sediment mobility – even if these require greater investment in field studies to derive them.

The importance of recognising geomorphic differences between sites

The overall aim of this research was to explore the idea that understanding geomorphic differences in rivers, particularly in terms of their bed sediment stability and supply, may improve understanding of which rivers are most vulnerable to changes in flow or nutrients with respect to algal blooms. We have shown that (i) periphyton removal commences at discharges when the sand and fine-gravel fractions of the bed surface become mobile; and (ii) differences in the frequency of sediment mobility between sites can help explain differences in periphyton abundance and can also identify sites where nuisance algae may develop. The key then is to understand why some sites are more mobile than others and to be able to recognise different geomorphic types of rivers to predict sediment mobility.

Mobility of the different size fractions of the bed-surface material depends on both the size-specific entrainment stress and the local grain stress, both of which are influenced by geomorphic controls, notably the size grading of the bed material. For example, boulders that are rarely, if ever, mobile increase the hiding factor on sand and fine gravel. Boulders and clast clusters also create form drag, while morphological units (e.g. riffles and pools) cause spatial variation in shear stress, both of which influence the amount of grain stress available locally to entrain bed-surface material.

Within the same hydrological region (i.e. across which the same runoff events occur) the balance of grain stress against entrainment stress determines the frequency of

mobility for a given size fraction. The effectiveness of abrasion on periphyton removal will also be influenced by the availability of sand and fine gravel on the bed surface, since if there is none to entrain there can be no abrasion. Francoeur & Biggs (2006), when testing the effects of sediment scour on periphyton removal in a laboratory, found that 86–100% of the maximum observed periphyton removal occurred in the first 5 min of scour, therefore, as long as sand is available it appears that removal can happen quickly. One might assume that a dilute bedload may achieve the same results as a more concentrated one but may simply require longer.

Differences in sediment supply and bed mobility have been used as a basis for classing rivers into different geomorphic types (e.g. Schumm, 1985; Church, 1992). For example, 'threshold' channels (*sensu* Church, 2006) are those where the framework of the bed is essentially immobile. Examples include channels with step-pool cascades, exposed bedrock or very large boulders, and a relative absence of sand and fine gravel. By contrast, in 'alluvial' channels all size fractions are mobilised during floods, hiding effects are less by virtue of less extreme ranges in grain size. Between these two end members there is a gradient of relative mobility. Thus, a geomorphic classification of channels across the gradient between threshold and alluvial offers some potential to distinguish rivers with periphyton accrual more or less sensitive to nutrient loading. It is of note from Fig. 5 that five of the six sites that are classified as low mobility (Makuri, Tiraumea, Makotuku, Makakahi and Rangitikei at Pukeokahu) could be classed as threshold channels by virtue of their low frequencies of sand mobility (<10%) and D_{50} mobility (<3%) and by their typically boulder-grade D_{90} (i.e. >128 mm, Table 1).

Application of this study's findings to periphyton management at the regional level requires ways to quickly estimate bed mobility at a site (and from that and the flow record the proportions of time that sand, fine gravel and general bed mobility occurs). Ideally, these require information on site bed-surface material size distribution, hydraulic data to relate flow to local bed shear stress and they also must deal with spatial variability in shear stress, stress partitioning and hiding effects on sediment entrainment. Although some approaches (e.g. Duncan & Biggs, 1998; Lorang & Hauer, 2003; Clausen & Plew, 2004) cover part of the problem, a major challenge lies with providing estimators that adequately deal with all aspects of site hydraulic and geomorphic properties.

In conclusion, we identified at most of our study sites a clear threshold flow that reduced periphyton abundance to low levels. This flow typically coincided with the range of flows required to move sand to fine gravel (up to 16 mm). We conclude from this that abrasion during frequent small floods appears to be the dominant physical mechanism keeping periphyton abundance at low levels. Our results also showed that the relationship between mean periphyton abundance (as mean chlorophyll *a*) and growth-promoting variable (mean SIN, SRP and water temperature) varied depending on the frequency of sediment mobility (both abrasion and molar action). The results highlight that removal frequency is the dominant control on periphyton abundance and that other factors become important when the removal frequency is low. This suggests that partitioning sites based on frequency of sediment mobility (either sand or the D_{50}) could improve predictability of sites at which there is potential for nuisance levels of periphyton to develop. We also found that all tested sediment-related flow metrics showed a stronger relationship with periphyton removal flows than the commonly used flow metric, three times the median flow. These results highlight the importance of recognising geomorphic differences between sites, in particular the frequency of sediment mobility, when trying to predict the effects of flow and nutrient changes on periphyton abundance. We note that further work is needed to predict periphyton abundance at any point in time at a given site.

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