## Investigating the impact of moving sand during summer spates on the spatial distribution of stream periphyton biomass in a gravel-cobble bed boreal river

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#### Abstract

The abrasive effects on periphyton biomass of saltating sand, that was transported over a stable gravel-cobble riverbed during summer flow events (spates), was studied on 35 riffles of an oligo-mesotrophic river in Quebec. A periphyton saltation abrasion model (PSAM) was developed from an existing bedrock erosion mechanistic model (Sklar and Dietrich 2004). The empirical PSAM models explained 56-59% of the variance in post-spate biomass on individual host-rocks following a low-magnitude, high-frequency spate.

Periphyton biomass was curtailed on riffle rocks when sand transport rates exceeded 64-180 g m<sup>-1</sup>event<sup>-1</sup> during spates. This perturbation threshold was confirmed by an *in situ* experiment that documented periphyton losses resulting from increasing rates of sand transport. Low profile substrates (2 cm) were scoured more thoroughly than high protruding substrates (6 cm), confirming the PSAM hypothesis that refuge potential increases with elevation above the stream bed relative to the mean sand saltation height.

An analysis of spatial patterns of periphyton biomass across riffles confirmed the tendency for a spate-related refuge habitat between the edge of the varial zone (zone of frequent wetting and drying) and the thalweg (deepest point) of the channel.

A hierarchical model (HPPM) that simulates how periphyton biomass is regulated by the flow of water and the flux of sand down a sedimentary link (segment of river along which grainsize and slope decreases systematically downstream) was developed and validated. Sedimentary links contained 3 channel types (hydrogeomorphic reaches, HGRs), each possessing significantly different morphological traits, ranging from straight-steep, cobblebed reaches (High-HGR) at the upstream end, to low-gradient, sinuous gravel-bed reaches (Low-HGR) downstream. For low-magnitude spates (e.g. 0.85Q<sub>Mean\_Annual</sub>), the most refuge (i.e. highest post spate biomass) was provided on riffles in Low-HGRs because sand transport rates were below the perturbation threshold. HPPM scenarios varying sand supply showed that link scale periphyton refuge area is very sensitive to normal variability in sand supply (e.g. a increase in sand on bed from 5% to 15% produced an 8 fold decrease in post-spate biomass). Further, biomass was universally low at higher levels of supply, characteristic of anthropogenically disturbed systems. Considering that these large scale losses occurred during spates with peak discharges that are exceeded 48% of the time annually, our results suggest that sand loading to river systems could severely limit biomass accumulation, and thus carbon and nutrient stores.

#### Résumé

Les effets abrasifs du sable en saltation sur la biomasse de périphyton, lorsqu'il est transporté au-dessus d'un lit de gravier et de galets stable durant les crues estivales, ont été étudiés sur 35 riffles d'une rivière oligomésotrophique québécoise. Un modèle d'abrasion du périphyton par saltation (PSAM) a été développé à partir d'un modèle mécanistique de l'érosion du soubassement. (Sklar et Dietrich, 2004). Les modèles PSAM empiriques expliquaient 56% à 59% de la variance de la biomasse après-crues sur les roches, suite à une période de crues de basse magnitude et de haute fréquence.

La biomasse du périphyton sur les roches des riffles était limitée par une vitesse de transport du sable qui excédait 64-180 g m<sup>-1</sup> événement<sup>-1</sup> durant une période de crues. Ce seuil de perturbation a été confirmé par une expérience *in situ*, où nous avons observé les pertes de périphyton causées par des vitesses croissantes de transport du sable. Le substrat à profil-bas (2 cm) a eu des pertes plus importantes de périphyton relativement au substrat saillant (6 cm), ce qui confirme l'hypothèse PSAM que le potentiel du refuge augmente avec l'élévation au-dessus du lit.

Une analyse de la distribution spatiale de la biomasse de périphyton dans les riffles a confirmé qu'une zone de refuge de crue existait entre les bords de la zone variable (zone fréquemment mouillée et séchée) et le thalweg du canal (le point le plus profond).

Un modèle de perturbation hiérarchique de périphyton (HPPM) a été développé pour simuler l'influence du transport de l'eau et le flux du sable sur la biomasse de périphyton à travers un lien sédimentaire (section de rivière de plusieurs km de longueur, où la dimension des roches diminue systématiquement en aval). Les liens sédimentaires sont divisés en 3 échelles de refuge : des lits de galets droits et raides (haute HGR) en amont, aux lits de gravier sinueux à faible gradient (bas HGR) en aval. Durant les crues de basse-magnitude (0.85  $Q_{Mean\_Annual}$ ), le refuge favorable du périphyton se trouvait dans les riffles de bas HGR, car les taux de transport du sable étaient inférieurs au seuil de perturbation. Les scénarios d'apport de sédiments testés dans HPPM ont aussi démontrés que le refuge à l'échelle du lien sédimentaire était sensible aux petits changements dans l'apport de sable (ex. 5-15% de sable sur le lit). De plus, la biomasse était plus basse pour les apports de sable élevés, charactérisant les systemes dérangés par l'homme. Si nous considérions que ses pertes on eu lieu durant les crues où la décharge maximale est exedée 48% du temps annuellement, nos

resultats suggèrent que l'apport de sable dans un système fluviale pourrait limiter l'accumulation de biomasse et les réserves de carbone et de nutriments.

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#### Statement regarding the role of co-authors

The four manuscripts in this thesis will be shortened and submitted for publication in peer-reviewed journals. For each manuscript, Prof. Michel Lapointe is a coauthor and third authorship is provided by Dr. Russell Steele on Chapter 3 and Prof. Antonella Cattaneo on Chapter 4. Contributions of co-authors to each manuscript are described below.

## Chapter 3: Modelling rock scale periphyton biomass remaining on a stable bed exposed to small spates: accounting for abrasion by saltating sand

Professor Lapointe provided stimulating debates regarding the strength of evidence available on processes responsible for spatial patterns of periphyton. A discussion with Prof. Marco Rodriguez helped focus efforts regarding exploratory multivariate statistical techniques for isolating the dominant factors affecting periphyton biomass from field data. Discussions with Prof. Peter Ashmore pertaining to an unrelated project led to the discovery of the 'tool and cover' based SAMB model, which later formed the basis of the paper. Dr. Russell Steele provided authorship on the statistical methods and results. Dr. Steele assisted with mapping causal pathways and gave a thorough analysis of the final models that I provided for testing. In the process, Dr. Steele suggested using linear mixed effects models to address issues related to sample design. Both Dr. Steele and Prof. Lapointe provided advice on model structure and gave intellectual and editorial comments on drafts of the manuscript which greatly improved the clarity of the text and cogency of arguementation.

### Chapter 4: Spatial patterns in periphyton biomass after low-magnitude flow spates: Geomorphic factors affecting patchiness across gravel cobble riffles.

Many discussions with Prof. Lapointe led to the design of the field study and the objective of examining cross riffle patterns in periphyton biomass. Prof. Cattaneo provided invaluable field advice on the best approach for quantifying periphyton biomass over the large scale required in this study. Further, Prof. Cattaneo also provided expertise in algal identification both in the field and in the lab. Veronique Trudeau helped me with spectrometry in the lab of Prof. Price (Department of Biology). Laboratory analyses of

nutrients (NO<sub>2</sub> NO<sub>3</sub>, NH<sub>4</sub>, TTN, TTP, PO<sub>4</sub>) were performed by the GEOTOP centre at the Université du Québec à Montréal. All other analyses were conducted by myself. Both Prof. Cattaneo and Prof. Lapointe provided intellectual and editorial comments on drafts of the manuscript.

### Chapter 5. A field experiment investigating how the height of the growth surface and the size of saltating sands affect the abrasion of stream bed periphyton.

Prof. Lapointe and Prof. Andre Roy encouraged me to take an experimental approach to obtain more direct evidence of the role of sand abrasion on periphyton. Many discussions with Prof. Lapointe led to the design of the experiment and the objective of isolating the threshold for disturbance by transported sand. Dr. Jose Correa (Math and Statistics Department, McGill) helped select multiple regression as the appropriate tool to evaluate differences in response between experimental runs. I performed all analyses included in the paper. Prof. Lapointe provided intellectual and editorial comments on drafts of the manuscript.

## Chapter 6. Modelling the effects of river sedimentary link structure and sand supply on downstream trends in periphyton refuge.

Many discussions with Prof. Lapointe centred on the objective of examining periphyton patterns at larger scales from early stages of the research process. Prof. Nigel Roulet encouraged the use of heuristic modelling to capture the main processes of the system to generate new insights and hypotheses. All programming and analysis was performed by myself. Dr. Steele also assisted in mapping causal pathways in the formulation of the overpassing sand transport model and he conducted parralel confirmatory analyses in HLM, MARS, CART and finally nonlinear regression. Dr. Desiree Tullos and Prof. Lapointe provided invaluable intellectual and editorial comments on drafts of the manuscript.

#### **Original Contributions to Knowledge**

The work presented in this dissertation provides original contributions in ecogeomorphology through the development of:

- 1. a mechanistically based periphyton saltation abrasion model (Ch. 3);
- thresholds for periphyton loss by spate related physical disturbance (sand abrasion, shear stress, velocity)(Ch. 4);
- a quantitative description of factors affecting the distribution of periphtyon refuge with: a) height of growth surface off the bed (Ch 3, 5), b) lateral position across riffles (Ch 4), c) reach scale differences in channel morphology (Ch 6), and d) distance down sedimentary links (Ch 6);
- 4. a model describing the transport of sand down a generic sedimentary link capable of modeling near threshold (over-passing) transport conditions (Ch. 6), and;
- 5. a hierarchical periphyton perturbation model to show the ecological effects of spate related disturbance at multiple spatial scales (Ch. 6).

The tools developed in this thesis will be useful in future studies seeking to: 1) quantify the role of human disturbances (e.g. urban development, drainage system modifications in response to climate change etc.) on periphyton biomass – base of the food chain in 3<sup>rd</sup> to 6<sup>th</sup> order gravel streams – through a sand supply variable (Ch. 6); and 2) predict for the first time, broad scale longitudinal and transverse spatial patterns of periphyton refuge habitats, which will facilitate the assessment of how quickly biomass recovers to pre-spate levels (Ch. 6). Knowledge of how geomorphology and sand supply affect spatial patterns in post-spate biomass is essential for instream benthic invertebrate and fish food resource mapping, identifying productive nodes in the river, and predicting how an increase in spate frequency and sand supply affect long term and large scale, along stream variability in biomass (Cada et al., 1987; Uehlinger et al., 1996; Nislow et al., 1999; Osmundson et al., 2002; Thorp et al., 2006; Ledger et al., 2008).

Spate disturbance has been shown to be a dominant factor governing the spatial distribution of periphyton biomass in gravel bed rivers (Biggs, 1995), but few studies

have investigated periphyton loss processes during low-magnitude, high-frequency spates (Uehlinger et al., 1996; Poff et al., 1997; Lake, 2000). The low magnitude spates that can recur many times during the period required for periphyton biomass to peak, typically transport sand entrained from surface interstices, channel margins and pools by a hopping motion (i.e. saltation) over a stable bed of gravel. The most studied local scale, spate related disturbance factors are hydraulic plucking by the shear force of water (Biggs and Thomsen, 1995; Stone, 2005), abrasion by suspended sediment (Francoeur and Biggs, 2006; Horner et al., 1990b), and complete mobilization of the upper layer of bed material by scour (Matthaei et al., 2003). Sand abrasion can cause significant periphyton losses (Culp et al., 1986; Francoeur and Biggs, 2006), but little is known about abrasion thresholds for saltating sand or about spatial patterns of refuge zones, where disturbance levels do not exceed these perturbation thresholds. Studies of periphyton refuge typically have focused on metre spatial scales, such as the shelter provided by the cracks in rocks (Bergey, 2005), in the lee of rocks (Francoeur and Biggs, 2006), on stable rocks or clusters of rocks (Francoeur et al., 1998) and across riffles (Ch. 4). This dissertation provides new insight into link- (sensu Table 2.1) and planform-scale refuge patterns. This knowledge is important because large, persistent refuge patches deliver algal cells to disturbed patches of riverbed located further downstream, assisting in the recolonization of these denuded surfaces. Thus the rate of recovery of biomass to pre-spate levels within rivers increases with the number, size and degree of connectivity of post-spate refuge patches (Dunning et al., 1992; Townsend et al., 1997).

Chapters 3 to 5 document small scale periphyton perturbation processes and present the sub-models and parametrisations that are required for the hierarchical periphyton perturbation model (HPPM) developed in the synthesis orientated Chapter 6.

Chapter 3 presents a model of periphyton abrasion by saltating sand (PSAM), which is the first attempt to merge the theoretical consideration of the sediment transport regime during sub-bankfull spates with a mechanistic model of bedrock abrasion by saltating sediment (Sklar and Dietrich, 2004), and a theoretical consideration of periphyton ecology. Previous studies of the abrasive potential of saltating sediment in moving water have focused on erosion rates of rock and cohesive clay, not periphyton (Kamphuis, 1990; Sklar and Dietrich, 2004). Through the development of PSAM, we present the idea that the amount of periphyton lost during a spate is a function of the immersion of the periphyton covered rock within the layer of intense sand transport (saltation layer) near the streambed. The amount of variance in rock scale observations of biomass explained by the PSAM model (i.e. 56% to 59%) is similar to the amount of variance explained by other studies predicting biomass from environmental conditions that aggregated data at larger spatial scales. In contrast, our model with similar predictive power, was resolved at the scale where periphyton abrasion occurs (i.e. rock scale) and did not average out this fine scale spatial heterogeneity in biomass over a large reach (e.g. reach scale), as previous studies have done. The results presented in Chapter 3 provides new insight into the biotic effects of frequent streambed abrasion through sand saltation that complements our more developed understanding of the effects of shear stress and finer suspended sediments on periphyton biomass during larger spates (Francoeur and Biggs, 2006). Our findings support the field study of Thomson et al. (2005), who suggested that sand saltation is a significant process for consideration when assessing periphyton removal from stable river beds. This dissertation work is also a step forward toward resolving Uehlinger's (1991) call for a better means of predicting biomass losses from small flow events (e.g. < 2MAD). The development of PSAM enhances our understanding of periphyton regulating processes, and may enable more accurate predictions of the distribution and resilience of the food resource upon which riverine food webs are based.

Chapter 4 presents field data documenting the threshold effect of sand transport rate on diatom dominated periphyton biomass. Periphyton perturbance thresholds have been reported for shear stress (Biggs and Thomsen, 1995; Stone, 2005) and velocity (Biggs and Close, 1989; Horner et al., 1990a; Rasmussen and Trudeau, 2007), but not for sand transport rates. Quantitative insight into the effects of suspended sand on periphyton loss had already been provided by flume studies (Francoeur and Biggs, 2006; Horner et al., 1990b), yet there was a lack of field studies documenting the effects of saltating sand on periphyton distribution. In Chapter 4, I also investigated an untested theory (see Jowett 2003) that, along riffle cross sections, a hydraulic refuge zone exists in the transition zone that is located between the "varial zone", where stranding and desiccation stress occurs at the channel edge, and the "thalweg zone" where high velocities and most sediment transport occurs. My field data are the first to validate such a transition zone refuge hypothesis (TZRH) for periphyton. Cross channel patterns in post-spate biomass were limited by the cross stream distribution of sand transport (rather than shear stress or velocity). The data provided unique insight into the existence of a bimodal distribution of sand transport across the channel. As expected, this pattern in transport explained the low periphyton biomass in the thalweg. However, low biomass was also found near the channel edge, where the secondary peak in transport occurred, despite the diminished flow strength at that location. This secondary shoreward peak in sand transport limited the high refuge potential of the transition zone.

Chapter 5 presents direct experimental evidence of periphyton abrasion by saltation under fixed flow conditions. While our earlier field studies (Ch 3, Ch 4) provided insight into the sediment-transport mechanisms potentially responsible for periphyton disturbance, their unconstrained observational design (i.e. uncontrolled field setting, exposure to a variety of flood intensities) precluded a discussion of the effects purely attributable to saltation abrasion. The *in situ* field experiment reported in Chapter 5 supported the hypotheses that: 1) host-rocks that protrude above the maximum saltation height retain higher biomass on their tops, because the periphyton residing there is protected from sand abrasion, and 2) abrasion losses of periphyton by predominantly suspended fine sand was less than abrasion losses associated with predominantly saltating coarse sand. The experiment also confirmed sand transport rate thresholds inferred from field data in Chapter 4. Low rates of sand transport (e.g.  $0.04 \text{ g m}^{-1}\text{s}^{-1}$ ) caused some diatom-dominated periphyton loss while moderate rates (e.g. > 0.2 g m<sup>-1</sup>s<sup>-1</sup>) lead to substantial scour of periphyton from a stable cobble bed stream, such as the SMR. The power function exponents relating periphyton biomasss and bedload transport rates were similar between the Skona River, where coarse bedload (gravel-cobble) was in transport (Stokseth, 1994), and the Sainte Marguerite river, where sand was in transport. This suggests that my study results may be more broadly applicable to similar diatom dominated river systems.

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Chapter 6 presents a multi-scale hierarchical periphyton perturbation model (HPPM) that is used to investigate how rock scale (mm-m) physical disturbances affect the spatial distribution of periphyton at the sedimentary link scale (100's m – km). Through the development of the HPPM, this study addresses and incorporates several pressing ecogeomorphology related research issues including: 1) how small scale processes operate within a larger scale context, 2) how sediment dynamics (i.e. as opposed to hydraulic fluctuations alone) affect small scale periphyton habitat, and 3) how sub-bankfull spates affect periphyton biomass (i.e. as opposed to extreme high or drought flows)(Lake, 2000; Thorp et al., 2006).

Unlike studies that use multivariate statistics to analyze unconstrained field data, our modelling approach (HPPM) enabled a causal assessment of how channel form and sand transport dynamics influence periphyton biomass under a fixed flow and sediment supply condition, at the reach and link scale. This sediment transport centred modelling approach both contrasts and complements studies defining unique habitat zones based on flow dynamics and channel pattern (Thoms and Parsons, 2003). For a generic boreal Canadian shield river, the HPPM results provided a quantitative validation of the hypothesis that the patchiness of post-spate periphyton biomass for a given spate magnitude varies significantly, depending on the amount of fine sediment on the bed prior to the spate (Tett et al., 1978; Power and Stewart, 1987; Poff et al., 1997; Francoeur and Biggs, 2006).

In contrast to studies focusing on eco-geomorphological interactions at channel junctions (i.e. between sedimentary links, which are river segments with a systematic downstream decrease in grainsize and channel slope, bounded by coarse sediment sources, Benda et al., 2004; Kiffney et al., 2006; Rice et al., 2006), our HPPM provided a physical basis and a new insight regarding how post-spate biomass is distributed <u>between</u> channel junctions that supply significant coarse bed material. HPPM simulations indicated that the downstream distribution of biomass within these units (i.e. sedimentary links) was nonlinear and bimodal. This dissertation will show that the highest biomass remaining (i.e. refuge) after a higher frequency low-magnitude spate (i.e. 0.85MAD) is found at the downstream end of the sedimentary link. Moderate post-spate biomass

occurs in the coarser upstream end of the link, where some refuge is provided by larger rocks elevated above the zone of intense sand transport near the bed. Mid-link stream segments had the lowest post-spate biomass because substrate surfaces were exposed and easily immersed in the saltation layer of sand during spates.

The work presented herein also inspires new hypotheses related to ecosystem disturbance. For example, previous studies suggest that hydraulic refuge at the larger watershed/network scale exists in headwater tributaries and biomass recovery to pre spate levels extends downstream with time since spate (Young and Huryn, 1996; Rempel et al., 1999). In contrast, our HPPM simulations suggest that refuge after a large spate would occur at the downstream end of a sedimentary link located in the headwaters of the stream network.

Our HPPM results provide new confirmatory evidence to support theories that associate the reach scale geomorphic form and function of different channel types (e.g. straight vs sinuous) with the unique ecological characteristics of these diverse habitat templates (Montgomery, 1999; Church, 2002; Chessman et al., 2006). For example, Chapter 6 shows how the downlink differences in refuge potential are linked to variability in channel type at the reach scale (Hydrogeomorphic Reaches). The HPPM results also show how the geomorphic context of a riffle (i.e. the hydrogeomorphic character of the upstream reach) affects the amount of sand arriving from upstream and thus the patchiness of post-spate biomass. This HPPM finding provides a novel example of how the broader scale context of the hydrogeomorphic reach must be considered, given that biomass can be controlled by processes operating at larger (and smaller) spatial scales; as advocated by Chessman et al. (2006).

#### Chapter 1

# Fine sediment transport and its abrasive effects on streambed periphyton in a boreal river.

#### **1.1 Introduction**

Urbanization and climate change are associated with an increase in the volume, frequency, and intensity of runoff, as well as an increase in fine sediment loads through soil erosion, mass wasting, and channel adjustment (Gregory et al., 1992; Goudie, 2006). Predictive models are required to assess how changes in physical habitat will affect the distribution of fish under this altered disturbance regime. Current instream habitat models relate the flow regime to fish preferences for physical habitat variables (Bovee, 1986; Lamouroux and Jowett, 2005), but some studies suggest that biotic factors such as food availability may be more important (Cada. G. F., 1987; Nislow et al., 1999; Osmundson et al., 2002). Furthermore, current models focus on properties of flow, and do not consider fine sediment effects on the food resource. In a recent review of ecological theory related to the structure, function and distribution of biota within lotic systems, Thorp et al. (2006) stressed the importance of developing a model that addresses change in food resources along the entire river network. Development of this model requires a shift in research focus to: 1) match the scale of environmental process with the appropriate scale of biological organization, 2) examine how a given process varies longitudinally and laterally along the river network, 3) understand how important small scale processes (traditional focus) are for larger spatiotemporal patches, where other variables operate.

Periphyton are the dominant primary producers in most temperate stream ecosystems thereby supporting upper trophic level organisms (Biggs, 1995). Periphyton commonly refers to all the microflora (algae, bacteria, and fungi) on the substrata of freshwater streams, rivers, lakes and other waterways (Wetzel, 1983)(Figure 1.1). The food quality of algae (especially diatoms) is high compared to other nonanimal benthic food (e.g. detritus) (Lamberti, 1996). Gregory (1983) found that virtually all invertebrate feeding groups consumed some form of algae, and thus algae directly affects fish productivity. For example, Osmundson et al. (2002) showed that periphyton biomass was positively related to fish distribution over 375 km of the Colorado river. Their study also found periphyton biomass was negatively related to the fraction of sand on the bed, suggesting that this food resource is sensitive to the amount of sand in the river. In other studies, an increase in the fraction of sand on the bed has been shown to dramatically increase the sand transport rate (Wilcock and Kenworthy, 2002), and presumably the potential abrasion of periphyton.



**Figure 1.1** a) Diatom dominated periphyton with an even distribution; b) Diatom dominated periphyton with patchy distribution.

A large body of research has shown that periphyton biomass increases with the availability of resources (e.g. light, nutrients, and temperature) and decreases with the frequency and magnitude of disturbances (e.g. spates, grazing) (Stevenson, 1996; Azim et al., 2005; Biggs and Kilroy, 2007). In gravel bed rivers, spate magnitude and time since disturbance predict up to 63% of biomass at the reach scale (Biggs and Close, 1989; Uehlinger, 1991). Researchers agree that high-magnitude, low-frequency spates are capable of "resetting" the periphyton biomass to low levels over large sections of river (Fisher et al., 1982; Uehlinger, 1991). However, little research attention has been given to the role of low-magnitude, high-frequency spates in governing the spatial distribution

of periphyton biomass (Uehlinger, 1991). Researchers concur that the physical disturbance effects associated with low-magnitude spates on stream benthos are patchier than the spatially extensive scour observed during high-magnitude spates (Power and Stewart, 1987; Brookes, 1996; Brooks, 1998; Matthaei et al., 2003). However, little is known about the size and extent of the area of periphyton perturbed by these events, or how this patchy mosaic of periphyton relates to differences in the channel morphology and the small scale process of periphyton abrasion by sand. To characterize the spatial distribution and the patchiness of post-spate periphyton, one must investigate two primary questions: 1) What local scale (i.e. rock/patch) physical disturbance factors are limiting periphyton biomass during these spates? and 2) How broadly are these limiting conditions distributed over the streambed for such a low-magnitude spate?

The most studied local scale, spate related disturbance factors are hydraulic plucking by the shear force of water (Biggs and Thomsen, 1995; Stone, 2005), abrasion by suspended sediment (Francoeur and Biggs, 2006; Horner et al., 1990b), and complete mobilization of the upper layer of bed material by scour (Matthaei et al., 2003). However, during low-magnitude spates, coarser materials (e.g. gravel, cobble, boulder) remain static, and a large percentage (> 40% in gravel bed rivers, (Lisle, 1995)) of the bedload moved is sand (0.063 mm  $< D_i < 2$  mm) (Stokseth, 1994; Grams et al., 2006). During low-magnitude events, this sand is typically transported by saltation (bouncing along the bed). Such sand movement may have a significant impact on stream benthos because sand can be continuously transported at baseflow conditions. Further, small additions of sand can dramatically increase the rate of transport (Wilcock and Kenworthy, 2002; Bond, 2004; Thomson et al., 2005). A few field studies suggest that the abrasive effects of saltating sand on stream benthos can be substantial (Culp et al., 1986; Thomson et al., 2005), but these studies have not focused on linking the mechanics of saltating sand with periphyton abrasion. Mechanistic studies of the abrasive potential of saltating sand (and larger sediment) in moving water have focused on erosion rates of bedrock (Sklar and Dietrich, 2004) and cohesive clay (Kamphuis, 1990; Thompson and Amos, 2004); not periphyton. Sklar and Dietrich (2004) synthesized much of this literature to develop a mechanistic bedrock saltation abrasion model (SAMB) that is based on the kinetics of

saltating sediment. Application of this SAMB model to periphyton remains unexplored. While there is some knowledge regarding thresholds in velocity (Biggs and Close, 1989; Horner et al., 1990a; Rasmussen and Trudeau, 2007) and shear stress (Biggs and Thomsen, 1995; Stone, 2005) that limit periphyton biomass, none have been determined for saltating sand.

As the extent of damaging physical conditions on periphyton expands over the streambed with increasing spate magnitude, the area of unaffected streambed presumably decreases in size. Patches of streambed resistant to the effects of spate related disturbances (e.g. hydraulic stresses) serve as periphyton refuge zones. These refuge zones supply downstream areas denuded of periphyton with algae for recolonization, thereby improving the river system's resilience to frequent spate disturbances (Stevenson, 1983; Sedell et al., 1990; Lake, 2000; Lutscher et al., 2007). Knowledge of how geomorphology and sand supply affect spatial patterns in post-spate biomass is essential for food resource mapping, identifying productive nodes in the river, and predicting how an increase in spate frequency and sand supply affect long term and large scale, along stream variability in biomass (Cada et al., 1987; Uehlinger et al., 1996; Nislow et al., 1999; Osmundson et al., 2002; Thorp et al., 2006; Ledger et al., 2008). Studies of periphyton refuge typically focus on small spatial scales, such as the shelter provided by the cracks in rocks (Bergey, 2005), in the lee of rocks (Francoeur and Biggs, 2006), on stable rocks or on clusters of rocks (Francoeur et al., 1998). Very few studies have investigated the spatial distribution and the factors affecting larger scale periphyton refuge.

Field studies have documented patterns in periphyton biomass both laterally across the channel (Tett et al., 1978; Sand-Jensen, 1988; Coleman and Dahm, 1990; Cattaneo et al., 1997), and longitudinally down km's of river (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). While insightful, these studies typically do not consider the role of pre-spate disturbance history, lack direct measurements of substrate disturbance, and do not consider the larger geomorphic context within which they are situated. There are numerous studies reporting watershed scale patterns in periphyton biomass (Vannote et al., 1980; Biggs and Close, 1989; Wright and Li, 2002; Naiman et al., 1987) designed to test an earlier theory (i.e. River Continuum Concept, RCC, Vannote et al., 1980) which viewed the river system as unidirectional and disturbance regime independent. The watershed scale clinal changes in biomass predicted by the RCC (i.e. downstream increase in biomass in 6<sup>th</sup> order rivers) were often obscured by spatial differences (i.e. patchiness) in smaller scale habitat variables (Biggs and Close, 1989; Wright and Li, 2002) and spate related disturbance effects (Young and Huryn, 1996).

Recent ecological theories regarding the distribution of biota in river systems incorporate the hierarchical, 3-Dimensional, patchy and dynamic nature of the river system (Frissell et al., 1986; Junk et al., 1989; Sedell et al., 1990; Wu and Loucks, 1995; Poff et al., 1997; Lake, 2000; Benda et al., 2004; Junk and Wantzen, 2004; Thorp et al., 2006). For example, in the River Ecosystem Synthesis (Thorp et al., 2006), the river network is viewed as a downstream array of "hydrogeomorphic patches" (here referred to as hydrogeomorphic reaches or HGRs, e.g. meandering, anabranched, braiding; mobile vs. armoured). These HGRs are defined based on the "hydro"logic regime over the bed of the reach (discharge variability being a surrogate representing variability in substrate stability, nutrient supply, temperature etc.) and "geomorphic" character of the reach (Thorp et al., 2006). The HGR provides boundary conditions that limit the biotic assemblage of organisms that are adapted to persist under those conditions (i.e. habitat template, Poff and Ward, 1990). Thus hydrogeomorphic patches can be defined at many spatial scales within a river system, and presumably these patches have a different resistance to disturbance (i.e. refuge potential).

Researchers have had some success showing differences in biomass and ecological structure between HGRs that have different channel planform characteristics; such as biomass differences between meandering reaches and braided reaches (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). However, Chessman et al. (2006) cautioned that the broader scale context of the HGR must also be considered, as biomass can be controlled by processes operating at larger (and smaller) spatial scales. Therefore, biomass regulating processes within HGRs must be considered within the context of larger geomorphic units such as sedimentary links (river segments with a systematic downstream decrease in grainsize and channel slope, bounded by coarse sediment sources which can include multiple HGRs). For example, similar plan-scale HGRs may differ in biotic assemblage between sedimentary links, if the amount of sand supplied to one link is much greater than the other link. Currently, there are no studies examining if periphyton refuge is "patchy" at the riffle, planform or sedimentary link scale, for a frequent spate or how this patchiness varies with sand supply.

Researchers generally agree that the abrasion of periphyton by suspended sand is an important biomass regulating process (e.g. Francoeur and Biggs, 2006) and likely affects large scale trends in biomass (Cattaneo, 1996; Osmundson et al., 2002; Jakob et al., 2003; Meyers et al., 2007), yet direct proof at large spatial scales is hard to establish because of: 1) difficulties in measuring small scale process variables over large areas, 2) difficulties in obtaining direct bed stability data (especially for sand, see Salant et al., 2006b), 3) inability to experimentally control spate magnitude or sediment load, and 4) a lack of consideration for the mechanics of saltating sand. This type of problem is much more amenable to a numerical modelling approach after parameterization of the key processes (e.g. Doyle and Stanley, 2006) using field data and laboratory experimentation, the approach followed in this thesis.

Although the role of frequent spates in governing lotic ecosystem form and function is accepted (Poff et al., 1997; Poole, 2002; Wiens, 2002; Junk and Wantzen, 2004), their role in governing spatial patchiness in periphyton refuge is largely unexplored (Power and Stewart, 1987). Saltating sand's capacity to erode clay and bedrock has been documented, and mechanistic models have been developed, but the influence of saltating sand on periphyton biomass has yet to be examined. We are unaware of any studies that indicate what levels of sand transport cause substantial periphyton removal, or how broadly these limiting conditions are distributed over the streambed for a low-magnitude spate. Nor are we aware of any studies that document or model how saltating sand varies laterally across the river or longitudinally along the river network. Thus, the effects of changing sand supply during a frequent spate on large scale

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patterns in periphyton biomass remain poorly understood. All these questions are studied here.

#### **1.2 Research Objectives:**

The study of physical disturbance processes that affect periphyton biomass has largely overlooked the potentially significant effect of saltating sand during frequent spates on periphyton biomass. Several fundamental questions need to be answered, including:

- Is the spatial distribution of periphyton biomass influenced by frequent trimming from sand transported during such spates?
- How is periphyton removed by transported sand and at what level does sand transport begin to curtail periphyton accumulation?
- How does channel morphology and sand supply affect the transport of sand and the distribution of post-spate periphyton laterally across riffles, between different channel types (HGRs), and longitudinally down sedimentary links?

From these general questions, I developed specific objectives, which are addressed in 4 papers (Ch 3-6) and summarized below. My objectives were achieved through field based empirical measurements, *in situ* experimentation, and a numerical model. The construction of this model required: a) developing a rock scale model to describe the process of periphyton abrasion by sand (Ch. 3-5); b) developing a rock scale sand transport model that accounts for sand advection from the upstream riffle (Ch. 6); c) documenting the geomorphic characteristics of a sedimentary link, and classifying morphologically distinct channel types (Ch. 6); d) developing a geomorphic model to characterize channel form ranging from the rock scale to the sedimentary link scale (Ch. 6); e) joining the three sub-models (Periphyton, Sand Transport, Geomorphic Template) in a hierarchical periphyton perturbation model (HPPM). In Chapter 6, I query the HPPM model under a range of sand supply conditions.

#### 1) Chapter 3 outline.

In Chapter 3, I examine if spatial patterns in biomass found after a series of lowmagnitude spates can be explained by the abrasion of periphyton by saltating sand. This unique analysis bridges the gap between the fields of sediment transport mechanics and periphyton ecology. The two central questions addressed in Chapter 3 are: 1) Can an existing mechanistic model of bedrock erosion by saltating particles (Sklar and Dietrich, 2004) be adapted to the case of periphyton abrasion by sand?; and 2) Does the amount of periphyton retained after a spate increase with protrusion of the growth surface above the saltation layer (i.e. layer next to the bed with intense sand transport)?

Periphyton biomass was monitored across 15 riffles distributed over 2.35 km of a mid-sized (280 km<sup>2</sup>) boreal river before and after a small spate (0.63MAD) with a weekly summer recurrence period. During the spate period, I measured sand transport rates, peak shear stress, baseflow velocity, and the height of abrasion on painted nails for model validation.

I then developed a periphyton saltation abrasion model (PSAM) based on an existing mechanistic model for bedrock erosion (Sklar and Dietrich, 2004). Modifications were made to the bedrock abrasion model to better represent the case of periphyton abrasion. My primary objective was to test the PSAM model's ability to describe post-spate periphyton biomass. I tested two primary hypotheses related to PSAM: 1) The PSAM tools effect (i.e. rate of sand transport over the bed) has a significant negative correlation with post-spate periphyton biomass; and 2) The PSAM cover effect (i.e. how exposed periphyton is to sand abrasion) is a predictor variable with a significant negative effect on post-spate biomass. In a separate analysis using a larger set of data, I tested a third hypothesis: 3) The threshold for the motion of sand divides high periphyton biomass at low sand transport rates, from low biomass at high transport rates.

#### 2) Chapter 4 outline.

In Chapter 4, I establish periphyton perturbation thresholds for sand transport rates, spate peak shear stress and average velocity during growth. I also examine how these stressors affect the spatial distribution of post-spate periphyton across riffles. Chapter 3 results indicated that saltating sand explained biomass abundance, when data

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was considered at the rock scale. However, little is known about how these abrasive conditions affect the spatial distribution of periphyton refuge across riffles.

My primary objectives were to: 1) Determine if thresholds in velocity, sand transport, and shear stress for periphyton loss exist, using field data collected during a small natural spate; 2) Test the hypothesis that a small spate-related refuge habitat exists between the edge of the varial zone (i.e. zone subject to frequent wetting and drying), and the deepest point of the channel, where high hydraulic stress and saltating sand reduce biomass.

#### 3) Chapter 5 outline.

In Chapter 5, an experimental study of periphyton removal by sand, I examine how the height of the growth surface above the bed and the size of transported sand affect periphyton losses. An *in situ* experiment was undertaken to address two objectives: 1) to validate the sand transport rate threshold for inferred periphyton losses that was found through the analysis of field data (Ch. 4) with direct observations of periphyton losses by saltating sand; 2) to compare the degree of periphyton biomass loss resulting from exposure to suspended fine sand (0.063-0.5 mm) versus saltating coarse sand (0.5-2.0 mm), for both low (2 cm) and high (6 cm) protruding substrates. I test the hypotheses that: 1) rock scale refuge increases (i.e. more biomass) with increased protrusion of the host-rock's growth surface above the stream bed; and 2) less periphyton is lost from the transport of fine sand versus coarse sand.

#### 4) Chapter 6 outline.

In Chapter 6, I develop and test a model that routes water and sand down a sedimentary link, scaling down spate related physical disturbances (discharge and sand supply) to periphyton covered rocks situated within a series of riffles. A rock scale periphyton perturbation model (PSAM, Ch. 3) is used to assess post-spate biomass at each rock, which is in-turn scaled up to the sedimentary link scale.

The primary objectives of this paper are to build a link scale model to investigate: a) How sedimentary link morphology affects the spatial distribution of periphyton refuge; and b) How link scale periphyton refuge varies with sand supply. I hypothesize that for a typical low-magnitude spate: 1) the longitudinal distribution of biomass in a sedimentary link is parabolic and concave upward for low-magnitude, high-frequency spates, assuming that multiple periphyton protection mechanisms are competitively operating during the spate, and 2) biomass varies between planform HGR types and is highest in the HGR located furthest downstream (sinuous gravel-bed HGRs), assuming that shear stresses during the spate are low enough at the downstream end of the link to inhibit periphyton detachment or intense sand transport; 3) biomass levels in the link are highly sensitive to global additions of sand on the bed; 4) low sand supply (e.g. below dams) results in a downstream increase in the sand transport rate and a decrease in periphyton biomass (Jakob et al., 2003; Meyers et al., 2007); and 5) high sand supply (e.g. below sand sources) leads to a downstream decrease in sand transport rate and a potential increase in periphyton biomass (Yamada and Nakamura, 2002).

A hierarchical periphyton perturbation model (HPPM) was developed to simulate the transport of sand down an idealized sedimentary link, consisting of three different channel types (HGRs). The HPDM model included the PSAM model, developed in Chapter 3. The geomorphic models that were used to create the idealized sedimentary link were developed from morphometric data collected from a reference river (described below) and regime theory.

#### **1.3 Research Site Description**

The study sites were located along the Ste-Marguerite River, which flows through deeply fractured granite and schist rocks of the Canadian Shield (Figures 1.2 and 1.3, Big Pool site lies at  $48^{\circ}26'56"$ N,  $70^{\circ}26'97"$ W). The Sainte Marguerite River once supported a world class Atlantic salmon fishery with a large population (1000's) of fish. In recent decades, the number of individuals returning to spawn has declined dramatically (e.g. Spawners < 500 individuals). The remaining salmon stocks are supported by an active fry stocking program. There are many potential causes for the population decline of Atlantic salmon, including instream habitat degradation due to land use change. The



**Figure 1.2** Location of the study reaches on the Sainte-Marguerite River within Quebec, Canada. Sampling in 2003 focused on 29 riffles distributed between the Cascade, Onesime, Big Pool and Bardsville reference reaches. Sampling in 2004 focused on 15 riffles distributed between the Big Pool and Meander reaches.



Figure 1.3 View looking downstream from within the Big Pool reach.

watershed has a substantial amount of Boreal forest cover that has been logged intermittently since settlement. While there is little other development within the watershed, substantial sections of the Principle Branch of the river in the 'meander' reach
(Fig 1.2) were straightened and relocated in the 1960's to accommodate highway development. The rivers morphology is still adjusting to these anthropogenic changes, downstream of the Big Pool link (Talbot and Lapointe, 2001a; b).

The morphology of the main stem of the river consists of a series of sedimentary links, which are long sections (100's m to km's) of river where, because of size selective alluvial transport, there is a systematic downstream decrease in bed material grainsize and stream slope (Rice and Church, 1998; Davey and Lapointe, 2007). These sedimentary links are separated by sediment input zones (e.g. tributaries and valley wall contacts) that deliver coarse sediment to the river. The coarse sediment sources locally often inhibit channel incision and thus also locally control the streambed base level (Benda et al., 2004). This typically leads to a shallow bed slope upstream of the coarse sediment source, and a steeper bed slope downstream. On the Sainte Marguerite, these base level controls are also found where the river has incised through boulder rich, raised beach ridges, talus cones and paraglacial colluvial deposits that bisect the river (e.g. debris flows and kame deltas). Sedimentary links associated with this latter type of base level control normally have a long boulder lined straight section of channel, and terminate in an abrupt downstream fining segment at the downstream end. The channel planform morphology may vary down sedimentary links. On the Sainte Marguerite river, down link changes in channel plan form generally grade from: 1) straight, boulder rapid at the upstream end, 2) to a sinuous, boulder-cobble channel with vegetated islands, 3) to a sinuous, cobblegravel bed, single-thread meandering channel, 4) to a meandering gravel channel with vegetated islands. Lower reaches of the river (e.g. < 30 km from the outlet) are incised into marine clays and sands, but I did not examine the channel forms associated with these deposits or pure sand bed reaches.

I conducted my research within 5 sedimentary links. The morphometric properties of riffles within these sedimentary links are provided in Table 1.1. The sedimentary link dimensions vary, from small basins (88.5 km<sup>2</sup>) with short fining segments (1.6 km) to large basins (568 km<sup>2</sup>) with long fining segments (9.18 km). The "Meander" Link segment (Figure 1.2) was selected because of the unusually high sand transport rates observed there; associated with artificial straightening and bed

readjustments since the 1960's. For example, sand content (defined by bulk sampling of the surface layer) on the bed is much higher and more variable in the Meander Reach (27  $\% \pm$  SD 18 %) than in the Big Pool reach (15  $\% \pm$  SD 6%). Meanders in the upper half of the Meander link segment (i.e. 3 riffles) was straightened in the 1960's, unlike the lower half of this segment (Talbot and Lapointe, 2001a; b).

The watershed receives an average of 1.2 m of precipitation annually. The water chemistry in the study sites, measured in the 2003 summer period (12 Weeks), was typical of oligo-mesotrophic Canadian Shield rivers (Lavoie et al. (2006) cf. Rasmussen and Trudeau, (2007)) with a neutral pH (Mean = 7.2) and low nutrients (Mean Values:  $TN = 374 \mu g/L$ ,  $NH_4 = 23 \mu g/L$ ,  $NO_2 + NO_3 = 41 \mu g/L$ ,  $TP = 32 \mu g/L$ ,  $SRP = 13.9 \mu g/L$ ), low conductivity (Mean = 26.2  $\mu$ S/cm), cool summer water temperatures (Mean<sub>July & August</sub> = 16.3 °C), and low turbidity (0-5 NTU at baseflow).

Thirty year, historical flow records from a nearby gauging station (i.e. Sainte-Marguerite, Nord-Est Branch gauge 062803, 1976-2003) were analyzed to characterize the flow regime of the river at the Big Pool reach (where a temporary gauge was only installed in 1995.) The annual daily peak discharge which is exceeded once in every two years is 83 m<sup>3</sup>/s at Big Pool. The mean annual discharge (MAD), the long term average discharge for a river, was 9.6 m<sup>3</sup>/s. The mean daily flow of 1.7 m<sup>3</sup>/s was exceeded 329 days per year (Q<sub>329</sub>). The spring flood peak on the Ste-Marguerite River is driven by snowmelt and typically occurs between 22 April and 9 May. Periphyton biomass accumulates during July-September, when low flows are relatively stable and over-bank events are rare.

Frequent summer rain showers over the basin headwaters during the growth period generate the low-magnitude spates that punctuate the growth cycle. Characterization of these spates required adoption of a broad definition of "spate". For the purpose of his study, Uehlinger (1996) defined a "spate" as 10Q<sub>329</sub>, noting significant periphyton losses and bed movement at this threshold on the Necker River in Germany. This is equivalent to 17 m<sup>3</sup>/s at Big Pool. In this study, we are also interested in even smaller, more frequent flows that potentially interrupt the growth cycle of periphyton in the summer. Based on long term discharge records, we will define a "spate" here as any

	No. of	Dist Upst	ance ream	Drainage Basin Area	Riffle @ Ba	Slope seflow	Median Particle Size (D <sub>50</sub> )	Riffle Width @ Bankfull Discharge	Riffle Depth @ Baseflow Discharge	Riffle Depth @ Bankfull Discharge
Reach	Riffles	Min	Max	Avg	Min	Max	Avg±SE	Avg±SE	Avg	Avg
		(km)	(km)	(km <sup>2</sup> )	(m/m)	(m/m)	(mm)	<b>(m)</b>	<b>(m)</b>	(m)
Cascade	4	84.17	85.76	88.5	0.0017	0.0080	56±13	30.4±1.3	0.38	0.80
Onesime	8	67.00	67.87	208.2	0.0006	0.0077	58±11	26.3±3.0	0.38	0.86
Big Pool	9	59.67	61.09	233.5	0.0006	0.0044	44±13	34.5±2.6	0.44	1.31
Meander	6	52.89	53.82	280.2	0.0012	0.0032	34±5	40.7±2.4	0.38	1.09
Bardsville <sup>1</sup>	8	33.29	42.47	568.5	0.0011	0.0056	97±15	53.4±2.9	0.48	1.51
River	35				0.0006	0.008	65±42	36.6±11.6	0.41	1.11
$\frac{1}{1-\text{Two sites}}$	35 at the dow	nstream	end of M	leander linl	k and one	site abo	$65\pm42$ we the conflu	$36.6\pm11.6$ ience on the N	0.41 forth West Bra	nch.

**Table 1.1** Summary of morphometric properties of five sedimentary links of the Sainte-Marguerite river.

flow event where daily discharge is measurably higher than the preceding and following day. Thus, we define a spate based on the magnitude and the frequency of the disturbance, independent of its effect on periphyton (i.e. perturbation intensity)(Lake, 2000). The average spate discharge at big pool over the period July-September (1991-2003) was 8.2 m<sup>3</sup>/s (i.e.  $4.8Q_{329}$ , 0.85MAD, exceeded 30% of the 1 July – 1 Sept. period and 48% of the time annually). Individual spates ranged between 2.3 m<sup>3</sup>/s (i.e.  $1.3Q_{329}$ , 0.23MAD, exceed 92% of the summer period) and 34.3 m<sup>3</sup>/s (i.e.  $20Q_{329}$ , 3.6MAD, exceed 0.006% of the summer period). The number of days between such spates ranged from 5.7 to 8.3 days, averaging 7.1 days. Spate peak flow was between 1.1 and 7.8 times the average discharge of the six days preceding the event, with average departure being a factor of 1.65. The baseflow discharge that occurred between these spates averaged 4.5 m<sup>3</sup>/s, a discharge exceeded 65% of the time during the summer growth period.

Gravel bed rivers that experience frequent spate disturbance and have low nutrients and water conductivity, are typically populated by diatoms, an early colonizing and spate resistant type of algae (Peterson, 1996; Stevenson, 1996; Azim et al., 2005; Biggs and Kilroy, 2007). On the Sainte Marguerite River, the periphyton community is diatom dominated, with a mean peak observed biomass of 31 mg/m<sup>2</sup> chlorophyll *a* (Rasmussen and Trudeau, 2007). A qualitative survey of algal taxa along the river was conducted in 2003. Diatoms were the most abundant class of algae and included *Tabellaria, Navicula, Gomphonema* (Figure 1.4), *Eunotia, Cymbella, Fragilaria, Pinnularia,* and *Synedra*. Chlorophytes (green algae) included *Ulothrix, Draparnaldia, Desmidium, Closterium, Bulbachaete, and Tetraspora*. Colonies of the cyanobacterium (blue green algae) *Nostoc* were commonly visible 2 weeks after floods on rock faces sheltered from the flow, with the more extensive coverage in shallows near the shore zones. Other cyanobacteria included *Gloeotrichia, Leptothrix, Calothrix, and Phormidium*. The only rhodophyte (red algae) identified was *Hildebrandia*.



**Figure 1.4** Example of diatom (*Gomphonema*) under an electron microscope (Stevenson, 2008).

### 1.4 Periphyton biomass characterization

Benthic biomass generally refers to the quantity of organic matter that has accumulated per unit area of streambed  $(mg/m^2)$ . Periphyton biomass is typically measured using either chlorophyll *a* (mg chl*a*/m<sup>2</sup>) or ash-free dry mass (mg carbon/m<sup>2</sup>). Chlorophyll *a* is a pigment contained in most algae, which enables autotrophic production through photosynthesis. It is thus an integrative measure of the interaction between growth and disturbance related controls on periphyton production. To measure chlorophyll *a*, periphyton is scraped and brushed from a known area of rock surface. A solvent is then used to extract the chlorophyll *a* from the sample. The chlorophyll *a* concentration, a relative measure of the autotrophic biomass, is then measured using a spectrophotometer. Stream periphyton communities usually contain 1-2% of chlorophyll *a* by weight (Biggs and Kilroy, 2007). Peak biomass values vary among different

communities: 300-400 mg/m<sup>2</sup> chlorophyll *a* for diatoms and *cyanobacteria* to >1200 mg/m<sup>2</sup> chlorophyll *a* for filamentous green algae (Stevenson, 1996). The second common biomass measure, the ash-free dry mass (AFDM), is a measure of the total amount of organic material (carbon) in the sample, including autotrophic and heterotrophic microorganisms, dead periphyton, micro-invertebrates and terrestrial debris. Chlorophyll *a* is more commonly used to measure periphyton biomass because it is quicker to measure than AFDM, orders of magnitude more accurate for low levels of biomass, and not biased by non-periphytic organic matter (Biggs and Kilroy, 2007).

This study required a very large number of periphyton biomass measurements (i.e. up to 1800) to be taken over a very short period of time following spates (i.e. days), to minimize the potential growth effects between observations. For example, concurrent measurements of periphyton biomass were required on 15 to 35 riffles. The width of river bed devoid of terrestrial plants (i.e. "active channel") at each riffle cross section were divided into 100 equally spaced points, and the stone beneath each point was selected without bias (Wolman, 1954). At each stone, periphyton abundance was characterized on top of each rock, using a rapid assessment technique proposed by the United States Environmental Protection Agency (USEPA, Stevenson and Bahls, 1999). The test involves an assessment of the thickness of the algal mat, as a means to rank the relative biomass into 6 categories (Table 1.2).

The USEPA ranking system was calibrated to periphyton biomass as chlorophyll a, using a minimum of 8 rocks in each rank (Table 1.2). Periphyton was removed from a fixed area (20 cm<sup>2</sup>) on each rock, using scalpel and brush. The algal suspension was filtered through 45 µm Whatman<sup>TM</sup> filters that were then kept frozen until analysis. Chlorophyll a was then extracted with 90% acetone for 24 h and the extracts were read in a spectrometer according to standard methods (APHA, 1995). A significant difference (p < 0.05) existed between mean Chla values associated with the different ranks, except for ranks 3 and 4 (Bonferroni ANOVA analysis; Table 1.2). Even though rank 4 had a visually thicker mat, Chla was lower than for rank 3, suggesting that the mat was dying off.

**Table 1.2** Results of one way analysis of variance (ANOVA) testing differences in periphyton biomass among USEPA ranks. USEPA rank categories are based on algal appearance and thickness (see Below Table). Periphyton biomass is based on chlorophyll *a* assays of periphyton removed from a small prescribed area of pure USEPA rank.

	Biomass –Chlorophyll <i>a</i> (mg/m <sup>2</sup> )			
Rank	Average	SE		
0	0.23*	0.04		
0.5	0.52*	0.07		
1	3.72*	0.63		
2	8.13*	1.45		
3	41.30*	5.05		
4	29.58	3.41		

 $2004 - F_{(5,87)} = 223, p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.05$ 

USEPA (Stevenson and Bahls, 1999) rapid periphyton protocol for ranking abundance of microalgae: Rank 0 - Substrate rough with no visual evidence of microalgae; Rank 0.5 - Slightly slimy but no visual accumulation of microalgae is evident; Rank 1 - Slimy with visual accumulation evident; Rank 2 - Moderately slimy with accumulations evident and between 0.5 mm to 1 mm thick; Rank 3 - Very slimy with accumulation layer from 1 mm to 5 mm thick; Rank 4 - Algae sloughs when wading in area or removing rock. Accumulation > 5mm thick.

# Chapter 2

# Assessing the role of physical disturbance on periphyton refuge: A review of the dominant biomass regulating processes

## **2.1 Introduction**

The purpose of this chapter is to identify research deficiencies that may explain the unpredictability of the spatial distribution of periphyton biomass. The objectives are to review literature regarding: 1) periphyton and their importance to the stream ecosystems, 2) spate disturbance and the importance of periphyton refuge, 3) small scale biological and physical controls limiting periphyton biomass, 4) the effect of lowmagnitude spates on periphyton losses, 5) the likely disturbance regime for non-bed mobilizing low-magnitude spates, 6) eco-geomorphological theory regarding how small scale biomass regulating processes are affected by their larger scale geomorphic context, and 7) spatial patterns of periphyton biomass at intermediate spatial scales (i.e. > rock or patch scale, < watershed) that provide insight into tenets of eco-geomorphological theory. A summary of promising research avenues is provided as conclusions (Section 2.6).

# 2.2 Periphyton and their importance in riverine ecosystems

Periphyton commonly refers to all the microflora on substrata of freshwater streams, rivers, lakes and other waterways (Wetzel, 1983). The microflora includes algae, bacteria, and fungi. Benthic algae that inhabit freshwater habitats are diatoms (Bacillariophyta), green (Chlorophyta), red (Rhodophyta) and blue-green (Cyanophyta -Bacteria) (Stevenson, 1996). Periphyton communities can be dominated by pioneering species, such as diatoms, in low nutrient streams that are frequently disturbed by rapid increases in discharge from rainfall events, referred to hereafter as spates. Diatom dominated periphyton is a brown slimy film that covers the stream bed. Some early pioneer taxa may dominate until maximum biomass is reached (*Gomphonema, Synedra, Cymbella*), but if sufficient time exists between spates, climax communities, such as green algae (e.g. Calothrix Phormidium), may become dominant. Green algae climax communities appear as a green slimy mat that is thicker than diatom dominated mats (e.g. > 1 cm) with strands of filamentous algae reaching lengths greater than 5 cm.

Periphyton are the dominant primary producers in most temperate stream ecosystems (Biggs, 1995). Vannote et al. (1980) predicts that benthic algae are the primary energy source in third to sixth order rivers. The food quality of algae is high compared to other nonanimal benthic food sources (e.g. detritus, (Lamberti, 1996). Virtually all invertebrate feeding groups investigated by Gregory, (1983) consumed some form of algae. Algae chemoregulate rivers by harvesting inorganic phosphorus and nitrogen and organic pollutants (Stevenson, 1996). Algae also provide habitat for other organisms (e.g. chironomids and meiofauna, (Stevenson, 1996). Current predictive models of fish distribution relate the flow regime to fish peferences for physical habitat variables (Bovee, 1986; Lamouroux and Jowett, 2005). However, some studies suggest that biotic factors, such as benthic food availability (macroinvertebrates and periphtyon), may be more important than flow conditions (Cada et al., 1987; Nislow et al., 1999; Osmundson et al., 2002).

### 2.2.1 Spate disturbance and the importance of periphyton refugia

Stream periphyton reside in a dynamic environment and they are morphologically and physiologically adapted to persist, in spite of frequent spate disturbance. Picket and White (1985) define disturbance in lotic systems as "any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment." Anthropogenic modifications to fluvial systems are occurring on a global scale and these changes dramatically alter the frequency and timing of water and sediment during spates. Spates range from lowmagnitude (Q < 1/3 mean annual discharge, MAD) high-frequency (weekly or monthly) events, to high-magnitude (Q > 3MAD) low-frequency (Q > 1:2 year flood) events. The effects of an altered spate regime on periphyton are as of yet unknown. In order to develop adaptive strategies for river system management, the effects of altered spate regimes need to be better understood, which is the aim of this thesis.

The ability of periphyton to persist during a period where the flow and sediment regime rapidly adjusts, depends on the availability of flow refugia (Sedell et al., 1990). Periphyton flow refugia are habitats where periphyton are sheltered from harsh conditions (e.g. unstable substrates or high velocities) at varying levels of discharge, where densityindependent losses of algae are small (Lancaster and Hildrew, 1993; Rempel et al., 1999). These flow refugia act as population sources for periphyton recolonization after spate disturbances. The spatial distribution of periphyton refuge is thought to be closely related to the spatial difference in the 'habitat template", which sets boundary conditions on what organisms can persist on a particular area of streambed (Poff and Ward, 1990). Essential elements of the habitat template are: 1) the physical habitat form (e.g. cluster of rocks), 2) habitat stability (e.g. rock movement during spates), and 3) variability in physiochemical resources (i.e. temperature, nutrients, velocity)(Poff and Ward, 1990; Thorp et al., 2006). Of these three elements, the physical form of riverine habitat is the easiest to define using a hierarchical classification of fluvial forms (e.g. Frothingham et al., 2002). The fluvial system can be viewed as a nested hierarchy of morphological features. Each holon in the hierarchy has a unique spatial scale and adjustment period (Frothingham et al., 2002). For example, at the network scale, tributaries form a dendritic path of the river, at the scale of the entire watershed (10-1000's kms). Morphometric river properties at this scale (e.g. slope) adjust over geologic time periods. At the other extreme, individual grains (sand, gravel cobble etc.,  $\mu$ m-m) adjust during spates that last for hours (Table 2.1). Each holon in the hierarchy is also nested. For example, planform scale units (segments with uniform planform characteristics, 10-100's m, e.g. high sinuosity vs low sinuosity) are nested within link scale unit (the segment bound by two tributary nodes, 1-10's kms). Thus, the habitat template for periphyton refuge can be defined at many spatial scales.

Most discussions of periphyton refugia have focused on small spatial scales, without giving consideration to larger-scale features. High, post-spate biomass has been associated with the shelter provided by the cracks in rocks (Bergey, 2005), in the lee of rocks (Francoeur and Biggs, 2006), on stable rocks or clusters of rocks (Francoeur et al., 1998), on patches of bed where the bed substrate was not scoured or buried by excavated bed material (Matthaei et al., 2003) and in pools vs riffles (Biggs et al., 2000). At the other extreme, longitudinal patterns in biomass have been investigated at the network scale, but the non-uniform role of spate disturbance in affecting these patterns was largely overlooked. These network scale studies showed that the downstream distribution of biomass is discontinuous and affected by habitat variability at smaller scales. We know of no studies that examine the patchiness of periphyton refuge at intermediate spatial scales (i.e. planform or link scale) that consider spate disturbances and their variability.

**Table 2.1.** Scale-based nested hierarchy of fluvial forms (Adapted from Frothingham et al., 2002)

Holon	Description	Spatial Scale	
Network scale	When viewed at the watershed level, the river is a dendritic network of many tributaries. The structure of the drainage network is hierarchical, consisting of links, defined in terms of magnitude (Shreve 1966) or stream order (Strahler 1952), and nodes, which are junctions of conjoining links.	scale of the entire watershed, 10-1000's kms	
Link scale*	The segment of river bound by two tributary nodes	> 10-14 channel widths, 1-10's kms	
Planform scale	Reaches with uniform planform characteristics	one meander wavelength, minimum length is 10-14 channel widths, 10-100's m,	
	e.g. high sinuosity vs low sinuosity		
Bar unit scale	Pool-riffle-point bar sequence	5-7 channel widths	
Bar element scale	Riffle or pool	2-3 channel widths	
Bedform scale	Unit bars, clusters of rocks, ripples	<1 channel width, cm-m	
Rock scale	Individual particles (gravel, cobble etc.) or particle clusters	μm-m	

\*as in link magnitude and not to be confused with the sedimentary link of Rice and Church, (1998) described in text.

Refugia function differently for different types and magnitudes of disturbance (Sedell et al., 1990). For example, biomass may vary between riffles and pools for small spates (Biggs, 1995), but periphyton may be reduced to low levels in both riffles and pools during high-magnitude spates (Grimm and Fisher, 1989). Most researchers agree that periphyton is lost over large areas of streambed during high-magnitude spates. The patchy distribution of periphyton is much harder to characterize for smaller events. During low-magnitude spates, growth may occur in some zones of the channel while losses occur in others zones (Humphrey and Stevenson, 1992). The amount of post-spate biomass retained on a given habitat template depends on the growth factors that limit biomass development prior to the spate, and the physical disturbance variables during the spate. Therefore two key questions in characterizing the spatial heterogeneity of periphyton refuge are: 1) What are limiting physical conditions for periphyton?, and 2) How broadly are these limiting conditions distributed over the streambed for a lowmagnitude spate? The research challenge involves defining the spatial extent of zones within the river system, where post-spate biomass is higher than average. We are interested in investigating if post-spate periphyton is patchy: 1) with rock elevation above the bed?, 2) across riffles?, 3) down kilometer long sections of river where slope and grainsize decrease?, or 4) between channel segments of differing planform?

Research in the development of a mechanistic understanding of periphyton biomass limiting processes is challenging. Periphyton biomass is highly variable in both time and space in rivers, and can span six orders of magnitude, which poses sampling difficulties (Chételat et al., 1999). Periphyton sampling is much more manageable at small spatial scales. The factors regulating biomass at small scales have been investigated extensively in the field using multivariate statistics to relate biomass (or biomass loss) to environmental variables (Sand-Jensen, 1988; Biggs and Close, 1989; Uehlinger, 1991; Stokseth, 1997; Matthaei et al., 2003). The amount of variance explained by these habitat associations does not exceed 60% and typically requires data to be aggregated over large areas of streambed. Thus, individual rock scale variability is lost. This suggests that the mechanisms operating at the "rock" scale are not yet fully investigated. Difficulties encountered in these studies are associated with lack of control on independent variables, interdependence among independent variables, difficulty in measuring the suite of variables over large areas, and difficulty obtaining direct measurements of key variables (e.g. turbulence or mechanical abrasion at the surface of the periphyton mat). Further, data regarding dynamic physical conditions over a habitat patch are often not available (Lake, 2000). Finally, the predictions are based on measures such as grain size, which do not directly address the mechanism affecting biomass levels

at the rock scale where they are operating (although see Warnaars et al., 2007). Laboratory studies have provided valuable insight into small scale processes. These studies benefit from the experimental control provided by laboratory conditions, but it is not obvious how representative these processes are during natural spates or how the larger scale geomorphic context affects these small scale processes.

# 2.3 Local controls on periphyton biomass accrual and loss

The local (i.e. bedform scale or smaller, Table 2.1) factors affecting periphyton growth (i.e. biomass accrual) and detachment have received much more attention than the study of large scale biomass patterns (Peterson, 1996; Stevenson, 1996; Azim et al., 2005; Biggs and Kilroy, 2007). There are growth mechanisms as well as loss mechanisms that affect periphyton biomass (Figure 2.1) (Biggs and Kilroy, 2007).





# 2.3.1 Local growth factors

The growth of algae is affected by the rate of cell division on the substrate. The rate of cell division is governed by the availability of resources (e.g. Light, Nutrients, Temperature, and dissolved CO<sub>2</sub>). These resources provide the building blocks and energy for photosynthesis and cell growth to occur. Of the growth factors, light is the most limiting resource, but it is only limiting at very low levels (e.g. 100-1000  $\mu$ mol photon<sup>-2</sup>s<sup>-1</sup> (e.g. bankside summer light > 1500  $\mu$ mol photon<sup>-2</sup>s<sup>-1</sup>). Light limitation partially depends on the clarity and depth of the water. Davies-Colley et al. (1992) found productivity was limited at 1000  $\mu$ mol photon<sup>-2</sup>s<sup>-1</sup>, when water clarity is 7 NTU (Nephelometric Turbidity Units ~ 1 m secci disc visibility). Biomass starts to decrease at 60% riparian forest canopy cover. Therefore, in clear flowing sub-alpine rivers with an open canopy cover, light is not a limiting growth factor.

If light absorption is saturated, periphyton growth may be controlled by inorganic nitrogen and/or phosphorus concentrations. The transition from nutrient limitation to nutrient saturation has been reported to be in the range of 0.6-15  $\mu$ g/l for inorganic phosphorus and 50-60  $\mu$ g/l for inorganic nitrogen compounds (Bothwell, 1989; Grimm and Fisher, 1989; Uehlinger et al., 1996). Bothwell (1989) found that nutrients are rarely limited at the surface of the periphyoton mat. The cells at the base of the mat are starved of nutrients because the cells on the surface absorb most of the nutrients. Consequently, higher ambient concentrations of nutrients penetrate further into the mat and promote the development of a thicker mat (Biggs et al., 2000).

If resources are in ample supply (i.e. saturated), then temperature becomes the third most important controller on the rate of periphyton mat development. For a diatom community characteristic of a Boreal river of eastern Canada, the optimum temperatures range is 10 - 20 degrees celcius (Park and Clough, 2007). Physiological stress occurs at high temperatures and slow growth rates result from low temperatures (Stokseth, 1994; Stevenson, 1996).

The water velocity over a patch of bed during low stable flow periods affects the rate of algal accumulation in periphyton (Dodd, 2002). The delivery of nutrients and the

removal of cell exudates in the laminar sub layer increases with the velocity of the overlying water thereby enhancing growth (Dodds, 2002). However, this positive effect of velocity on periphyton growth is tempered by velocity induced losses, which vary by algal growth form (Figure 2.2). For example, velocity has a positive effect on the growth rate of stalked diatoms. At velocities exceeding 0.5 m/s, it is assumed that the rate of biomass loss exceeds the growth rate (Biggs and Close, 1989; Horner et al., 1990a; Rasmussen and Trudeau, 2007). These losses are associated with hydraulic plucking of algae by the shear force of water, however sand transport is also possible at these velocities (Kamphuis, 1990). The spatial heterogeneity of velocity in the river during low stable flow periods can strongly influence the spatial distribution of periphyton in the absence of spate disturbance (Biggs, 2000).



**Figure 2.2** Periphyton biomass as a function of water velocity for different growth forms of algae (Adapted from Biggs and Kilroy, 2007).

## 2.3.2 Local biotic and abiotic loss factors

Periphyton losses through grazing by fish and macroinvertebrates are small relative to abiotic factors in river systems with high hydraulic variability. For example, Jowett and Duncan (1990) characterized hydraulic stability using the coefficient of variation of long term discharge records in New Zealand. Rivers with a coefficient of variation of discharge between 0.85-1.25 had a high baseflow and frequent highmagnitude spates, which disturbed the streambed and did not allow plant and animal communities to develop fully (Biggs et al., 1990). Thus, the spatial distribution of periphyton biomass was governed by physical disturbance (i.e. vs grazing) on New Zealand rivers with a coefficient of variation of discharge greater than 0.85. In contrast, rivers with a coefficient of variation for discharge less than 0.85 had low variability of flow that was controlled by large lakes or springfed. The streamflow was mainly baseflow with a few small floods. These streams were rich in nutrients and supported large amounts of stream life.

Spate disturbance has been shown to be a dominant factor governing the spatial distribution of periphyton biomass in gravel bed rivers (Biggs, 1995). Spate related physical disturbances include sloughing from high velocities or hydraulic shear (Biggs and Thomsen, 1995; Stone, 2005), abrasion by suspended sands and silts (Francoeur and Biggs, 2006; Horner et al., 1990b), and abrasion through bed excavation, and burial (Matthaei et al., 2003). During spates, bed sediments may remain stable, roll along the bed, move in a hopping motion close to the bed called "saltation", or be fully suspended within the water column. During sub-bankfull spates, sand is typically transported by saltation, while silts and clay travel in suspension as washload. Gravel typically travels in traction during bankfull flows. As the spate intensity increases, progressively larger bed materials pass through these phases of transport (e.g. even fine gravel can become suspended if shear stresses are high enough). During high-magnitude spates, large areas of the bed may be scoured to the depth of the larger bed materials (i.e. substrate). When this bed armour is broken, and all the substrate sediments are in motion, periphyton losses are largest.

Periphyton losses may occur solely by the shear force of the water in the overlying water column of rivers, in the rare case when no sediments are being transported. Laboratory studies have isolated the effects of shear stress on periphyton loss (Biggs and Thomsen, 1995; Stone, 2005). For example, Stone (2005) exposed periphyton grown on ceramic tiles to 10, 20, 30 and 40 Pascals of shear stress in a sediment free flume and found a strong positive and linear relationship between the % biomass lost (AFDM) and the shear stress (i.e. %Loss = 1.78Stress,  $R^2 = 0.99$ , unspecified taxonomic composition). This relation suggests that 50% of the biomass was removed when shear stresses were 28 Pa. In a similar laboratory study, Biggs and Thomsen (1995) found that non-filamentous diatoms (*Fragilaria, Cymbella, Achnanthes*) experienced 50% removal (i.e. from 48 mg/m<sup>2</sup>) when shear stresses were 51 Pa and no sediments were being transported. The 28-51 Pa required for 50% loss far exceeds the stress required to transport silt in suspension and is 6-10 times the stress required for the initiation of 1 mm sand transport on a typical cobble bed (Wilcock and Kenworthy, 2002). Thus, if fine sediments are present on the bed, additional periphyton may be lost due to the abrasive effects of suspended sediments and saltating sand.

There are more studies examining the effects of suspended sediment on periphyton (Horner et al., 1990a; Francoeur and Biggs, 2006) than saltating bedload (Culp et al., 1986; Thomson et al., 2005). Using laboratory conditions, both Francoeur and Biggs (2006) and Horner et al. (1990a) reported a rapid (5-15 minutes) 20-40% reduction in algal biomass resulting simply from increased flow velocity with no sediment transport. Horner et al. (1990a) reported an additional 4 to 13% loss in algal biomass associated with test velocities of 0.6 m/s and the addition of suspended clay and silt sized clastic sediment. Similarly, Francoeur and Biggs (2006) reported an additional 0-40% loss of periphyton biomass by suspended sand and silt (i.e. 84.2% < 0.5 mm, 100% < 3 mm), after the initial velocity increase.

Engineering studies have shown that saltation is extremely effective in abrading both clay (Kamphuis, 1990; Thompson and Amos, 2004) and bedrock (Sklar and Dietrich, 2004). It is implied that relatively non-cohesive periphyton would be similarly vulnerable. Further, saltating sediment has been shown to be more abrasive than suspended sediments, because saltating grains have more frequent and direct contact with the bed (Kamphuis, 1990; Sklar and Dietrich, 2004). Despite the potential implications of saltating sand on periphyton losses, there have been few field studies addressing the effect of sand transport on periphyton losses in gravel bed rivers (Stokseth, 1994; Thomson et al., 2005). For example, Thomson et al. (2005) studied the responses of algal assemblages to the passage of a sandy sediment slug released from a dam removal on Manatawny Creek, Pennsylvania. The authors found that the passage of the sediment slug increased the amount of sand on the bed from 1 to 15% and was associated with a 25% lower algal biomass and a 20% reduction in diatom species richness. In a separate field study, Stokseth (1994) monitored periphyton losses on the boulder bed of the Skona River, Norway resulting from four large spates (i.e. 2.8MAQ-15MAQ). Stokseth (1994) simulated sediment transport rates for these spates using a computational model. The author found that the simulated sediment transport rate (i.e. total beload, not just sand) and water temperature were negatively related to biomass ( $n = 5 R_{Adj}^2 = 0.954$ ). While this relation used the total bedload transported, more than 40% of the bedload was predicted to be sand. However, direct measurements relating sand transport rates to periphyton biomass losses are required, to test the validity of this relation for frequent spates, where the bedload is predominantly sand or finer sediment.

While past field studies have provided some valuable insight into the sedimenttransport mechanisms potentially responsible for periphyton disturbance (Culp et al., 1986; Bond, 2004; Thomson et al., 2005), their unconstrained experimental design (i.e. uncontrolled field setting, exposure to a variety of flood intensities) precluded a discussion of the effects purely attributable to saltation. Further, cross correlation in the variables that control periphyton biomass make it difficult to isolate the dominant physical disturbance processes responsible for periphyton losses. For example, low periphyton biomass is positively correlated with substrate mobility, which is in-turn positively correlated with flow strength and negatively correlated with particle size. To complicate matters further, flow strength is also related to growth rates. Consequently, host-rock particle size has been used to predict periphyton biomass with varied degrees of success and this bivariate relation merely reflects the cumulative effects of a series of interacting regulatory variables. Previous field studies have noted high biomass on fine sediments (sand, silt) in depositional zones where velocities are low (Tett et al., 1978; Sand-Jensen, 1988; Coleman and Dahm, 1990; Cattaneo et al., 1997) and on larger hostrocks, presumably because of their stability and proximity to growth enhancing velocities (Hynes, 1970; Uehlinger, 1991; Meyers et al., 2007). Intermediate to these extremes,

high variability in periphyton biomass has been associated with sandy gravels relative to clean gravel/cobbles or sand deposits (Tett et al., 1978). Despite the drawbacks associated with field studies, more large scale field studies are required to: 1) understand how saltating sand is distributed and moves within the river system, and 2) understand how saltation interacts with other physical disturbance factors for spates of different magnitudes.

In addition to further field study, direct experimental evidence of periphyton abrasion by saltating sand is also required to help develop a mechanistic understanding of periphyton loss through saltation abrasion. The study of Culp et al. (1986) focused on losses to macroinvertebrates from saltating sand. The in situ experiment examined the effects of saltating 0.5-2 mm sand on macroinvertebrate drift (i.e. losses) on Coronation Creek, B.C. The study was motivated by the fact that the 0.5-2 mm sand fraction increased in deposits after clear cut logging, but the composition of silts and clays had not changed. Culp et al. (1986) reported that the sand fraction was easily transported during spates. In the experiment, the fraction of sand on the bed was artificially increased from 17% to 27% over a patch of bed with bed velocities between 0.34-0.39 m/s. The saltating sand reduced total benthic macroinvertebrate densities by more than 50% in 24h. Culp et al. (1986) urged future research designed to establish the importance to the benthos of the composition, concentration, and timing of fine sediments inputs under standardized hydraulic conditions (e.g. constant discharge and shear stress).

### 2.3.3 Short term temporal changes in periphyton biomass

Short term temporal changes in periphyton biomass are illustrated in Figure 2.3. High-magnitude spates capable of breaking the bed armour can "reset" biomass to very low levels (e.g. Figure 2.4). After these resetting events, pioneer taxa colonize the bare substrate. Once the colonizing cells are extablished, the rate of algal growth can become exponential if resources are not limited (Figure 2.3). Biomass accumulates to a maximum value and then decreases through autogenic sloughing. Autogenic sloughing occurs when die off increases in the mat due to reduced nutrient exchange and reduced light



Figure 2.3 Diagram of the accrual cycle (Adapted from Biggs and Kilroy, 2007).



**Figure 2.4** Time series of discharge and biomass showing how spates truncate the growth cycle (Adapted from Biggs and Kilroy, 2007).

penetration inhibited by the increasing thickness of the overlying mat. The maximum biomass is generally dictated by the nutrient level and ambient velocity. These two physical factors regulate the balance between the growth rate and removal rate of cells by hydraulic plucking. If stable flow conditions persist, a balance is reached between growth and loss, and the periphyton mat reaches its carrying capacity. The time required for periphyton communities to reach peak biomass increases with maximum attainable biomass and decreases with nutrient availability. The time of accrual ranges from days to 7 weeks, but meso-oligotrophic rivers typically have values between 14-40 days (Biggs and Kilroy, 2005).

# **2.3.4** The effects of spate magnitude on periphyton losses and the scale of spatial patchiness

Not all spates reset the periphyton community. The amount of periphyton lost varies with spate magnitude. In gravel bed rivers, spate magnitude and time since disturbance predict 60% of biomass at the reach scale (Biggs and Close, 1989; Uehlinger, 1991). For example, in a study of the Swiss pre-alpine Necker river (126 km<sup>2</sup>, Gr-Cbl make up 90 % of channel, 20 m reach), Uehlinger (1996) measured 95% periphyton losses (chlorophyll a) for a spate with a peak discharge of 7.6MAD, 50-60% losses for a spate with peak discharge 3MAD, and 20% loss for a spate with a peak discharge of 2MAD. In a separate study of Sycamore Creek, Arizona (505 km<sup>2</sup>, bedrock and cobble/ boulder riffles, 6 reaches), Grimm and Fisher., (1989) also found that the percentage of losses decreased with spate magnitude (Figure 2.5). Again, large spates (> 3.5MAD) removed 90% periphyton chlorophyll a. The percent of biomass removed during smaller spates was more variable for a given spate discharge. For example, a 50% reduction in chlorophyll *a* occurred during smaller spates over a wide range of discharges (range = 0.17-1.39MAD). This suggests that 50% loss of chlorophyll *a* occurred for spates that are less than half of bankfull stage. For the same arid river system, Doyle and Stanley, (2006) predicted that the optimum flow for biomass accumulation (i.e. optimum between accumulation and loss) was 0.23MAD (< 1/3 bankfull stage). Collectively, the Sycamore Creek studies suggest that there is a very narrow range of high-frequency spate conditions



**Figure 2.5** Percent change in periphyton chlorophyll *a* as a function of discharge for Sycamore Creek Arizona 1984-1987 (Data from Table 1 of Grimm and Fisher (1989)). Grimm and Fisher (1989) qualitatively noted that coarse sand transport typically occurred between 2-3  $m^3/s$ .

that separates conditions promoting maximum biomass from conditions promoting 50% losses on that river system.

The area of stream bed fully mobilized generally increases with increasing spate magnitude (Wilcock et al., 1996; Matthaei et al., 1999; Lisle et al., 2000; Grams et al., 2006). Consequently, periphyton refuge zones decrease in size with increasing spate magnitude because the area of unstable streambed increases in size. For example, on the river Izar (2800 km<sup>2</sup>, D75 = 6.5, 800 m reach), the bed movement was patchy within an 800 m reach and varied with discharge (Matthaei et al., 2003). For a spate with a peak discharge of 4.2MAD, Matthaei et al. (2003) found that 27% of the substrate was scoured, 37% of the bed was buried by transported gravel, and 36% of the bed was undisturbed. More of the bed was stable (50%) during a smaller spate (2.4MAD) with only 20 % fill, and 30 % scour. The spatial pattern was similar to that of the larger event, but stable bed patches were more common.

During low-magnitude, high-frequency spates, coarser materials (e.g. gravel, cobble, boulder) remain static, whereas sand particles (< 2 mm) can be mobilized (Wilcock and Kenworthy, 2002). In gravel bed rivers, a large percentage of the bedload moved is sand (> 40% in gravel bed rivers, (Lisle, 1995)) and it is typically transported by saltation (Stokseth, 1994; Grams et al., 2006). Since sand is ubiquitous within gravel bed rivers and mobilized many times during a 1-2 month accrual period, it may be possible that trimming of periphyton during low-magnitude high-frequency spates strongly influences the spatial distribution of periphyton biomass. Thus, it is important to investigate the role of saltation on periphyton removal, and to characterize the patchiness of saltation abrasion within the river system during low-magnitude spates.

For lower-magnitude spates, the amount of biomass lost is variable, relative to high-magnitude spates (Grimm and Fisher, 1989). The variable effect of a spate of a particular magnitude on periphyton is thought to result from numerous antecedent conditions including: 1) the amount and types of sediment in storage in the channel. If sand and fine gravel is in low supply prior to a spate, then the spate is presumed to cause fewer losses of biomass than if these sediments were ample.; 2) the amount of pre-spate biomass (Power and Stewart, 1987; Uehlinger, 1991; Lake, 2000). Thick periphyton mats are more susceptible to detachment than low profile sheltered mats (e.g. Figure 2.6); 3) the species composition. Some algal forms are more tightly attached to the bed than others; and, 4) the physiological condition of periphyton. Periphyton with a high percentage of dead algal cells is easier to detach from the bed (Tett et al., 1978; Cummins et al., 1984; Power and Stewart, 1987; Uehlinger et al., 1996). During a low-magnitude spate, sand and mud entering and moving within the channel are thought to lead to a patchy distribution of periphtyon (Power and Stewart, 1987; Yamada and Nakamura, 2002). These fine sediments are thought to scour periphyton where flow energy is high and smother periphyton mats in low energy zones of the channel (Power and Stewart, 1987; Yamada and Nakamura, 2002). Humphrey and Stevenson, (1992) hypothesized that small spates may even promote algal growth because of the elevated nutrients they bring and the resulting sloughing of dead algae, thereby promoting fresh growth. The experimental results of Humphrey and Stevenson (1992) inferred that sub-scouring spates

will probably inhibit algal growth in nutrient-poor streams Conversely, they could also stimulate algal growth during small spates in low velocity zones of the channel (<10-20 cm/s) of nutrient-rich streams. Thus, in nutrient poor systems populated by a periphyton mat of stalked diatoms, spates that do not mobilize the coarse bed material may produce growth in areas in the channel where velocities are < 0.2 m/s, and losses where velocities exceed 0.5 m/s.



**Figure 2.6** The contours show the net specific rate of change of chlorophyll *a* (k = 1/x dx/dt) as a function of pre-spate period chlorophyll *a* ( $mg/m^2$  - Chl*a*) and maximum spate discharge ( $m^3/s$ ) (Adapted from Uehlinger et al., 1996). Growth persists in the white area and loss dominates the shaded area. The flow required for detachment decreases with increasing biomass. The graph was developed from the output of an empirical dynamic periphyton model fitted to 2 years of Necker river data.

### 2.4 Sand abrasion as a local disturbance factor

#### 2.4.1 Saltating sand as a control on periphyton biomass: The missing element?

Persistent reductions in the amount of periphyton biomass left after highfrequency spates reduces the rate of recovery of benthic algae biomass (Uehlinger, 1991), which may result in resource limitations to upper trophic levels (Stevenson, 1996). Even though the role of saltating sand in periphyton abrasion is conceptually understood, the mechanistic underpinnings require further investigation and illucidation.

A mechanistic understanding of how saltating river bed materials erode bedrock is much more developed than the case of periphyton abrasion (Sklar and Dietrich, 2006). The kinetics of saltating sediment in flowing water has been studied using dimensional analysis to scale flow and sediment parameters with properties of saltating sediment (e.g. saltation height, length, velocity). Required measurements are collected in a laboratory flume under simplified experimental conditions (e.g. flat beds) (Bagnold, 1973; Francis, 1977; Kamphuis, 1990; Lee and Hsu, 1994; Nino and Garcia, 1994; Nino and Garcia, 1998; Lee et al., 2000; Lee et al., 2002; Abbott and Francis, 2004). Sklar and Dietrich (2004) condensed the findings of these studies into a mechanistic saltation abrasion model (SAMB) that predicts rates of bedrock erosion. SAMB is a mechanistic model of bedrock abrasion which is conceptually based on the 'tool and cover effects' of saltating sediment. The 'tool effect' refers to the erosion of the bedrock surface by the impact of saltating particles (i.e. the tools). The 'cover effect' refers to the protection of a bedrock surface from saltation abrasion by a gravel layer which occasionally overlies the bedrock surface. In SAMB, the erosion rate of bedrock by a saltating particle is a function of: 1) the volume eroded per unit impact, 2) the number of particle impacts per unit time and area, and 3) the degree of exposure to this physical disturbance (Sklar and Dietrich, 2004). According to the SAMB model, bedrock erosion starts during the rising limb of a spate, when the increasing flow strength initiates saltation of fine sediments. As the spate intensity increases, more bedrock is eroded because more (and larger) sediment is saltating, which increases the number and efficiency of erosional bed contacts. During this progression of increasing flow strength, the height of each particle's hop increases, eventually reaching a maximum. Particles then become suspended, or have a flatter saltation trajectory (Francis, 1977). When this occurs, transported particles are less effective at eroding the bed rock, because the particles have fewer and less direct contact with the bed. The "saltation layer" of saltating sand is bounded by the streambed and maximum saltation heights (Figure 2.7). Presumably, substrate surfaces lying above the



**Figure 2.7** Three types of sediment transport over a coarse gravel bed. The top of the saltation layer is shown as the maximum saltation height.

saltation layer are abraded less than substrates immersed in the saltating stream. However, this hypothesis has not been tested with regards to periphyton.

### 2.4.2 Controls on sand transport within a gravel bed river.

A key variable in the SAMB model is the rate of grain contact with the bed, which is highly dependent on the sand transport rate. Again, more is known about small scale factors that affect sand transport than their broad scale expression within the river network. This is because the frequency of bed sediment movement and the transport pathways these sediments take during spates are harder to measure for sand than for coarser substrates (e.g gravel cobble). Coarser substrates are easier to track over large spatial scales (e.g > planform scale) during spates, because a range of established tracing techniques are available for gravel cobble sized material (Salant et al., 2006b). At the local scale, laboratory and field experiments have shown that the sand transport rate increases with the ease at which the sand grain is entrained (Wilcock and Kenworthy, 2002). The entrainment of a grain from the bed of a river is typically determined using sediment transport functions that are based on the temporally averaged bulk properties of flow. The sediment transport rate ( $Q_{sa}$ ) is given by:

$$Q_{sa} = \alpha \phi^{\beta} \quad (2.1)$$

where  $\phi$  is excess shear stress,  $\alpha$  and  $\beta$  are fitted constants. The excess shear stress is given by:

$$\phi = \frac{\tau}{\tau_{crt}} \tag{2.2}$$

where,  $\tau$  is the shear stress during the event and  $\tau_{crt}$  is the critical shear stress (i.e. the stress required to initiate movement of a particle on the riverbed). The total shear stress is given by DuBoys as:

$$\tau = \rho g dS \qquad (2.3)$$

where,  $\rho$  is the density of water (kg/m<sup>3</sup>), *g* is the acceleration due to gravity (m/s<sup>2</sup>), *d* is the flow depth (m), and *S* is the energy grade line, which is often assumed to be the local water surface slope (m/m).

The application of bedload transport formulae to mixed grain sizes requires the consideration of the degree of hiding of the grain amongst the adjacent bed particles (Parker, 1990). If a grain  $(D_i)$  is larger than surrounding bed material  $(D_{50})$ , then it is more exposed to flow and it is more easily moved than a small grain surrounded by larger rocks. Thus, if a sand grain is much smaller than the surrounding substrate  $(D_{sa}/D_{50} = \text{Low})$ , then the sand grain is hidden to the effects of flow. Wilcock and Kenworthy, (2002) presented a two fraction model where the effect of sand supply on the bed is also considered in the determination of critical stress. The authors found that the critical shear stress for sand (and for gravel) decreased with increasing fraction of sand on the bed (Figure 2.8). This results in sediment movement at lower shear stresses when higher amounts of sand are present on the bed.

Wilcock and Kenworthy (2002) used both field and flume data to fit their sediment transport model, which is presented below and illustrated in Figure 2.9. The y axis in Figure 2.9 is the sediment transport rate as in equation (2.1) but it is made dimensionless to collapse the transport curves for sand and gravel onto the same function:

$$W_i^* = \begin{cases} 0.002\phi^{0.75} & for \ \phi > 1.35 \ (2.4) \\ 14\left(1 - \frac{0.894}{\phi^{0.5}}\right)^{4.5} & for \ \phi \ge 1.35 \ (2.5) \end{cases}$$

where,  $W_i^*$  is the dimensionless sediment transport rate for size fraction *i* and:

$$W_i^* = \frac{(S_g - 1)gq_{bi}}{F_i u_*^3} \tag{2.6}$$

where,  $S_g$  is the specific gravity of sediment,  $q_{bi}$  is the volumetric transport rate per unit width of size *i*,  $F_i$  is the proportion of size *i* on the bed surface, and  $u_*$  is the shear velocity (i.e.  $u_* = \sqrt{\tau/\rho}$ ).



**Figure 2.8** Graph showing the reduction of the dimensionless reference shear stress for sand  $(\tau_{rs}^*)$  with increasing sand content on the bed  $(F_{sa})$  (Adapted from Wilcock and Kenworthy, 2002).

The x axis in Figure 2.9 is the dimensionless stress as given in equation (2.2) except the  $\tau_{crt}$  refers to a reference stress ( $\tau_{ri}$ ) required to cause an imperceptibly small transport rate (i.e.  $W_i^* = 0.02$ ) for particle size *i*. The  $\tau_{rs}$  term for sand is given by the function shown in Figure 2.8. Note how rapidly the sand transport rate increases above this  $W_i^* = 0.02$  theshold (Figure 2.9).

Thus, areas of bed where  $W_i^* > 0.02$  for sand fractions during a spate should have low biomass relative to areas of bed with lower sand transport rates. It is clear that sand transport rates increases dramatically when  $W_{sand}^* > 0.02$  (Figure 2.9). However, no one has yet tested, if patches of riverbed with negligible sand transport (e.g.  $W_{sand}^* < 0.02$ ) have high periphyton relative to patches of riverbed with high sand transport rates.



**Figure 2.9** Dimensionless sediment transport rate ( $W_i^*$ ) versus excess shear stress  $(\tau/\tau_{ri})$ . (Adapted from Wilcock and Kenworthy, 2002).

While the method of Wilcock and Kenworthy (2002) calculates a transport rate based on the local scale of sand on the bed and the bed architecture, the method does not directly address the delivery of sand from upstream during the "overpassing" phase of transport (Ferguson et al., 1989). During the overpassing phase, sand advected from upstream is transported over a static local bed. Because of the momentum of saltating sand, and its exposure to higher layers in the flow, the stress required to initiate movement of the sand grain from the riverbed is greater than the stress required to keep it in motion. This principle is illustrated in the Figure 2.10 where the entrainment velocity for 0.5 mm sand is > 0.1 m/s and the settling velocity is approximately 0.5 m/s (Pidwirny, 2008). While generally accepted as valid, there is little physical evidence supporting the existence of the "overpassing" phase of transport. The presence of overpassing sand would lead to an under estimation of sand transport rates using the method of Wilcock and Kenworthy (2002). The underestimation is typically accounted for by lowering the critical shear stress in a calibration exercise. This underestimation error would be greatest when shear stresses are near the thresholds for both initiating sand entrainment and for sustaining sand transport (i.e. during low magnitude spates); two variables that vary with the geomorphic setting. Consequently, the overpassing phase for sand sized bed material may be important in the prediction of transport rates during low-magnitude, high-frequency spates, but insignificant during higher-magnitude spates, when the critical shear stress for sand is vastly exceeded on all riffles.



**Figure 2.10** Diagram of Hulstrom (1970) showing water velocity thresholds for erosion, transport and deposition of different particle sizes (Adapted from Pidwirny, 2008). Note the difference between the erosion velocity and the settling velocity in the sand fraction associated with over-passing transport. This diagram assumes a certain flow depth and bed roughness.

#### 2.5 Broad scale spatial patterns in periphyton biomass and refuge.

Difficulties predicting broad scale patterns in biomass (i.e. > bedform scale) may result from inadequate consideration of saltation abrasion, which operates at smaller spatial scales. Small scale patterns in biomass give rise to emergent patterns at larger scales. Thorp et al. (2006) contend that important research avenues for the advancement of eco-geomorphological theory include: 1) determining how important small scale processes (traditional focus) are for larger spatiotemporal patches where other variables operate, and 2) examining how a given process varies longitudinally and laterally along the river network (Thorp et al., 2006). This section contains a review of the theoretical framework that has developed regarding contextualization of small scale processes within a broader geomorphic context. The section also contains a review of what is known of intermediate scale biomass patterns.

### 2.5.1 Ecogeomorphology and spatial context

Ecological theory regarding the spatial distribution of biota in river systems has developed substantially over the last 30 years (Frissell et al., 1986; Junk et al., 1989; Sedell et al., 1990; Wu and Loucks, 1995; Poff et al., 1997; Lake, 2000; Benda et al., 2004; Junk and Wantzen, 2004; Thorp et al., 2006). Early empirical studies have shown that periphyton biomass does not always increase steadily along a continuum of increasing light and nutrients with distance down the river network (1<sup>st</sup> to 6<sup>th</sup> order), as predicted by the River Continuum Concept (Vannote et al., 1980; Biggs and Close, 1989; Wright and Li, 2002; Naiman et al., 1987). For example, Osmundson et al. (2002) found periphyton biomass decreased downstream as the amount of sand on the bed and the average velocity increased. Other field studies have shown that discontinuities in biomass are attributed to habitat variability (e.g. velocity, nutrients) at smaller spatial scales (e.g. grain, bar element) and spate disturbance history (Young and Huryn, 1996; Biggs et al., 1998; Wright and Li, 2002; Naiman et al., 1987). Four of the basic ecological principles that have gained acceptance since early studies testing RCC include: 1) the morphology of a river and the biomass regulating processes are hierarchical in nature (cf. Frissell et al., 1986; Hildrew and Giller, 1994; Townsend and Hildrew, 1994; Frothingham et al., 2002). Periphyton biomass is not only governed by local factors like water velocity, but by differences in nutrients supply, which can vary between drainage basins (Biggs and Gerbeaux, 1993).; 2) temporal patterns in biomass are discontinuous and punctuated by spate disturbances (Power and Stewart, 1987; Biggs, 1995; Poff et al., 1997; Lake, 2000; Uehlinger, 2000). High-magnitude low-frequency spates can reset biomass to low levels (Uehlinger, 1991).; 3) rivers are not solely unidirectional flows of

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energy and matter and ecological processes operate in four dimension (i.e. lontitudinal, lateral, vertical, and time)(Poole, 2002; Wiens, 2002; Junk and Wantzen, 2004). Periphyton growth can be influenced by nutrients delivered both vertically from the hyporheic zone (Doyle and Stanley, 2006) and longitudinally from upstream catchments (Biggs and Gerbeaux, 1993).; 4) rivers are a mosaic of dynamic patches (e.g. physical habitat, disturbance intensity, species abundance) which vary in composition, size, and recovery stage (e.g. Heirarchical Patch Dynamics, Wu and Loucks, 1995). Tett et al. (1978) found that periphyton biomass levels were correlated to patches of substrate of differing calibre. High biomass was found on patches of gravel and patches of sand, wheras biomass was low on sandy gravel patches. Mattaehi et al. (2003) found post-spate biomass varied between patches of bed that were scoured, patches that had experienced deposition or patches with no net change in bed elevation. Biomass was highest on undisturbed patches.

When these four principles are combined with the concept of the habitat template, the river system can be viewed as a nested array of habitat patches (e.g. riffles within plan units within links), with each patch having a different resistance to spate disturbance and thus refuge potential. The spatial distribution of periphyton must be heterogeneous (i.e. patchy) for refuge to exist at the scale of observation of interest. For a low-magnitude spate, it is not clear if periphyton is spatially heterogeneous across riffles, or between planform units nested in link units. Thus we do not know where periphyton refuge is high for this type of event (e.g. on one side of riffles located in a certain channel type at the upstream end of a link?). It is important to develop assessment tools and theory to identify these zones for protection.

### 2.5.2 Hydro-geomorphic controls on periphyton biomass at the planform scale

An example of the habitat template applied at the planform scale is given in the Riverine Ecosystem Synthesis (Thorp et al., 2006). In the RES the river network is viewed as a downstream array of hydrogeomorphic patches (here referred to as hydrogeomorphic reaches or HGRs, e.g. meandering, anabranched, braiding; mobile vs. armoured). These hydrogeomorphic reaches are defined based on the hydrologic regime over the patch of bed, using long term discharge records (i.e. to estimate substrate stability and to serve as a surrogate for physiochemical variaibility) and geomorphic character of the patch at the plan scale (e.g. channel type) (Thorp et al., 2006). The HGR provides boundary conditions that limit the biotic assemblage of organisms who are adapted to persist under those conditions (i.e. habitat template). When the ecological structure (e.g. biomass, diversity and community composition) and function (e.g. gross primary production) of the HGR is considered, these templates can be referred to as ecogeomorphic patches (or functional process zones, Thorp et al., 2006). There is mounting evidence that ecosystem structure and function varies with HGRs (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). For example, Coleman and Dahm (1990) found periphyton biomass was 11 times higher in a low gradient beaver pond affected reach versus a steep-straight incised reach. Chessman et al. (2006) cautioned that comparisons of ecological elements between HGRs must be interpreted within the larger spatial context, because ecological limitations may be imposed at a larger scale by different biomass regulating factors (e.g. HGRs nested in link). Despite recent advancements in the investigation of the ecological structure of plan scale HGRs, we know of no systematic attempts to investigate the periphyton refuge potential for different channel types on Boreal Atlantic salmon rivers.

# **2.5.3** Hydro-geomorphic controls on longitudinal trends in periphyton biomass at the link scale: Sedimentary link form and function.

The planform habitat patches (Plan-HGRs) are nested within larger geomorphic features called "sedimentary links". A sedimentary link is the section of river between significant coarse, lateral sediment inputs (Rice and Church, 1998). In sedimentary links, the sediment transport behaviour changes systematically downstream (Rice and Church, 2001). Sediment is selectively transported and abraded down the link, resulting in a downstream decrease in bed material size and channel slope. An example of the habitat template applied at the link scale is given in the Network Dynamics Hypothesis (Benda et al., 2004). The network dynamics hypothesis portrays the river as a downstream array of sedimentary links separated by features such as tributaries, sediment sources, and dams,

which reset downstream trends in physical habitat (Rice and Church, 2001; Benda et al., 2004; Ferguson et al., 2006; Rice et al., 2006).

Within the sedimentary link, abrupt changes in channel form may be present as the river responds to the diminishing ability of the stream to transport coarse material downstream. The ability of the stream to do work (e.g. Specific stream power = SSP) decreases down the sedimentary link because the channel slope decreases, but the channel discharge remains relatively constant between tributaries (Knighton, 1999). Distinctly different channel morphologies can be partitioned into channel types at the planform scale (e.g. wandering, meandering single thread, braided) based on SSP thresholds (Ferguson, 1981; Hicken and Nanson, 1984; Brookes, 1987; Nanson and Croke, 1992; Van Den Berg, 1995; Bravard and Peiry, 1999). Geomorphologists have recognized that different channel types vary in terms of their sensitivity to disturbance (i.e. changes in discharge and sediment load) and how quickly these channel types recover to a more stable state (Brookes, 1987; Rosgen, 1996). Ecologists have used these geomorphic units to define plan-scale HGRs, with unique faunal assemblages adapted to the heterogeneity in physical habitat and response/recovery traits of these various channel types (Thorp et al., 2006). The influence of position of these plan-scale HGRs within sedimentary links on differences in channel morphological diversity and stability, and subsequent effects on stream biota, have been largely overlooked.

Eco-geomorphological studies of sedimentary links investigated the hypothesis that high biodiversity is associated with high habitat variability at the transitions between links (Kiffney et al., 2006). A few studies investigated longitudinal trends in algal biomass at the link scale but did not consider the influence of sedimentary link structure (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). Differences in biomass in these studies were correlated to rock size and indices of stability of the coarser substrate. The role of fine sediment was also inferred from biomass patterns and distance from the zones where sediments were either supplied or removed. Specifically, periphyton biomass was high adjacent to sediment sinks (dams, lakes), but decreased downstream (or fluctuates more frequently), presumably as more potentially abrasive fine sediments were added to the system (Cattaneo, 1996; Jakob et al., 2003; Meyers et al., 2007). Conversely, Yamada and Nakamura (2002) found a downstream increase in periphyton biomass as fine sediment from a quarry was stored in an over-widened and channelized reach of channel, presumably protecting the downstream reach from fine sediment effects (e.g. scour or smothering). Researchers concur that the abrasion of periphyton by fine sediments is an important biomass regulating process (e.g. Francoeur and Biggs, 2006) and likely affects link scale trends, yet direct proof at the link and network scale is hard to establish because of: 1) difficulties in measuring small scale process variables over large areas, 2) difficulties obtaining direct bed stability data (especially for sand, see Salant et al., 2006b), 3) inability to experimentally control spate magnitude or sediment load, and 4) a lack of consideration for the mechanics of saltating sand. It is not obvious from theory how biomass will vary down a sedimentary link and this type of problem is much more amenable to a numerical modelling approach (e.g. Doyle and Stanley, 2006).

# 2.5.4 Hydro-geomorphic controls on lateral biomass patterns at the bar element scale: Riffle scale hydro-geomorphic patches.

At a much smaller spatial scale, bar unit-HGBU's (e.g. riffles) are nested within planform-HPRs (Frothingham et al., 2002). These riffles can be divided transversely into bedform scale HGP's (Bedform-HPBF's) based on the frequency of inundation and the ecological function (Rempel et al., 1999). There is a lack of a unifying theory regarding how spates affect the cross riffle distribution of periphyton biomass between bedform-HGBF's. Jowett (2003) proposed a plausible yet untested theory regarding the location of macroinvertebrate refuge zones within riffle cross sections following spates. This refuge related hypothesis may apply to periphyton. Jowett (2003) reasoned that most sediment transport and high velocities occurs in the thalweg zone, therefore this zone would have poor habitat. Further, poor habitat conditions would also occur in the varial zone due to stranding and desiccation stress. Thus, the best refuge habitat should exist in a transition between the varial zone and the thalweg because physical disturbance was minimal in this zone (Jowett, 2003). Few studies have reported transverse patterns of periphyton biomass (Tett et al., 1978; Fisher et al., 1982; Sand-Jensen, 1988; Rolland et al., 1997). These previous studies do not provide sufficient data to test the Jowett (2003) hypothesis.

# **2.6 Conclusions**

The spatial distribution of benthic algae still eludes modelling, due to high variability of controlling factors in both time and space (Cattaneo et al., 1993). The interactions between the abiotic and biotic controls that affect periphyton biomass reviewed in this chapter are summarized in Figure 2.11. Of these biotic and abiotic factors, the role of saltating sand on periphyton disturbance has received the least attention. Yet, engineering studies of the effects of saltating sand on bedrock have demonstrated its substantial potential for erosion. These studies also suggest that saltation is more erosive to bedrock than suspended sediments, which have been shown to effectively abrade periphyton.



**Figure 2.11** Diagram of local controls on periphyton biomass that are well documented. The blank box represents saltation and was not included in the figure to indicate that the least is known about this potentially significant disturbance factor.

Periphyton models attempting to isolate factors affecting large scale spatial patterns in periphyton biomass may fail to reach acceptable predictive power, because the negative effects of saltating sand on periphyton biomass at shorter spatio-temporal scales were not considered. Despite the large body of knowledge regarding the effects of spate disturbances on spatial and temporal patterns in periphyton biomass, there is a need to investigate how the erosive properties of saltating sand limits the spatial distribution of periphyton biomass within river systems. The characteristics of refuge zones remaining after these spates have not been investigated at intermediate scales (e.g. planform, link) or for low-magnitude high-frequency spates. These research avenues relating small scale saltation kinetics to large scale patterns in periphyton biomass directly parallel some research topics requisite for the advancement of eco-geomorphological theory including: 1) determining how important small scale processes (traditional focus) are for larger spatio-temporal patches where other variables operate, 2) examining how a given process varies longitudinally and laterally along the river network, 3) matching the scale of environmental process with the appropriate scale of biological organization, 4) further developing a lotic model that addresses change in food resources along the entire river network (Cattaneo et al., 1993; Thorp et al., 2006). Knowledge of the distribution and resilience of food organisms will help affirm how particular habitats meet fish needs within the context of global scale anthropogenic manipulation to river systems (Franzine et al., 2002).
#### Context and connecting statement for chapter 3

In this chapter, we investigate the factors that influence in-stream periphyton biomass remaining on the tops of rocks lying on the channel bed, after a low-magnitude spate. The model structure is based on components of an existing mechanistic model of bedrock erosion by saltating sediment. The model is fit to field data to investigate if sand transport over a stable coarse bed can explain spatial patterns in periphyton biomass. We also present a statistical approach to properly account for the degree of independence of spatially clustered data that is typical of ecological studies of lotic systems. This approach involved using a series of linear mixed effects models with both Akikie and Bayesian (AIC/BIC) model selection criteria.

Elements of the periphyton perturbation theory developed in this chapter are further refined in chapter 4 using field data, and corroborated with the results of an *in situ* experiment which are presented in chapter 5. The periphyton perturbation model developed and parameterized in this chapter is a vital component of the hierarchical periphyton perturbation model presented in chapter 6. Chapter 6 will show how the small scale processes investigated in this chapter give rise to periphyton refuge patterns at much larger scales of observation.

#### Chapter 3

## Modelling rock scale periphyton biomass remaining on a stable bed exposed to small spates: accounting for abrasion by saltating sand

James J.W. Luce, Russell Steele and Michel F. Lapointe

#### Abstract

The periphyton that cover the substrata of rivers contains the dominant primary producers in most temperate stream ecosystems, yet little is known about how sand transported along the bed affects the algal biomass of periphyton. Saltating sand is transported by a hopping motion along the river bed for flow increases (spates) ranging from baseflow to bankfull condition. Saltating sediment has been shown to be efficient at eroding cohesive (clay) and brittle (rock) bed materials. Therefore, an empirical model that considers periphyton losses associated with the kinetics of saltating sand should assist in explaining the spatial distribution of biomass in river systems. We investigated the effects of saltating sand on periphyton biomass at rock and 1.5 m patch scales during a low-magnitude, high-frequency spate (0.6 x mean annual discharge, 7 day summer mean return period) where sand was moving over a stable, coarse bed pavement.

A saltation abrasion model for periphyton (PSAM) was developed from an existing mechanistic saltation abrasion model for bedrock (SAMB, Sklar and Dietrich, 2004). Modifications (new variables) are introduced within the bedrock abrasion model to better represent specific periphyton abrasion processes (host-rock Exposure Index and Immersion Index within saltation layer). Periphyton was monitored at the rock scale (n = 1500) before and after a period of several small spates across 15 riffle crests (100 rocks across each of the riffle crests) distributed over 2.35 km of a mid-sized (280 km<sup>2</sup>) Canadian Shield river. Physical disturbance factors for periphyton were isolated by selecting reaches with no significant differences in growth factors, and by sampling periphyton directly after the spates. During the spate period, we also measured sand transport rates, peak shear stress, baseflow velocity and the height of saltation abrasion on painted nails.

A simplified version of PSAM was tested using nonlinear regression and three linear mixed effects models (LME) with best model selection criteria (Bayesian Information Criteria, Akaike Information Criteria) on rock scale data. For rocks exposed to high sand transport rates (> 100 g  $m^{-1}$  event<sup>-1</sup>), the best PSAM models (linear and nonlinear) explained 56-59% of the variance in biomass at the rock scale. Both nonlinear and linear models predicted post-spate biomass with similar accuracy. However, the LME models allowed us to account for heteroscedasticity in residuals, resulting in a more conservative and statistically robust assessment of model parameter significance. The local sand transport rate, representing the "tool effect" in the PSAM model, had a strong negative and significant effect on post-spate biomass, to the exclusion of peak spate shear stress and independently from baseflow (conditioning) velocity. The "cover effect", represented by two indices of periphyton exposure to the tools effect, was also negative and significant, as hypothesized. However, the cover effect explained less variance in post-spate biomass than the tools effect. When all data were considered, the reference sand transport rate for the sand motion threshold (W\*>0.002, Wilcock and Kenworthy, 2002) divided patches of bed with high maximum periphyton biomass (chlorophyll a > 10 $mg/m^2$ ) from patches of bed with low maximum periphyton biomass that were characterized by higher transport rates (especially when W\*>0.02). Sand (0.5-2mm) was primarily saltating during the small but high-frequency spates, and the spatial distribution of low periphyton biomass was predicted from the PSAM models.

#### **3.1 Introduction**

Periphyton biomass accrual is governed by the balance between growth and disturbance factors (Stevenson, 1996; Azim et al., 2005; Biggs and Kilroy, 2007; Warnaars et al., 2007). In gravel bed rivers, spate magnitude and time since disturbance predict up to 63% of biomass variance at the reach scale (Fisher and Grimm, 1988; Biggs and Close, 1989; Uehlinger, 1991; Schweizer, 2007). Spate related physical disturbances include sloughing from hydraulic shear (Biggs and Thomsen, 1995; Stone, 2005), abrasion by suspended sediments (Francoeur and Biggs, 2006; Horner et al., 1990b), and abrasion through bed excavation, and burial (Matthaei et al. 2003). Periphyton refuges retain more biomass than areas not sheltered from physical disturbance. Periphyton

refuge is found in rock crevices (Bergey, 2005), in the lee of rocks (Francoeur and Biggs, 2006), on large stable rock and rock clusters (Francoeur et al., 1998), or patches of bed sheltered from transported sand or gravel. Francoeur and Biggs (2006) speculated that increasing height above the bed provides refuge from fine sediment abrasion. During larger spates (e.g. 3-8 times mean annual discharge, with a frequency of 6-19 spates per year), 50-95% of the periphyton community is lost, especially if the bed is scoured, and the larger clasts of the bed pavement are mobile (Fisher and Grimm, 1988; Biggs and Close, 1989; Uehlinger, 1991; Matthaei et al., 2003). During small spates, sand can be mobilized from pools, channel margins and bed surface interstices, even when the shear force of water (i.e. shear stress) is low and bed surface gravels are static (Wilcock and Kenworthy, 2002). Thus a large percentage (>40%, Lisle, 1989; 1995; Wilcock et al., 1996) of the sediment moved in such small spates is sand (< 2 mm), which travels over a stable armoured bed of larger periphyton covered rocks (i.e. host-rocks) (Stokseth, 1994; Grams et al., 2006). The majority of this sand load moves by a hopping motion called saltation, if the flow energy is not sufficient to cause sustained suspension. Researchers have hypothesized that abrasion by fine sediment over a stable bed may be responsible for periphyton removal during moderate spates (Horner and Welch, 1981; Fisher and Grimm, 1988; Horner et al., 1990b). Here, we quantify how sensitive periphyton biomass is to increasing saltating sand flux during small spates, and to what extent host-rock height above the bed provides refuge for periphyton.

Existing studies of the abrasive potential of saltating sediment in moving water have focused on erosion rates of rock and cohesive clay; not periphyton . Sklar and Dietrich (2004) synthesized much of this literature to develop a mechanistic bedrock saltation abrasion model (SAMB) based on the kinetics of saltating sediment. SAMB is conceptually based on the 'tool and cover effects' of saltating sediment. The 'tool effect' refers to erosion of the bedrock surface by the impact of saltating particles (i.e. the tools). The 'cover effect' refers to protection of a bedrock surface from saltation abrasion by a gravel layer which occasionally overlies the bedrock surface. According to SAMB, as flow energy progressively increases, bedrock erosion starts with the intiation of saltation. Erosion rates increase to a maximum at moderate velocities, then decrease again as particles hit the bed less frequently and at more glancing angles. Erosion rates approach zero when particles go into suspension. For bedrock, maximum rates of erosion occur if gravel is saltating. Periphyton is much less resistant than bedrock. Even suspended clay and sand have a significant abrasive effect on periphyton (Francoeur and Biggs, 2006; Horner et al., 1990b). Substantial losses in benthic algae and macroinvertebrates have been associated with transported sand in the field (Culp et al., 1986; Bond, 2004; Thomson et al., 2005). The theoretical basis provided by SAMB for the abrasive potential of saltating sediment will be modified here to provide a novel framework (PSAM – Periphyton Saltation Abrasion Model) to quantify the impacts of saltating sand on periphyton biomass during frequent spates.

Primary production in unshaded rivers is driven by periphyton, and the distribution of biomass remaining after a spate affects how quickly the periphyton community recovers from disturbance. Our ability to both identify potential periphyton refuge zones and model biomass dynamics depend on identifying the key processes responsible for the periphyton disturbance (Fisher et al., 1982; Uehlinger et al., 1996; Rempel et al., 1999). The empirical linkages between saltation kinetics and periphyton biomass provided here by PSAM are required to assess the ecological implications of anthropogenically induced alterations to the timing and magnitude of spates and fine sediment delivery (Gregory et al., 1992; Goudie, 2006).

The general purpose of our study is to investigate how periphyton biomass is limited by transported sand during low-magnitude but high-recurrence spates. We will first in section 3.2.2 adapt SAMB, an existing mechanistic model for bedrock erosion by saltating sediment, to conceptualize periphyton erosion from a host-rock by saltating sand (0.5-2 mm). In this conceptual model of periphyton saltation abrasion (C-PSAM), we propose alternative exposure terms to consider the refuge provided to periphyton by stream bed architecture. From this theoretical base, we develop statistical models (PSAM) for predicting periphyton biomass in a gravel bed river after a small spate (i.e. 0.6 times the mean annual discharge).

Our primary objective was to test how well the PSAM model describes post-spate periphyton biomass. We tested two primary hypotheses related to PSAM:  $H_{1_1}$ : The

PSAM tools effect (i.e. rate of sand transport over the bed, Section 3.2.2) is a significant predictor of periphyton biomass;  $H_{1_2}$ : The PSAM cover effect (i.e. how exposed periphyton is to sand abrasion, Section 3.2.2) is a significant predictor of periphyton biomass. In a separate analysis using a larger set of data, we test a third hypothesis:  $H_{1_3}$ : The threshold for motion of sand divides high periphyton biomass at low sand transport rates, from low biomass at high transport rates.

The first two hypotheses were tested using nonlinear regression and a group of linear mixed effects models. First, nonlinear regression is used to fit an approximation of the conceptual model structure of PSAM. This analytical approach combines the advantages of a statistical model formulation, tolerating the lower measurement precision associated with field data, with a simple parameterization that closely represents the behavior of the original mechanistic model. An error analysis of the nonlinear, least squares model led to the development of a similar but more statistically robust, linear least squares PSAM model. This linear model supported the validity of the nonlinear model and enabled a more conservative assessment of the significance of parameter estimates. In testing Hypothesis 3, we expressed the sand transport rate in terms of a classic dimensionless transport rate both to make our observations testable at other spatial scales, and to relate our results to an existing two fraction model for sand and gravel transport (Wilcock and Kenworthy, 2002; Salant et al., 2006b).

We suspect that the known difficulties researchers have experienced regarding the prediction of periphyton biomass in space and time (Cattaneo et al., 1993; Stone, 2005) may have resulted from inadequate accounting for saltation, an intermittent and patchy process. The development of PSAM enhances our understanding of periphyton regulating processes, and may enable more accurate predictions of the distribution and resilience of the food resource upon which riverine food webs are based.

#### **3.2 Model Development**

#### 3.2.1 Bedrock Saltation Abrasion Model (SAMB)

In the main SAMB model (Sklar and Dietrich, 2004), the erosion rate of bedrock (E, mm/yr) by a saltating particle is given by:

$$E = V_i I_r F_e \tag{3.1}$$

where,  $V_i$  is the volume eroded per grain impact (m<sup>3</sup>/impact),  $I_r$  is the impact rate on the bed (Impacts m<sup>-2</sup> s<sup>-1</sup>) and  $F_e$  is the degree of bedrock exposure, given as the area of exposed bedrock to total area of channel including alluvial cover (m<sup>2</sup>/m<sup>2</sup>). The "tool effect" is the erosive effect of mobile sediment striking the bed and given by  $V_i I_r$ . The "cover effect" is the protective effect of alluvial bed material covering the bedrock (F<sub>e</sub>). In SAMB, these three variables are calculated using calibrated sub-models.

According to SAMB, the height of each particle hop increases with flow strength but eventually reaches a maximum. Particles then either become suspended, or have a flatter saltation trajectory (Francis, 1977). Thus, a "saltation layer" near the bed forms and it is bounded by maximum saltation height for that sediment mixture and flow strength (Figure 3.1). If the bedrock is exposed, erosion rates increase with flow strength as the



**Figure 3.1** Definition of terms. Rocks 1-3 are examples of host-rocks, sampled for periphyton biomass. The protrusion height is measured relative to the mean bed matrix elevation and can be positive or negative.

saltation layer thickens and transport intensity increases. Bedrock erosion rates decrease to zero if the bed becomes covered with gravel ( $F_e = 0$ ) as the supply of sediment from upstream exceeds the ability of the river to transport it.

### **3.2.2 Modifications to SAMB for Conceptual Periphyton Saltation Abrasion Model** (C-PSAM)

The mechanistic form of the periphtyon saltation abrasion model (PSAM) was derived from SAMB by expressing equation (3.1) in terms of periphyton and rearranging to solve for post-spate biomass ( $PB_{T2}$ ) which yields C-PSAM:

$$PB_{T2} = PB_{T1} - \rho_{mat} V_{ip} I_{r_sa} F_{ep} (T_2 - T_1)$$
(3.2)

where,  $PB_{T1}$  is the biomass before the spate (kg/m<sup>2</sup>),  $\rho_{mat}$  is the density of the periphyton mat (kg/m<sup>3</sup>),  $V_{ip}$  is the periphyton volume eroded per impact (m<sup>3</sup>/Impact),  $I_{r\_sa}$  is the time-mean impact rate of sand on the bed (Impacts m<sup>-2</sup>s<sup>-1</sup>) of a specified diameter (In this study we measured 0.5-2 mm sand transport because smaller sand is prone to suspension.),  $F_{ep}$  is the degree of periphyton exposure, and  $(T_2 - T_1)$  is the time between pre- and post-spate biomass sampling.

The other main modification we make to SAMB is in the exposure term ( $F_e$ ) in equation (3.1). In SAMB, this term is defined as the ratio of bedrock area free of protective alluvial cover to total bed area. However, periphyton is sheltered by vertical exposure more than by alluvial cover. We assume here that the degree of exposure for periphyton ( $F_e$ , equation (3.2)) to flow related disturbances is a function of how high the particle top protrudes above (or below) the mean bed matrix level (Figure 3.2). The bed matrix is the fine material (e.g. sand granules, medium gravel i.e. less than 16 mm) which occupies the spaces between coarser framework bed material (e.g. gravel cobble). The "flattest" surface at the base of the coarse bed material is the mean local matrix elevation (Fisher et al., 1982). The protrusion of a periphyton covered rock above (or below) this mean matrix level may affect either how much the rock is "exposed" to bombardment relative to the surrounding substrate or how much protection is provided by being located well above the abrasive saltation layer. To address the degree of exposure within PSAM



**Figure 3.2** The degree of scour on a rocks surface should partially be a function of the saltation height (SH) relative to the top of the rock or protrusion height (PH). When the immersion index (SH/PH) exceeds unity, then the rock should be fully immersed in saltating sand. Increasing saltation height between Figures 3.2a-c could be from increasing flow intensity or decreasing sand size for same flow.

we include 2, nondimensional relative exposure indices for host-rocks: a "exposure index" ( $F_{ep\_El}$ ) and an "immersion index" ( $F_{ep\_Il}$ ).

The first index, the exposure index ( $F_{ep\_EI}$ ), is the protrusion height of the periphyton covered rock of interest (i.e. host-rock), divided by the median protrusion height of a patch (Mean width = 1.4 m) of rocks surrounding this host-rock. Thus, as the exposure index increases with protrusion height, relative to the median protrusion height, the periphyton loss term in PSAM (i.e.  $-\rho_{mat}V_{ip}I_{r\_sa}F_{ep}(T_2 - T_1)$ ) increases, resulting in less post-spate periphyton. This exposure index is similar to the hiding index used in sediment transport studies (Parker, 1990), except that we use mean protrusion height above the matrix rather than the median particle size as a reference length scale. The second  $F_{ep}$ , the immersion index ( $F_{ep\_II}$ ), was designed to also consider the potential positive effect of increasing protrusion height on periphyton biomass. This index is the ratio of the mean saltation layer thickness to protrusion height of the host-rock (Figures 3.2a, b, c). If this immersion index has a value greater than or equal to 1, then the host-rock is fully immersed in saltating sand (Figure 3.2c). Thus, as the immersion index

increases with saltation height, for a given host-rock protrusion height, the periphyton loss term in PSAM (i.e.  $-\rho_{mat}V_{ip}I_{r\_sa}F_{ep}(T_2 - T_1)$ ) increases, resulting in the prediction of less post-spate periphyton.

We anticipate that the periphyton biomass remaining after a spate decreases with an increase in both the immersion index and the exposure index, if the bed was abraded by sand. The degree of colinearity and the effect on periphyton of these 2 variables will be tested empirically.

#### **3.2.3 Model Assumptions**

Our objective was to test the ability of the variables underlying C-PSAM (equation (3.2)) to predict rock scale (sensu "grain scale" of Frothingham et al., 2002), post-spate biomass at hundreds of locations on a natural river. Consequently, C-PSAM was not tested directly because the laboratory type control required was not achievable in the field. Instead, we first fit to field data a nonlinear regression model motivated by C-PSAM (equation (3.2)):

$$PB_{T2} = PB_{T1} - V_{water}^{\beta 2} I_{r\_sand\_t}^{\beta 3} F_{ep}^{\beta 4} + e$$
(3.3)

where, *PB* is in mg/m<sup>2</sup> of chlorophyll *a*,  $V_{water}$  is the average water velocity at baseflow (i.e. conditioning velocity, m/s),  $I_{r\_sand\_t}$  is the sand transport rate measured between *T*1 and *T*2 (g m<sup>-1</sup>event<sup>-1</sup>),  $F_{ep}$  is either the immersion index or hiding index (or both), and *e* represents random model error. Equation (3.3) does not include the mat density ( $\rho_{mat}$ ) because only a diatom dominated periphyton community is considered. The event duration ( $T_2 - T_1$ ) from equation (3.2) may also be held constant if data are from one event. The  $V_{ip}$  of equation (3.2) was also excluded from equation (3.3) because it is estimated to be a very small quantity (e.g.  $10^{-24}$ ) assuming a tensile strength of 2.2-6.2 MPA for algae (Johnson et al., 1996), a narrow particle size range (0.05 mm – 2 mm), and a realistic range of particle impact velocities (< 0.4 m/s).

The error terms, *e*, must be independent of other model parameters and have constant variance (i.e. multivariate term for heteroscedasticity) for all observations in order for us to make appropriate statistical inference (i.e. not overstate *p*-values). In

order to strengthen our results in the presence of violations of these two assumptions, we also fit linear regression models of the form:

$$\log PB_{T2} = \alpha + \beta_1 \log PB_{T1} - \beta_2 \log V_{water} - \beta_3 \log I_{r\_sand\_t} - \beta_4 \log F_{ep} + e^*$$
(3.4a)

or when transformed:

$$PB_{T2} = 10^{\alpha} PB_{T1}^{\beta 1} V_{water}^{-\beta 2} I_{r\_sa\_sand\_t}^{-\beta 3} F_{ep}^{-\beta 4} 10^{e*}$$
(3.4b)

which differs from model (3.3) in three important ways. First, it addresses possible, nonconstant variance by assuming a multiplicative (rather than additive) error. Second, it allows for some additional flexibility in the model by not assuming a simple offset term for the pre-spate biomass ( $PB_{T1}$  in equation (3.3)), but rather tries to estimate the offset from the data ( $PB_{T1}^{\beta 1}$  in equation (3.4b)). Finally, linear regression models can yield far less correlation between parameter estimates than nonlinear regression models, lending additional stability to the inference.

Equation (3.4a) was inspired by SAMB and thus meant to account for saltation abrasion losses. Direct losses can also occur purely by abrasion by suspended sediment loads and high shear stresses during the spate ( $\tau_{spate}$ ; Biggs and Thomsen 1995, Stone 2005). Consequently, equation (3.4a) was amended to include  $\tau_{spate}$  as a covariate:  $\log PB_{T2} = \alpha + \beta_1 \log PB_{T1} - \beta_2 \log V_{water} - \beta_3 \log I_{r\_sand\_t} - \beta_4 \log F_{ep} - \tau_{spate} + e^*$ (3.4c)

We assumed suspended sediment losses were negligible because data was collected during a period when 0.5-2 mm sand was primarily saltating. Regardless, suspended sediment effects are expected to be more evenly distributed across the channel than sand saltation abrasion effects.

In the context of C-PSAM, the variable  $V_{water}$  in equations (3.3) and (3.4) is a surrogate variable representing particle impact velocity, which affects the volume eroded per impact ( $V_{ip}$ ). Based on SAMB, an increase in  $V_{water}$  increases the particle impact velocity and a larger volume of bedrock (periphyton here) is removed per impact (Sklar and Dietrich, 2004). However, as stated earlier, we anticipate  $V_{ip}$  to be negligible. Yet, flow velocity at baseflow (i.e. conditioning velocity,  $V_{water}$ ) is also a growth related variable with a nonlinear effect on pre-spate biomass ( $PB_{T1}$ ). At very low velocities (e.g. mean < 0.1 m/s), biomass increases as higher velocities increase the exchange of nutrient and exudates across algal cell walls (Horner and Welch, 1981). At higher velocities (e.g. mean > 0.1 m/s), the cell removal rate by flowing water increases. When the cell removal rate by flowing water exceeds the growth rate, then the conditioning velocity ( $V_{water}$ ) limits biomass accumulation (Biggs and Stokseth, 1996; Horner et al., 1990b). We assume a simple power function between  $V_{water}$  and  $PB_{T2}$  in our models, assuming most of the data have  $V_{water} > 0.10$  m/s. We also assume that other growth related variables that affect  $PB_{T1}$  (e.g. light, nutrients and temperature) vary little within the relatively short study reaches based on field observations.

#### **3.3 Materials and Methods**

#### **3.3.1 Site Description**

Study sites were located along the Sainte-Marguerite River, which flows through deeply fractured granite and schist rocks (Figure 3.3, 48°26'56"N, 70°26'97"W). Water chemistry in this boreal watershed is typical of oligo-mesotrophic, Canadian Shield rivers (Grenier et al., 2005). The periphyton community consisted primarily of diatoms and included *Tabellaria, Navicula, Gomphonema, Eunotia, Cymbella, Fragilaria, Pinnularia,* and *Synedra*. At Big Pool, the 1.8 year return period flow is 82 m<sup>3</sup>/s and the mean annual discharge (MAD) is 9.6 m<sup>3</sup>/s. Periphyton biomass accumulates throughout the July to September period, when flows are relatively stable and over-bank events are rare.

We adopted a broad definition of spate to characterize the magnitude and frequency of small runoff events that punctuate the growth period using long term discharge records. Here, the spate peak is the daily average discharge on the day when this discharge is higher than the preceding and following day and preceeded by at least three days of stable flow. Flow records from the Sainte Marguerite river for the period of July to September, for the years 1991 to 2003, indicate that the average spate peak discharge at Big Pool was 8.2 m<sup>3</sup>/s (i.e. exceeded 25% of the summer period, exceeded



**Figure 3.3** Location of the study reaches on the Ste. Marguerite River within Quebec, Canada. Sampling in 2004 occurred on 15 riffles distributed between the Big Pool (9 riffles) and Meander (6 riffles) reaches.

48% of the time annually) but ranged between 2.3 m<sup>3</sup>/s (i.e. exceed 92% of the summer period) and 34.3 m<sup>3</sup>/s (i.e. exceed 0.006% of the summer period). The period between spates ranged from 5.7 to 8.3 days, averaging 7.1 days. Spate magnitudes were between 1.1 and 7.8 times the average discharge of the six days preceding the event, with average departure being a factor of 1.65. The baseflow discharge that occurred between these spates averaged 4.5 m<sup>3</sup>/s, a discharge exceeded 65% of the time during the summer growth period.

Rock scale instream data were collected at a number of locations across 9 distinct riffles in the Big Pool reach (BPR) and 6 riffles in the Meander reach (MR) during the  $2^{nd}$  &  $3^{rd}$  August 2004 and the  $26^{th}$  &  $27^{th}$  August 2004 (Figure 3.4). During this monitoring period, a series of small spates occurred, the largest of which had a maximum instantaneous discharge of 6.1 m<sup>3</sup>/s (24 August 2004) and was large enough to cause a measurable first-flush turbidity response (see turbidity spike in Figure 3.4). The peak discharges during these small spates was just lower than the mean summer spate discharge (8.2 m<sup>3</sup>/s) that is typical of the periphyton growing season.

#### **3.3.2 Instream Measurements**

**Periphyton biomass.** Periphyton data was collected the 2<sup>nd</sup> & 3<sup>rd</sup> August 2004 (BP1, pre-spate), and the 26<sup>th</sup> & 27<sup>th</sup> August 2004 (BP2, post-spate). This latter periphyton sampling occurred 2 days after the larger 24 August 2004 spate of the sampling period, approximating the mean summer spate (Figure 3.4). Measurements of periphyton biomass at the top of each rock, rock protrusion height, b-axis and water depth were taken at 100 rocks across each of the 15 riffle transects (Figure 3.5a). Sample rocks were selected by blindly choosing the rock located directly below regular increments on a tape measure strung taught across the cross section (Leopold et al., 1964). A rapid assessment technique was used to assess relative biomass of micro algae on top of each rock (Table 3.1)( Stevenson and Bahls, 1999). As part of a calibration process, eight rocks (minimum) from each rank were sampled for chlorophyll *a* measurement. The periphyton was removed from a 0.2 m<sup>2</sup> area on each calibration rock using scalpel and brush. Chlorophyll *a* was extracted using standard methods (APHA, 1995). There was a significant difference (*p* = 0.05, *n* = 10) between all rank means except for ranks three and four, indicating die off in the thicker rank 4 samples (Table 3.2).

**Sand transport rate.** Ten sand traps were placed across each riffle transect at regular increments within the active channel (i.e. the area of channel bed devoid of vascular vegetation due to frequent spate disturbance). The closed sided sediment traps were inserted flush with the surrounding substrate and consist of a one litre plastic



**Figure 3.4** Stage and turbidity records from Big Pool showing the timing of field sampling activities. The 'largest' spate (24th August 04) during the monitoring period shown (27 July 04 - 1 September 04) caused a strong spike in turbidity.



**Figure 3.5** a) Typical riffle cross section sampling arrangement, where 100 rocks were sampled for periphyton abundance (USEPA rank) and protrusion height. Approximately 10 sediment traps were used to determine sand transport rates across the transect during the previous spate period. Staff gauge readings were required to estimate peak spate depths from reach specific discharge hydrographs. b) The height of paint abrasion was measured at sediment traps using abrasion pins placed at the edge of sediment traps (Flow direction is towards the viewer).

Rank	Criteria
0	Substrate rough with no visual evidence of microalgae
0.5	Slightly slimy but no visual accumulation of microalgae is evident
1	Slimy with visual accumulation evident.
2	Moderately slimy with accumulations evident and between 0.5 mm to 1 mm thick.
3	Very slimy with accumulation layer from 1 mm to 5 mm thick
4	Algae sloughs when wading in area or removing rock. Accumulation > 5mm thick

**Table 3.1** USEPA rapid periphyton protocol for ranking abundance of microalgae (Stevenson and Bahls, 1999).

**Table 3.2** Results of one way analysis of variance (ANOVA) testing differences in periphyton biomass among USEPA ranks. All data were collected during the post-spate periphyton survey. USEPA rank categories are based on algal appearance and thickness (Table 3.1). Periphyton biomass is based on chlorophyll *a* assays of periphyton removed from a small prescribed area of pure USEPA rank.

	Biomass – Chlorophyll a (mg/m <sup>2</sup> )						
	2004						
Rank	Average	S.E.					
0	0.23*	0.04					
0.5	0.52*	0.07					
1	3.72*	0.63					
2	8.13*	1.45					
3	41.30*	5.05					
4	29.58	3.41					
$2004 - F_{(5,87)} = 223, p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.001, R = 0.96, R^2 = 0.96; R^2 = $							
0.05							

container filled with clean 16-32 mm gravel. The traps capture particles smaller than 5 mm in bedload or saltation load. The trap line was located 30 cm downstream of the test rocks. Trap lids were opened 2 August 2004 and closed 26 August 2004 (Figure 3.4). The contents were dried at 105 °C and shaken in a set of sieves for 20 minutes to determine the mass of 0.5-2 mm sand trapped. The mass of transported sand was divided by the width of the trap (i.e. 12 cm) to give  $I_{r\_sand\_t}$  as a mean rate per meter width and spate duration (g m<sup>-1</sup>event<sup>-1</sup>).

**Protrusion height.** The protrusion height was measured at each host-rock. The protrusion height is the height between the top of the host-rock and the mean matrix elevation over a reference area of  $0.25 \text{ m}^2$  (Figure 3.1).

**Conditioning velocity.** The conditioning velocity measurements are 1.5 minute long readings taken at all sand traps using a Gurley No. 625D Pygmy meter at 0.4 times the flow depth during a period of inter-spate baseflow (Figure 3.5). Measurements were taken between the 18<sup>th</sup> and 23<sup>rd</sup> of August 2004. Linear interpolation was used to estimate conditioning velocities for rocks located between traps.

**Peak shear stress.** Peak shear stress for the stronger 24 August 2004 spate was also estimated at each rock. For rocks where flow was obstructed by upstream features (e.g. large boulders, woody debris), shear stress estimates were made separately from those for unobstructed rocks. The calibrated shear stresses for unobstructed ( $\tau_{Unobs}$ ) and obstructed ( $\tau_{obst.}$ ) flow sites are given by:

- - - -

$$\tau_{Unobs.} = 2.932 + 0.510\tau_{DuBoys} + 1.171RR - 2.432DFT \quad (3.5)$$
$$(R^{2}_{adj} = 0.66, SE = 0.22 \text{ Pa}, n = 50)$$
$$\tau_{Obst.} = 0.577 + 0.385\tau_{DuBoys} \qquad (3.6)$$
$$(R^{2}_{adj} = 0.52, SE = 0.13 \text{ Pa}, n = 41)$$

where,  $\tau_{DuBoys}$  is an estimate of shear stress at each rock based on the DuBoys equation (Chang 1988), RR (Relative Roughness) is the ratio rock b-axis/flow depth at spate peak, and DFT (Dimensionless Distance from the Thalweg) is the distance of the rock from the deepest part of the channel as a fraction of local active channel width. Shear stresses (square root) and bed roughness (Log) were transformed to satisfy the assumption of normality. Equations (3.5) and (3.6) were calibrated shear stress estimates based on: 1) a velocity profile based method and conditioning velocity measurements (Wilcock et al., 1996), and 2) DuBoys estimates with local water depth at each sampled rock and local water slope at each riffle representing the conditions during velocity sampling. Water surface slopes over riffles were measured using a Sokkia<sup>™</sup> B2C level during base flow conditions (Stage = 0.11 m) and spate conditions (Stage = 0.49-0.55 m). Linear

regression (p < 0.05) was used to determine the slope over  $\ge 3$  bankfull channel widths, centered on each riffle. Water stage at each riffle cross section was estimated for the 24 August 2004 spate using a linear regression between observed stage at each riffle cross section and stage at a pressure transducer at each reach. Water depths at each rock were calculated by subtracting the elevation of the riffle section water surface at the spate peak from the streambed elevation, at each rock.

#### 3.3.3 Calculation of Exposure Indices

The host-rock **exposure index** is predominantly positive (but it can be negative when the host-rock is below the mean matrix level) and is given by:

$$F_{ep\_EI} = \frac{P_i}{P_{50}}$$
(3.7)

where,  $P_i$  is the protrusion height of the host-rock and  $P_{50}$  is the median protrusion height of a patch of 10 rocks centred around the host-rock.

The **immersion index** is given by:

$$F_{ep\_II} = \frac{Hs_{Sklar and Dietrich}}{P_i}$$
(3.8)

where,  $Hs_{Sklar and Dietrich}$  is an estimate of the average local saltation height and  $P_i$  is the protrusion height of the host-rock. The average saltation height at each rock was estimated using the method of Sklar and Dietrich (2004):

$$Hs_{Sklar and Dietrich} = 1.44 \left(\frac{\tau^*}{\tau_c^* - 1}\right)^{0.5} D_s \tag{3.9}$$

where,  $\tau^*$  is the shear stress at the spate peak, made dimensionless by the size of sand in motion ( $D_s = 2$  mm), and  $\tau_c^*$  is the dimensionless critical shear stress when sand motion is initiated. The dimensionless shear stress at the spate peak is given by:  $\tau^* = \tau/(S_g - 1)\rho g D_{sa}$ , where  $\tau$  is the shear stress given by equations (3.5) or (3.6) as appropriate,  $S_g$  is the specific gravity of sediment, and  $D_{sa}$  is the diameter of sand in transport.  $S_g = \rho_s / \rho_w$  and  $\rho$  is the density (kg/m<sup>3</sup>) of sediment ( $\rho_s$ ) and water ( $\rho_w$ ). The method of Wilcock and Kenworthy (2002), to determine critical shear stress for entrainment of mixed sand and gravel beds ( $\tau_r^*$ ), was used to calculate  $\tau_c^*$  (i.e.  $\tau_c^* \sim \tau_r^*$ ) at each rock. By their method,  $\tau_c^*$  decreases as the fraction of sand on the bed increases, and as a particle becomes less hidden by the surrounding substrate. The fraction of sand in surface substrate was measured at each sand trap location using a McNeil type sampler with an opening diameter of 0.25 m (McNeil and Ahnell, 1964). The sampler excluded bed material larger than 34 mm and captured all material coarser than 0.063 mm. Samples (2 to 4 kg) were taken to the depth of the largest substrate rock. Samples were sieved to extract the 0.5 to 2 mm sand. This subsample of sand was divided by the total sample mass to determine the fraction of sand in the surface substrate at each sediment trap.

It was not practically feasible to collect enough direct measurements of average saltation height during the spate period to directly evaluate the ability of equation (3.9) to predict saltation heights for gravel-cobble river beds. Alternatively, we measured the height of the abraded section of paint, measured from the substrate insertion point to the top of the dulled paint, on 12 inch painted steel pins exposed to saltating sand during a spate (24 August 2004, Figure 3.5b). This Abrasion Height (*AH*) has a strong positive relation with the average saltation height estimate (i.e. equation (3.9),  $Hs_{Sklar and Dietrich}$  vs measured *AH*  $R^2_{adj} = 0.73$ , n = 20, Appendix A).

We also developed a regression equation for estimating *AH* that more accurately predicts *AH* ( $R^2_{adj} = 0.92$ , n = 20, Appendix A), relative to the predictive strength of equation (3.9). The abrasion height estimate (*AH<sub>e</sub>*) is given by (see Appendix A):

$$AH_e = 0.015 + 0.085P_{50} - 0.046F_{sa} + 0.051FR + 0.045SC_{2mm} \quad n = 56$$
(3.10)

where,  $P_{50}$  is the median protrusion height of a patch of 10 rocks,  $F_{sa}$  is the fraction of sand on the bed, *FR* is the flow Froude Number at baseflow, and  $SC_{2mm}$  is the suspension criteria for 2 mm sand at the spate peak discharge. The suspension criteria is the shear velocity (*u*\*) divided by the fall velocity (*w*) of a particle in standing water (i.e.  $SC_{2mm} = u^*/w_{2mm}$ , where  $u^* = \sqrt{\tau_{spate peak}/\rho_{water}}$ ), and indicates the transition from saltating motion to suspension at a value of one.

#### **3.3.4 Statistical Analysis**

We fit nonlinear least squares regression models in the form of equation (3.3). Three models were fit where the exposure term  $(F_{ep})$  was either the host-rock exposure index  $(F_{ep\_El})$ , the immersion index  $(F_{ep\_Il})$ , or the Abrasion Height estimate, to investigate which parameter provides the best fit. These models provided promising results (Section 3.4.1) but an analysis of model residuals identified two potential problems in the nonlinear least squares analysis. First, we observed some strong correlation between parameter estimates, leading to potentially unstable model inference (i.e. overstated *p*-values). Second, the residuals displayed non-constant variance (heteroscedasticity) in several models, which can also invalidate the resulting inference.

Non-constant variance can result from multiple sources, although this can often (although not always) be attributed to 1) a multiplicative error structure in the observed data (i.e. errors increase rapidly with the estimate of the dependent variable), 2) unmeasured covariates, and/or 3) correlation within groups of observations. These three sources are discussed below.

First, a multiplicative error structure is typical in this type of data (Schweizer, 2007 and Table 3.2). Nonlinear regression models have a linear error structure. Alternatively, linear regression models using log transformed variables (equation (3.4b)) have a multiplicative error structure. Further, different error structures can be modelled using a special class of linear model (i.e. random effects models, described below) by specifying different variance-covariance matrices. Consequently, we used linear mixed effects models (described further below) to address this potential source of non-constant variance.

Second, our study was designed to minimize the influence of unmeasured covariates. However, we were concerned with level of achievable accuracy of the average saltation height (equation (3.9)) considering it had not been applied to coarse gravel beds before. Thus we also included the abrasion height estimate (equation (3.10)) as a covariate in our statistical models because equation (3.10) more accurately predicted measured paint abrasion heights than the average saltation height estimate (equation

(3.9)) over a narrow range of abrasion height data (n = 20). The abrasion height estimate also performed better over a wider range of abrasion height data (n = 56), explaining 65% of the variance in abrasion height data.

Third, our data was prone to correlation within groups of observations. The transect style sampling design creates two potential sources of dependence amongst observations. One type of dependence is correlation in the model errors (i.e. residuals) within riffle cross sections compared to between cross sections. The other source of dependence is at the observation level, that observations located more closely to each other within the cross section may have correlated errors.

We used a class of linear mixed effects models (Verbeke and Molenberghs, 2000), which allow us to try to compensate for the degree of correlation between cross sections, while properly leveraging the number of replications within cross sections. We compared three different classes of models, described in order of increasing complexity. The first class of model is standard multiple regression model (LM) which assumes that after controlling for fixed effects there is no additional correlation within cross sections, either due to cross section related heterogeneity of variance or due to spatial correlation. The second class of model accounts for between cross section heterogeneity of variance in error terms (i.e. assumes that unexplained model deviations will be more similar within a cross section than between cross sections). For the second class of models, we used two types of additional spatial correlation functions to model within cross section model error, linear (Random Effects Linear - Re\_L) and Gaussian decay (Re\_G) in spatial correlation as a function of within cross section distance.

We tested various permutations of PSAM equation (3.4), selectively adding conditioning velocity, peak spate shear stress and abrasion height estimates (Section 3.4.2) as covariates. The conceptual framework for this analysis is shown in Figure 3.6. A variety of information criteria were used to choose which predictors are retained in our linear, mixed effects regression models. The Bayesian Information Criteria (BIC) and Akaike Information Criteria (AIC) in particular were emphasized, as they contrast two different modelling objectives. The BIC attempts to optimize over correct covariate selection (Schwarz, 1978), whereas the AIC tries to maximize the predictive ability of the model (Akaike, 1973). In general, we have tried to find the statistical models that optimize one (or both criteria), although we focused our search on models that were scientifically reasonable. We also present the standard  $R^2$  statistics and hypothesis testing *p*-values for individual coefficients in our selected models, to aid in the interpretation of our results. Of the PSAM regression models selected by these criteria, we present the most appropriate type of linear mixed effects model (i.e. LM, Re\_L, Re\_G) to adequately address potential sources of unstable model inference.



**Figure 3.6** Conceptual framework for periphyton growth (left side) and removal (right side), showing PSAM model components (i.e. dark boxes) and primary hypotheses.

**Threshold Analysis.** We hypothesized that a threshold sand transport rate that divides imperceptibly low transport from high transport, would also divide patches of bed with high periphyton biomass, from patches of bed with low biomass, respectively. The sand transport rate at each trap was made nondimensional ( $W_{sa}^*$ ) using the method in Wilcock and Kenworthy, (2002) and the complete 2004 dataset (i.e. including sand transport cases < 100 g m<sup>-1</sup> event<sup>-1</sup>). The time average fractional transport rate for 0.5-2mm sand ( $qb_{sa}$ ) was calculated based on the elapsed time the traps were open (25 days). The local fraction of 0.5- 2 mm sand within the bed surface was measured using McNeil

scoop sample. The shear velocity was calculated from the trap-local shear stress at the peak of the 24 August 2004 event. We superimposed the threshold transport rate on a plot of the average biomass versus the median  $W_{sa}^*$ .

#### **3.4 Results**

Of the 1500 host-rock sample locations we monitored in the active channel, only 74% were submerged in the baseflow channel at both periphyton sampling occasions. Periphyton was only sampled on host-rocks in this wetted zone. Within this sample of wetted host-rocks, coupled measurements of sand transport rate and periphyton biomass were available for 82% of the rocks. These data were used to test our third hypothesis (i.e. the threshold analysis, Section 3.3.4). Twenty percent of these data (n=183) had sand transport rates greater than 100 g<sup>-1</sup>m<sup>-1</sup>event<sup>-1</sup>, and were used to evaluate the PSAM related hypotheses (Figure 3.6, Sections 3.3.1 to 3.3.3). For this subsample of data, the variables used in the regression analyses are summarized in Table 3.3. We eliminated cases with extremely low event sand transport rates (< 100 g m<sup>-1</sup> event<sup>-1</sup>), on the basis that the relationship between sand transport and periphyton biomass is nonlinear in this low range, and likely subject to more noise from unmeasured variables related to the periphyton accrual process. The goal of our analysis is to determine how well PSAM variables predict post-spate biomass on individual host-rocks using field data, therby providing evidence for the general hypothesis that saltation abrasion is a significant process during small spates, where sand is transported over a coarse, stable bed. We summarize the results of our statistical analyses in Table 3.4 (nonlinear PSAM models, equation (3.3)) and Table 3.5 (linear PSAM models, equation (3.4)).

#### **3.4.1 Nonlinear Models**

Nonlinear models were fitted for sand transport conditions exceeding 100 g m<sup>-1</sup> event<sup>-1</sup> (Table 3.4). The models included post-spate biomass, conditioning velocity, sand transport rate and either the exposure index (Model 1a), immersion index (Model 1b) or abrasion height estimate (Model 1c). The nonlinear model that included the immersion index (1b) provided the best fit, explaining 59% of the variance (Table 3.4, Model 1b):

Rock Scale Variables	Min.	25%ile	50%ile	Mean	75%ile	Max.	Transfor- mation***
Biomass <sub>Post</sub> (mg chla/m <sup>2</sup> )*	0.23	0.23	0.52	3.53	3.72	41.3	Log
Biomass <sub>Pre</sub> (mg chla/m <sup>2</sup> )*	0.23	0.23	0.23	2.01	0.52	41.3	Log
Conditioning Velocity (m/s)	0.04	0.38	0.54	0.54	0.66	0.93	SQRT
Sand Transport (g m <sup>-1</sup> event <sup>-1</sup> )	101	280.1	948.9	1148	1839	3090	Log
Peak Shear Stress (Pa)	2.34	4.51	6.8	9.12	12.33	28.01	SQRT
Immersion Index (dim)	0.51	0.57	0.64	0.71	0.77	1.46	Log
Exposure Index (dim)	0.19	0.94	1.93	2.52	2.99	14.88	Log
Abrasion Height estimate for sand (m)	0.01	0.03	0.03	0.03	0.04	0.06	None

**Table 3.3** Summary of variables used in the linear and nonlinear statistical models and abrasion height calibration model.

Variables used in the calculation of cover effect indices and abrasion height estimate.

Protrusion Height (m)**	0.02	0.03	0.04	0.05	0.06	0.51	Log
Suspension Criterion for 1 mm Sand (dim)	0.37	0.51	0.63	0.7	0.85	1.28	None
Froude Number (dim)	0.02	0.2	0.26	0.25	0.3	0.47	None
Fraction Sand on Bed	0.12	0.19	0.23	0.23	0.26	0.42	None
Reference Stress for 2 mm Sand (Pa)	2.18	2.5	3.21	3.59	4.24	11.75	None
Dimensionless Reference Stress for 2 mm Sand	0.07	0.08	0.1	0.11	0.13	0.36	None

n = 183 (i.e. 20% of the periphyton covered riverbed), \* - Biomass increased between PB<sub>T1</sub> and PB<sub>T2</sub> as time since last bed moving spate increased (See section 3.5.1), \*\* Negative protrusion heights were found on 2.8% of the total sample of host-rocks (n = 1500) and none of the host-rocks in this subsample (n = 183). \*\*\* Transformations for LME models and not nonlinear regressions.

$$PB_{T2} = PB_{T1} + V_{water}^{-0.784} I_{r \ sand \ t}^{-0.202} Immersion \ Index^{-0.396}$$
(3.11)

Unlike in equation (3.3), pre-spate biomass is added to the term that includes water velocity, sand transport rate and immersion index in equation (3.11). The positive sign of this three variable term indicates that a very small net increase in biomass occurred during the 25 day period in between pre- and post- periphyton sampling occasions (Table 3.3). As predicted (equation (3.3), Figure 3.6), the amount of additional biomass decreased with conditioning velocity, sand transport rate and degree of immersion of the host-rock in the saltating stream.

In model 1b, the coefficients for velocity and the immersion index both had 95% confidence intervals that did not include 0, indicating a statistically significant contribution to the nonlinear model. However, the confidence interval for the sand transport coefficient slightly exceeded zero. Error diagnostic analysis showed two potential problems with Model 1b. First, we noticed a large degree of correlation between the sand transport and immersion index parameters (Pearsons correlation coefficient = 0.77). Second, there seemed to be highly non-constant variance in the residuals when plotted against predicted values. Since residuals did not appear to be randomly distributed and clustered by cross section, we used linear mixed effects models (Sections 3.3.4, 3.4.2) in order to further investigate the effect of sand transport rate.

#### **3.4.2 Linear Mixed Effects Models**

The nonlinear models in section 3.4.1 and the linear mixed effects models presented here are linked because a logarithmic transformation of nonlinear equation yields a linear model in the logarithms of the predictor and response variables (cf. equations (3.3) and (4b)). This principle allows us to use two types of linear models, both with fixed (independent variables in PSAM models) and random (grouping variable, e.g. cross section) effects to further test model assumption violations from the nonlinear model. The measured velocity values were in a range such that the square root transformation and the log transformation of the two variables yielded almost identical results. Because of this similarity, we felt justified in presenting the results (Table 3.5)

**Table 3.4** Nonlinear regression model  $PB_{T2} = PB_{T1} - V_{water}^{\beta 2} I_{r\_sand\_t}^{\beta 3} F_{ep}^{\beta 4} + e$  (eq. (3.3)) where  $V_{water}$  is conditioning velocity,  $I_{r\_and\_t}$  is sand transport rate, and  $F_{ep}$  is either the exposure index (*EI*, i.e. eq. (3.7)), immersion index (*II*, i.e. eq. (3.8)), or abrasion height estimate (*AH*, m, i.e. eq. (3.10)). For variable units see Table 3.3 and note that variables were not transformed.

Model	Model	p <sup>2</sup>	Conditioning	Sand	Exposur	o Indicos	Abrasion Height	
	Туре	ň	velocity	transport	Exposur	emaices		
			(β <sub>2</sub> )	(β <sub>3</sub> )	(β <sub>4EI</sub> )	(β <sub>411</sub> )	(β <sub>4AH</sub> )	
1a	Nonlin.	No				х	х	
		model						
1b	Nonlin.	0.59	-0.784	-0.202	Х	-0.396	Х	
1c	Nonlin.	0.46	6.864	-5.152	Х	Х	-8.107	

 $R^2$  is adjusted. Coefficients are not standardized. The "X" indicates that the predictor was not included in equation (3.3) for that regression run. The "—" indicates that no parameter estimates are available because the model could not converge.

for the linear regression using a square root transformation for velocity because of the presence of zero velocity values

(i.e. 
$$\log PB_{T2} = \alpha + \beta_1 \log PB_{T1} - \beta_2 \sqrt{V_{water}} - \beta_3 \log I_{r\_sand\_t} - \beta_4 \log F_{ep} + e^*$$
).

In model 2a (Table 3.5), we are testing if the same variables contained in our best nonlinear model (1b) remain significant after accounting for random effects. The standardized beta values shown in Table 3.5 are an indication of the variables relative contribution to the model. After subjecting the initial model 2a ( $PB_{T2} = \alpha + \beta_1 PB_{T1} + \beta_2 V_{water} + \beta_3 I_{r_{sand_t}} + \beta_4 F_{ep_{11}} + \beta_6 \tau_{spate_{peak}} + e^*$ ) to our model selection criteria (e.g AIC, BIC), both the immersion index and peak spate shear stress were not retained in our best model (i.e.  $PB_{T2} = \alpha + 0.26PB_{T1} - 0.43V_{water} - 0.21I_{r\_sand\_t} + e^*$ , Table 3.5). As observed in the nonlinear model, pre-spate biomass had a significant positive effect on post-spate biomass. Again, both the conditioning velocity and the local sand transport rate had highly significant, negative effects on post-spate biomass, as anticipated through our model development. The standard linear model (LM) could not be used to represent Model 2a because the random effects were significant (RE-G) indicating that there was significant correlation of model errors related to both cross sections membership and close proximity of sampled rocks within cross sections (i.e. Gaussian vs. Linear spatial correlation).

In model 2b, the exposure index was added to the initial model 2a. Note that the best model 2b (i.e.  $PB_{T2} = \alpha + 0.24PB_{T1} - 0.43V_{water} - 0.21I_{r\_sand\_t} - 0.13F_{ep\_EI} + e^*$ , Table 3.5) is very similar to model 2a in terms of parameter estimates and amount of explained variance but the exposure index is a significant predictor of biomass. An increase in exposure decreased the post-spate biomass, as predicted by PSAM theory. Again, the immersion index was not retained in the best model 2b, and a random effects model (RE-G) was required to avoid overstating the significance of parameter estimates.

**Table 3.5** Best linear mixed effects models selected using AIC, BIC selection criteria. The beta values correspond to:  $PB_{T2} = \alpha + \beta_1 PB_{T1} + \beta_2 V_{water} + \beta_3 I_{r\_sand\_t} + \beta_4 F_{ep} + \beta_5 AH + \beta_6 \tau_{spate\_peak} + e^*$  (eq. (3.4) base); where,  $PB_{T2}$  and  $PB_{T1}$  are post- and prespate biomass respectively,  $V_{water}$  is conditioning velocity,  $I_{r\_sand\_t}$  is sand transport rate, and  $F_{ep}$  is either the exposure index ( $F_{ep\_EI}$ , i.e. eq. (3.7)), immersion index ( $F_{ep\_II}$ , i.e. eq. (3.8)). If random effects were significant (e.g. model errors are not independent of the cross section from which they were sampled), and some spatial correlation of predictor variables exists between adjacent rocks sampled within each cross section, then a random effects model with a Gaussian spatial correlation function (RE-G) is reported (i.e. 2a, 2b). If the assumption of multivariate normality and independence of observations were met, then a standard multiple linear regression is the appropriate type of model (LM, Model 2c).

Model	Model	R <sup>2</sup>	Pre-spate	Cond.	Sand	Immer-	Exposure	Abrasion	Peak
	Туре		biomass	velocity	transport	sion	Index	Height	spate
						Index			shear
									stress
		<u>.</u>	$(\beta_1)$	(β <sub>2</sub> )	(β <sub>3</sub> )	$(\beta_{4II})$	$(\beta_{4EI})$	(β <sub>5</sub> )	(β <sub>6</sub> )
2a	RE-G	0.50	0.26 ***	-0.43***	-0.21**	ni	х	Х	ni
2b	RE-G	0.51	0.24***	-0.43***	-0.21**	ni	-0.13**	х	ni
2c	LM	0.56	0.36***	ni	-0.22***	-0.14*	-0.16**	-0.41***	ni

Beta values are standardized and  $R^2$  is adjusted. 'X' indicates that the variable was not entered as a predictor in the expanded model; 'ni' indicates that the predictor did not withstand the scrutiny of our model selection criteria (see section 3.3.4) and was not retained in the best model, \*p<0.05; \*\*p<0.01; \*\*\* p<0.001

The best linear model (2c) according to the AIC and BIC criteria included the abrasion height estimate (i.e. estimate of height of abraded paint, equation (3.10)) and both the immersion index (i.e. average saltation height/host rock proturstion height) and the exposure index. Model 2c explained the most variance ( $R^2_{adj} = 0.56$ ) in the post-spate biomass of the three linear models but not as much as the more parsimonious nonlinear model (1b). In both the linear and nonlinear models the sand transport rate and the exposure term(s) of PSAM (i.e. $F_{ep}$ ) were significant predictors of post-spate biomass. Despite preconceptions that there may be allot of cross correlation between  $F_{ep\_El}$ ,  $F_{ep\_Il}$  and AH, all three variables have significant independent effects on post-spate biomass.

In all models in Table 3.5, the sand transport rate consistently and significantly predicts post-spate biomass on individual host-rocks. Increased sand transport intensity was associated with decreased biomass, even in the presence of other predictors. For example, in models 2a, b, and c of Table 3.5, the *p*-values for the sand transport coefficients were 0.002, 0.002, and 0.00004, respectively. We also note that after controlling for sand transport by its inclusion in models 2b, c, we do not see a significant negative effect of shear stress (i.e. not included in models 2b, c), but the effect of higher conditioning velocity persists.

One potential source of non-constant variance is the omission of a covariate (e.g. immersion index,  $F_{ep\_II}$ ) that represents an important aspect of the process being modeled (e.g. the cover effect). Since the predictive power of  $F_{ep\_II}$  in PSAM depends in part on how accurately the saltation height is measured (here estimated using  $Hs_{Sklar and Dietrich}$ , equation (3.9)), large measurement errors in Hs<sub>Sklar and Dietrich</sub> could have similar negative statistical effects to entirely excluding this cover effect variable from the PSAM model. The introduction of a more accurate estimate of saltation height, such as the abrasion height estimate (*AH*, equation (3.10)), into the PSAM model (e.g. model run 2c) should ensure that the immersion index cover effect is more adequately represented in PSAM, and should promote constant variance in model residuals. The inclusion of the *AH* in model 2c (Table 3.5, 2c) eliminated both significant between cross section heterogeneity, and significant within cross section spatial correlation. Consequently PSAM could be

modeled using a standard multiple regression model (LM) in model run 2c because no statistical assumptions were violated for this simpler type of model. In the presence of abrasion height, the exposure index (p=0.008) and the immersion index (p=0.02) are still statistically significant, however, these two indices provided relatively little additional explanatory power (increasing the percentage of variability explained by the model by less than 2% (from 54% to 56%, not shown on Table 3.5)). Together, the three cover effect related variables explain 6% (from 50% to 56%, Table 3.5) of the unique variance in post-spate biomass.

#### 3.4.3 Comparing the nonlinear and linear regression results

We compared the predicted values from the nonlinear and linear regression models, in particular, model 1b from Table 3.4 and 2c from Table 3.5. The correlation between the two sets of predicted values was quite high ( $R^2_{adj} = 0.94$ , p < 0.001), and the two models yield similar predicted post-spate biomass values. There was less agreement between fitted values for large values of post-spate biomass, likely due to the fact that the linear mixed model can produce a better fit than the nonlinear model for these high biomass values. Regardless, the percentage variance explained by the two models differed by only 3%. Thus, the linear mixed model results support the significance of the results of section 3.4.1, in spite of the potential problems encountered when diagnosing the nonlinear model. The main difference between these two models (1b and 2c) is that the significance and contribution of cover effect variables (Immersion Index, Exposure Index, Abrasion Height) are more conservatively stated in the more statistically robust model 2c.

#### **3.4.4 Sand transport threshold**

The preceding statistical analyses focused on data where the sand transport rate exceeded 100 g m<sup>-1</sup>event<sup>-1</sup>. In this section, all data from 2004 are examined, including rocks exposed to low transport rates (<100 g m<sup>-1</sup>event<sup>-1</sup>). Further, data are no longer at the rock scale but aggregated into patches consisting of measurements encompassing three rocks (Figure 3.7). Transport rates were made dimensionless (i.e. converted from g m<sup>-1</sup>event<sup>-1</sup> to  $W^*$  values, Wilcock and Kenworthy 2002). The threshold for the initiation



**Figure 3.7** The average  $\pm$  1SD periphyton biomass as a function of median dimensionless sand transport rate (W\*<sub>sa</sub>) for 307 patches of river bed consisting of three rocks each. The periphyton data was measured after a small spate (i.e. 0.6MAD) on the Sainte Marguerite river that occurred on the 24<sup>th</sup> August 2004. The transport rate is barely perceptible at W\*<sub>sa</sub> = 0.002 but increases rapidly within the gray shaded area.

of sand transport ( $W_r^*=0.002$ , Wilcock and Kenworthy 2002) clearly divided patches of bed with high average biomass, where transport rates were less than  $W_r^*$ , from patches of bed with low average biomass (mean chl*a* <10 mg/m<sup>2</sup>), particularly where the median dimensionless sand transport rates exceeded 0.02.

This threshold analysis used data aggregated at the patch scale, while the PSAM regression analyses (Sections 3.4.1, to 3.4.3) used chlorophyll *a* measured on top of individual rocks. Figure 3.8 shows how the variability in biomass (CV) increases with the spatial scale of data aggregation (e.g. patch, riffle, link) using regression analysis data (n = 183). The coefficient of variation in chlorophyll *a* was highest at the largest spatial scale, indicating that analyses using data aggregated at this large scale homogenize small scale variability in periphyton biomass. At any scale larger than the 1 m patch on scoured



**Figure 3.8** The coefficient of variation (CV) for periphyton chlorophyll *a* as a function of size of geomorphic unit over which data are averaged. The total sample (n = 183 rocks) was divided into 4 successively smaller geomorphic units and the average CV for each unit is shown. Periphyton biomass data that are averaged over many kilometres contain a high degree of smaller scale variability.

sections of the Sainte Marguerite River bed, the standard deviation of periphyton biomass exceeds the mean biomass value (CV > 1).

#### **3.5 Discussion**

We monitored periphyton disturbance after a series of very low-magnitude, highfrequency spates (largest spate = 0.6 Mean Annual Discharge, with a mean weekly recurrence period in summer) during which we measured substantial (but patchy) sand movement over a stable gravel-cobble bed. The biomass removal resulting from a spate of this magnitude was not expected to be dramatic (see Uehlinger et al., 1996) but these events recur at least 4 times more frequently than the time required for the periphyton community to reach peak biomass (30-120 days, Bouletreau et al., 2006) and are thus expected to strongly influence spatial patterns in summer biomass in this boreal river system. These disturbances may exert significant controls on trophic flows in these streams.

#### 3.5.1 How well does PSAM explain post-spate biomass?

Our best PSAM regression models explained 56-59% (adjusted) of the variance in post-spate periphyton biomass (Models 2c, 1b). The models are resolved at the individual host-rock scale, but consider conditions in the substrate patch within which the rock is situated. Various studies relating changes in periphyton biomass to physical variables (e.g. time since last spate, spate magnitude) have explained up to 63% (unadjusted) of the variance. However this was achieved by averaging this small scale heterogeneity in biomass over longer reaches (e.g. riffles – 2 km's, Figure 3.8) (e.g. Uehlinger et al., 1996, 2 km). Consequently, these previous studies did not focus on explaining the mechanisms governing rock and patch scale variability in the spatial distribution of periphyton biomass as we have done. On the Sainte Marguerite River, the hidden variability in periphyton biomass is 2 to 3 times higher when biomass estimates are aggregated over kilometer length reaches versus averaged over metre scale patches (Figure 3.8). On other rivers, longitudinal studies using larger scale data aggregation found that time since last bed moving "flood" (i.e. high-magnitude spate) was by far the most significant predictor of periphyton biomass, followed by water temperature and photosynthetically active radiation (PAR) over the last 14 days (Schweizer, 2007; Schuwirth et al., 2008). We have controlled for these variables as much as possible by: 1) sampling directly after a spate capable of causing a spike in turbidity, 2) sampling within two reaches of river where water temperature and nutrients are not significantly different (DIN and DRP,  $F_{(3,73)}$ , p >(0.05) during the summer, and 3) selecting reaches in which light is not limited by more than 60% tree canopy coverage.

Ideally, PSAM should be tested with periphyton measurements taken immediately before  $(PB_{T1})$  and after  $(PB_{T2})$  a spate disturbance to accurately quantify losses during the spate. Having such measurements would permit the loss term in equations (3.2) and (3.3) to be regressed directly with periphyton losses  $(PB_{T1} - PB_{T2})$ . While we have used the terms pre- and post-spate biomass in our PSAM regression models, it is more appropriate to use the terms pre- and post- "spate period" because a series of small spates occurred between the two periphyton sampling dates (Figure 3.5). Consequently, the amount of biomass lost during any one spate could not be quantified with certainty, and

our PSAM model results characterize the effects of a series of small spates of similar magnitude. It was only possible to measure high biomass accumulation over the 25 day monitoring period on rocks subject to low sand transport rates ( $W^* < 0.02$ , Figure 3.7). Where sand transport rates were relatively high (i.e.  $Q_{sa} > 100$  g m<sup>-1</sup>event<sup>-1</sup>, Tables 3.3), a minor increase in biomass occurred. We suspect this increase in biomass is due to an increase in time since last large, bed moving spate as observed elsewhere (Schweizer, 2007). Our first periphyton sampling occurred 56 days after the last major spring discharge peak ( $Q_{max}$  c. 27 m<sup>3</sup>/s), a discharge large enough to cause extensive periphyton removal over large areas of bed, based on our observations of a spate of similar magnitude in 2003. Our second sampling was commenced 76 days after this large spring spate, and thus some biomass accumulation was to be expected between sampling occasions. As hypothesized however, PSAM regression models indicate biomass accumulation in these high sand transport zones was limited by high velocity during the growth period, as well as high sand transport rates (tool effect) and periphyton exposure (cover effect) during the low magnitude spate of 24 August 04 (Tables 3.4 and 3.5).

**Significance of the tool effect.** The tool effect was represented by the sand transport rate measurements. As hypothesized  $(H_{1_1})$  the tool effect on post-spate period biomass was strong, negative and significant (Table 3.5). These results were consistent between all tested models (Tables 3.4, 3.5). We found no evidence to suggest that the negative influence of sand transport on periphyton biomass was simply because sand transport co-varied with other physical disturbance variables for cases with sand transport rates > 100 g m<sup>-1</sup> event<sup>-1</sup> (Sections 3.4.1, 3.4.2). The sand transport rate was consistently a strong predictor of biomass in the presence of all other predictors (i.e. including spate peak shear stress) second only to pre-spate biomass (Tables 3.4, 3.5). Pre-spate biomass had a positive effect on post-spate biomass for the low biomass levels present on the Sainte Marguerite river. On other rivers where biomass levels are higher, a negative relationship between pre-spate biomass leads to higher periphyton losses during spates, because thicker mats protrude further into the flow field, making them more prone to sloughing. In thick periphyton mats, cells at the base of the mat tend to die off, making the mat more

susceptible to detachment. The cells die off because the amount of light and nutrients delivered to the base of the mat decreases as the mat thickness increases (Stevenson, 1996). On the Sainte Marguerite river, there were very few areas where mats were thick enough for light and nutrient limitation, so the negative effect of pre-spate biomass was not reflected in our models.

We focused on the process of periphyton abrasion by saltating 0.5-2 mm sand using direct measurements of sand transport during a spate period. Although not focusing on saltation abrasion effects, other studies have shown that the rate of transported sediments, ranging from silt/clay to gravel, cause periphyton losses in the field (Stokseth, 1994) and in the laboratory (Horner and Welch, 1981; Francoeur and Biggs, 2006; Horner et al., 1990b). Stokseth (1994) measured periphyton losses from gravel bed load transport on the boulder bed of the Skona River, Norway, resulting from four large spates (i.e. 2.8-15 times mean annual discharge) but did not directly measure the transport rate as we have done. Rather, sediment transport rates were simulated using a computational model. Stokseth (1994) did find that the simulated rate of transported bedload (i.e. coarse sand and gravel) and water temperature were negatively related to post-spate biomass (n = 5spates,  $R_{Adi}^2 = 0.954$ ) on a system where 40% of the transported bed load was sand. Flume studies have shown that periphyton losses from suspended sediments increase with sediment concentration, even after accounting for the effect of flow velocity (Horner and Welch, 1981; Francoeur and Biggs, 2006; Horner et al., 1990b). Similarly, on the Sainte Marguerite river, saltating sand had a negative effect on periphyton biomass that was independent of sloughing effects from both the conditioning velocity and the shear force of water at the peak of the spate discharge (e.g. Tables 3.5, 2c).

Significance of cover effect variables. In our PSAM model, the cover effect in limiting abrasion was represented by the host-rock exposure index (equation (3.7)) and immersion index (equation (3.8)). As hypothesized  $(H_{1_2})$ , these cover effect variables were highly significant inverse predictors of post-spate biomass in our best models (e.g. Model 2c). However, cover effect variables explained less of the variance in periphyton biomass than expected (i.e. 6%), considering bedrock erosion study results. Specifically, Sklar and Dietrich (2006) found that the cover effect of alluvium overlying bedrock

explained more variance in observed bedrock erosion than the tool effect of saltating sediment. It is possible that this effect is less significant for periphyton than for alluvial transport over bedrock because the cover effect on periphyton is quickly exhausted during spates by the sheer number of sand grains bombarding substrates, even at low sand transport rates. However, we suspect that uncertainties associated with estimating how high sand saltates, and how these saltation heights relate to periphyton scour heights, inhibit a more rigorous assessment of the relative contribution and significance of cover effects within PSAM.

The immersion index was designed to indicate the extent to which the periphyton covered rock was submersed in saltating sand. The immersion index was a strong and significant negative predictor of post-spate biomass in our nonlinear model (1b). The residuals analysis of this nonlinear model suggested that the significance of the immersion index was overstated. However, the immersion index was significant in our random effects models (Models 2a & 2b) and linear model (Model 2c), and this significance was not overstated because all model assumptions were satisfied.

Our ability to test the significance of the immersion index is limited by how well the saltation height (equation (3.8), numerator) can be predicted. While the saltation height estimate method of Sklar and Dietrich (2002), equation (3.9) predicted measured abrasion heights reasonably well ( $R^2_{adj} = 0.73$ , Appendix A), inclusion of a more accurate ( $R^2_{adj} = 0.92$ , Appendix A) estimate of abrasion height (e.g. equation (3.10)) in PSAM improved the model fit (cf. Model 2b and 2c) and resulted in a random distribution of model residuals. Consequently, random effects models were no longer required to model PSAM and a simple multiple linear regression (LM) could be used without violating model assumptions.

The PSAM regression analyses confirmed our second, cover effect related hypothesis, yet the analysis did not provide clear direction regarding which exposure term best described the protective effect provided to periphyton by the bed structure. Rather, our results suggest that further study of both the immersion index and the exposure index is warranted. Experimentation is also required to further develop our understanding of how sand saltation height relates to the height periphyton is scoured from the rock. These studies may require the experimental control provided by flume-like conditions.

# **3.5.2** Does the threshold for motion of sand divide high periphyton biomass at low sand transport rates, from low biomass at high transport rates?

Our third hypothesis was clearly supported by our data. We have seen that the regression models fit to the subset of non-negligible sand transport data strongly indicate a negative effect of increasing transport on periphyton. Moreover, when all the spate data were considered, there was an abrupt, nonlinear reduction in periphyton biomass on rocks across the conventional nondimensional threshold for sand transport. Dimensionless sand transport rates between the threshold for sand movement ( $W^* = 0.002$ ) and that for relatively high rates of transport ( $W^* = 0.02$ ) occur with a very small change in shear stress (Wilcock and Kenworthy, 2002). This narrow range in dimensionless sand transport rates clearly divided rocks with high biomass at low transport rates, from rocks with low biomass and high transport rates. This evidence strongly suggests that periphyton was abraded by saltating sand during these small but frequent spate(s). To our knowledge, no comparable data exist.

#### 3.5.3 Model limitations, bias and confounding effects

Forty one percent of the variance in periphyton biomass was not explained in our best models. This variance can be attributed to measurement imprecision and unaccounted growth or disturbance factors. As stated previously, we have controlled for most of these factors as best we could under field conditions (Section 3.5.1). We did not control for biomass loss from grazing, which can be significant on some systems (Dudley and D'Antonio, 1991; Wohl and Carline, 1996). This is unlikely on the Sainte Marguerite River given the oligotrophic status and frequent spate cycle (Section 3.3.1).

Our biomass measurements did not account for periphyton found in the sheltered lee of substrates and they should be considered conservative estimates of the amount of post-disturbance biomass (see Francoeur and Biggs, 2006). Our shear stress estimates are based on bulk properties of flow because direct measurement at the surface of the
periphyton was not practically feasible. We propagated measurement errors in our shear stress estimates from slope, water level and velocity measurements, and these errors average 20% of the estimated shear stress. These values can increase dramatically if the water surface slope varied across the riffle but our selection of cross section location minimized this effect. Fortunately, our shear stress measurement error was smaller than the difference between the low threshold for sand transport and high reported shear stress diatom detachment thresholds (Biggs and Thomsen, 1995; Wilcock, 2004; Stone, 2005). The higher detachment threshold for periphyton relative to sand likely explains why peak spate shear stress was not included in our best models. This discrepancy in detachment thresholds implies that periphyton mat development may inhibit sand transport in a manner similar to silk producing insects (Statzner et al., 1999).

In other field studies, higher biomass has been associated with larger host-rocks because they are typically more stable (Tett et al., 1978; Meyers et al., 2007). Our data suggest that host-rock instability is not a prerequisite for periphyton removal. However, host-rock size is important, as it is closely related to how high the periphyton growth surface is elevated above the bed. We do not expect the positive effect of elevation off the bed to be indefinite as suggested by our models. The refuge potential provided by height of growth surface off the bed must diminish at some point because rocks protruding above the saltation layer are subject to the well documented abrasive effect of suspended sediment and sloughing induced by the shear force of water (Biggs and Thomsen, 1995; Stone, 2005; Francoeur and Biggs, 2006; Horner et al., 1990b).

Our analysis implies that the periphyton directly removed by the shear stress at the spate peak was not significant. This may understate the role of shear stress in periphyton abrasion because the distribution of shear stress in both space and time during the spate has a strong effect on sand transport intensity. Thus shear stress indirectly affects periphyton biomass through its influence on the intensity of substrate abrasion.

We used linear mixed effects models to address the statistical issues due to the non-random distribution and interdependent nature of model residuals but we could have used either nonlinear mixed effects models or structural equation models (i.e. path analysis). However, it was not clear in our case that the data would support such complicated approaches or yield more insightful conclusions. This is because our sample size is relatively small for these two procedures. Further, we had already thoroughly investigated sources of heterogeneity of variance and variable dependence in our dataset using the statistically robust linear random effects models.

#### **3.5.4 Broader Applicability**

Our results show that rock scale patterns in periphyton biomass can be described by the process of saltation abrasion on the Sainte Marguerite River. Thus biomass was controlled by the nonlinear relation between bed morphology, sand supply and flow strength captured by the sand and gravel transport model of Wilcock and Kenworthy (2002). This may partially explain why small scale periphyton biomass patterns have been so hard to predict elsewhere (Cattaneo et al., 1993; Uehlinger et al., 1996), because sand availability and transport measurements are typically not considered. It may also explain why no relation between substratum size and biomass has been found that can be generalized unconditionally (Tett et al., 1978; Fisher and Grimm, 1988; Francoeur et al., 1998). PSAM theory contends that periphyton biomass can increase with host-rock size if these rocks protrude above the saltation layer and provide refuge to periphyton. However, there may be no relation between post-spate biomass and host-rock size if all substrates are thoroughly scoured by saltating sand during high-magnitude spates. SAMB theory and laboratory tests suggests that the abrasive potential of saltating sand is greater than suspended sands because saltating sand grains have more direct and effective contact with the bed, relative to suspended sands (Sklar and Dietrich, 2001; 2004). This study provides some insight into the biotic effects of frequent streambed abrasion through sand saltation, to compliment our more developed understanding of the effects of shear stress and finer suspended sediments on periphyton biomass.

Our findings support the field study of Thomson et al. (2005) who suggested that saltation is a significant process for consideration when assessing periphyton removal from stable river beds. This work is a step toward resolving Uehlinger's (1991) call for a better means of predicting biomass losses from small events (e.g. < 2MAD) and our best model (1b, 2c) may be combined with tested models of accrual (See Stone, 2005;

Bouletreau et al., 2006) to heuristically study spatial and long term temporal trends in periphyton refuge within drainage basins under different climatic and instream modification regimes (see Uehlinger, 2000). The abrasive effects of saltating sand on periphyton losses may be beneficial at moderate levels but could conceivably reduce the food base supporting the food web of gravel bed streams, if the frequency of spate disturbance consistently truncates the growth cycle. Given the interconnected nature of saltating sand, suspended sediment transport and shear velocity of flow, we encourage conducting flume experiments to test the mechanistic form of PSAM using a range of particle sizes, algal communities and streambed architecture.

### **3.6 Conclusions**

A model of periphyton abrasion by saltating sand (PSAM) was developed from theoretical consideration of the sediment transport regime during sub-bankfull spates, a mechanistic model of bedrock abrasion by saltating sediment (Sklar and Dietrich, 2004), and theoretical consideration of periphyton ecology (Section 3.2.2). Our best PSAM model(s) explained 56% to 59% of the variance in periphyton biomass remaining on riffle substrate after a series of small spates (e.g. <0.6MAD, with a mean weekly recurrence period during the growing season, see Sections 3.3.1). The amount of variance in biomass explained by the PSAM model is similar to the variance explained by other studies predicting biomass from environmental conditions using data aggregated at larger spatial scales. However, our model was resolved at the scale at which periphyton abrasion occurs (i.e. rock scale) and did not average out small scale spatial heterogeneity over a large reach (e.g. planform scale) as other studies have done. The tool effect of the abrasion model was represented by sand transport rates during the spate period. This negative effect had a strong and significant contribution to the prediction of post-spatebiomass, independent of direct hydraulic effects (Section 3.4.2). We represented the cover effect of the abrasion model in part using an immersion index. This index indicated the extent to which the growth surface (i.e. top of the rock) was immersed within saltation layer (the layer next to the bed where sand moved by a hopping motion). The immersion index was also a significant PSAM model component (Section 3.4.2). This finding supported our hypothesis that the amount of shelter provided to periphyton from saltating

sand grains (i.e. refuge potential) increases with height above the stream bed (i.e. where the sediment concentration is lower). Our results imply that a change in spate frequency and sand supply, due to land use change or climate change, has the potential to (and may have already) dramatically alter the periphyton related stores of carbon, nitrogen and food for upper trophic levels within the Sainte Marguerite river. It is imperative to test the universality of PSAM to provide the tools required to better assess the impact of these long-term global environmental threats to our river systems. The once lucrative and world class sport fishery on the Sainte Marguerite river is currently near collapse, and the causes of this near extirpation of Atlantic salmon have yet to be discovered.

#### Context and connecting statement for chapter 4.

The PSAM theory developed in chapter 3 dictates that more post-spate periphyton biomass (i.e. refuge) are found on patches of bed that have low rates of sand transport, and on top of rocks where periphyton are sheltered from the abrasive effect of saltating sand. In chapter 4, I investigate what intensity of physical disturbance constitutes "shelter" for the periphyton of the Ste Marguerite river. I also investigate how spatial heterogeneity in the intensity of spate-related, physical disturbance affect the spatial distribution of periphton refuge across riffles.

Periphyton refugia have been investigated at very small scales (e.g. rock, patch) but few studies have examined the factors affecting biomass retention across riffles after spates. Flow refugia for stream benthos have been hypothesized to exist between the edge of the channel, which is subject to frequent wetting and drying, and the centre of the channel where high hydraulic stress and sediment mobility reduce biomass. This hypothesis has not been tested for periphyton and there are few periphyton studies reporting cross channel trends in biomass. From these studies, three lateral biomass patterns are apparent, of which only the two support for the flow refugia hypothesis at the riffle scale. High biomass is generally associated with either (presumably undisturbed) sand and silt in low velocity zones, or (presumably stable) gravel. If less periphyton is found on the surface of a host particle then it is generally assumed that that particle was mobile during the spate, yet supportive measurements of sediment transport are typically inexistant. The analysis presented in Chapter 4 attempts to explain the cross riffle patterns in periphyton biomass as a function of the abrasion of stable substrates by sand mobilized during frequent spates. In this study we contribute to the development of a unifying theory with respect to channel morphology, flow condition, disturbance thresholds, and periphyton refuge habitat across riffles.

The physical disturbance thresholds documented in this chapter were tested experimentally; the results are presented in chapter 5. While the focus here in chapter 4 is on across stream refuge, link scale periphyton refuge patterns are examined in chapter 6.

## Chapter 4

# Spatial patterns in periphyton biomass after low-magnitude flow spates: Geomorphic factors affecting patchiness across gravel cobble riffles

James J.W. Luce, Antonella Cattaneo and Michel F. Lapointe

## Abstract.

During small, frequent flow spates (i.e. order  $10^1$  day recurrence), the gravelcobble river bed is stable, but flows are often strong enough to transport large quantities of sand by a hopping motion called saltation. The effects of saltating sand on periphyton biomass are not well doccumented. Since small spates occur many times during the periphyton's growth period and sand mobilization on gravel-cobble beds can be patchy, saltating sand could strongly influence the spatial distribution of periphyton biomass. We tested the hypothesis, analogous to Jowett's (1999) hypothesis concerning macroinvertebrate biomass, that a spate-related refuge habitat exists in a transition zone located between the edge of the varial zone (i.e. zone of frequent wetting and drying), and the thalweg (i.e. deepest point) of the channel where high hydraulic stress and saltating sand reduce biomass. We studied an oligo-mesotrophic river in Quebec, documenting periphyton biomass across 15 riffles after 3 summer spate periods. Generalized linear models were used to examine cross-riffle trends in post-spate periphyton biomass, spate related sand transport and shear stress, and velocity during pre-spate growth. Our results indicate that sand transport patterns controlled the spatial distribution of periphyton biomass after a small spate (0.63MAD) with an average recurrence interval of 7 days. Low periphyton biomass ( $< 10 \text{ mg/m}^2$ ) was found where sand transport rates exceeded 64-180 g m<sup>-1</sup> event<sup>-1</sup>, peak shear stresses were greater than 15 Pa and average baseflow velocities were higher than 0.5 m/s. As observed elsewhere, no cross-riffle refuge was found after a higher magnitude spate (3MAD) when disturbance thresholds were exceeded across the entire riffle face. As hypothesized, the highest biomass found after small spates occurred in the transition zone. Biomass increased away from the thalweg as sand transport rates decreased. Biomass continued to increase towards the edge of this

zone unless disturbed by high rates of sand transport that were associated with a small secondary peak in sand transport rate.

## **4.1 Introduction**

The effects of large runoff events or "spates" capable of mobilizing the bed surface armour and removing up to 95% of periphyton standing stocks have been well documented on gravel-cobble bed rivers (Fisher and Grimm, 1988; Biggs and Close, 1989; 1991). These large spates reset the periphyton community and initiate a 30-120 day recovery period required to re-establish carrying capacity (Uehlinger et al., 1996; Bouletreau et al., 2006). The physical processes regulating periphyton biomass during smaller, more frequent spates (e.g. in this study 0.85Mean Annual Discharge, 0.85MAD), 4 spates on average per summer month) have received less attention. As these small, summer season spates can occur many times during the typically long recovery periods that separate periphyton resetting events (Weng et al., 2001; Biggs and Kilroy, 2007), their frequency and scour effectiveness may ultimately control peak summer periphyton biomass patterns.

During such small spates, the shear force of water is often too low to mobilize coarse bed material (e.g. gravel-cobble pavement) but high enough to entrain sand from the river bed (Wilcock and Kenworthy, 2002). Consequently, a high percentage of sediment movement during small spates (e.g. > 40 %, Lisle, 1989; Stokseth, 1994; Lisle, 1995; Wilcock et al., 1996) consists of sand moving over larger (e.g. gravel-cobble) and stable pavement rocks (Stokseth, 1994; Grams et al., 2006). Sand abrasion can cause significant periphyton losses (Culp et al., 1986; Francoeur and Biggs, 2006; Ch. 3) but little is known about abrasion thresholds or about spatial patterns of threshold exceedances; for example, how this disturbance is distributed across the stream bed during small spates. This knowledge is important because large, persistent refuge patches, deliver algal cells to disturbed patches of riverbed located further downstream to assist in the recolonization of these denuded surfaces. Thus the rate of recovery of biomass to pre-spate levels within rivers increases with the number, size and degree of connectivity of post-spate refuge patches (Dunning et al., 1992; Townsend et al., 1997).

Presumably, small spates result in less extensive periphyton removal and a patchy spatial distribution of biomass at the riffle scale.

Riffles can be divided transversely into 4 zones based on frequency of inundation and ecological function (Figure 4.1a). The shore zone is seasonally flooded but remains dry for most of the summer growth season (Rempel et al., 1999). A varial zone exists between the shore zone and the baseflow water's edge. In this zone, algae are periodically stressed by desiccation due to recurrent wetting and drying related to the frequent spates that occur during the summer (Jowett, 2003; Bouletreau et al., 2006). The thalweg zone is typically near the centre of the channel and characteristically has the highest flow depths and velocities. Observations of sediment transport indicate that the transport zone for coarse bed material is predominantly in the thalweg but expands and contracts with event magnitude (Gaeuman et al., 2005). The transition zone, intermediate between thalweg and varial zones, is characterized by reduced velocities. However, in channels with higher sand loadings, preferential lanes of sand transport can be observed along the edge of the transition zone (Powell et al., 1999; Bravo-Espinosa et al., 2003; Gran et al., 2006). Such sand rich marginal zones results from the effect of secondary, helicoidal circulation at high flows shifting saltating sands towards the innner convex sides of streambeds (Dietrich and Smith, 1984; Whiting and Dietrich, 1993).

A few studies have documented transverse patterns of periphyton biomass in streams (Tett et al., 1978; Fisher et al., 1982; Sand-Jensen, 1988; Rolland et al., 1997). Three patterns have been described (Figure 4.1b). In the first pattern (P1), biomass increases away from the thalweg to average depth then decreases (Tett et al., 1978; Sand-Jensen, 1988; Rolland et al., 1997). The second pattern (P2) is similar but biomass continues to increase from the thalweg to the inner edge of the varial zone (Tett et al., 1978; Fisher et al., 1982). A homogeneous cross channel distribution with low biomass has been observed after large spates (P3 –Low) (Tett et al., 1978; Sand-Jensen, 1988) or at high levels after extended stable flow periods (P3-High) (Fisher et al., 1982; Sand-Jensen, 1988). These lateral differences in biomass were related to the negative effect of flow velocity, positive effect of substrate stability and varying effect of particle size (Tett et al., 1978; Fisher et al., 1982; Rolland et al., 1997). Laterally diminishing flow strength



**Figure 4.1** a) Half-riffle bed profile from the thalweg to the bankfull channel edge showing water surfaces (W/S) at low, stable growth condition, during a frequent spate, and during an infrequent larger spate. b) Different patterns of periphyton biomass (P1-P3, discussed in text) across riffles reported in the literature (Tett et al., 1978; Fisher et al., 1982; Sand-Jensen, 1988; Rolland et al., 1997). c) Distribution of physical disturbance factors that may affect periphyton biomass according to the literature.

intuitively explains the P2 pattern but the mechanisms responsible for a near shore decrease in biomass (P1) remain unclear.

Jowett (2003) proposed that a macroinvertebrate refuge zone existed across the river in the transition zone between the thalweg and varial zone. Such a transition zone refuge hypothesis (TZRH) may also apply to periphyton. Jowett (2003) reasoned that most sediment transport and high velocities occurs in the thalweg zone so this zone would be a poor habitat. Further, unfavourable conditions would also occur in the varial zone due to stranding and desiccation stress. Thus, the best refuges should exist in a transition zone between the varial zone and thalweg where physical disturbance is minimal (Jowett, 2003).

The purpose of this study is to examine the physical disturbance mechanisms controlling cross channel patterns in periphyton biomass and test the extension of the TZRH hypothesis to periphyton.

### 4.2 Methods

## 4.2.1 Study site description and spate disturbance regime

The study sites were distributed along the boreal Sainte Marguerite River, which flows through deeply fractured granite and schist rocks of the Canadian Shield , Quebec, Canada (Figure 4.2, 48°26'56", 70°26'97"W). We monitored periphyton disturbance by summer spates in 2 reaches: Big Pool (BPR) and Meander (MR, Table 4.1). The watershed receives an average of 1.2 m of precipitation annually. Water chemistry in 2003 was typical of oligo-mesotrophic Canadian Shield rivers (Table 4.2). The widths of the 15 study riffles varied from 25.3 m to 48.0 m, and light levels over these riffles were not limited by riparian canopy cover.

Historical flow records from a close by gauging station were analyzed to characterize the flow regime of the river at the Big Pool reach. For the period 1976-2003, the mean annual discharge (MAD) was 9.6 m<sup>3</sup>/s. The spring flood peak on the Sainte Marguerite River is driven by snowmelt and typically occurs between late April and mid May. The 2 year return period flood is 83 m<sup>3</sup>/s at Big Pool. Periphyton biomass accumulates during July-September when base flows are generally low (e.g. 2.5 m<sup>3</sup>/s exceeded 90% of time annually) and relatively stable and over-bank events are rare.



**Figure 4.2** Location of the study reaches on the Ste. Marguerite River, Quebec, Canada. Sampling occurred on 15 riffles distributed between the Big Pool (9) and Meander reaches (6).

However, small and frequent spates do occur during this growth period. Flow records for the July-September (91 day) period for the years 1991-2003 were analyzed to characterize the magnitude and frequency of summer spates. Here we defined "spates" as any rapid increase in flow when the daily discharge is higher than the preceding and following day. The average peak discharge for the series of summer spates was 8.2 m<sup>3</sup>/s (i.e. 0.85MAD) but varied between 2.3 m<sup>3</sup>/s and 34.3 m<sup>3</sup>/s. There are frequent summer rain showers over the basin headwaters, and the number of days between these spates ranged from 5.7 to 8.3, averaging 7.1 days. The peak flows of these spates were between 1.1 and 7.8 (Mean = 1.65) times the average discharge of the 6 days preceding the event. The average baseflow between spates was 4.1 m<sup>3</sup>/s.

	Number of	Distand upstrea mouth	e am of	Drain - age basin area	Riffle water s @ base	e slope eflow	Mediar particle (D <sub>50</sub> )	n e size	Bankf width	ull	Base- flow depth	Bank- full depth
Reach	riffles	min (km)	max (km)	avg (km²)	min (m/m)	max (m/m)	Med (mm)	CV	avg (m)	SD (m)	avg (m)	avg (m)
Big Po	ol 9	59.67	61.09	233.5	0.0006	0.0056	53	1.75	34.5	7.8	0.44	1.31
Meano	ler 6	52.89	53.82	280.2	0.0004	0.0029	44	1.30	40.7	5.8	0.38	1.09

**Table 4.1** Summary of morphometric characteristics of monitored reaches.

**Table 4.2** Summary of water quality data for the 2003 summer season and medianvalues for typical Canadian Shield Rivers

Description	Ste. Marguerite R.	Typical Can. Shield
	Mean	Median
	(June – Sept. 2003)	Grenier et al. (2005)
Total Phosphorus (µg/L P)	32	17
Soluble phosphorus (µg/L P)	14	10
Total Nitrogen (μg/L N)	374	210
Nitrates-nitrites (µg/L N)	41	52
Ammonia (µg/L N)	23	20
рН	7.2	7.3
Conductivity (μS/cm)	26.2	38
Water Temperature (oC) <sup>1</sup>	16.3	0.2
<sup>1</sup> Average temperature at Big Pool logger	considering the entire 2003 and	2004 monitoring periods

## **4.2.2 Field procedures**

Data were collected in 2003 and 2004 during 3 sampling periods with variable spate sizes (0.6MAD to 3MAD). We measured peak spate shear stress and sand transport rates during sampling periods 1 and 3 and periphyton biomass at the end of all 3 periods (see Table 4.3). Velocity was measured during ambient stable flow conditions characteristic of the growth period (i.e. conditioning velocity). The first sampling period (SP1 in Table 4.3) was characterized by 3 major spates, the largest of which was 3MAD. A spate of this magnitude only occurred once in the previous twelve years considering

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Sampling Period	Period	Reach	Condition	ning Velocity	(m/s)	Peak S	c Spate stress (P	Shear a)	g m <sup>-1</sup> er	risport e /ent <sup>-1</sup> )	Periph	/ton Bio (mg/m <sup>2</sup>	mass )
			Mean±SD	Range	Sample Date	Mean	CV	Spate Peak	Mean	CV	Mean	CV**	Date Sampled
SP1 (5 spates	18/07/03	BPR	na*	na*	na*	23.2	0.5	17/08/03	1015	0.7	0.6	1.4	22/08/03
- large)	30/08/03	MR	na	na*	na*	na	па	па	па	na	na	Na	па
SP2 (2+	2/07/04	BPR	na*	na*	na*	9.2	0.8	1/07/04	na	na	3.8	2.1	2/08/04
spates - small)	2/08/04	MR	na*	na*	na*	5.4	0.7	1/07/04	na	na	4.2	2.2	2/08/04
SP3 (4 spates	2/08/04 to	BPR	0.45±0.4	0.01-0.93	18- 23/08/04	10.9	0.6	24/08/04	228	2.5	5.1	2.0	26/08/04
- small)	26/08/04	MR	0.34± 0.2	0.0-0.93	18- 23/08/04	5.7	0.7	24/08/04	538	1.6	6.7	1.8	26/08/04
BPR = Big F Reach. **No	ool Reach; ote that the C	MR = Mea 3V values	Inder Reach; na are relatively lov	<ul> <li>not available</li> <li>v due to our for</li> </ul>	; na*- Stage d cus on post sp	lata suggests : ate disturbanc	similar to	Period 3; n=4 s and use of th	06 in Big Poo e calibrated L	Reach (n=3 SEPA index	15 in 2003); to determine	n=349 in chla; w	Meander hich has
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daily discharge records for the summer period (July-Sept). The second and third sampling periods (SP2, SP3) were characterized by a series of small spates with an approximate weekly summertime recurrence period (Figure 4.3). The largest of these spates was only 0.63MAD but was associated with the largest increase in turbidity. Spates smaller than 0.63MAD were associated with very minor increases in turbidity. The most complete and detailed measurements of biomass and physical disturbance were collected during the third sampling period. Our analysis primarily focuses on SP3, while analysis of small events is supplemented with SP2 data. We will briefly present SP1 data to show how cross stream trends in biomass and physical disturbance variables are distributed during a low-frequency, high-magnitude summer spate.



**Figure 4.3** Stage and turbidity records at the Big Pool reach showing the sequence of spates relative to periphyton and sand trap data collection.

**Hydraulic conditions.** – A data logger monitoring station was installed in the middle of each of the 2 study reaches to measure average flow depth, temperature, and turbidity at 15 minute intervals, using pressure transducers (Druck<sup>™</sup>, Level Logger<sup>™</sup>), a copper constantan temperature sensors, and optical backscatter sensors (OBS<sup>™</sup>), respectively (Figure 4.3). Discharge rating curves were developed based on flow measurements covering the full range of wadeable flows. We also developed regression curves relating the stage at the data logger (Campbell Scientific<sup>™</sup> 21X) with the stage measured on a staff gauge at each riffle. These regressions were used to estimate flow depth at each cross section, for any stage measured at the closest permanent data logger station.

**Physical habitat.** – A topographic survey of a longitudinal profile and a transverse cross section at each successive riffle was conducted using a Wild 206 total station. Cross section study sites were one third of the channel width upstream of the crest of the riffle, to best approach steady uniform flow conditions at summer stages. Survey stakes were established at each end of each cross section. A measuring tape was affixed to these stakes for rapid location of positions on cross sections to permit georeferencing observations of velocity, shear stress, periphyton, and sand transport.

**Periphyton data.** – The width of river bed devoid of terrestrial plants (i.e. the "active channel") at each riffle cross section was divided into 100 equally spaced points and the stone beneath each point was selected without bias (Wolman, 1954). At each stone, we measured the b-axis and water depth using a ruler. Periphyton abundance was characterized on top of each rock using a rapid assessment technique proposed by the United States Environmental Protection Agency (USEPA, Stevenson and Bahls, 1999). The test involves an assessment of the thickness of the algal mat as a means to rank the relative biomass into 6 categories (Table 4.4). Each observation of abundance was the rank present on the top of the rock regardless of the extent of coverage.

The USEPA ranking system was calibrated to periphyton biomass as chlorophyll *a* (Chl*a*) using a minimum of 8 rocks in each rank (Table 4.4). Periphyton was removed

from a fixed area (20 cm<sup>2</sup>) on each rock using scalpel and brush. The algal suspension was filtered through 45 µm Whatman<sup>TM</sup> filters that were then kept frozen until analysis. We then extracted Chl*a* with 90% acetone for 24 h and read the extracts in a spectrometer according to standard methods (APHA, 1995). A significant difference (p < 0.05) existed between mean Chl*a* values associated with the different ranks, except for ranks 3 and 4 (Bonferroni ANOVA analysis; Table 4.4). Even though rank 4 had a visually thicker mat, Chl*a* was lower than for rank 3, suggesting that the mat was dying off.

**Table 4.4** Results of one way analysis of variance (ANOVA) testing differences in periphyton biomass among USEPA ranks. USEPA rank categories are based on algal appearance and thickness (see Table legend). Periphyton biomass values are based on chlorophyll *a* assays of periphyton removed from a small prescribed area of pure USEPA rank.

	Biomass –Chlorophyll <i>a</i> (mg/m <sup>2</sup> )	
Rank	average	SE
0	0.23*	0.04
0.5	0.52*	0.07
1	3.72*	0.63
2	8.13*	1.45
3	41.30*	5.05
4	29.58	3.41

 $2004 - F_{(5,87)} = 223, p < 0.001, R = 0.96, R^2 = 0.93; * p < 0.05$ 

USEPA (2000) rapid periphyton protocol for ranking abundance of microalgae: Rank 0 - Substrate rough with no visual evidence of microalgae; Rank 0.5 - Slightly slimy but no visual accumulation of microalgae is evident; Rank 1 - Slimy with visual accumulation evident; Rank 2 - Moderately slimy with accumulation layer from 1 mm to 5 mm thick; Rank 4 - Algae sloughs when wading in area or removing rock. Accumulation > 5mm thick.

Sediment traps. – At each riffle cross section, the active channel width was divided into 6 to 24 segments and a sediment trap was placed in the middle of each segment. The sediment trap consisted of a 1 litre plastic container filled with clean 19-36 mm gravel. This device trapped particles < 8 mm travelling along the bed. On each section, the traps were positioned 30 cm downstream of the periphyton sampling line and

installed flush with the bed. Traps were opened prior to the spates and covered within 48 hours following the event peak (Figure 4.3). All traps were opened or closed within a 3 h period to standardize transport times for a given spate. Trap contents were dried at 105 °C and sieved for 20 minutes to determine the mass of 0.5-2 mm sand. The cumulative event sand transport rate (g m<sup>-1</sup>event<sup>-1</sup>) was obtained from the total trap mass captured for that event divided by the width of the trap. Linear interpolation was used to estimate sand transport rates at rocks situated between sediment traps.

**Conditioning velocity.** – The conditioning velocity was measured at 91 trap locations (Table 4.3) only during sampling period 3 in stable baseflow conditions that occurred between periphyton surveys. Average velocities were based on 1.5 minute long readings (a Gurley No. 625D Pygmy meter) taken at 0.4 times the flow depth. Near bed velocities were measured 2 cm above the bed. Linear interpolation was again used to assign velocities to sampled rocks between sediment traps.

**Peak shear stress.** – Peak spate shear stress was estimated at each rock sampling location based on the DuBoys equation:

$$\tau_{DuBoys} = \rho g dS \tag{4.1}$$

where  $\rho$  is the density of water, *g* is the gravitational constant, *d* is the local water depth and *S* is the local water surface slope (Chang, 1988). This equation assumes, as a first approximation, relatively uniform flow (depth and velocity) over each rock and weak lateral velocity gradients. Water surface slopes over riffles were measured using a Sokkia<sup>TM</sup> B2C level during base flow conditions (Depth = 0.11 m) and spate conditions (Depth = 0.49-0.55 m). Linear regression (p < 0.05) of water surface elevation versus distance downstream was used to determine the water survace slope over riffle cross sections. The regression considered a distance of 3 bankfull channel widths, centered on each riffle. Water stage at each riffle cross section was estimated using models that related observed stage at each riffle cross-section, to stage at a pressure transducer in each reach. Spate peak water depths were estimated at each rock by subtracting the local elevation of the water surface at the spate peak from the local streambed elevation at the rock. Rock scale predictions of shear stress using the DuBoys equation tend to overestimate local shear stresses, especially when flow is nonuniform and hydraulically rough (e.g. Stone, 2005). Therefore, we compared the DuBoys estimates (equation (4.1)) with those based on the alternate local velocity profile method (Wilcock et al., 1996). In this approach, the peak shear stress was calculated separately for sites where flow was obstructed by upstream features (e.g. large boulders, woody debris) and for unobstructed sites. Based on these data, the DuBoys shear stress estimate was corrected for relative roughness (RR = rock b-axis/flow depth) and dimensionless distance from thalweg (DFT= distance of rock from the deepest part of the channel/active channel width). Shear stresses (square root) and bed roughness (log) were transformed to satisfy the assumption of normality. The corrected DuBoys shear stress estimates for unobstructed flow sites are given by:

$$\tau_{Unobs.} = 2.932 + 0.510\tau_{DuBoys} + 1.171RR - 2.432DFT$$
(4.2)  
$$(R^{2}_{adj} = 0.66 \text{ SE} = 0.22 \text{ Pa}, n = 50)$$

The corrected shear stress for the sites with upstream flow obstructions were given by:

$$\tau_{Obst.} = 0.577 + 0.385\tau_{DuBoys}$$
(4.3)  
$$(R^2_{adi} = 0.52 \text{ SE} = 0.13 \text{ Pa}, n = 41)$$

*Water quality* - Water chemistry was monitored weekly for 11 weeks, at BPR and downstream of MR, during the 2003 growing season. Laboratory analyses of nutrients (NO<sub>2</sub> NO<sub>3</sub>, NH<sub>4</sub>, TTN, TTP, PO<sub>4</sub>) were performed by the GEOTOP centre at the Université du Québec à Montréal. During sample collection, we measured pH and conductivity using a HANNA<sup>TM</sup> HI 98128 (±0.05 pH, ±0.5°C) probe and a HI 98311 (±2% f.s. EC, ±0.5°C) probe. The 15 minute mean stream temperatures were also recorded (Campbell Scientific 21X, copper-constantan probe) at BPR and MR for the periods 19 July to 2 September in 2003, and 28 July to 2 September in 2004.

#### 4.2.3 Data analysis

Using data from both reaches (BPR and MR) and focusing on period SP3, mean periphyton biomass was plotted against each physical disturbance variable (i.e. sand transport, peak spate shear stress and conditioning velocity) at the patch scale (i.e. all sampled rocks nearest a given sediment trap) using individual bivariate plots. The resulting distributions were examined visually for thresholds dividing harsh physical conditions with low periphyton biomass, from less intense physical conditions allowing high biomass to persist. We used Classification and Regression Tree analysis (CART) in SYSTAT (11.0/2005, Systat Software Inc., Richmond) to determine if a statistically sound threshold exists between low-disturbance, high-biomass patches of bed and high-disturbance, low-biomass patches. The dependent variable (*periphyton biomass*) and independent physical disturbance variables did not require transformation. We conducted a naïve bootstrapping (n = 1000) of the CART model to determine confidence limits around the statistically determined threshold.

Cross stream patterns in biomass and physical disturbance variables, the focus of this paper, were then examined in BPR and MR using SP3 data. To permit within reach comparisons between cross sections, the across channel distance was standardized by dividing the distance of rock from the thalweg by the total active channel width. Dimensionless distance data were grouped into 7 categories (< 0.1, 0.2, 0.3, 0.4 0.5, 0.6, > 0.6). For each reach, a Bonferroni 1-way ANOVA design and Generalized Linear Model (GLZ) was used to test for significant differences in periphyton biomass between the categories of dimensionless distance from the thalweg (Tabachnick and Fidell, 2001). This analysis was repeated for shear stress, sand transport, and velocity (11.0/2005, Systat Software Inc., Richmond).

A GLZ analysis of biomass during period SP2 was also conducted to supplement detailed insights from the small spate (i.e. SP3). A GLZ analysis of SP1 data summarized the effects of physical disturbance during the series of large spates on the distribution of periphyton.

#### 4.3 Results

### 4.3.1 Periphyton data and disturbance history

A wide range of biotic and abiotic conditions were monitored during the 3 sampling periods as shown previously in Tables 4.1 and 4.3 and in Figure 4.3. Periphyton biomass following a very large spate (3.0MAD) in sampling period 1 (SP1) was the lowest and and least variable of the 3 sampling periods (Table 4.3). Biomass was higher in SP2, 78 days after the largest spring spate peak (i.e. freshet) of 2004, and 31 days after a 0.6MAD spate. The highest biomass was measured during SP3, 102 days after the largest spring freshet and immediately after a 0.63MAD spate (24 August 2004).

A qualitative survey of algal taxa along the river was conducted prior to SP3. Diatoms were the most abundant class of algae and included *Tabellaria, Navicula, Gomphonema, Eunotia, Cymbella, Fragilaria, Pinnularia,* and *Synedra*. Chlorophytes included *Ulothrix, Draparnaldia, Desmidium, Closterium, Bulbachaete, and Tetraspora*. Colonies of the cyanobacterium *Nostoc* were commonly visible 2 weeks after floods on rock faces sheltered from the flow, with the more extensive coverage in shallows near the shore zones. Other cyanobacteria included *Gloeotrichia, Leptothrix, Calothrix, and Phormidium*. The only rhodophyte identified was *Hildebrandia*.

#### 4.3.2 Effects of velocity, sand transport rate and shear stress

To elucidate the cross-sectional patterns of periphyton resulting from gradients in disturbance variables, we first analyze evidence for threshold values for the effect on periphyton from each of these stressors. Periphyton biomass at the start of sampling period 3 (Figure 4.3b, i.e. early August 2004, end of SP2) was compared against velocities measured during the SP3 base flow period that preceded the 24<sup>th</sup> August 2004 spate. Velocity measurements are not concurrent with periphyton biomass sampling but the stage was similar during velocity and periphyton sampling periods. Thus, conditioning velocity measurements represent a stable flow period with weekly spates that have a peak discharge less than 0.63MAD. Figure 4.4a shows that very low periphyton biomass (i.e. < 5 mg chla/m<sup>2</sup>) was found on patches of stream bed exposed to

near bed velocities exceeding 0.25 m/s (Figure 4.4a) and average velocities exceeding 0.5 m/s (not shown in Figure 4.4). At near bed velocities less than 0.25 m/s, it was possible to find patches of bed with biomass as high as 41 mg  $chla/m^2$ . A near bed velocity of 0.3 m/s is a threshold value associated with the initiation of sand movement (Thompson and Amos, 2004).

The dominant size fractions in sediment traps in low level transport were 0.25-0.5 mm, 0.5-1 mm and 1-2 mm sand, in order of decreasing presence, within the broad clay to medium gravel (i.e. up to 16 mm) size range. For 0.5 to 2 mm sand, which is primarily transported by saltation, transport rates less than 180 m<sup>-1</sup>event<sup>-1</sup> (Figure 4.4b, SP3) were weakly related to periphyton biomass after the 24<sup>th</sup> August 2004 spate. It was possible to find patches of bed with up to 41 mg chl*a*/m<sup>2</sup> on these sheltered patches of streambed In contrast, the effect of sand transport rate on periphyton biomass above 180 g m<sup>-1</sup>event<sup>-1</sup> was negative. Stream bed patches that experienced sand transport rates exceeding 180 g m<sup>-1</sup>event<sup>-1</sup> had mean biomass values lower than 5 mg chl*a*/m<sup>2</sup>. Biomass was less than 2.5 mg chl*a*/m<sup>2</sup> at very high rates of transport (e.g. 3000 g m<sup>-1</sup>event<sup>-1</sup>). Patches of bed with periphyton biomass up to 41 mg chl*a*/m<sup>2</sup> were found where peak shear stresses during the 24<sup>th</sup> August 2004 spate were lower than 15 Pascals (Figure 4.4c). At shear stresses exceeding 15 Pa, periphyton biomass was only 15% to 20% as abundant.

The three stressor variables in Figure 4.4 are typically cross-correlated. To examine the nature of these correlations we performed a Bonferroni Pearson Correlation analysis between periphyton biomass (ln), bed velocity, sand transport rate (ln) and peak spate shear stress ( $\sqrt{}$ ). There was no significant positive correlation between the sand transport rate and peak spate shear stress (p=0.43). Significant correlations (p<0.001) were found among all other variable combinations but the strength of these relationships was relatively weak ( $R^2_{min} = 0.08$  to  $R^2_{max} = 0.24$ ). The disturbance variables were negatively correlated with periphyton biomass as expected. The sand transport rate was positively correlated with the bed velocity ( $p=6.7 \times 10^{-14}$ ,  $R^2 = 0.18$ ).



**Figure 4.4** a) Relationship between mean ( $\pm$ SD) periphyton biomass at the end of sampling period 2 (i.e. beginning of sampling period 3, SP3) and conditioning velocity measured at 2 cm above the bed. Each point represents a mean of three rocks directly associated with velocity measurement locations. b) Mean periphyton biomass ( $\pm$ SD, n = 3 rocks, adjacent to traps) following a series of small spates in SP3 as a function of b) mean ( $\pm$ SD) cumulative observed sand transport in local sediment trap, and of c) mean ( $\pm$ SD) peak spate local shear stress. The envelope curves define the maximum periphyton biomass for a given level of physical disturbance. Disturbance thresholds above each plot are approximate. The threshold for average velocity (0.51 m/s) is not shown.

While the threshold values associated with the envelope curves shown in Figures 4.4 a-c show a clear reduction in biomass on patches of bed exposed to disturbance values exceeding these threshold values, we conducted a more rigorous statistical assessment of these thresholds. A bootstrapped classification and regression tree (CART) analysis was conducted to more objectively define the disturbance values that divide (i.e. split values) patches of bed with high-biomass that were exposed to low-disturbance intensities, from patches of bed with low-biomass that were exposed to high-disturbance intensities. The bootstrapping analysis showed (Table 4.5) that the upper 90<sup>th</sup> percentile split values for all disturbance variables are similar to the envelope curve inspired thresholds shown in Figure 4.4 (e.g. 180 g m<sup>-1</sup>event<sup>-1</sup> in Figure 4.4 cf. 186 g m<sup>-1</sup>event<sup>-1</sup> in Table 4.5). The mean CART split values were lower than the envelope curve thresholds (e.g. 65 g m<sup>-1</sup>event<sup>-1</sup> Table 4.5 vs 180 g m<sup>-1</sup>event<sup>-1</sup> Figure 4.4b). CART split values were also found at very low disturbance levels (e.g. 6.5 g m<sup>-1</sup>event<sup>-1</sup>, Table 4.5) showing that biomass levels were negatively influenced by disturbance values that were much lower than the envelope inspired thresholds shown in Figure 4.4.

**Table 4.5** Bootstrapped (n = 1000) classification and regression tree (CART) analysis summary statistics of disturbance thresholds (first regression tree split) separating statistically different (p<0.05) populations of chlorophyll a. PRE is similar to  $R^2$ .

Disturbance Variable	Mean CART			$10^{th}$	90 <sup>th</sup>	PRE
	Split Value	SD	Median	<b>%</b> <sup>tile</sup>	<b>%</b> <sup>tile</sup>	±SD
Bed Velocity (m/s)	0.12	0.07	0.08	0.04	0.23	0.25±0.13
Mean Velocity (m/s)	0.29	0.14	0.31	0.08	0.51	0.24±0.13
Sand Transport (g m <sup>-1</sup> event <sup>-1</sup> )	65	144	133	6.5	186	0.24±0.13
Shear Stress (Pa)	7	4	5	3	14	0.22±0.12

### 4.3.3 Across reach patterns

The transition zone hypothesis dictates that biomass is lowest across a riffle in the thalweg were high disturbance levels exceed periphyton perturbation thresholds. During the smallest spates (SP3), there was a decrease in conditioning velocity (Figure 4.5a), sand transport rate (Figure 4.5b) and peak shear stress (Figure 4.5c) with distance from the thalweg in both BPR and MR. Of the 3 physical disturbance variables, only the sand transport threshold (64 to 180 g m<sup>-1</sup>s<sup>-1</sup>) was exceeded.

In the transition zone of both BPR and MR, the conditioning velocity (Figure 4.5a) and peak shear stress (Figure 4.5c) decreased shoreward and remained below threshold values (0.51 m/s, 15 Pa) for large reductions in biomass. The major difference in physical disturbance between reaches was that in BPR, sand transport rates exceeded 64 to 180 g m<sup>-1</sup>s<sup>-1</sup> at the shoreward edge of the transition zone (Figure 4.5b) whereas in MR, the shore edge was associated with below threshold average sand transport rates (Figure 4.5b) and coarser substrate (Figure 4.6).



**Figure 4.5** Generalized linear model results showing across riffle trends in the mean (± SE) a) conditioning velocity, b) sand transport rate, and c) peak shear stress c) as a function of the distance from the thalweg normalized by active channel width. Each plot shows separate trends for the Big Pool reach (BPR) and the Meander Reach (MR) for a small spate sampling period (SP3). Figures b and c also show the trends associated with the large spate sampling period (SP1). Horizontal "Threshold" lines indicate disturbance value above which only very low periphyton biomass exists (Figure 4.4). The horizontal grey bands illustrate Classification and Regression Tree (CART) analysis results (Table 4.5) as explained in the text.



**Figure 4.6** Generalized linear model results showing across riffle trends in the average (± SE) bed particle size as a function of the dimensionless distance from the thalweg. Separate trends are shown for the Big Pool reach (BPR) and the Meander Reach (MR).

In BPR during SP3, the mean substrate diameter increased shoreward in the transition zone (Figure 4.6). There was no positive relation between flow strength and particle size in this transition zone.

Periphyton biomass in BPR was highest in the centre of the transition zone (i.e. Figure 4.7a) where sand transport rates were lowest. This cross stream pattern in biomass was very similar during both SP2 and SP3. In the MR, biomass increased with distance from the thalweg, increasing sharply at the shoreward edge of the transition zone (Figure 4.7b). The spate disturbance levels were similar between SP2 and SP3. Therefore, we suppose that the cross stream distribution of physical disturbance variables may have been similar between the 2 periods but detailed measurements were only available for SP3.



**Figure 4.7** Generalized linear model results showing across riffle trends in the average (± SE) periphyton biomass (as Chl*a*) as a function of the distance from the thalweg normalized by active channel width for the a) Big Pool Reach (BPR) and b) Meander reach (MR). Trends were determined for periods SP2 and SP3 at both reaches and for SP1 only at BPR. Note the different scale for periphyton Chl*a* in a) and b). The line at 10 mg/m<sup>2</sup> is provided as reference.

The cross-stream distribution of biomass, after the strong spates in SP1 (i.e. 3.0MAD), was homogeneous and only averaged 0.6 mg chla/m<sup>2</sup> (Figure 4.7a, Table 4.3).

In the thalweg zone, the magnitude of both sand transport (Figure 4.5b) and shear stress (Figure 4.5c) exceeded established thresholds and decreased with distance from thalweg (Figures 4.4b, 4.4c). In the tranzition zone, the sand transport rate greatly exceeded 180 g m<sup>-1</sup>event<sup>-1</sup> but shear stress decreased below 7-15 Pa toward shore (Figures 4.5b, 4.5c). Surprisingly, the cross stream distribution of sand transport rates (Figure 4.5b) was bimodal as observed during small spates. Specifically, sand transport rates did not simply decrease shoreward with decreasing flow strength. Further, the larger peak was located near the shore and not in the thalweg. Periphyton biomass did decrease shoreward (Figure 4.7a) but did not vary significantly between distance categories.

### 4.4 Discussion

#### 4.4.1 Abiotic controls on periphyton biomass

Periphyton biomass was significantly lower where coarse sand was transported at rates exceeding 64 to 180 g m<sup>-1</sup> event<sup>-1</sup> (Figure 4.4b). This finding is novel because quantitative insight into the effects of abrasive sediments on periphyton loss had been mostly provided by flume studies examining the effects of suspended silt and sand (Francoeur and Biggs, 2006; Horner et al., 1990b). In a field study, Thomson et al. (2005) studied the responses of algal assemblages to the passage of a sediment slug that was released following a dam removal on Manatawny Creek, Pennsylvania. The authors found that the amount of sand on the bed surface increased from 1% to 15%, and this was associated with a 25% reduction in algal biomass and a 20% reduction in diatom species richness. Sand transport rates were not reported by Thomson et al. (2005), however, Wilcock and Kenworthy (2002) demonstrated that increasing the amount of sand on the bed from 1% to 15% reduces the threshold shear stress (i.e. critical shear stress) for sand movement by a factor of 3 (i.e. 5 Pa vs 15 Pa). This substantial reduction in critical shear stress for sand entrainment can cause very large increases in the sand transport rate. Thus, the potential to abrade periphyton by transported sand increases with the fraction of sand on the bed even with constant discharge conditions.

During natural spates, the amount of periphyton lost depends on a combination of stressor variables such as hydraulic plucking and abrasion, and pre-spate algal conditions such as strength of algal attachment to the substrate (Power and Stewart, 1987; Grimm and Fisher, 1989; Uehlinger et al., 1996). In this study, frequent sand abrasion appeared to be the predominant factor limiting the across riffle distribution of periphyton biomass. Shear stresses greater than 15 Pa were associated with a large reduction in biomass but this threshold was not exceeded over large areas of the bed during the small spates. Further, the detachment thresholds for tightly algae are higher than the thresholds for the initation of saltating sand (Biggs and Thomsen, 1995; Wilcock and Kenworthy, 2002; Stone, 2005). For example, a shear stress of 15 Pa is 3-4 times higher than the critical shear stress for sand on a cobble bed with 15% sand on the bed surface (Wilcock and Kenworthy, 2002). This shows that available sand can be actively transported at shear stresses between 3 Pa to 15 Pa. In a flume study, Biggs and Thomsen (1995) showed that a shear stress of 15 Pa was associated with a 20% to 23% loss (Chl a) in tightly attached algae (e.g. Fragelaria, Cymbella) and a 55% to 67% loss in weakly attached algae (e.g. Gomphonema, Ulothrix). In a similar study, Stone (2005) found a strong positive, linear relationship between the percent biomass (AFDM) lost from ceramic tiles and the shear stress (i.e. %Loss = 1.78Stress (Pa),  $R^2 = 0.99$ ). This relation dictates that at 15 Pa, periphyton biomass is reduced by 28%, in general agreement with the findings of Biggs and Thomsen (1995) for tightly attached algae. Other laboratory flume studies have shown that, in addition to the losses experienced by an increase in shear stress in sediment free water (e.g. 40% loss Chl a), further losses of periphyton biomass occur when fine sediments are suspended in the water (Horner et al., 1990a; Francoeur and Biggs, 2006). Horner et al. (1990a) found an additional 4% to 13% of biomass was lost through abrasion by suspended silt. Similarly, Francoeur and Biggs (2006) reported that suspended sands can cause up to a 40% reduction in biomass, which was independent of initial hydraulic detachment losses. While abrasion losses of periphyton by suspended sediments can be as high as 40%, engineering studies of clay and bedrock erosion have shown that the erosion by saltating sand exceeds that of suspended sand (Kamphuis, 1990; Sklar and Dietrich, 2004).

Periphyton losses were not measured on the Sainte Marguerite River, however, the average biomass was 71% lower on patches of bed with peak spate shear stress greater than 15 Pa, relative to patches of bed exposed to lower shear stresses (Figure 4.4c). The flume study results suggest that a 71% reduction in periphyton biomass could not result, soely from sloughing by shear stress for a tightly attached algal community; such as the diatom dominated periphyton community found on the Sainte Marguerite River. A 71% reduction in biomass would also require abrasion losses from suspended and saltating sands, and sloughing of the less abundant loosely attached algae at lower shear stresses (i.e. 4-10 Pa, Thomsen et al. (1999) as reflected in our 10<sup>th</sup> percentile split value of 6.5 Pa, Table 4.5).

## 4.4.2 Is the transition zone refuge hypothesis applicable to periphyton?

The distribution of periphyton biomass across 15 riffles after 2 sampling periods (SP2, SP3) subject to small spates (i.e. 0.63MAD, ~ weekly mean recurrence period) supported the Transition Zone Refuge Hypothesis (TZRH). Specifically, the highest biomass was found between the varial zone and the thalweg. The distribution of physical disturbance variables across riffles that was measured during the third sampling period (SP3) also supports the TZRH. Sand transport rate, peak spate shear stress and conditioning velocity decreased with distance from thalweg as predicted. Of the 3 physical disturbance variables we considered, only the sand transport rate exceeded a disturbance threshold in the thalweg zone. Sand transport was therefore the biomass limiting variable. In the transition zone (TZ), biomass increased shoreward, except where sand transport exceeded 64-180 g m<sup>-1</sup> event<sup>-1</sup>. In the Meander Reach (MR), biomass continually increased towards the edge of the transition zone (pattern P2, Figure 4.1) with laterally decreasing flow velocity and sediment mobility. In the Big Pool Reach (BPR), the bell shaped distribution of biomass in the transition zone (pattern P1, Figure 4.1) was associated with high levels (e.g. > 180 g m<sup>-1</sup> event<sup>-1</sup>) of sand transport at the shoreward edge of the zone.

The TZRH hypothesis was not supported by the laterally homogeneous pattern (P3 Low) of biomass observed after the large rare 2003 spate (Figure 4.7a). However,

our data do support the qualitative observation of other researchers who contend that during large spates, widespread and substantial reductions in periphyton standing crop are likely to occur by scour of immobile riffle rocks by transported sand (Fisher et al., 1982; Gregory et al., 1992; Goudie, 2006).

There are relatively few studies documenting transverse patterns of periphyton biomass (Tett et al., 1978; Fisher et al., 1982; Sand-Jensen, 1988; Rolland et al., 1997). Of the 10 cobble bed studies reported in the literature, 5 presented the bell shaped lateral pattern of periphyton biomass (e.g. P1 Figure 4.1), 3 had the laterally increasing P2 pattern, one showed the laterally homogeneous P3-Min pattern, and one the P3-Max pattern. The P2 pattern is thought to result because the fine substrates near the shore are less disturbed and the rate of recovery after spates is more rapid (Tett et al., 1978; Sand-Jensen, 1988). The P1 pattern was considered anomalous and associated with rapid velocities near the bank (Sand-Jensen, 1988). Low periphyton biomass was generally associated with high velocities and smaller substrates presumed to be more mobile (Tett et al., 1978; Fisher et al., 1982; Rolland et al., 1997). Our observations support the hypothesis proposed by Tett et al. (1978) that the highest biomass occurs at the edge of channel unless this area is disturbed. High intensity sand transport was the shoreward abiotic disturbance in the Sainte Marguerite river.

#### 4.4.3 The effects of geomorphic state on the availability of periphyton refuge

More biomass was retained on riffles with the P2 biomass pattern than riffles with the P1 pattern (Figure 4.7). The refuge potential associated with P1 pattern riffles was limited by the presence of a secondary peak in sand transport at the transition zone-varial zone boundary (Figure 4.5b). Therefore it is important to understand the factors that promote this secondary peak in sand transport, in order to predict how changes in channel form and sand supply may promote shifts between P2 and P1 response patterns. There are 3 factors which promote the paradoxical secondary peak in sand transport at the edge of the channel, despite the laterally decreasing flow energy: 1) Lines of preferential sand transport develop on the side of the channel where sand is supplied from a source (e.g. point bar, tributary) located directly upstream of the riffle (Powell et al., 1999; Gran et al., 2006); 2) Sand is laterally transferred from the thalweg towards the shore from secondary flow currents related to channel curvature and cross section asymmetry (Bridge and Jarvis, 1982; Dietrich and Smith, 1984); and 3) For a given shear stress, stationary sand grains on the riverbed are easier to move near the channel edge than in the thalweg. With distance from the thalweg, the fraction of sand on the bed increases (i.e. sand supply) and the median bed particle size decreases (i.e. increasing exposure to flow) (Ikeda, 1989; Lisle, 1989; Wilcock and Kenworthy, 2002). Consequently, sand grains are more exposed to flow and are more available for transport at the edge of the channel, relative to the thalweg. Considering these 3 sediment transport mechanisms, the shift from a P2 response pattern to a P1 response pattern in a river system is more likely, as sand supply, cross section asymmetry and channel sinuosity increase. These factors promote stronger secondary flow velocities and lateral sediment sorting.

#### **4.4.4 Study Assumptions and Limitations**

Our data strongly support the hypothesis that frequent trimming by sand transport was the main biomass limiting variable in field conditions on the Sainte Marguerite River. A Pearson correlation analysis showed that the effect of sand transport was independent of the effect of shear stress. At large spatial scales, other growth and disturbance factors could also limit periphyton biomass. However, in this study all sites were selected in close proximity to each other to limit differences in nutrients, light, and temperature. We found no significant differences (p < 0.05) in nutrients and temperature between reaches encompassing the study area during weekly sampling in July and August 2003 (Unpublished Data). Aquatic macroinvertebrate density data was not collected but substantial grazing is unlikely in zones where sand transport rates are high (Culp et al., 1986).

The GLZ analysis suggests that the P1 or P2 pattern can occur on either side of a riffle. However, riffle cross sections were generally asymmetrical (i.e. the thalweg was skewed towards one bank) and the P1 and P2 pattern was typically observed on the lower energy side of the channel (i.e. wide-shallow half vs narrow-deep half adjacent to the thalweg).

## 4.5 Conclusions

Our results show that periphyton refuge during summer spates exist where local sand transport rates are less than 64-180 g m<sup>-1</sup>event<sup>-1</sup> and where average base flow velocities were less than 0.29-0.51 m/s, a velocity range capable of transporting sand (Kamphuis, 1990). Low biomass was also associated with local peak spate shear stresses exceeding 7-15 Pa. The highest biomass was generally found in the sheltered zone between the thalweg and varial zone, on the low energy side of the channel.

Further studies now need to determine how broadly applicable our thresholds for algal disturbance are, and particularly to see how physiological stress and algal community composition affect detachment. Quantification of detachment thresholds for sand abrasion may permit more accurate assessments of food resource distribution for macroinvertebrates and fish within river systems. The effects of fine suspended sands have been studied in flume experiments (Francoeur and Biggs, 2006) We suggest replicating this type of experimental study for saltating sands because sand is in frequent contact with the bed at low velocities during this mode of transport (i.e. hopping).

Sand transport models have been developed and applied with success to predict sand fluxes in river systems (Wilcock and Kenworthy, 2002; Wilcock and Crowe, 2003; Salant et al., 2006b). Dynamic models that couple flow, sediment transport, periphyton detachment thresholds and growth processes provide a means to assess how changing hydrologic regime and sediment supply will affect periphyton in rivers (Stone, 2005; Bouletreau et al., 2006). These models are required to evaluate the resistance of periphyton communities to projected future increases in the volume and intensity of runoff, as well as in fine sediment loads through soil erosion, mass wasting, and channel adjustment (Gregory et al., 1992; Uehlinger, 2000; Goudie, 2006).

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#### Context and connecting statement for chapter 5.

Saltation is a mode of sediment transport by which sand particles move downstream with a near-bed hopping motion. Quantitative studies and a mechanistic understanding of this important mechanism of streambed periphyton abrasion are lacking. In anthropogenically disturbed watersheds, an increase in the streambed sand fraction has been shown to reduce the biomass of benthic alga and macroinvertebrates by abrading their relatively static host-rocks (Thomson et al., 2005). The results presented in Chapters 3 and 4 showed how periphyton biomass in the Boreal Sainte Marguerite River was increasingly limited with increasing sand transport rates, above a threshold rate of 64-180 g m<sup>-1</sup>event<sup>-1</sup>. In Chapter 3 the immersion index of PSAM was a significant predictor of post-spate biomass in a model also containing sand flux, indicating that rocks protruding above the saltation layer are protected from sand abrasion. In the observational studies in Ch3 and Ch4, biomass losses could not be reliably quantified and confounding effects, such as sloughing from high shear stresses, had to be isolated statistically. In this chapter I experimentally examine how periphyton losses from the abrasion of transported sand are affected by sand concentration, height of periphyton above the bed, and size of sand in transport, under near constant shear stress conditions. Empirical quantitative models of these effects are presented. The approach involved exposing periphyton-covered rocks to a suite of sand sizes and transport rates on a test patch of the bed of the Ste. Marguerite River, Québec during a period of stable flow.

# Chapter 5

# A field experiment investigating how the height of the growth surface and the size of saltating sands affect the abrasion of stream bed periphyton

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## Abstract

The benthic algae contained within periphyton, the slimy biofilm covering rocks on the bed of rivers, are at the base of the food chain, sustaining organisms at higher trophic levels. The influence of large spates capable of moving large bed material on periphyton losses is well documented and researchers have also focused on the mechanisms of sloughing by hydraulic shear and abrasion by suspended sediment. Recently, the important role of saltating sand in abrading substrates during frequent, lowmagnitude spates has been recognized (Ch 4). These studies infer periphyton losses from statistical associations between measured transport rates and post-spate biomass across sites. However, we are unaware of studies that have experimentally examined in detail how periphyton losses are affected by sand saltation characteristics. In this paper we present the results of a field experiment designed to compare the degree of loss of periphyton biomass resulting from exposure to saltating fine sand (0.063-0.5 mm) versus coarse sand (0.5-2.0 mm) for both low (2 cm) and high (6 cm) protruding substrates. The experiment was carried out under steady discharge conditions, with a bed shear stress typical for a spate with a mean period of recurrence (weekly here) less than the time for periphyton to reach carrying capacity. Under these conditions our analysis confirmed significant periphyton losses starting at ~ 50 g m<sup>-1</sup> event<sup>-1</sup>, consistent with natural spate data sets (64 g m<sup>-1</sup> event<sup>-1</sup>). However such losses begin at 9 g m<sup>-1</sup> event<sup>-1</sup> if the sand is coarse (0.5-2 mm vs. 0.063-0.5) and predominantly saltating (i.e. vs suspended). Substrates closer to the bed lose more periphyton than elevated substrates confirming the hypothesis that refuge potential increases with elevation above the bed. For the frequent

small spate conditions tested, coarse sand moved primarily by saltation. Fine sand (<5 mm) also saltated but a large percentage of the fine sand load was transported primarily by suspension, and had a less erosive effect on periphyton than saltating coarse sand.

#### **5.1 Introduction**

Large spates (e.g. > 2 x mean annual discharge, or 2MAD) have been widely recognized as a dominant physical disturbance factor regulating the spatial distribution of periphyton (Biggs, 1999) and macroinvertebrates (Rempel, 2000). However, there have been relatively few studies addressing the abrasive effect of saltating sand on stream benthos during smaller spates that can recur on a weekly basis during the primary algal growth season (Culp et al., 1986; Bond, 2004; Thomson et al., 2005). Any persistent reductions in the amount of periphyton biomass left after such frequent, summer spates can reduce the rate of recovery of benthic algae biomass (Uehlinger, 1991) which may provide resource limitations to upper trophic levels in streams such as benthic invertebrates and fish (Stevenson, 1996). During these frequent, minor spates (< 2MAD), sand particles (< 2 mm) can be mobilized at low flow shear stresses (Wilcock and Kenworthy, 2002), while coarser materials (e.g. gravel, cobble, boulder) may remain static (Stokseth, 1994; Grams et al., 2006, Ch. 3). During minor spates, sand is typically transported in saltation: which refers to particles bouncing along and bombarding the bed (Figure 5.1). Saltation is an intermediate form of transport between suspension and traction. With increasing flow strength, fines will travel predominantly in suspension within the water column (Figure 5.1). Engineering studies have shown that because of the frequency and energy of sand impacts, saltation is extremely effective in abrading clay (Kamphuis, 1990; Thompson and Amos, 2004) and even capable of eroding bedrock (Sklar and Dietrich, 2004). It is thus plausible that relatively non-cohesive periphyton may be even more vulnerable to this stressor, and therefore an important disturbance variable during frequent, small summer spates. While the influence of saltating sand on periphyton has received little attention, Culp et al. (1986) conducted an experimental study of sands abrasive effect on reducing macroinvertebrate biomass. Culp et al. (1986) concluded that saltating sediments may have a major influence on macroinvertebrate drift and survivorship, and stressed the need "to establish the importance to the benthos of the

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Figure 5.1 Three types of sediment transport over a coarse gravel bed.

composition, concentration, and timing of fine sediments inputs under standardized conditions of flow and tractive force."

In contrast to the mechanics of saltation abrasion, the effect of suspended sediment abrasion on periphyton have been isolated using laboratory flume experiments (Horner et al., 1990a; Francoeur and Biggs, 2006). The authors reported significant losses (e.g. up to 40%) of periphyton biomass directly attributable to suspended sediments. Currently, observational field studies on gravel bed rivers are the primary source of insight regarding the how saltating sand affects periphyton biomass. However, few field studies exist, and direct measurements of sand transport rates are rarely obtained in these studies. For example, Thomson et al. (2005) found that the passage of the sediment slug increased the amount of sand on the bed from 1-15% and was associated with a 25% lower algal biomass on Manatawny Creek, Pennsylvania. Unfortunately no sand transport rates were reported. Stokseth (1994) found that the <u>simulated</u> bedload transport rate (considering sand <u>and</u> gravel) and water temperature were negatively related to biomass ( $n = 5 R_{Adj}^2 = 0.95$ ) during spates (i.e. 2.8MAD-15MAD) on the Skona River, Norway.

In a previous field study we investigated the abrasive potential of saltating sand on the spatial distribution of post-spate periphyton after a series of small spates (i.e. 0.6MAD) on the Sainte-Marguerite River (Ch. 3, Ch. 4). Low periphyton biomass (< 10 mg/m<sup>2</sup>) was found where sand transport rates exceeded 64-180 g m<sup>-1</sup>event<sup>-1</sup>, peak shear stresses were greater than 15 Pa and average baseflow velocities higher than 0.5 m/s (Ch. 4). To examine the interactions between these variables we proposed a semideterministic periphyton saltation abrasion model (PSAM) in chapter 3 which was partly based on the bedrock saltation abrasion model (SAMB) of Sklar and Dietrich (2004). In Sklar and Dietrich's mechanistic SAMB model of bedrock abrasion, the erosion rate of bedrock by a saltating particle was a function of: 1) the volume eroded per unit impact, 2) the number of particle impacts per unit time and area, and 3) the degree of exposure to this physical disturbance (Sklar and Dietrich, 2004). According to their SAMB model, bedrock loss starts during the rising limb of a spate when the increasing flow strength initiates saltation of fine sediments. As the spate intensity increases, the volume of bedrock loss increases because more (and larger) sediment is saltating which increases the number and efficiency of erosional bed contacts. During this progression of increasing flow strength, the height of each particle hop increases but eventually reaches a maximum. At higher flows, particles either become suspended, or have a flatter saltation trajectory (Francis, 1977). Thus, a 'saltation layer' near the bed forms which is bounded by maximum saltation height for that sediment mixture (Figure 5.1).

Our saltation abrasion model for periphyton (PSAM, Ch. 3) is an empirical regression model predicting periphyton biomass after a spate period using key SAMB predictors including sand transport rate, an index of degree of exposure to abrasion, prespate biomass, as well as pre-spate flow velocity (Ch. 3, Model 1b). The first SAMB variable, the volume of material eroded per contact, was assumed constant because a narrow particle size range was considered (0.5mm to 2mm sand). The second SAMB variable, the grain contact rate, was represented by the sand transport rate measured during the spate. The third SAMB variable, index of exposure, was represented in PSAM by an "immersion index", defined as the height of the saltation layer at the peak of the spate, relative to the protrusion height of the host-rock above the average bed matrix surface level (Figure 5.2). The bed matrix is the fine material (e.g. sand granules, medium gravel i.e. less than 16 mm) which occupies the spaces between coarser framework bed materials (e.g. gravel cobble). The PSAM model was fited to uncontrolled data from 15 riffles subject to small spates (i.e. largest spate was 0.6MAD) on the Sainte Marguerite River. We found that 59% of the variance in post-spate periphyton could be explained by


**Figure 5.2** Definition of terms. Rocks 1-3 are examples of host-rocks, sampled for periphyton biomass. The protrusion height is measured relative to the mean bed matrix elevation and is typically positive but can be negative.

pre-spate biomass, spate event sand transport rate and periphyton exposure defined as a function of the height of the growth surface above the mean bed. These findings suggested that the number of contacts (i.e. transport rate) and height above the bed are important determinants for periphyton removal.

While the immersion index was a significant predictor in the empirical PSAM model (Ch. 3), no direct experimental evidence exists confirming the refuge effect provided by the elevated level of a growth surface relative the saltating layer. Further, while periphyton losses from sand abrasion were implied by the threshold analysis in Ch. 4, and PSAM model in Ch. 3, direct measurements of loss could not be obtained during the uncontrolled field experiment. Specifically, periphyton loss could not be quantified with certainty because the unpredictable timing of spates led to a large elapsed time between pre- and post-spate periphyton surveys, which was long enough for some nonspate related biomass accumulation (or loss) to occur. Further, variable flow stress during the natural spates created uncertainty regarding how long transport occurred at each sediment trap. There may be large differences in transport times between sediment traps located in areas that differed greatly in terms of flow strength. Consequently, cumulative sand transport rates (g  $m^{-1}$  event<sup>-1</sup>) could not be related to instantaneous transport rates measured in g  $m^{-1}s^{-1}$  (Ch. 4) with a high degree of certainty. The experiments presented here will allow us to do this.

In this paper, we conduct an *in situ* field experiment to examine how sand moves (e.g. saltating versus suspended) over a cobble bed during typical small spate conditions, and the effect this transport has on periphyton losses. We focused on high-frequency spate conditions because anthropogenic influences can cause an increase in spate frequency and delivery of fine sediment. Even at baseflow conditions, a small increase in sand supply can cause large increases in sand transport rates (Bond, 2004). Thus, we conducted our experiment with fixed flow strength, typical for riffles during a small spate, but over a very large range in sand supply including conditions typical of sand over-loaded cobble systems.

The general objective of this Chapter is thus to provide direct, controlled tests of the effects of the size, transport rate and vertical extent of saltating sand on periphyton abrasion. Consequently, for a typical, small spate condition, our specific objectives are to evaluate: 1) if both coarse and fine sands are saltating; 2) if the nonlinear, threshold response reported in Chapter 4 is confirmed, between increasing sand transport rates and periphyton biomass loss; 3) if height above the bed provides more shelter to periphyton from saltating sand, as modelled by the Immersion index of PSAM; and, 4) if coarse sediments have a more abrasive effect on periphyton than fine sediment as predicted by SAMB (Sklar and Dietrich, 2004). To achieve our objectives we compare biomass losses from host-rock exposure to (presumably suspended) fine sand (0.063-0.5 mm) versus (presumably saltating) coarse sand (0.5-2.0 mm) for both low (2 cm) and high (6 cm)protruding substrates. In order to assess how broadly applicable our experimental results were to other sites, we compared our results across a number of field studies (Ch. 3, Ch. 4, Stokseth 1994, Culp et al. 1986). To achieve this objective, it was necessary to convert our experimental findings into a number of different metrics of sand transport rates (e.g. g  $m^{-1}$  event<sup>-1</sup>, g m<sup>-1</sup>s<sup>-1</sup>) and biomass (e.g. post-spate biomass in mg/m<sup>2</sup>, % biomass lost) that were used in these other studies.

# 5.2 Methods

### **5.2.1 Experimental Design**

Selection of Representative Riffle and Spate Condition. Our study was conducted on the Sainte-Marguerite River (SMR) (e.g. Big Pool Reach, BPR lies at  $48^{\circ}26'56''N$ ,  $70^{\circ}26'97''W$ ). This gravel-cobble, Boreal river is snow melt dominated and the largest flow events of the year typically occur in the spring. The 1.8 year return period flow near the test reach is 82 m<sup>3</sup>/s (Big Pool Reach, BPR) but local floodplain inundation was observed at flows as low as low 40 m<sup>3</sup>/s, which have a return period of 1.05 years. The mean annual discharge (MAD) at BPR was 9.6 m<sup>3</sup>/s. A mean daily flow of 1.7 m<sup>3</sup>/s is equalled or exceeded 329 days of the year (Q<sub>329</sub>) for the period 1976-2003.

We sought a very short patch of bed (2 m) within a riffle where shear stress conditions during stable base flow were: 1) typical of a small summer spate, and 2) lower than that shown to limit biomass (< 15 Pa, Ch. 4), yet 3) high enough to transport available sand at a high rate. We would seed the bed upstream of the patch in order to simulate sand transport over a much broader range than what typically occurs during a small spate in a stable river. Consequently, we tested sand transport conditions up to the much higher transport rates usually associated with larger infrequent discharge events, or with sand rich gravel beds.

Site selection first required defining typical "average summerspate" conditions. For his purposes, Uehlinger (1996) defined a "spate" as  $10Q_{329}$  noting significant periphyton losses and bed movement at this threshold. Here we are interested in smaller (i.e. <  $10Q_{329}$ ), more frequent flows that interrupt the growth cycle of periphyton in the summer. We will define a spate as any flow event when daily discharge is measurably higher than the preceding and following day. Over 13 years the average spate discharge during the July-September (1991-2003) period was 8.2 m<sup>3</sup>/s (i.e. 4.8Q<sub>329</sub>, 0.85MAD, exceeded 25% of the summer period and 48% of the time annually) but ranged between 2.3 m<sup>3</sup>/s (i.e. exceed 92% of the summer time) and 34.3 m<sup>3</sup>/s (i.e. exceed 0.006% of the summer time). The baseflow discharge that occurred between these spate disturbances averaged 4.5 m<sup>3</sup>/s, a discharge exceeded 65% of the time during the summer growth period. The number of days between summer spates varied from 5.7 to 8.3 days, averaging 7.1 days. Thus, a typical average summer spate here is 0.85MAD with a weekly recurrence.

To identify the hydraulic and sediment transport characteristics to be simulated over the test patch, we collected sand transport and peak spate shear stress in two reaches during a small spate ( $Q_{max} = 6.1 \text{ m}^3/\text{s} = 3.6Q_{329}$ , exceeded 54% of the time annually) which occurred on 24 August 2004, and in four reaches during a series of large spates  $(Q_{max} = 30.6 \text{ m}^3/\text{s} = 18Q_{329}$ , exceeded 7.8% of the time annually) in August 2003. The average values of sand transport and shear stress at riffles (n = 29) for these natural spates are given in Table 5.1. The data in Table 5.1 were used as a guide to bound sand transport conditions during the experiment and to select the test patch. We did not capture data for our "average summer" spate ( $Q_{max} = 8.6 \text{ m}^3/\text{s} = 4.8 Q_{329}$ ) but our 2004 spate here was close in magnitude (i.e.  $6.1 \text{ m}^3/\text{s}$ ) and provided a lower limit for the average peak spate shear stress (8-13 Pa, Table 5.1). This spate flow event is exceeded 50% of the time during the growing season (i.e., 45.5/91 days). The peak summer discharge during 2003 was 30.6  $\text{m}^3$ /s which is close in magnitude to the maximum summer event recorded (i.e.  $34.3 \text{ m}^3/\text{s}$ ) for the period 1991-2003 (not including the extremely rare 1996 summer flood). A flow of 30.6  $m^3/s$  is typically exceeded < 1% of the time (i.e., 15 hours) during the algae growing season (July-September) and creates riffle shear stresses of 25-50 Pa (Table 5.1).

Five riffles were inspected as possible experiment sites based on how well the shear stress and sand transport rate criteria were met. The test riffle selected is in the Meander Reach (MR). Experimental runs were completed on 11 August 2005. The fixed shear stress (14 Pa) and range of sand transport conditions (0-3200 g m<sup>-1</sup>event<sup>-1</sup>) used in our experimental runs are given in Table 5.1, for comparison with the 2 monitored spates. Shear stress conditions over the test patch reasonably represent a typical small spate but in this system, the maximum sand transport rates triggered over the patch during the experiment are more typical of a large spate.

We also compared the sediment transport conditions over the test patch to those over natural spate affected patches by comparing indices of sediment movement potential **Table 5.1** Summary of average peak flow and sand transport condition for five reaches of the Ste. Marguerite river during two natural spates measured in 2003 and 2004. The experimental conditions tested during the *in situ* experiment in 2005 were bounded by these field examples.

	Large Spate <sup>1</sup> – 3MAQ, 18Q <sub>329</sub>				Small S			
	Median	Depth	Shear Stress	Sand	Depth	Shear Stress	Sand	Shear Stress
	Particle Size			Transport			Transport	<b>Critical</b> <sup>5</sup>
Reach	Avg±SD	Avg±SD	Avg±SD	Range	Avg±SD	Avg±SD	Range	Avg±SD
	( <b>mm</b> )	( <b>m</b> )	(Pa)	(g m <sup>-1</sup> event <sup>-1</sup> )	( <b>m</b> )	(Pa)	(g m <sup>-1</sup> event <sup>-1</sup> )	(Pa)
Cascade	56±27	$0.66 \pm 0.1$	36.9±20.1	619-1526				3.9±1.1
Onesime	58±31	$0.68 \pm 0.1$	24.3±15.2	200-1198				5.2±3.5
Big Pool	44±38	$1.09\pm0.3$	26.7±14.3	155-1303	$0.49{\pm}0.1$	12.5±6.9	6-318	6.0±3.5
Meander	33±13				$0.57 \pm 0.5$	7.8±3.3	22-342	2.9±0.9
Bardsville	97±42	1.22±0.4	51.9±26.6	440-2099				5.3±2.5
		Experimental Conditions		Exj	perimental Con	ditions		
Test Patch	<sup>3</sup> 60	0.29	<sup>4</sup> 14	0-3200	0.29	<sup>4</sup> 14	0-3200	3.48
<sup>1</sup> Event 3 17 A	August 2003; <sup>2</sup> Ev	ent 1, 25 Au	igust 2004; <sup>3</sup> Wc	olman (1954) coun	t.; <sup>4</sup> Using Wil	lcock et al. (199	96); <sup>5</sup> Using Wild	cock and

Kenworthy, (2002) assuming 2 mm sand and patch D<sub>50</sub>.

(i.e. Suspended sediment criterion, Mobility Ratio) between the two spates and over the test patch (Table 5.2). The suspended sediment criterion is the ratio of the shear water velocity to the fall velocity of a particle. When this ratio is 1 or greater the particle is suspended in the water column. We calculated this ratio for 0.063 mm silt and 0.5 mm and 2 mm sand. The suspended sediment criterion for the test patch was very similar to those experienced during the small spate (bottom line, Table 5.2). The finer fractions (0.063, 0.5 mm) were suspended but 2 mm sand was not. We also calculate a "mobility ratio" which is the reach averaged shear stress during the peak of the spate divided by the critical shear stress required to move the median particle size on the barhead adjacent to the riffle (Lapointe et al., 2000). Lapointe et al.(2000) showed that when this ratio is greater than 0.8 on the SMR, a patchy mosaic of bed scour occurs. The mobility ratio was calculated using the median particle size over the riffle test patch and was found to be 0.25, which is lower but similar to the small spate monitored in 2004 ( $Q_{max} = 6.1 \text{ m}^3/\text{s} = 3.6Q_{329}$ ). The coarse bed material was very stable. Tables 5.3 and 5.1 summarizes the hydraulic conditions over the test patch.

**Table 5.2** Summary of average indices of sediment suspension  $(U^*/W_f)$  and bed scour and fill (Mobility Ratio) for five reaches of the Ste. Marguerite river during two spates. Particles are deemed to begin to travel in suspension when the suspension criteria  $(U^*/W_f)$  exceeds 1. Lapointe et al. (2000) measured bed scour and fill (> 20 cm) in the Sainte Marguerite River and found that it occurred for the flows they monitored when the mobility ratio exceeded 0.8.

	Na	tural S	oate Coi	nditions	Natural Spate Conditions			
-	La	rge Spate	e <sup>1</sup> – 3MAC	<b>Q, 18Q</b> <sub>329</sub>	Small Spate <sup>2</sup> – 0.6MAQ, 3.6Q <sub>329</sub>			
-	Suspension Criterion (U*/W <sub>f</sub> )			Mobility Ratio <sup>3</sup>	Suspension Criterion (U*/W <sub>f</sub> )			Mobility Ratio <sup>3</sup>
-	Silt 0.063 mm	Med. Sand 0.5 mm	Crs. Sand 2 mm		Silt 0.063 mm	Med. Sand 0.5 mm	Crs. Sand 2 mm	
Reach			-	Avg±SD				Avg±SD
	(dim)	(dim)	(dim)	(dim)	(dim)	(dim)	(dim)	(dim)
Cascade	38.1	2.9	0.7	0.68±0.27				
Onesime	30.5	2.3	0.6	0.45±0.23				
Big Pool	32.5	2.5	0.6	1.0±0.87	21.8	1.7	0.4	0.34±0.31
Meander					17.8	1.4	0.3	0.34±0.22
Bardsville	45.5	3.8	0.8	0.59±0.37				
	Experimental Conditions			I	Experim	ental Co	nditions	
Test Patch	24.7	1.9	0.5	0.25	24.7	1.9	0.5	0.25

**Experimental procedures.** The experiments required artificially seeding sand on the bed by hand. This sand was mined from an adjacent point bar and sieved into two fractions: 0.06-0.50 mm and 0.5-2.0 mm. Three experimental runs were conducted to document cumulative periphyton abrasion from test rocks of various heights exposed to 7 increasing levels of sand transport of particles of these 2 fractions (Table 5.4). In Run 1, the test rocks protruded 2 cm above the mean bed level of the surrounding bed matrix

Parameter	Value
Average Flow Velocity <sup>1,2</sup>	0.65 m/s
Bed Velocity <sup>1,2,3</sup>	0.42 m/s
Froude Number	0.38
Reynolds Number	143 760
Reach Length	2 m
	$\frac{2}{2}$

**Table 5.3** Experimental conditions over the patch of bed used for all three simulated spates (Runs 1-3).

<sup>1</sup>Velocity measurements taken with a Gurley No. 625D Pygmy meter.; <sup>2</sup> Measurement at 0.4 x flow depth.<sup>3</sup> Measurement taken 2 cm above the bed.

**Table 5.4** Experimental conditions tested for each of the three runs. Water depth and velocity were constant during all three runs.

		Run 1	Run 2	Run 3
		n=3 rocks	n=3 rocks	n=3 rocks
		2 cm Protrusion	2 cm Protrusion	6 cm Protrusion
Seeding	Seeding Mass	Sand in Transport	Sand in Transport	Sand in Transport
Iviass		0.5 – 2.0 mm	0.063 – 0.5 mm	0.5-2.0 mm
Per Level	Cumula-	Cumulative Mass	Cumulative Mass	Cumulative Mass
	tive	of Sand Transported	of Sand Transported	of Sand Transported
(g)	(g)	(g)	(g)	(g)
0	0	0	0	0
10	10	1.2	2.2	0.6
11.9	21.9	2.0	3.0	1.7
15.6	37.5	2.9	4.3	2.5
25	62.5	4.5	6.0	3.2
112.5	175	10.7	10.6	6.6
450	625	157.6	31.8	24.2
1600	2225	386.4	98.9	276.8
	Seeding Mass Per Level (g) 0 10 11.9 15.6 25 112.5 450 1600	Seeding Mass         Seeding Mass           Per Level         Cumula- tive           (g)         (g)           0         0           10         10           11.9         21.9           15.6         37.5           25         62.5           112.5         175           450         625           1600         2225	Run 1Seeding MassSeeding Mass $2 \text{ cm Protrusion}$ Per LevelCumula- tiveCumulative Mass of Sand Transported(g)(g)(g)00101011.921.92562.5112.5175112.51751002225386.4	Run 1Run 2Seeding MassSeeding MassSeeding Mass $2 \text{ cm Protrusion}$ $2 \text{ cm Protrusion}$ Per LevelCumula- tiveCumulative Mass of Sand TransportedCumulative Mass of Sand TransportedCumulative Mass of Sand Transported(g)(g)(g)(g)(g)000010101.22.211.921.92.03.015.637.52.94.32562.54.56.0112.517510.710.6450625157.631.816002225386.498.9

(<20 mm) and were exposed to seeded 0.5-2.0 mm sand. Test rocks in Run 2 also protruded 2 cm from the mean bed level but were exposed to finer seeded sand (0.063-0.50 mm). The protrusion height was increased to 6 cm by decreasing the burial depth of</li>

the host-rock for Run 3, where the rocks were exposed to 0.5-2.0 mm sand. All 3 runs were exposed to 7 levels of sand transport quantity (Table 5.4).

Flow velocity was monitored before and after the three test runs and found to be constant during all three runs (Table 5.3). The same patch of bed was used for all trials, providing control on flow roughness (i.e. constant 0.29 m depth and  $D_{50}$  of 60 mm). All periphyton-covered test rocks were taken from the downstream end of the test riffle; from a source area having uniform flow velocity (0.05 m/s) during growth.

Each test rock was selected individually to insure the same degree of antecedent biomass was present, constraining the rock size and shape as much as feasibly possible. All the rocks required for the analysis were moved to a staging area with the same low velocity conditions as their growth position. The orientation of the rock relative to the downstream direction of flow was noted in its growth position and later maintained during installation at the test patch.

Although the experiment sought to recreate a gradient in sand transport rates analogous to those measured during the near bankfull spate of 2003, it was nevertheless carried out under conditions of constant shear stress in a test riffle of relatively limited length. This was necessary to isolate sand grain size as the sole disturbance factor explaining observed losses in biomass. Sand transport rates can increase under stable competent flow conditions by simply increasing the fraction of sand on the bed available for transport (Wilcock and Kenworthy, 2002; Curran and Wilcock, 2005). Although it was difficult to consistently achieve specific sediment transport rates, the addition of successively larger amounts of sand on the bed did result in successively higher sand transport rates. The required seeding mass per exposure level was selected through trial and error experimentation on 5 August 2005 to achieve the desired range of observed sand transport intensity over test rocks (Table 5.4).

**Test run procedures**. The experimental set up employed in each run is shown in Figure 5.3. A sediment trap was installed within a plastic sleeve embedded in the substrate to facilitate rapid removal and replacement between sand exposure levels.



**Figure 5.3** Plan view of the set up used for each of the three experimental runs (see Table 5.4). For each run, three periphyton covered rocks were placed at the appropriate protrusion height (PH) and exposed to seven consecutive and progressively higher levels of sand transport. After each level of sand transport, periphyton biomass and mass of sand transported past the rocks was measured.

Three periphyton-covered cobbles were placed ~ 3 cm apart and upstream of the sediment trap with their tops at the appropriate protrusion height above the mean elevation of the bed matrix. The rocks were shielded from flow during placement to ensure any pre-seeding loss in periphyton biomass could be attributed to the flow velocity near the bed (0.42 m/s) rather than to the faster water above it (0.65 m/s). The biomass on each rock was assessed both at their low-velocity (0.05 m/s) growth position and after installation at the test patch to determine how much periphyton loss occurred during installation. The first mass (i.e. 10 g) of sand was then placed in the seeding area which was located 0.3 m upstream of the test rocks (Table 5.4). Sand was delivered to the bed by placing a board upstream of the test rocks, emptying the sand in the lee of the board from containers and then removing the board to allow transport. Movement of this sand past the rocks was observed with the aid of a mask and snorkel. The duration from the start of the sand exposure until sediment transport was no longer observable was

recorded. To measure the actual transport rate, the trap was then capped, removed, labelled and replaced with a new trap for the next exposure level. After each exposure level, the biomass remaining on the rocks was assessed visually and photographed *in situ* as described in the next section. This process was repeated for the next sand exposure level (i.e. 11.9 g) and so on until all treatment levels were completed, effectively mimicking the sediment transport regime of a near-bankfull event. At the completion of Run 1, the test rocks were removed, the water column above the substrate agitated to assist in the removal of any lingering sand grains, and the experimental procedure was repeated for Runs 2 then 3.

Velocity profiles were collected prior to Run 1 and after Run 3 using a Gurley No. 625D Pygmy meter. The velocity profiles had twenty points taken between 2 cm above the substrate and 2 cm below the water surface. Shear stress condition during the test was estimated from these data based on methods in Robert (1996; 1997).

### 5.2.2 Measurement

**Measuring Protrusion Height.** The protrusion height is a measure of the degree of exposure for each rock. We measured the protrusion height as the height of the top of the rock above or below the average matrix elevation considering a reference area of 0.5 m by 0.5 m centered on the rock. The bed matrix is the fine material (e.g. < 10 mm) which occupies the spaces between coarser fabric bed material (e.g. 60 mm) and constitutes the 'flattest' surface at the base of the gravel mixture.

**Determination of periphyton biomass.** A rapid assessment technique developed by the U.S. Environmental Protection Agency (USEPA) was used to rank the biomass of micro alga contained in the periphyton of the test rock without disturbing the rock (Stevenson and Bahls, 1999). The test involves a visual and tactile assessment of the thickness and sliminess of the algal mat to rank the relative biomass into 5 categories (Table 5.5). The touch test for sliminess was required to distinguishing between ranks 0 and 0.5 but avoided otherwise to minimize disturbance. For each biomass assessment, a master sketch for that test rock was marked with polygons corresponding to the USEPA rank they represented. The fraction of area exhibited by each rank was estimated by eye **Table 5.5** Results of one way analysis of variance (ANOVA) testing differences in periphyton biomass among USEPA ranks. USEPA rank categories are based on algal appearance and thickness (see table legend). Periphyton biomass are based on chlorophyll *a* assays of periphyton removed from the rock area exposed to flow in 2003 or a small prescribed area of pure USEPA rank in 2004.

	2003		2004		
Rank <sup>1</sup>	Average	SE	Average	SE	
0	1.3*	0.5	0.23*	0.04	
0.5	5.9*	1.1	0.52*	0.07	
1	15.7*	1.7	3.72*	0.63	
2	24.7*	2.6	8.13*	1.45	
3			41.30*	5.05	
4			29.58	3.41	

Periphyton Biomass – Chlorophyll  $a (mg/m^2)$ 

Rank<sup>1</sup> - USEPA (2000) rapid periphyton protocol for ranking abundance of microalgae: *Rank 0* - Substrate rough with no visual evidence of microalgae; *Rank 0.5* - Slightly slimy but no visual accumulation of microalgae is evident; *Rank 1* - Slimy with visual accumulation evident; *Rank 2* - Moderately slimy with accumulations evident and between 0.5 mm to 1 mm thick; *Rank 3* - Very slimy with accumulation layer from 1 mm to 5 mm thick; *Rank 4* - Algae sloughs when wading in area or removing rock. Accumulation > 5mm thick.

\* p < 0.05

2003 -  $F_{(3,70)} = 53.5$ , p < 0.001, R = 0.83,  $R^2 = 0.70$ 2004 -  $F_{(5,87)} = 223$ , p < 0.001, R = 0.96,  $R^2 = 0.93$ 

to the nearest five percent. Each rank was then converted to chlorophyll a (mg/m<sup>2</sup>) using a calibration curve described in Chapter 4 and shown in Table 5.5. The chlorophyll avalue for each rank was then multiplied by the fraction of the rock that it covered. These values were summed for each rock to determine the total periphyton biomass (i.e. Periphyton Chlorophyll a). The periphyton loss was determined by subtracting the periphyton biomass at sand exposure level i from the initial biomass, dividing by the initial biomass and multiplying by 100. The *total periphyton loss* was calculated using the initial periphyton biomass present before movement from growth position. The *periphyton loss attributable to sand transport* was calculated using the initial biomass retained after exposure to the velocity increase associated with rock installation at the test patch.

**Fine sediment traps.** The sediment traps consist of a one-litre plastic container filled with clean 16-32 mm gravel and installed with the rim flush with the bed. Trap contents were dried at 105 °C and shaken in a set of sieves for 20 minutes to determine the mass of sand (0.063-0.5 mm and 0.5-2 mm) trapped. The *cumulative sand transport* (g m<sup>-1</sup>event<sup>-1</sup>) past the test rocks is given by the mass trapped, divided by the width of the trap (Table 5.4). The *sand transport rate* (g m<sup>-1</sup>s<sup>-1</sup>) was determined by dividing the cumulative sand transport value by the time elapsed between sand release and trap collection.

### 5.2.3 Analysis

**Comparison of periphyton losses by run.** A comparison of Run 1 with Run 2 was required to assess if larger sand was more abrasive on periphyton than finer sand. A comparison of Run 1 with Run 3 was required to test if higher substrates were less abraded than lower substrates. Multiple regression was used to test for significant differences in the slopes and intercepts between three test run trend lines representing the rate of periphyton biomass removal with increasing *cumulative sand transport* (Kutner, 2004, Section 11.4) Finally, we tested for equality in the error term variances between runs using the Levine Test (Kutner, 2004, Section 3.6).

**Comparison of periphyton losses with inferred losses from Sainte Marguerite River data and other field studies**. The results of the three test runs were compared with results from Chapter 4 and other field studies (Culp et al., 1986; Stokseth, 1994). For a comparison of experimental results with the results in Chapter 4, we plotted our test run results on a graph showing an envelope curve which defined the upper limit of average *periphyton biomass* for given levels of *cumulative sand transport* for natural summer spates in the SMR. Two analyses were conducted using sand transport rate data rather than cumulative sand transport rate data to compare the results with the works of Culp et al. (1986) regarding disturbance thresholds and Stokseth (1994) regarding disturbance gradient. To compare our results with those of Stokseth (1994) we used linear regression to characterize the disturbance gradient between *periphyton biomass* and *sand transport rate*. Data from all three experimental runs were pooled for this regression analysis. To compare our results with those of Culp et al. (1986) we used Classification and Regression Tree analysis (CART) in SYSTAT (11.0/2005, Systat Software Inc., Richmond) to investigate if a statistically sound threshold exists between low transport-low biomass losses and high transport-high loss conditions. The dependent variable (*total periphyton loss*) and independent variable (*sand transport rate*) did not require transformation. We conducted a naïve bootstrapping (n = 100) of the CART model to determine confidence limits around the statistically determined threshold. Data from all three experimental runs were pooled for the CART analysis.

### 5.3 Results

### **5.3.1** General observations of test runs

**Spatial pattern of periphyton loss**. Initial placement of the test rocks within the higher velocity yet unseeded water of the study reach resulted in periphyton sloughing, especially on their upstream faces and tops. During the first few sand transport treatments, a small area became reduced in periphyton biomass on the top of the rocks and on slightly angled edges of the rock face. Progressive reductions in periphyton occurred through three mechanisms, including expansion of the denuded area, increased number of individual denuded areas, and evenly distributed reductions over substantial areas of the rock. At the end of the treatments, the least amount of periphyton was found on the upper upstream face of the test rocks. Very little periphyton remained on the lower upstream face, while the most was retained on the downstream face.

**Sand transport over a coarse bed.** Sand transport was observed as it passed over the bed surrounding the test rocks. Three observations of this transport process are of note. First, during very high sand transport conditions, some low-lying rocks between the seeding area and test rocks were temporarily buried in sand. Under these conditions, a sheet of sand covered the periphyton, protecting it from saltating grains. Second, coarse sand grains were observed 'ramping' up the face of imbricated rocks (Figure 5.1),

increasing saltation height above the bed. Finally, as sand moved past rocks during high transport treatments, a sand deposit built up and then receded at the base of the rock. Considering this, it is possible that periphyton could colonize a partly buried rock during stable flow conditions and the next flood remove the fine material at the base of the rock, exposing an uncolonized surface. Thus, the "trim line" observed on post-spate rocks can result from this process of matrix excavation and exposure of uncolonized surfaces.

# **5.3.2** Effects of protrusion height and calibre of transported sand on periphyton biomass retention.

For each of the 3 runs, the response of periphyton to increasing cumulative sand transport is characterized by four stages of adjustment (Figure 5.4). Threshold values of cumulative sand transport were selected to divide these adjustment stages. Initially, low levels of sand transport did not affect the periphyton biomass up to a rate of approximately 9 g m<sup>-1</sup>event<sup>-1</sup>. Second, there was a phase of rapid reduction in periphyton biomass when cumulative sand transport levels were between 9 g m<sup>-1</sup>event<sup>-1</sup> and 40 g m<sup>-1</sup> event<sup>-1</sup>. Third, there were more gradual periphyton losses when sand transport rates exceeded 40 g m<sup>-1</sup>event<sup>-1</sup>. Finally, all three response lines (Runs 1-3) converge when cumulative sand transport values exceed 800 g m<sup>-1</sup>event<sup>-1</sup>. This suggests that the mitigative effects of protrusion height above the bed and size of transported sand were negligible when sand transport rates reached that high level.

Effects of host-rock protrusion height on periphyton biomass. The immersion index in the PSAM model (Ch. 3) dictates that the height of the growth surface above the bed provides protection to periphyton from saltating sand. Our experimental results from runs 1 and 3 support this assertion. For saltating coarse sand (0.5-2 mm), there was a more sudden decrease in periphyton biomass on test rocks in the low-lying substrate condition (Run 1, 2 cm protrusion), relative to periphyton on those that protruded higher above the bed (Run 3, 6 cm protrusion, Figure 5.4). There were two key differences between Runs 1 and 3 (effects of protrusion height), depending on the phase of adjustment. First, when sand transport rates were between 9 g m<sup>-1</sup>event<sup>-1</sup> and 40 g m<sup>-1</sup>event<sup>-1</sup>, the rate of decrease of periphyton biomass per unit of sand transport was greater



**Figure 5.4** Mean periphyton biomass (± 1 SD, 3 replicates per run) for three experimental runs where successively larger treatments of sand were transported past periphyton covered rocks under fixed shear stress conditions. The protrusion height refers to the distance between the top of the rock and the average bed matrix level. The 'sand size' refers to the range of particle sizes seeded during the experimental runs.

for low lying substrates than it was for high substrates. Second, once sand transport exceeded 40 g m<sup>-1</sup> event<sup>-1</sup> there was a difference in the subsequent removal pattern of periphyton biomass, which was characterized using multiple regressions. The periphyton biomass on low-lying substrates (Run 1) declined negligibly with increasing sand transport rate (Slope = -0.104), but the biomass on substrates with 6 cm protrusion from the bed declined appreciably from a higher initial biomass (Slope = -0.299, Figure 5.4, Table 5.6).

Effect of sand calibre on periphyton biomass. At a fixed rock height and total sand mass, coarse sand increased the removal of periphyton biomass (Run 1, 0.5-2 mm); relative to finer sand (Run 2, 0.063-0.5 mm, Figure 5.4). There were two key differences between Runs 1 and 2 in the pattern of periphyton biomass loss depending on phase of adjustment. First, when cumulative sand transport rates were between 9 g m<sup>-1</sup> event<sup>-1</sup> and 40 g m<sup>-1</sup> event<sup>-1</sup>, the initial rate of decrease of periphyton biomass per unit of sand

**Table 5.6** Multiple regression of cumulative sand transport (g m<sup>-1</sup>event<sup>-1</sup>) on periphyton Chlorophyll a (mg/m<sup>2</sup>) comparing the periphyton response between three experimental runs for sand levels > 50 g m<sup>-1</sup>event<sup>-1</sup>. Variables were log transformed.

Experimental Treatment	Intercept	Slope	
Run 1) 2 cm protrusion, 2 mm	0.908 *	-0.104*	
Sand	(i.e. 8.1 mg/m <sup>2</sup> )		
Run 2) 2 cm protrusion, 0.063-	1.297	-0.298	
0.5 mm Sand	(i.e. 19.8 mg/m <sup>2</sup> )		
Run 3) 6 cm protrusion, 2 mm	1.395	-0.299	
Sand	(i.e. 24.8 mg/m <sup>2</sup> )		
* significantly different from other runs at Kutner 2004, Section 11). $R^2_{Adjusted} = 0.78$	$p < 0.01$ , $R^2 = 0.81$ . Regression compares 5E = 0.11	aring multiple lines (see	

transport is greater for periphyton subjected to coarse sand (Run 1), relative to the fine sand treatments (Run 2). Second, when sand transport rates exceeded 40 g m<sup>-1</sup>event<sup>-1</sup>, the periphyton biomass subjected to coarse sand did not decline with increasing sand transport (Slope = -0.104) but the biomass on substrates subjected to fine sand transport (Slope = -0.298) was gradually reduced (Table 5.6).

The ratio of flow shear velocity to sand particle fall velocity was found to exceed 1 (Table 5.2) for particles finer than 0.5 mm given the flow conditions during the experimental runs, suggesting that the predominant mode of transport for that size fraction is through suspension (Sklar and Dietrich, 2004). Theory and our observations indicate that the majority of the fine sand was transported in suspension (Run 2), but the predominant mode of transport for coarse sand was saltation (Run 1).

The mitigative effect of protrusion height on reducing periphyton losses from abrasion was statistically indistinguishable (p=0.99) from that of fine sediment moving predominantly in suspension. For sand transport rates exceeding 40 g m<sup>-1</sup>event<sup>-1</sup>, periphyton biomass was lost at the same rate from rocks protruding 6 cm and subjected to

coarse sand (Table 5.6, Run 3, slope = -0.299) as the rate from low lying rocks subjected to fine sand transport (slope = -0.298).

## 5.3.3 Comparison of sand transport thresholds with previous field and flume studies

In this section we compare our experimental findings with the results of previous studies to confirm sand transport threshold limits, and to assess how broadly applicable our experimental results are to other field conditions (Ch. 4, Culp et al., 1986; Horner et al., 1990a; Stokseth, 1994; Francoeur and Biggs, 2006). The results are summarized in Table 5.7 and discussed below.

Study	Biomass (mg/m <sup>2</sup> ): Threshold Transport Rate (g m <sup>-1</sup> event <sup>-1</sup> )	Biomass (mg/m <sup>2</sup> ) vs Transport Rate (g m <sup>-1</sup> event <sup>-1</sup> )	% Biomass lost by abrasion during experiment, independent of velocity effects.	Biomass Loss (%): Threshold Transport Rate (g m <sup>-1</sup> s <sup>-1</sup> )
Chapter 5 Experiment	9 g m <sup>-</sup> event <sup>-</sup>	$PB_{T2} = 5.66Q_s$ at a water temp. of $16^{\circ}C$	20% to 48% from	Mean = $0.04 - 1.8$
Results	to		suspended sand	g m <sup>-1</sup> s <sup>-1</sup>
	$40 \mathrm{g}\mathrm{m}^{-1}\mathrm{event}^{-1}$			associated with up to a 48% loss of periphyton biomass.
Chapter 4	10 <sup>th</sup> %tile = 6.5			
Observational Results	Mean = 65			
hesuits	90 <sup>th</sup> %tile = 186			
Stokseth (1994)		$PB_{T2} = 5.15Q_s^{-0.24}$ at a water temp. of $16^{\circ}C$		
Horner et al. (1990)			4% to 13% from suspended silt	
Francoeur and Biggs (2006)			0% to 40% from suspended sands	
Culp et al. (1986)				Mean = 0.10±0.03 g m <sup>-1</sup> s <sup>-1</sup> associated with a 50% loss in macroinvertebrate biomass.

Table 5.7 Summary of experimental results and the findings of previous studies.

**Chapter 4 comparison.** In Chapter 4 we reported a threshold type reduction in periphyton biomass with cumulative sand transport exceeding 64 g m<sup>-1</sup>event<sup>-1</sup> based on uncontrolled field observations (Figure 5.5). We measured both variables at 29 riffles in 2003 and 15 riffles in 2004 on the SMR, Québec. Each riffle was instrumented with between 4 and 10 sediment traps, and each trap was coupled with measurements of periphyton biomass from three rocks located upstream of the traps. These data thus represent a broad range of channel conditions, ranging from straight, boulder-dominated to sinuous, gravely reaches, and flow rates ranging from near baseflow to near bankfull flows. A bootstrapped CART analysis in chapter 4 indicated that the threshold split values that divide high biomass at low transport rates from low biomass at higher transport rates averaged 64 g m<sup>-1</sup>event<sup>-1</sup> but varied from 6.5 g m<sup>-1</sup>event<sup>-1</sup> (10<sup>th</sup> percentile) to 186 g m<sup>-1</sup>event<sup>-1</sup> (90<sup>th</sup> percentile). Interestingly, there is broad agreement between experimental data from Runs 1 through 3 reported above and this more extensive, two



**Figure 5.5** Mean periphyton biomass ( $\pm$  1 SD, n = 3 rocks) following natural spates in 2003 (triangles) and 2004 (inverted triangles) as a function of cumulative observed sand transport in local sediment trap. The envelope for maximum periphyton biomass for a given level of cumulative sand transport was drawn by eye.

year field program (Figure 5.5). The envelope curve which bounds the field data also generally bound the experimental results, and their overall trends in biomass reduction with increasing transport rate are similar. The 2003-2004 field data indicate a drastic curtailment of periphyton biomass for patches of riverbed associated with sand transport rates exceeding 64-180 g m<sup>-1</sup>event<sup>-1</sup>. The experimental runs reveal that biomass reductions can occur at transport rates as low as 9 g m<sup>-1</sup>event<sup>-1</sup>, in general agreement with the 10<sup>th</sup> percentile split value reported in Chapter 4.

**Stokseth (1994) field study comparison.** A regression of *sand transport rate* (g  $m^{-1}s^{-1}$ ) and *periphyton biomass* (mg/m<sup>2</sup>) was performed on our experimental data for comparison with the findings of Stokseth (1994). Data from the three experimental runs were pooled. The biomass was found to decline with sand transport according to the following power function:

Biomass Chla (mg/m<sup>2</sup>) = 5.66 Sand Transport Rate<sup>-0.26</sup> (5.1)  

$$n = 27 R_{Adj}^2 = 0.60, p < 0.001$$

A direct comparison can be made between the equation of Stokseth (1994) shown in Table 5.7 and our equation (5.1), despite the different units used for the dependent variable because there is a direct linear relationship between these metrics (i.e. Chla and AFDM) for the range of data being compared. There are distinct similarities in the constant (i.e. 5.66 vs. 5.15), and exponents (i.e. -0.26 vs. -0.24) in these two equations.

**Comparison with flume studies.** The effects of sand transport rate on percent periphyton lost from pre disturbance levels (left y axis) or from the biomass left after installation in the test area (right y axis) are shown in Figure 5.6. Data from all three runs are shown and each point represents an average of 3 replicate rocks. The line shown is a distance weighted least squares smoother with a tolerance of 0.9. Initially, 30-50% of the pre-disturbance biomass was lost due to the 0.05 to 0.41 m/s velocity increase associated with removal of the rocks from the growth area and placement in the test area.

Classification and Regression Trees (CART) were then used to determine if a statistically sound separation exists between low transport-low loss and high transport-



**Figure 5.6** The effects of sand transport rate on average percent periphyton lost relative to both the pre-disturbance biomass measured at the growth location (left axis) and the biomass retained after relocation to the test site but before sand treatments commence (right axis). Cases are the average of three sampled rocks and all three experimental runs are shown. The trend line is a distance weighted least squares smoother with a tolerance of 0.9. A threshold of 0.04 g m<sup>-1</sup>s<sup>-1</sup> (lower and upper split value at 95% confidence interval = 0.27-0.52 g m<sup>-1</sup>s<sup>-1</sup>; lower and upper  $R^2$  at 95% confidence interval = 0.69-0.76) was determined using a bootstrapped CART model (n = 100 iterations).

high loss. The dependent variable (*total periphyton loss*, Figure 5.5) and independent variable (*sand transport rate*) did not require transformation. A naïve bootstrapping (n = 100) of the CART model was performed to determine confidence limits around a mean predicted separation value. The mean split value was 0.04 g m<sup>-1</sup>s<sup>-1</sup>, SD = 0.034 g m<sup>-1</sup>s<sup>-1</sup>;  $R^2 = 0.69$ -0.76) dividing two statistically different populations; low transport-low loss and high transport – high loss (Figure 5.6).

Using laboratory conditions, Horner et al. (1990a) reported a 4% to 13% loss in algal biomass exposed to suspended clay and silt sized clastic sediment. In a similar flume study, Francoeur and Biggs (2006) reported a 0% to 40% loss of periphyton biomass by suspended sand (i.e. 84.2% < 0.5 mm, 100% < 3 mm), after an initial velocity increase. Similarly, we found a 20% to 48% reduction in diatom-dominated periphyton

biomass for sand transport rates exceeding 0.04 g m<sup>-1</sup>s<sup>-1</sup>, considering both suspended and saltating sands (Figure 5.6). As in the flume studies, the reduction in biomass was directly attributable to abrasion by sand and independent of losses associated with the shear force of water. In our experiment, we found an initial 30% to 50% decrease in biomass in less than 15 minutes of exposure to an increase velocity in sediment free water, as reported in previous flume studies (Francoeur and Biggs 2006, Horner et al. 1990).

**Culp et al. (1986) comparison.** Figure 5.6 shows that up to 48% of periphyton biomass loss occurred at sand transport rates between 0.04 to 1.8 g m<sup>-1</sup>s<sup>-1</sup> (Table 5.7). In a similar type of *in situ* field experiment, Culp et al. (1986) found a 50% reduction in macroinvertebrate biomass from saltating 0.5 to 2 mm sand at a rate of  $0.104\pm0.034$  g m<sup>-1</sup>s<sup>-1</sup>. Culp et al. (1986) observed saltating sand scouring the bed during the experiment but periphyton losses were not quantified.

### **5.4 Discussion**

In all experimental runs, an increase in sand transport intensity resulted in larger periphyton losses, as implied from field data relating post-spate biomass to sand transport rate during natural spates (Ch. 3 & Ch. 4). In chapter 4, low biomass (Mean <  $10 \text{ mg/m}^2$ ) on patches of bed exposed to transport rates greater than 64 g m<sup>-1</sup>event<sup>-1</sup> (6.5 to 180 g m<sup>-1</sup>event<sup>-1</sup>) imply that losses occur for these high rates of sand transport but measurements of loss were not available to test this assumption. Here, our experimental results confirmed that large losses of periphyton occur through saltating sand abrasion at rates greater than 40 g m<sup>-1</sup>event<sup>-1</sup> (9 to 200 g m<sup>-1</sup>event<sup>-1</sup>). Variability in the loss rate of periphyton was attributable to differences in host-rock height and the caliber of sand being transported over the bed.

### 5.4.1 Protrusion height related effects on periphyton abrasion

The immersion index developed in chapter 3 implies that for a given flow and saltation intensity, rocks that extend above the saltation layer contain more periphyton than lower lying substrates. Similarly, researchers have described a "trim line" at a

certain elevation above the bed matrix that divides host-rocks with high protrusion heights and biomass from rocks with low protrusion heights and biomass (Stevenson, 1996). Here, we found that elevated substrates (Run 3) retained more post-disturbance periphyton than low lying substrates (Run 1) for all but the highest sand transport rates tested. We attribute this result to a decrease in sediment concentration with distance above the bed. The spatial pattern of periphyton observed at moderate sand transport rates was similar to that reported by other researchers (Francoeur and Biggs, 2006, Ch. 3). Specifically, periphyton biomass was noticeably lower on the top of the rock, moderate on the lower-upstream face and highest on the sheltered downstream face. The scour of periphyton on the top of host-rocks 6 cm off the stream bed was not anticipated, because flume studies predict 1-2 cm saltation heights (Sklar and Dietrich, 2004). There are two possible explanations for this result. First, saltation heights over a coarse bed are much higher than for flat beds. This was certainly the case in our experiment, as we observed sand grains saltating up, and launching off of imbricated rocks. In fact, one possible explanation for not observing the hypothesized trim line is that the 6 cm protrusion height was too low, below the maximum saltation height for those conditions. The second possible explanation is that the sand abrading the top of the host-rocks was suspended and not saltating. This scenario was also possible because the 0.5-2 mm sand was near the threshold for suspended transport (Table 5.2).

### 5.4.2 Sand calibre related effects on periphyton abrasion.

For the flow conditions tested, we found that coarse sand (0.5 mm to 2 mm) moved primarily by saltation, and fine sand (<0.5 mm) moved primarily in suspension (Table 5.2). Thus we could not isolate fine sand saltation effects on periphyton from coarse sand saltation effects. However, our results provide clear evidence that fine (predominantly) suspended sand was less abrasive to periphyton than coarse (predominantly) saltating sand, for identical sand seeding masses, and the hydraulic condition tested. There are two possible reasons for this result. First, as the percentage of sand moving as suspended load increases, the abrasive effect of sand on periphyton decreases because the suspended grains have less frequent contact with the stream bed than saltating sand grains (Dade and Friend, 1998). Second, saltating sand grains impart 142

more kinetic energy on the streambed because they are heavier than suspended grains and strike the bed at at a more direct (less glancing) angle than suspended sand grains. Consequently, saltating sand contacts should remove more periphyton per contact. Flume studies report a 0 to 40% reduction in periphyton biomass from suspended sediment. We found comparable, if not slightly higher losses (20-48%) of periphyton when both fine sand and coarse sand abrasion test runs were considered.

# **5.4.3** The importance of bedload transport rates in the prediction of post-spate periphyton biomass.

Stokseth (1994) found stronger negative relationships between periphyton and bedload transport (i.e. > 0.16 mm), relative to between periphyton and suspended load (i.e. 0.001-0.5 mm) in the Sokna River, Norway. Both the Skona river and SMR are similar in channel dimension, are diatom-dominated, and are adjusted to frequent spate disturbance. Stokseth's (1994) equation relating post-spate biomass from bedload transport rates for sand and gravels was nearly identical to our equation (5.1) (Section 5.3.3), which was developed from experimental data for sand transport. Consequently, our study results may be more broadly applicable to similar river systems and lower spate intensities, relative to the spate conditions tested by Stokseth (1994).

#### **5.4.4 Significance and future work**

Our ability to predict the amount of periphyton in river systems is very important because it allows us to assess the rate of recovery of the periphyton biomass after spates and floods. Surfaces that are scoured 'clean' of periphyton take longer to reach carrying capacity, and provide fewer algal spores for recolonization, relative to those surfaces that retain some measure of biomass. Consequently, small changes in spate frequency due to a change in climate or land use have the potential to significantly reduce the periphyton biomass. A significant reduction in periphyton biomass within rivers can influence the productivity of organisms occupying higher trophic levels. Our results show that periphyton losses can occur at very low levels of sand transport 0.027 g m<sup>-1</sup>s<sup>-1</sup>. Large periphyton losses from saltating sand occurred at transport rates between 0.04 and 1.8 g m<sup>-1</sup>s<sup>-1</sup>. Similarly, substantial reductions (50%) in macroinvertebrate densities from

saltating sand have been reported for cobble beds exposed to sand transport rates between 0.07 and 0.14 g m<sup>-1</sup>s<sup>-1</sup> (Culp et al. 1986). Thus, low levels of saltation can remove both substantial amounts of benthic food resources (i.e. diatom dominated periphyton) and the macroinvertebrates that graze upon these algae. The effects of these biomass losses that occur during frequent spates on the upper trophic levels (e.g. fish, crustecans and molluscs), have yet to be explored.

More work is required to incorporate the process of periphyton abrasion by saltating sediment into a mechanistic, numerical modelling scheme to better assess the resistance and recovery potential of river systems. This will require determining detachment thresholds for different algal communities, both within and outside of the optimal temperature range for these taxa assemblages. Our study has shown the importance of impact intensity, represented by sand transport rate, in determining degree of periphyton loss. More research is also required into the continued refinement of methods for the accurate prediction of sand transport rates (e.g. Curran and Wilcock, 2005; Grams et al., 2006). Many researchers have contributed to our understanding of the saltation process in flowing water, but extension of these research efforts into coarse beds would be beneficial (e.g. Hardy, 2005; Sambrook Smith and Nicholas, 2005).

### **5.5 Conclusions**

There are two major difficulties in assessing periphyton biomass (Uehlinger, 1991). First, periphyton sampling frequency in flood-prone rivers has to be appropriate for the rivers discharge regime. We have approached this problem by simulating spate conditions by the controlled release of increasingly larger masses of sand and by using a variety of sand sizes. Second, there is a very high spatial variability in periphyton biomass (Cattaneo et al., 1993). This study has demonstrated that a critical element in determining the spatial distribution of biomass in these systems is the intensity and mode of transport of sand over a coarse bed.

Global climate change and urbanization threaten to increase the volume and intensity of runoff, as well as the entrainment of fine sediments through soil erosion, mass wasting, and channel adjustment (Gregory et al., 1992; Goudie, 2006). The major implication of the findings described here is that that low rates of sand transport (e.g. 0.04 g m<sup>-1</sup>s<sup>-1</sup>) can cause diatom-dominated periphyton loss and moderate rates (e.g. > 0.2 g m<sup>-1</sup>s<sup>-1</sup>) can lead to significant scour of periphyton from a stable cobble bed stream, such as the SMR. This is significant because small changes in sand supply or flow level can lead to large changes in sand transport rates (Wilcock and Kenworthy, 2002).

### **Context and connecting statement for chapter 6**

In Chapter 3, we developed and tested a periphyton saltation abrasion model (PSAM) which explained up to 59% of the spatial variation at the rock scale in periphyton biomass after low-magnitude spates. PSAM was based primarily on the process of saltating sand abrasion. In Chapter 4, we documented thresholds of periphyton disturbance by flow velocity (0.5 m/s), shear stress (15 Pa) and sand transport (64 to 180 gm<sup>-1</sup>event<sup>-1</sup>) and examined their cross-stream distribution to test the hypothesis that periphyton refuge is highest between the extreme conditions of the thalweg and varial zones. Chapter 5 confirms the statistical inferences made in Chapters 3 and 4 regarding periphyton loss processes through direct observations of saltating sand during an *in situ* field experiment. Tall substrates retained more periphyton than low profile substrates because they were more sheltered from abrasion, as represented in the PSAM immersion index. While the focus of Chapter 4 was cross-riffle refuge patterns, in Chapter 6, we examine along river patterns in periphyton refuge. We couple the rock scale PSAM with a hierarchically structured geomorphic template, which is based on data from five reference sedimentary links located on the Sainte Marguerite River. The model is used to investigate how channel morphology and sand supply affect the longitudinal distribution of periphyton biomass during a typical spate. Model behavior is compared to field studies that infer how sand supply affects longitudinal trends in biomass from observations of biomass below dams/lakes and quarries.

# Chapter 6

# Modelling the effects of river sedimentary link structure and sand supply on downstream trends in periphyton refuge

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## Abstract

Periphyton are at the base of the riverine food web and subject to anthropogenically induced stresses such as shifts in discharge and sediment regimes. Models to assess how these periphyton stresses are differentially distributed within drainage networks are lacking. Periphyton models have been developed at small spatial scales, although the need to examine how these processes are affected by larger scale geomorphic form and process is pressing. In this paper, we develop a hierarchical periphyton perturbation model (HPPM) that simulates how the transport of water and mobile sands down a sedimentary link (e.g. segment of river between coarse supply zones along which grainsizes decrease systematically downstream from coarse cobbles to gravel) influences longitudinal trends in post-spate periphyton biomass. The HPPM is composed of a multi-scale geomorphologic template and smaller scale hydraulic, sand transport, and periphyton perturbation sub-models. The geomorphic template models were based on data from 35 reaches within 5 sedimentary links along a Canadian Boreal Atlantic salmon river. Once validated, the HPPM was used to examine the effects of variability in channel morphology and sand supply on post-spate periphyton biomass for a low-magnitude high-frequency spate (0.85 x mean annual discharge, 50% exceedance annually) during which sand is transported over a stable gravel-cobble bed.

The morphology along sedimentary links varied from low-gradient, sinuous gravel-bed channels to high-gradient, straighter cobble-bed channels. Monitored links contained 3 morphologically distinct channel types (hydrogeomorphic reaches or HGRs): Low-HGR (10-30 W/m<sup>2</sup> at bankfull discharge), Medium-HGR (30-60 W/m<sup>2</sup>), and High-HGR (60-80 W/m<sup>2</sup>). The HPPM predicts that the downlink distribution of post-spate periphyton biomass was nonlinear. The highest post-spate biomass (i.e. refuge) within

the sedimentary link was found in the downstream gravel bed reach (Low-HGRs). Periphyton abrasion decreased downstream in Low- and Medium-HPG's because less sand was being transported as flow energy decreased. Near the upstream limit of the links, biomass increased slightly going upstream, due to a sheltering effect caused by the upstream increase in rock height exceeding the upstream increase in saltation height of sand. The HPPM model predicted a downstream decrease in biomass under low sand supply conditions in High\_HGRs as observed below dams and lakes (Cattaneo, 1996; Jakob et al., 2003; Meyers et al., 2007). Further, a downstream increase in biomass under high sand supply conditions was predicted down the entire link by the HPPM, as observed downstream from a quarry (Yamada and Nakamura, 2002). Sensitivity analyses showed that even during constant, low-magnitude discharge conditions, periphyton biomass down the entire link decreased by a factor of 8 when the fraction of sand on the bed was increased from 5% to 20%, confirming that the effect of a spate on periphyton biomass is strongly influenced by pre-spate sand supply.

### **6.1 Introduction**

The food web of mid-sized temperate, gravel-cobble bed rivers is based on periphyton (Vannote et al., 1980; Gregory, 1983; Biggs, 1995; Lamberti, 1996), which is vulnerable to erosion by transported sand during low-magnitude, high-frequency spates (e.g. < 30% bankfull stage, < 1 mean annual discharge (1MAD)) (Power and Stewart, 1987, Ch. 3). At the scale of an individual rock (i.e. "rock scale" see Table 6.1), periphyton biomass increases with the availability of resources (e.g. light, nutrients, temperature) and decreases with disturbance (e.g. hydraulic plucking, abrasion by mobile sediment) (Stevenson, 1996; Azim et al., 2005; Biggs and Kilroy, 2007). During spates, periphyton is scoured from patches of streambed where harsh physical conditions exist (e.g. sand transport rates > 64 to 180 g m<sup>-1</sup>event<sup>-1</sup>, average velocities > 0.5 m/s, shear stresses > 15 Pa, Ch. 4). Large spates capable of mobilizing coarse bed materials (e.g. > 3MAD) reset the periphyton community to low levels over large areas (e.g. km's) of streambed (Tett et al., 1978; Uehlinger et al., 1996). Researchers concur that the physical disturbance effects associated with low-magnitude spates is patchier than that of high-

Holon	Description	Spatial Scale	
Network scale	When viewed at the watershed level, the river is a dendritic network of many tributaries. The structure of the drainage network is hierarchical, consisting of links, defined in terms of magnitude (Shreve 1966) or stream order (Strahler 1952), and nodes, which are junctions of conjoining links.	scale of the entire watershed, 10-1000's kms	
Link scale*	The segment of river bound by two tributary nodes	> 10-14 channel widths, 1-10's kms	
Planform scale	Reaches with uniform planform characteristics	one meander wavelength, minimum length is 10-14	
	e.g. high sinuosity vs low sinuosity	channel widths, 10-100's m,	
Bar unit scale	Pool-riffle-point bar sequence	5-7 channel widths	
Bar element scale	Riffle or pool	2-3 channel widths	
Bedform scale	Unit bars, clusters of rocks, ripples	<1 channel width, cm-m	
Rock scale	Individual particles (gravel, cobble etc.) or particle clusters	μm-m	

**Table 6.1** Scale-based nested hierarchy of fluvial forms (Adapted from Frothingham et al., 2002).

\*as in topological link and not to be confused with the sedimentary link of Rice and Church, (1998) described in the text.

magnitude spates (Power and Stewart, 1987; Brookes, 1996; Brooks, 1998; Matthaei et al., 2003). However, little is known about the size and extent of perturbed area or how it relates to channel morphology and small scale processes.

During low-magnitude spates, coarser materials (e.g. gravel, cobble, boulder) remain static, and a large percentage (> 40% in gravel bed rivers (Lisle, 1995)) of the bedload moved is sand ( $D_i < 2$  mm) (Stokseth, 1994; Grams et al., 2006). This sand is typically transported by saltation (bouncing along the stream bed), a highly abrasive form of transport for periphyton (Figure 6.1). Such sand can be transported even at baseflow conditions, and small additions of sand can dramatically increase the rate of transport (Wilcock and Kenworthy, 2002; Bond, 2004; Thomson et al., 2005). Patches of streambed resistant to the effects of disturbances from saltating sand or hydraulic stresses serve as periphyton refuge zones. Such refuge zones can occur at any spatial scale within the drainage network (Table 6.1) and supply downstream areas denuded of periphyton



**Figure 6.1** The degree of scour on a rocks surface should partially be a function of the saltation height (SH) relative to the top of the rock or protrusion height (PH). When the immersion index (SH/PH) exceeds unity then the rock should be fully immersed in saltating sand. Increasing saltation height between figure b) and figure d) could be from increasing flow intensity or decreasing sand size for same flow.

with algae for recolonization, thereby improving the river systems resilience to frequent flow disturbances (Stevenson, 1983; Sedell et al., 1990; Lake, 2000; Lutscher et al., 2007). Knowledge of how geomorphology and sand supply affect spatial patterns in postspate biomass is essential for food resource mapping, identifying productive nodes in the river, and predicting how an increase in spate frequency and sand supply affects long term and large scale along stream variability in periphyton refuge (Cada et al., 1987; Uehlinger et al., 1996; Nislow et al., 1999; Osmundson et al., 2002; Thorp et al., 2006; Ledger et al., 2008).

Empirical studies have shown that periphyton biomass does not always increase steadily along a continuum of increasing light and nutrients with distance down the river network (1<sup>st</sup> to 6<sup>th</sup> order) (Vannote et al., 1980; Biggs and Close, 1989; Wright and Li, 2002; Naiman et al., 1987). Osmundson et al. (2002) observed that periphyton biomass decreased down the drainage network as the amount of sand on the bed and the average velocity increased. Discontinuities in biomass are attributed to habitat variability (e.g. velocity, nutrients) at smaller spatial scales (e.g. grain, bar element, Table 6.1) and to

spate disturbance history (Young and Huryn, 1996; Biggs et al., 1998; Wright and Li, 2002; Naiman et al., 1987). These principles are reflected in the Riverine Ecosystem Synthesis (RES, Thorp et al., 2006) that views the river network as a downstream array of hydrogeomorphic patches (HGP's, e.g. meandering, anabranched, braiding; mobile vs. armoured). These particular "patches" are plan-scale (Table 6.1) in size and commonly referred to as "reaches" by geomorphologists. We will subsequently refer to plan scale hydrogeomorphic patches as Hydrogeomorphic Reaches (HGRs), recognizing that a reach can be a patch as defined by landscape ecologists. These hydrogeomorphic reaches are defined based on the hydrologic regime over the streambed (discharge variability being a surrogate representing variability in substrate stability, nutrient supply, temperature etc.) and geomorphic character of the reach (Thorp et al., 2006). The HGR provides boundary conditions that limit the biotic assemblage of organisms that are adapted to persist under those conditions (i.e. habitat template, Poff and Ward, 1990). When the ecological structure of the HGR is considered, these templates can be referred to as ecogeomorphic reaches (or functional process zones, Thorp et al., 2006). There is mounting evidence that ecosystem function varies with HGR structure (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). For example, Coleman and Dahm (1990) found periphyton biomass was 11 times higher in a low gradient, beaver pond affected reach versus that in a steep, straight incised reach. Chessman et al. (2006) cautioned that comparisons of ecological elements between HGRs must be interpreted within the larger spatial context, because ecological limitations may be imposed at higher holons in the hierarchy of biomass regulating factors (e.g. plan-scale HGRs nested in links, see Table 6.1).

Channel types (HGRs) can thus vary between features such as tributaries, sediment sources and dams, which reset downstream trends in physical habitat (Rice Ferguson Hoey (Rice and Church, 2001; Benda et al., 2004; Ferguson et al., 2006). The section of river between points or zones with significant, coarse lateral sediment inputs is a "sedimentary link" (Rice and Church, 1998). Along any given sedimentary link, the sediment transport behaviour changes systematically downstream (Rice and Church, 2001; Davey and Lapointe, 2007). Sediment is size-selectively transported and abraded downstream, resulting in a downstream decrease in bed material size and adjusted channel slope along a link. The ability of the stream to do work on a unit bed area (e.g. Specific stream power = SSP = discharge x slope /channel width) decreases down the sedimentary link because the channel slope decreases, although the channel discharge remains roughly constant between tributaries (Knighton, 1999). Within a given sedimentary link, abrupt changes in channel form may be present. Distinct channel morphologies can be partitioned into channel types (~ HGRs) based on *SSP* thresholds (Ferguson, 1981; Hicken and Nanson, 1984; Brookes, 1987; Nanson and Croke, 1992; Van Den Berg, 1995; Bravard and Peiry, 1999).

Eco-geomorphological studies of sedimentary links have focused on biodiversity at transitions between links (Rice et al., 2001; Kiffney et al., 2006; Rice et al., 2006). However, a few studies have investigated longitudinal trends in biomass at the link scale (e.g. km's, Table 6.1)(Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007). Periphyton biomass was observed to be high, close downstream to sediment sinks (dams, lakes), but to decrease (or fluctuate more frequently) with distance downstream of these sinks, presumably as more potentially abrasive fine sediment is added to the system (Cattaneo, 1996; Jakob et al., 2003; Meyers et al., 2007). Conversely, Yamada and Nakamura (2002) found a downstream increase in periphyton biomass as fine sediment from a quarry source was stored in an over-widened and channelized reach of channel, presumably buffering the downstream reach from scour (or from smothering by silt).

Research has clearly shown that the abrasion of periphyton by fine sediments is an important biomass regulating process (e.g. Francoeur and Biggs, 2006) and likely affects link scale trends. However, direct tests of this effect at the link and drainage network scale (Table 6.1) are hard to conduct because of: 1) logistical difficulties involved in measuring variables such as velocity and periphyton over large areas, 2) difficulties in obtaining direct bed stability data (especially for sand, see Salant et al., 2006b), 3) inability to experimentally control spate magnitude or sediment load, and 4) a poor understanding of the mechanics of saltating sand, the main abrasion agent (Ch. 3-5). This type of multifaceted problem is much more amenable to a numerical modelling approach

after parameterization of the key processes (as per Chapters. 3, 4, 5, for example see Doyle and Stanley 2006).

Numerical models can clarify how competing biomass regulating processes, operating at small spatial scales, can result in emergent patterns at larger spatial scales. The eco-geomorphological system considered here is sufficiently complex that it is not obvious how rock scale (e.g. host-rocks) periphyton biomass regulating processes are expressed within a sedimentary link or how sensitive they are to sand supply. It is not clear how sand transport rates vary down a sedimentary link, and affect periphyton losses through abrasion. For example, sand transport rates may decrease downlink with decreasing flow shear stress; however, transport rates could remain high, or even increase downstream, if the stress required to move sand decreases rapidly down the sedimentary link due to a downstream increase in the fraction of sand on the bed.

In addition to uncertainties regarding longitudinal trends in periphyton perturbation by transported sand, gradients in sedimentary link morphololgy and spate magnitude may also potentially affect the longitudinal distribution of biomass. To illustrate this point we consider four possible longitudinal trends in biomass down a sedimentary link that grades from coarse-cobble to gravel riffles: 1) No pattern, 2) a downlink decrease, 3) a downlink increase, or 4) a nonlinear trend. In pattern 1, biomass may not vary down link when detachment thresholds for algae (e.g. Sand transport < 120g m<sup>-1</sup> event<sup>-1</sup>, Velocity < 0.5 m/s, Ch 4) are exceeded over all the riffles down the link, regardless of the differences in geomorphic character of each riffle. Field studies conducted over smaller spatial scales suggest that this homogeneous trend in biomass is more likely to be found after large spates of an unknown magnitude (Uehlinger 1991). In pattern 2, biomass may increase down link for lower magnitude spates, since these perturbation thresholds are less likely to be exceeded at the downstream end of the link where lower shear stresses are found. This hypothesis is based on the premise that velocity decreases down a sedimentary link. Contrary to what happens at the drainage network scale, flow velocity should decrease downstream within a sedimentary link because the channel slope decreases with little or no change in discharge (or growth related factors); especially if the sedimentary link is contained within a topological link.

Thus, periphyton is less likely to be disturbed by velocities greater than 0.5 m/s at the downstream end of the link. The third pattern is contrary to the second pattern. Specifically, biomass may increase uplink, despite the upstream increase in flow velocity, because the uplink increase in streambed grainsize provides more streambed substrate surfaces that are elevated above the layer of high intensity sand transport near the channel bed (Figure 6.1, Ch 3). Finally, the downstream trend in biomass may not be linear. Specifically, biomass may be high at the upstream and downstream end of a link (i.e. trends two and three) because biomass is protected at each end of the link through different mechanisms.

We investigate four inter-related themes in this paper:

1. What are the geomorphological characateristics of the HGRs of the Sainte Marguerite river and how are these habitats distributed down sedimentary links? Do these HGRs have similar geomorphological characteristics as channel types identified on other rivers?

2. Does the periphyton biomass following a low-magnitude, high-frequency spate vary downstream between these HGRs? Which HGR provides the most periphtyon refuge? In general, are HGRs relevant habitat templates that can be used to describe the patchiness of periphyton after small spates?

3. Similarly, which of the 4 potential down link patterns (no pattern, downlink decrease, downlink increase, nonlinear) of post-spate biomass predominates in a gravel-cobble bed sedimentary link? What combination of factors lead to the down link pattern in post-spate biomass?

4. How sensitive are biomass levels in sedimentary links to global additions of fraction sand on the bed ( $F_s$ ) and supply from upstream ( $Q_{sa\_in}$ )? More specifically: a) Does low sand supply (e.g. below dams) result in a downstream increase in sand transport rate and decrease in periphyton biomass (e.g. Jakob et al., 2003)? and b) Does high sand supply (e.g. below sand sources) lead to a downstream decrease in sand transport rate and potential increase in periphyton biomass (Yamada and Nakamura, 2002).

To investigate these questions, we collected field data to parameterize a hierarchical periphyton perturbation model (HPPM). The HPPM simulates the transport of water and sand down a sedimentary link that is divided into different channel types (HGRs) as a function of *SSP* levels. The HPPM consists of four sub-models: geomorphologic, hydraulic, sand transport, and periphyton perturbation. The geomorphic template is based on the average morphometric characteristics of 35 planform reaches in 5 sedimentary links along the Sainte Marguerite River, a Canadian, Atlantic salmon river. The geomorphic template consists of a group of models that use regime theory and other empirical relations to define morphometric characteristics (Chang, 1988). The geomorphic template is represented by a nested hierarchy of scales: sedimentary link, planform, bar element (i.e. riffle), and grain (i.e. host-rock) scales (Table 6.1). The HPPM calculates periphyton biomass at the rock scale, based on driving forces controlled at the link and network scales. From these rock scale calculations, periphyton biomass and physical disturbance variables were simulated along the link and for a range of sand supply scenarios.

Through the development of the hierarchical periphyton perturbation model (HPPM), this study addresses and incorporates several pressing ecogeomorphology related research issues, including: 1) examining how small scale processes operate within a larger scale context, 2) investigating sediment dynamics over HGRs (i.e. as opposed to hydraulic fluctuations alone), and 3) investigating sub-bankfull spate effects on biota (i.e. as opposed to focusing on extreme high or drought flows, Lake, 2000; Thorp et al., 2006). The HPPM provides a framework for testing eco-geomorphological theory and (with further testing) mapping of food resources at a large spatial scale. From a river management perspective, the HPPM also permits an initial assessment of the spatial extent and severity of periphyton perturbation resulting from alterations in a rivers sand load and flood frequency, two disturbance factors that vary with changes in land use and climate.

## 6.2 Methods

Four steps were required to achieve our objectives: 1) Divide sedimentary links into channel types (hydrogeomorphic patches) based on field link data (Section 6.2.2); 2) Develop a hierarchical periphyton perturbation model (HPPM) based on process parameterizations from our reference river (Section 6.2.2); 3) Verify and validate the HPPM model with longitudinal data from one reference link and two spates (Section 6.2.3); and 4) Simulate downstream trends in periphyton biomass in the reference link for a low-magnitude, high-frequency summer spate, while considering three distinct sand supply scenarios at the head of the link that are: i) an average fraction of sand on the gravel-cobble bed and average sand supply to the head of the reference link (i.e. initial sand supply) based on our reference field conditions; ii) varying the fraction of sand on the bed to reflect sand starved to sand rich (disturbed) conditions; and iii) varying the initial upstream sand supply up to an extreme, but realistic rate (Section 6.2.3).

### 6.2.1 Study Sites: Reference link and spate data

The reference river (Sainte Marguerite River, SMR) flows through deeply fractured granite and schist rocks of the Canadian Shield, Quebec, Canada (Figure 6.2,  $48^{\circ}26'56"$ ,  $70^{\circ}26'97"W$ ). The spring (April, May) flood peak is driven by snowmelt. At Big Pool (drainage basin area = 233 km<sup>2</sup>), the 2 year return period flood is 83 m<sup>3</sup>/s and the mean annual discharge (MAD) is 9.6 m<sup>3</sup>/s. The July-September baseflow in 2004 was 2.4 m<sup>3</sup>/s (0.25MAD, exceeded 90% of the time annually). The periphyton community is diatom dominated and typical peak biomass (e.g. 31 mg/m<sup>2</sup> chl*a*, Rasmussen and Trudeau 2007) occurs in August. The average peak discharge for frequent spates occurring during the primary growth season (July-Sept) was 8 m<sup>3</sup>/s or 0.85MAD (Min=2.3m<sup>3</sup>/s, Max = 34.3 m<sup>3</sup>/s) with a mean recurrence period 7.1 days (Range 5.7-8.3). Here, a spate is defined as any rise in daily discharge greater than the preceding or following day that occurs 3 or more days after a previous discharge peak. This average summer spate peak (8 m<sup>3</sup>/s) flow is exceeded 25% of the time at weekly mean intervals during the summer period (July-Sept.) and 48% of the time annually.
The morphometric data used to develop the geomorphic template for channel types along a link were collected at 35 riffles located within five sedimentary links (Tables 6.2 & 6.3). One cross section was surveyed on each riffle in each link (except Bardsville where only every 5<sup>th</sup> riffle was sampled). Cross sections were positioned one third of the channel width upstream of the crest of the riffle, where flow conditions are more uniform within the cross section. A topographic survey of the longitudinal profile and a transverse cross section at each riffle was done using a Wild 206 total station. Planimetric characteristics were measured from high resolution, airborne videography (10 cm resolution). Substrate grainsize was measured in the field across each riffle (Wolman, 1954, n = 100). Data loggers (Campbell Scientific<sup>TM</sup> 21X) were used to monitor average



**Figure 6.2** Location of the study reaches on the Sainte Marguerite River within Quebec, Canada. Sampling in 2003 focused on 35 riffles distributed between the Cascade, Onesime, Big Pool and Bardsville reference reaches. Sampling in 2004 focused on 15 riffles distributed between the Big Pool and Meander reaches.

	No.	Distance		Drainage	Riffle Slope @		Median Particle	Width @ Bankfull	Baseflow	Riffle Depth
	of	Upst	ream	Area	Base	eflow	Size (D <sub>50</sub> )	Discharge	Depth	@ Bankfull Discharge
Sedimentary Link	Rif- fles	Min	Max	Avg	Min	Max	Avg±SE	Avg±SE	Avg	Avg
		(km)	(km)	(km <sup>2</sup> )	(m/m)	(m/m)	(mm)	(m)	(m)	(m)
Cascade	4	85.17	85.76	88.5	0.0017	0.0080	56±13	30.4±1.3	0.38	0.80
Onesime	8	67.00	67.87	208.2	0.0006	0.0077	58±11	26.3±3.0	0.38	0.86
Big Pool	9	59.67	61.09	233.5	0.0006	0.0044	44±13	34.5±2.6	0.44	1.31
Meander	6	52.89	53.82	280.2	0.0012	0.0032	34±5	40.7±2.4	0.38	1.09
Bardsville <sup>1</sup>	8	33.29	42.47	568.5	0.0011	0.0056	97±15	53.4±2.9	0.48	1.51
River	35				0.0006	0.008	65±42	36.6±11.6	0.41	1.11
1 – Two sites	at the do	wnstream e	end of Mea	nder link and	d one site a	bove the c	onfluence o	n the North W	est Branch.	

**Table 6.2** Summary of morphometric properties of five sedimentary links of the Sainte Marguerite river.

Table 6.3	Summary	of bankfull	discharge,	specific stream	power an	d sand	transport
rates mea	isured in fiv	ve reference	e links of tl	ne Sainte Margu	ierite Rive	er.	

	Specific st (Bar	ream power nk full)	Bank Full Discharge	Sand (0.5-2 mm) transport rate (summ spate data measured in 2003)	
Sedimentary Link	Avg.	Min-Max		Avg±SD	Min-Max
	(W/m²)	(W/m²)	(m³/s)	(g m <sup>-1</sup> event <sup>-1</sup> )	
Cascade	30	10-52	18.8	1136 ±403	619 -1526
Onesime	42	11-87	37.2	802±403	200-1198
Big Pool	26	6-44	40.8	632±366	155 – 1303
Meander	23	12-32	47.2		
Bardsville	53	19-80	82.6	1444±529	440 -2099
River	35	6-87	48		155 -2099

flow levels and turbidity at fifteen minute intervals near the centre of each link.

Regression curves related the stage at this data logger station with the stage measured on a staff gauge at each riffle. Local water surface slopes over riffle cross sections were measured using a Sokkia<sup>TM</sup> B2C level during base flow conditions (Depth = 0.11 m) and near bankfull conditions (Depth = 0.49 to 0.55 m). Linear regression (p < 0.05) of

measured water surface elevation versus distance downstream along each riffle was used to calculate the local water surface slope.

Measurements of periphyton biomass and rock scale physical disturbance factors were collected during 2003 and 2004. The 2003 sampling period (18 July 2003 to 30 August 2003) was characterized by three major spates, the largest of which was 3MAD (17 August 2003). The 2004 sampling period (2 August 2004 to 26 August 2004) was characterized by a series of smaller spates. In 2004, the largest spate was only 0.63MAD (24 August, 2004). Over each riffle cross section, we measured: 1) post-spate periphyton biomass, 2) sand transport rates, 3) peak spate shear stress, 4) flow velocity, and 5) fraction of sand on the bed. Post-spate periphyton biomass was quantified using USEPA Rapid assessment protocol (5 categories based on mat thickness) on the top of 60, evenly spaced rocks, selected without size bias (Wolman, 1954; Stevenson and Bahls, 1999). The amount of chlorophyll a was measured using spectrophotometry (24 h extraction using 95% acetone) on 10 rocks within each USEPA rank (Parsons et al., 1984). A Bonferoni Anova was used to quantify the degree of discrimination between USEPA ranks. Sand transport rates were measured at 4 to 10 Sedibac<sup>TM</sup> sediment traps per riffle capturing particles < 8 mm; 3) estimated peak spate shear stress at each rock using DuBoys equation (Chang, 1988). This DuBoys estimate was calibrated to an alternative estimate of shear stress (Wilcock et al., 1996) using velocity measurements (Appendix B.2, 3.2). Velocity was measured for 1.5 minutes at 0.4 flow depth using a Gurley No. 625D Pygmy meter at all sediment trap locations during stable flow conditions (18-23 August 2004). The fraction of sand on the bed (McNeil and Ahnell, 1964, samples truncated at 32 mm) was measured at all trap locations after the 2004 spate period. Davey (2004) provided bulk sample grainsize data (pavement and subpavement layers) for adjacent barhead and thalweg locations.

#### 6.2.2 HPPM Model Approach

The HPPM estimates post-spate periphyton biomass at the rock scale, based on driving and disturbance forces operating at the link and network scales. A detailed account of the modelling procedures is given in Table 6.4 and the governing equations are

I able o.4 Summary o	d labour	Locedures L	oy spanan su	cale and associated boundary con	ligitions, sud-titouel co	omponents and parameterization sources.
Deutacing Conditione		Modelliing	Procedure:	s by Spatial Scale	Model Cemenent	Doromotorization Mothod
	Vetwork	Link	Bar Element	Bedform/Grain		
1	Select the	position of lir	I nk in the wate	srshed		
Drainage Basin Area	Determine	e design disch and be	harges (Q1.8, aseflow disch	, Q1.05), spate discharge (Qspate) H arge (Qbase)	Hydrologic submodels	Empirical Hydrologic Models fit to Ste Marguerite River (SMR)
Down Link Gradient in Specific Stream Power (SSP)	2)	Divide link i Determine L Determine c	nto 20 riffles Link Length Jown link grac	ranging from 5 - 80 W/m <sup>2</sup> s silent in bed grainsize and channel	Morphometric submodels	Channel Form (Kondolf 2003) Morphometric Empiricism (Poff et al 2006) Width- Regime function (Griffiths 1981) fit to SMR D50 - Empirical fit to SMR
Width & SSP			Determine rif	the slope 5	Slope selection model	Slope - Width regime function/ Width specific stream power = 1
Asymmetric Channel		3)	Calculate not	mal depth for Q1.8	Hydraulic submodel A	Normal Depth (Henderson 1966) using
Geometry Discharge + Channel			Calculate noi Divide riffle c	rmal depth for Q <sub>base</sub> and Q <sub>spate</sub> cross section into 11 segments	2	Channel Area (Ferguson et al 2003), Mannings, Limerinos (1978)
Asymmetry		4)	Calculate be-	d grainsize across the CX	-ateral sorting submodel	Regression - parameterized using SM River data
Water surface slope		5)		Calculate conditioning velocity	Hydraulic submodel B	Mannings, Limerinos (1978)
Sand supply at Link top Fraction Sand on Bed				Calculate spate shear stress	Hydraulic submodel C	Average Shear Stress (Chang 1988, p 38) compensated for roughness & distance to thalweg
Protrusion Ht = 55% D50				Calculate spate sand transport 8	and transport submodel	Overpass compensating sand transport model
				Calculate protrusion height		(Luce et al 2007) Empirical fit to SMR.
				Calculate residual periphyton F biomass.	<sup>o</sup> eriphyton submodel	Periphyton Saltation Abrasion Model (PSAM) (Luce, Steele, Lapointe 2008)
	(9		Riffle - Calcu periphyton bi	ulate central tendency measures for iomass and disturbance variables		8
		Link - Plot r biomass an power gradi	neasures of c d disturbance ient or distanc	central tendency for periphyton > variables versus specific stream ce downstream.	Display down-link trends	
-	Network - procedure lesser drai	Select new li s to determin inage basin a	ink location in the downstrear trea.	the watershed using above the material and the second sin a link of greater or the second sec	Display down-watershed rends	

.... U V G Tahla provided in Appendices A.1 and A.2. The model was constructed in Microsoft Excel (2007) utilizing Solver and Visual Basic. The six basic steps involved in applying the periphyton model to a geomorphic zone are to: 1) Select the position of the given link within the network and calculate bankfull discharge given the drainage basin area; 2) Divide the link into 20 riffles ranging in *SSP* from 5 to 80 W/m<sup>2</sup> and calculate the range of geomorphic characteristics within the link (Figure 6.3); 3) Calculate the local riffle cross section geometric template of characteristics and equally divide the riffle into 12 host-rock locations (details below, Figure 6.3a); 4) Calculate the grain size characteristics of the patch surrounding each host-rock (details below); 5) For the small test spate, calculate the periphyton model parameters (Figure 6.4a, b) and periphyton biomass (Figure 6.4c) for each of the 12 equally spaced rocks across each riffle, and; 6) Average periphyton biomass for each riffle and plot down-link trends. The main sub-models are discussed in the following sections.

Geomorphic template sub-models. Bankfull riffle cross section dimensions were calculated using regime theory. Regime models of channel form typically consider water discharge (Q), sediment discharge ( $Q_s$ ) and median size ( $D_{50}$ ) as independent variables and channel width (W), depth (d) and slope (S) as dependent variables (Chang, 1988; Pizzuto, 1992; Eaton et al., 2004). The geomorphic template is a generic representation of a series of riffles down a sedimentary link, with flow and sediment transport characteristics representing those monitored on the reference Sainte Marguerite river. Consequently, we transformed our downstream SSP gradient into a downstream grain size distribution using a regression equation relating median grain size to bankfull SSP (Appendix B.2, 1.2, distribution illustrated in Figure 6.3b). Further, data from these reference riffles were used to fit a regime equation for bankfull channel width developed by Griffiths (1981; 1984) using nonlinear regression (i.e.  $W_1 = 14.747 Q_{bfl}^{0.514} S^{0.238}/$  $D_{50}^{0.142}$ ,  $Q_{bfl}$  = bankfull discharge,  $D_{50}$  = median grain size of riffle). The equation represents the bankfull width for a predominantly stable river where there is a balance between Q,  $Q_s$  and channel form. Width was also specified as  $W_2 = SQ/SSP$ . A 'stable' slope was calculated by iteratively solving for S when  $W_2 = W_1$ . Our approach avoided solutions requiring the optimization of bedload transport, or minimization of stream



**Figure 6.3** The bankfull channel geometry across simulated riffles was calculated a) for different levels of bankfull specific stream power down a sedimentary link with constant discharge. For these calculations, b) a downstream reduction in grain size was assumed using a regression equation of cross section median particle size as a function of specific stream power fitted to field data from the Sainte Marguerite river. c) The slope and bankfull channel geometry was calculated (see Section 6.2.2) for all 20 riffles in the simulated sedimentary link longitudinal profile.

power expenditure. These latter approaches result in the design of threshold type channels regardless of river scale, unlike natural channels that may have higher levels of excess shear stress with distance downstream (Benda et al., 2004).

To calculate the bankfull channel dimensions (e.g. Figure 6.3a), we iteratively solved for normal depth using an estimate of bankfull discharge ( $Q_{bfl}$ ) and S, W, and  $D_{50}$  for each riffle. The bankfull discharge was constant within a given link and specified by a regression between field measurements of bankfull discharge as a function of drainage basin area (Appendix B.2, 1.1). The normal depth calculation assumed an asymmetric channel geometry (Ferguson, 2003) and used the continuity of flow, the Manning's velocity equation (Chang, 1988), and the Limerinos (1970) roughness function. To compensate for not using a backward step calculation, which accounts for backwatering

behind the riffle crest at low flows, the local riffle water surface slope was empirically scaled to dimensionless discharge (fraction bankfull) as given in Appendix B.2, 2.7-2.9). By this scaling procedure, the difference between bankfull (measured in May 2004) and low flow (measured in August 2004), water surface slope decreases for higher stream power riffles (i.e. less backwater effect at low flow for steeper reaches).

Each of the five reference links were simulated using the HPPM, by specifying their average drainage basin area, to compare simulated bankfull morphometric properties (e.g. width, depth) to measured bankfull morphometric properties and thus verify the geomorphic model components. The relations between predicted and observed morphometric properties were highly significant (p < 0.0005) with only slight biases.

Assigning morphometric properties to the bankfull riffle: cross channel sediment sorting and flow depths. Having established the bankfull channel dimensions, the normal depth at riffles, was then calculated for: 1) the discharge during growth conditions ( $Q_{base} = 0.24$ MAD, Figure. 6.4a), and 2) the reference spate discharge to be tested ( $Q_{Ref} = 0.85$ MAD). The water depth at each rock was calculated for these discharges by subtracting the local water stage from the bed elevation at each station. The cross stream distribution of median grain size varied across each riffle based on a regression equation from SMR data relating lateral fining rate and dimensionless distance (i.e. distance from bank/bankfull width) from the deep side of the channel (i.e. cut bank) (Appendix B.2, 2.4, 2.5). By this equation, the median bed material became finer with distance from the thalweg. Similarly, the fraction of sand on the bed increased away from the eroded bank at a rate that was a function of the dimensionless distance from the cut bank (Appendix B.2, 2.6, also see Lisle, 1989).

Sand transport sub-model. The sand transport rate over the spate at each of the 12 rocks across each cross section was calculated using nonlinear regression models based on observed Sainte Marguerite river sand transport data, using a combination of the mechanistic functions of Wilcock and Kenworthy (2002) and Henderson (1966) (Appendix C, Luce et al., 2008). The nonlinear models consider the excess shear stress at the rock as well as the amount of sand advected from the upstream reach. The transport



**Figure 6.4** Modelled longitudinal profile showing the location of a) a riffle with bankfull specific stream power 35 W/m<sup>2</sup>, where the depth of flow is determined for a discharge characteristic of the growth period and of a test discharge. b) These depths are used to calculate the conditioning velocity characteristic of low flow, peak spate shear stress for the test discharge and sand transport for 10 patches across each cross section, based on local sand fraction,  $D_{50}$  and shear stress. c) In turn, these outputs are used to determine the post-spate periphyton biomass.

rate at each rock, for weak to moderate sand transport rates (i.e. 100 g m<sup>-1</sup>event<sup>-1</sup>  $< Q_{sa\_rock} < 1400$  g m<sup>-1</sup>event<sup>-1</sup>), is given by:

$$Q_{sa\_rock\_i_1} = (5.76\phi^{4.4})_{rock/patch} \left( Q_{sa\_in} \left( \frac{SSP_{below}}{SSP_{above}} \right)^2 \left( \frac{D_{us}}{D_{riffle}} \right)^{\frac{3}{2}} \right)_{reach} (6.1) \quad R^2_{adj} = 0.68$$

where,  $\phi$  is the excess shear stress for 2 mm sand on a gravel bed given by Wilcock and Kenworthy (2002). The  $\phi$  term increases with fraction of sand on the bed, degree of exposure to flow and shear stress over the patch. The 5.76 and 4.4 in equation (6.1) are constants fitted to data from the small 2004 spate (e.g.  $Q_{peak} = 6.2 \text{ m}^3/\text{s}$ ) considering only patches of bed where sand transport rates exceeded 100 g m<sup>-1</sup> event<sup>-1</sup>. The ( )<sub>*Reach*</sub> factor is derived from the Einstein Brown sediment transport formula and assumes a given sediment size and specific gravity, a wide channel, and a constant Chezy C (Henderson, 1966; Wilcock, 2004). The variable  $Q_{sa_in}$ , is the average sand transport rate from the riffle immediately upstream,  $(SSP_{below}/SSP_{above})^2$  is the ratio of SSP of the upstream inter-riffle reach  $(SSP_{above})$  and downstream inter-riffle reach  $(SSP_{below})$ . The  $(SSP_{below}/SSP_{above})^2$  term indicates the magnitude of downstream reduction in the ability of the stream to do work. The  $(D_{us}/D_{riffle})^{3/2}$  term is the ratio of median grain size at the riffle  $(D_{riffle})$  of the host- rock to the median grain size of the upstream riffle  $(D_{us})$ . This  $(D_{us}/D_{riffle})^{3/2}$  term increases with coarseness of the upstream riffle relative to the riffle where transport rate is being estimated, and it is an indirect measure of the downstream rate of change in transport potential, since particle size is proportional to the critical shear stress required to intiate sediment transport.

For near threshold conditions (<100 g m<sup>-1</sup>event<sup>-1</sup>) the sand transport rate was given by:

$$Q_{sa\_rock\_i_2} = (1.31\phi^{1.22})_{rock/patch} \left( Q_{sa\_in} \left( \frac{SSP_{below}}{SSP_{above}} \right)^2 \left( \frac{D_{us}}{D_{riffle}} \right)^{\frac{3}{2}} \right)_{reach} (6.2) R^2_{adj} = 0.30$$

Equation (6.2) was fit to data from the small 2004 spate (e.g.  $Q_{peak} = 6.2 \text{ m}^3/\text{s}$ ) considering only low sand transport (i.e.  $Q_{sa} < 100 \text{ g m}^{-1}\text{event}^{-1}$ ) patches. While the  $R^2$  is much lower than for equation (6.1), previous studies have demonstrated that the effect of sand abrasion on periphyton removal is negligible for these low transport rates (Ch. 4, Ch. 5). The sand transport rate was then averaged for the 12 rocks across the riffle and this riffle average sand transport rate became the  $Q_{sa in 1}$  term for the downstream riffle.

For very high rates of  $Q_{sa\_in}$  (i.e. > 1400 g m<sup>-1</sup> event<sup>-1</sup>),  $Q_{sa\_in}$  for each riffle was given by the mean of:

$$Q_{sa\_rock\_i_3} = 8.4 (10^{2.20+0.665\log\phi})$$
 (6.3)  $R^2_{adj} = 0.15$ 

for each of the 12 rocks in the upstream cross section, if  $Q_{sa\_in\_1}$  exceeded 1400 g m<sup>-1</sup> event<sup>-1</sup>. Equation (6.3) is a regression equation fit to 94 observations of sand trap data collected during the much larger 2003 spates (e.g.  $Q_{peak}$ Spate 3 = 30.1 m<sup>3</sup>/s). While the amount of explained variance in equation (6.3) is low, the overall HPPM model output is insensitive to  $Q_{sa}$  in this range of conditions. Equation (6.3) is generally evoked during

very high rates of sand transport (e.g. >  $1400 \text{ g m}^{-1}\text{event}^{-1}$ ) that far exceed the sensitive range for periphyton loss (e.g. 64 to 180 g m<sup>-1</sup>event<sup>-1</sup>, Ch. 4).

Sand deposition occurs in the inter-riffle reach if the transport rate from the upstream riffle (i.e.  $Q_{sa_in}$ ) exceeds the transport rate of the modeled riffle (i.e.  $Q_{sa_out} = \overline{Q_{sa_rock}}$ ). The amount of sand storage occurring at this inter-riffle reach scale is governed by the reach factor (i.e. ( )<sub>reach</sub>) in equations (6.1) and (6.2). The amount of sand stored in the reach upstream of a riffle increases (i.e.  $Q_{sa_in}$  is reduced) as the downstream rate of change in *SSP* and median grainsize increases. Alternatively, the upstream inter-riffle reach tends to transfer sand (i.e. less storage) if the downstream change in *SSP* and grainsize is small. In the HPPM, the fraction of sand deposited on the bed. We did not budget through time the fraction of sand ( $F_{sa}$ ) and gravel on the bed during model runs. This is because the small spates we modeled are too short in duration and transport rates are too small to significantly change  $F_{sa}$  during the spate. The absence of a function to update the fraction of sand on the bed has no significant effect (i.e. changed  $F_{sa} < 0.5\%$ ) on the majority of our test runs (see Sections 6.2.3 and 6.4.4).

**Periphyton biomass sub-model.** The post-spate periphyton biomass in the HPPM was calculated using a linear empirical form of the periphyton saltation abrasion model (PSAM, Ch 3) with parameters determined by field data in the reference system (Appendix D):

$$PB_{T2} = 2.488 - 1.776V_{water} - 0.412I_{rsa} - 0.472F_{ep\_EI} - 1.486F_{ep\_II} - 7.693AH_{2mm}$$

$$(6.4) \quad R^2_{Adj} = 0.56, \, p < 0.001$$

where,  $PB_{T2}$  is periphyton biomass after a spate (mg chl*a*/m<sup>2</sup>, log),  $V_{water}$  is conditioning velocity (m/s, square root),  $I_{rsa}$  is the amount of sand moved during the spate per unit channel width (g m<sup>-1</sup>event<sup>-1</sup>, log),  $F_{ep\_EI}$  is a host-rock exposure index (log, equation (6.5)),  $F_{ep\_II}$  is the immersion index (log, equation (6.6)), and  $AH_{2mm}$  is an estimate of abrasion height (equation (6.8)). The rock protrusion height (i.e. the distance from the top of the rock to the mean matrix level) was given by  $0.55D_i$  based on a field calibration. The host-rock exposure index is given by:

$$F_{ep\_EI} = \frac{P_i}{P_{50}} \tag{6.5}$$

where,  $P_i$  is the protrusion height of the host-rock, and  $P_{50}$  is the median protrusion height (approx  $0.55D_{50}$ ) of a substrate patch centred on the host-rock. Note higher  $F_{ep\_EI}$  means the host-rock is more exposed. The immersion index is given by:

$$F_{ep\_II} = \frac{Hs_{Sklar and Dietrich}}{P_i}$$
(6.6)

where,  $Hs_{Sklar and Dietrich}$  is the average saltation height calculated using Sklar and Dietrich (2004):

$$Hs_{Sklar and Dietrich} = 1.44 \left(\frac{\tau^*}{\tau_c^*-1}\right)^{0.5} D_s \tag{6.7}$$

where,  $\tau^*$  is the shear stress at the spate peak, made dimensionless by the size of sand in motion ( $D_s = 2 \text{ mm}$ ), and  $\tau_c^*$  is the dimensionless critical shear stress when sand motion is initiated. The dimensionless shear stress for the spate peak is given by:  $\tau^* = \tau/(S_g - 1)\rho g D_{sa}$ , where  $\tau$  is the local shear stress,  $S_g$  is the specific gravity of sediment, and  $D_{sa}$  is the diameter of sand in transport.  $S_g = \rho_s/\rho_w$ , and  $\rho$  is the density (kg/m<sup>3</sup>) of sediment ( $\rho_s$ ) and water ( $\rho_w$ ). The method of Wilcock and Kenworthy (2002) to estimate critical shear stress for mixed sand and gravel beds was used to calculate  $\tau_c^*$  (i.e.  $\sim \tau_r^*$ ) at each rock. By their method, sand resting on a gravel bed becomes more mobile (i.e.  $\tau_c^*$  decreases) as the fraction of sand on the bed increases and as the sand grain to be transported becomes more exposed to flow (i.e.  $D_{sa}/D_{50}$  increases). The Sklar and Dietrich (2004) saltation height model was strongly correlated with the height of abrasion measured on painted nails on the SMR ( $R_{adj}^2 = 0.73$ , SE = 0.11, p < 0.001, n=20, see section 3.3.3).

The Abrasion Height (*AH*) was given by:

$$AH = 0.015 + 0.085P_{50} - 0.046F_{sa} + 0.051FR + 0.045SC_{2mm}$$
(6.8)  
SE=0.007,  $R^2_{adj}$ =0.92, p<0.002; n=20.

where, AH were measurements of the height of abrasion of painted pins after a spate where saltation was the predominant mode of transport,  $P_{50}$  is the median protrusion height of the substrate patch,  $F_{sa}$  is the fraction of sand on the bed, FR is the Froude Number, and  $SC_{2mm}$  is the suspension criteria for 2 mm sand.

Here PSAM equation (6.4) was used to calculate the periphyton biomass remaining on each rock after the reference spate (Figure 6.4c). The conditioning velocity was calculated using the water depth at  $Q_{base}$ ,  $D_{50}$  and Limerinos (1970) roughness equation. The depth of flow at each rock was calculated using the normal depths for  $Q_{base}$  and  $Q_{Ref}$ . The shear stress and sand transport were calculated for  $Q_{Ref}$  using the DuBoys equation (Chang, 1988) and the sand transport sub-model, respectively (Section 6.3, Figure 6.4b). Finally, down link patterns in post-spate periphyton biomass were displayed by plotting average cross section biomass versus stream power.

### 6.2.3 Analysis

**Analysis of down link trends in channel form.** Multivariate Adaptive Regression Splines (MARS, San Diego, California) were used to evaluate thresholds in morphometric properties of the 35 reference riffles (i.e. median grainsize, bar area, fraction of sand on the bed, width to depth ratio, relative roughness, radius of curvature) as a function of bankfull, specific stream power.

**HPPM model verification: 2004 Event.** The HPPM model was run to simulate periphyton biomass down the Big Pool Link (240 km<sup>2</sup>) resulting from the small, 24 August 2004 spate data ( $Q_{Peak} = 6.2 \text{ m}^3/\text{s} = 0.64\text{MAD}$ ). This link was selected because the most complete data sets are available for BPR and the link is intermediate in scale within the reference links. The boundary conditions were: 240 km<sup>2</sup> drainage basin area, 15% sand on the bed down the entire link, and 5 g m<sup>-1</sup>event<sup>-1</sup> supplied to the upstream end of the link. The observed and predicted baseflow conditioning velocity, spate peak shear stress, sand transport rates and post-spate periphyton biomass were plotted against bankfull stream power to verify sub-model components and to assess how well our generic link represents data from actual links. **HPPM model validation: 2003 Event**. The Big Pool Link HPPM model was rerun to simulate periphyton biomass remaining after the large spate ( $Q_{Peak}$ = 30.6 m<sup>3</sup>/s = 3.2MAD) monitored in 2003. The periphyton data for this large spate are independent of the 2004 calibration data used to develop the HPPM periphyton sub-model and thus provides an event based validation.

The effect of link morphology and sand supply  $(Q_s, F_{sa})$  on periphyton biomass. A sedimentary link with generic link morphology (i.e. including Low-, Medand High-HGRs) was used to simulate the effects of a low-magnitude (0.85MAD, Section 6.2.1) high-frequency spate (with Q equalled or exceeded 48% of the time annually). As in the validation runs, the fraction of sand on the bed for this reference simulation was assumed to be 15% and the drainage basin area was 240 km<sup>2</sup>. The sediment supply at the upstream end of the link was increased from 5 to 10 g m<sup>-1</sup>event<sup>-1</sup> (based on a linear regression of cross section average sediment transport rate at the upstream end of the BPR link, measured using sediment traps versus spate peak discharge  $R^{2}_{adj} = 0.76$ , p = 0.03, n= 5). The 10 g m<sup>-1</sup> event<sup>-1</sup> is reference simulation provides the basis for visual comparison between all subsequent simulation runs. Simulation runs were conducted by sequentially changing sand supply and fraction of sand on the bed over the same generic link morphology. The range of tested parameter values are given in Table 6.5. The discharge was held constant for these simulation runs. The objective of this sensitivity analysis was to test the HPPM under a large, yet realistic range of parameter values, to ensure the model behaviour is realistic and sensitive to the appropriate parameters, relative to field studies and theory (Rykiel, 1996).

Parameter Units Values Tested										
Sand Supply	(g m <sup>-1</sup> event <sup>-1</sup> )	1	10	90	250	500	2700			
Fraction Sand	(%)	5	10	15	20	25	30			
Bolded values are the reference case.										

**Table 6.5** Range of parameter values tested in the sensitivity analysis.

### **6.3 Results**

### 6.3.1 Down link gradients in channel form: Hydrogeomorphic patch characteristics

On the Sainte Marguerite river, sedimentary properties of riffles  $(D_{50}, \frac{D_{50}}{d}, Barhead F_{sa})$  varied smoothly down a bankfull specific stream power gradient  $(SSP_{min} = 6 SSP_{max} = 87 \text{ W/m}^2$ , Table 6.3, Figure 6.5). However, morphometric properties (Bend curvature, fraction bar area, aspect ratio, relative roughness, roughness relative to width, maximum reach  $F_{sa}$ , Figure. 6.5) had a discontinuous spatial distribution (i.e. zonal distributon). The *SSP* thresholds that divided significantly different trends in morphometric properties based on the MARS analysis were 30 W/m<sup>2</sup>, 50 W/m<sup>2</sup> and 60 W/m<sup>2</sup> (Figure 6.5b,c, vertical lines). These three *SSP* thresholds overlap with thresholds identified by other researchers (Nanson and Knighton, 1996; Kondolf et al., 2003; Burge, 2005)(Figure 6.5a). Two distinct planforms were identified. Specifically, riffles with *SSP*'s exceeding 50 W/m<sup>2</sup> were located in straighter reaches (high bend curvature radius relative to bankfull channel width,  $R_c/w > 5$ ) and associated with higher bankfull width to depth ratio and decrease in sediment stored in lateral bars. Riffles with *SSP*'s less than 50 W/m<sup>2</sup> possessed tighter meander bends (i.e. low  $R_c/w$ ), and the area of the channel occupied by lateral bars increased.

When bar unit to rock scale morphometric properties were also considered, three different channel types were distinguishable (Figure 6.5d): Low-HGR (SSP = 10-30 W/m<sup>2</sup>), Medium-HGR (SSP = 30-60 W/m<sup>2</sup>), High-HGR (SSP = 60-90 W/m<sup>2</sup>). We are referring to the channel types as hydrogeomorphic reaches (HGR) under the assumption that differences in hydraulic regime are reflected in channel form (Schumm, 1963). Low-HGRs had median substrates ranging from coarse gravel to very coarse gravel, and possessed both tight bends and sandy lateral bar (e.g. point-bar) deposits. High-HGRs had riffles with median substrates ranging from very coarse gravel to large cobbles. These riffles were broad, shallow (Figure 6.5, High W/d) and hydraulically rough (High



**Figure 6.5** a) Distribution of specific stream power (*SSP*) thresholds dividing morphological differences in channel form (Brookes, 1996; Kondolf et al., 2003; Burge, 2005). b) Differences in channel morphometric properties along a gradient in *SSP* for the Sainte Marguerite river, Quebec (data from 5 sedimentary links, 35 cross sections). The trend lines shown are fitted using a LOWESS (Tol. = 0.6) smoothing function. The vertical bars show thresholds in*SSP*, calculated using multivariate adaptive regression splines (Salford Systems, 2006), that divide d) three hydrogeomorphic reach types with significantly different morphometric properties. No vertical rectangle means a continuous linear trend exists.

 $D_{50}/d$ ). Medium-HGRs were transitional between Low- and High-HGRs and divided by the 50 W/m<sup>2</sup> threshold previously discussed.

# 6.3.2 Observed and simulated down stream trends in periphyton biomass and physical disturbance variables within a gravel-cobble sedimentary link.

**Model Validation:** Downstream trends in predicted and observed a) shear stress, c) sand transport and d) periphyton biomass were compared for the weaker  $(6.2 \text{ m}^3/\text{s})$ 2004 spate (Figure 6.6) and stronger ( $30.4 \text{ m}^3/\text{s}$ ) spate observed in 2003 (Figure 6.7). There was agreement between predicted and observed shear stress (Figures. 6.6a, 6.7a), average conditioning velocity (Figures 6.6b, 6.7b) and sand transport (Figures 6.6c, 6.7c). In the smallest event sand transport rates predicted by the model (Figure 6.6c) were generally below 50 g m<sup>-1</sup> event<sup>-1</sup>, as observed in the field. Note however, that much higher sand transport rates were observed in five sites (33% of sites, Figure 6.6c, riffle labels given). The higher observed transport rates at these sites were attributed to a higher fraction of sand on the bed (25% to 40%, Sites BP2, BP8, T7) than assumed in the HPPM run (15%), larger depth than modelled (Sites BP8, BP2, T3) or steeper slope (Sites T3, T4). All five sites were associated with channel instability at either a meander cut off (BP8), artificial channel straightening (Sites T3, T4, T7) or other anomalous channel form (BP2 was semi-alluvial). In the stronger 2003 spate, six sites (30% of sites, Figure 6.7c) had much lower observed values in sand transport than predicted. These six sites had a much lower fraction of sand on the bed and a lower sand supply from upstream than assumed in the HPPM runs (Figure 6.7c).

Too few sites were sampled in 2004 to validate model predictions for *SSP*s less than 10 W/m<sup>2</sup> or greater than 70 W/m<sup>2</sup> (Figure 6.6d). Overall, both the predicted and observed (DWLS smoother) biomass for the weaker 2004 spate increased downstream in Low- and Medium-HPG's (Figure 6.6d). Differences between the fraction of sand on the bed assumed in the model ( $F_{sa}$ = 15%) and the fraction of sand on the bed measured in the field ( $F_{sa}$ = variable) were primarily responsible for prediction errors. When the fraction of sand on the bed used in the HPPM was held constant down the link, the biomass then increased upstream for *SSP*s greater than 70 W/m<sup>2</sup>. The sparse 2004 periphyton data did



**Figure 6.6** Trend lines show predicted riffle mean values (i.e. thick line) for a) peak spate shear stress (± SD of Riffle), b) conditioning velocity (± SD of Riffle), c) sand transport rate and d) periphyton biomass (± SE of prediction) down a sedimentary link for a spate discharge of 6 m<sup>3</sup>/s with a constant fraction of sand ( $F_{sa}$ =14.7%), sand input of 5 g m<sup>-1</sup> event<sup>-1</sup> and drainage basin area of 240 km<sup>2</sup>. Data points on Figures b) to d) are cross section average values measured at natural riffles located both within the Big Pool (DBA=240 km<sup>2</sup>) and Meander (DBA=280 km<sup>2</sup>) links, representative of the small summer spate of 6 m<sup>3</sup>/s monitored in 2004. Labels given on panel c) are riffle site names.



**Figure 6.7** Trend lines show predicted riffle mean values (i.e. thick line) for a) peak shear stress (± SD of Riffle), b) conditioning velocity (± SD of Riffle), c) sand transport rate (± SE of prediction), and d) periphyton biomass (± SE of prediction) down a sedimentary link for a spate discharge of 30 m<sup>3</sup>/s with a constant fraction of sand ( $F_{sa}$ =14.7%), sand input of 1465 g m<sup>-1</sup>event<sup>-1</sup> and drainage basin area of 240 km<sup>2</sup>. Data points on Figures b) to d) are cross section average values measured at natural riffles located both within the Big Pool (DBA=240 km<sup>2</sup>), Onesime (DBA=206 km<sup>2</sup>) and Cascade (DBA=89 km<sup>2</sup>) links and are representative of the large summer spate (30.6 m<sup>3</sup>/s) monitored in 2003.

not validate this prediction. However, the average biomass weakly increased upstream in the reference link (m = 0.025,  $r_{adj}^2 = 0.13$ , p = 0.033) after the large-magnitude spate in 2003 (Figure 6.7d). The sand transport rates that occurred uplink during the 2003 spate

 $(Q_{sand} > 1000 \text{ g m}^{-1}\text{event}^{-1})$  greatly exceeded damaging levels for periphyton, thus the weak upstream increase in biomass was presumably due to the sheltering effect of larger substrates in these coarser reaches. Overall however, biomass was reset to low levels (e.g. Mean Chla < 10 mg/m<sup>2</sup>) down the entire sedimentary link in 2003, in close agreement with the HPPM prediction. The HPPM predicted a slight increase in biomass for *SSP*s less than 20 W/m<sup>2</sup>. This HPPM prediction was supported with biomass observations on only two riffles. The scarcity of data for these low *SSP*s (10 to 20 W/m<sup>2</sup>) inhibit a more a rigorous validation of HPPM model behavour for these low *SSP*s.

# 6.3.3 Simulated reference link base case: Link scale geomorphic gradients and periphyton biomass trends.

To examine the influence of link morphological gradients on the downlink distribution of sand transport, peak spate shear stress, conditioning velocity and postspate periphyton biomass, we simulated an average summer spate condition (i.e. 0.85MAD) and average sand supply conditions ( $F_{sa}$  = 15% sand on bed, 10 g m<sup>-1</sup> event<sup>-1</sup> at the upstream end Figure 6.8) along a generic link with Low-, Medium- and High-HGRs. The predicted downlink trend in biomass is parabolic (e.g. Figure 6.8a), with biomass decreasing  $(4 \text{ mg/m}^2 \text{ to } 1 \text{ mg/m}^2)$  downstream to the Med-HPG zone and subsequently increasing  $(1 \text{ mg/m}^2 \text{ to } 20 \text{ mg/m}^2)$  going further downstream. The minimum in biomass at 50  $W/m^2$  is associated with the transition between Medium- and High-HGRs (Figure 6.5), with high shear stress (Figure. 6.8c), peak sand transport rates (Figure. 6.8b) and the maximum degree of host-rock immersion in saltating sand (Immersion Index, Figure 6.9a, Figure 6.1). High-HGRs were characterized by moderate biomass which increased going upstream, despite the increasing peak spate shear stresses. The upstream increase in biomass (Figure 6.8a) was associated with a continuous decrease in immersion index (Figure 6.9a) and sand transport rate (Figure 6.8b). Sand transport at High-HGR riffles was supply limited in this cobble rich zone. Specifically, the high shear stresses (Figure 6.8c) were capable of transporting more sand than what was supplied (e.g.  $10 \text{ g m}^{-1}\text{event}^{-1}$ at the upstream end). The amount of sand available for transport increased downstream, because each successive riffle not only received sand eroded from the upstream riffle but



Average Summer Spate (Q<sub>peak</sub>= 8 m<sup>3</sup>/s) Model Run

**Figure 6.8** Modelled downs link trends in a) periphyton biomass and b) sand transport, c) peak shear stress and critical shear stress for the initiation of sand movement and d) conditioning velocity for a reference case. Reference case conditions include: constant discharge of a small frequent spate (0.85MAD), an upstream sand supply of 10 g m<sup>-1</sup> event<sup>-1</sup>, constant downstream fraction sand on the bed of 15%, and a drainage basin area of 240 km<sup>2</sup>.



**Figure 6.9** Modelled down link trends in a) immersion index (equation (6.6)), exposure index (equation (6.5)) of host-rock and b) net sand transport rate (i.e. downstream rate – upstream rate) showing zones of deposition and erosion for the reference case. Figure c) shows a DWLS smoother (Tol. = 0.9) of Sainte Marguerite river fraction bar area and fraction of sand in the substrate of barhead samples. Black dots denote knot points separating significantly different trends calculated using Multivariate Adaptive Regression Splines (MARS).

also contributed sand eroded *in situ* (Figure 6.9b). The downstream increase in sand transport rate was also associated with a decrease in median bed grainsize (i.e. cobble to coarse gravel), increasing the exposure of sand to flow (Figure 6.9a) and reducing the stress required to entrain sand (i.e. critical shear stress for sand, Figure 6.8c) among the cobbles.

The sand transport rate peak at 50 W/m<sup>2</sup> (Figure 6.8b) indicates that sand deposition and erosion were balanced at this point down the link (Figure 6.9b). Deposition exceeded erosion downstream of the 50 W/m<sup>2</sup> threshold (i.e. Medium- and Low-*SSP* reaches) as the shear stress decreased below levels (10-15 Pa) required to transport the available sand load (Figure 6.8c). It is interesting to note that the 50 W/m<sup>2</sup> threshold also separated high *SSP* channels that appear to merely supply or transfer sand (i.e. lack lateral bars) from lower *SSP* channels that stored sand (i.e. sinuous channels with a downstream increase in fraction of bar area)(Figure 6.9c).

The rapid decrease in sand transport rate at the Low- to Medium-HGR boundary predicted by the HPPM (Figure 6.8b) was associated with the mean shear stress, decreasing to near threshold levels for sand entrainment on a coarse gravel bed (i.e. ~ 5 Pa). Barring information on pure sand reaches at the downstream end of links (not collected here), biomass was highest in Low-HGR gravel bed reaches, because sand transport rates were at a link minimum there, and conditioning velocities also decreased below 0.5 m/s across the entire channel.

#### 6.3.4 Simulated effects of changing sand supply

Effect of sand supply on the bed. To examine the influence of river bed sand availability on the downlink distribution of periphyton biomass we simulated an average summer spate condition (i.e. 0.85MAD) but varied the fraction of sand on the bed between 5% and 30%, bracketing our reference case based on SMR conditions (i.e. 15%, Figure 6.10a, b). The change in periphyton biomass in these model runs was directly attributable to the fraction of sand on the bed because the discharge and initial, upstream sand supply (10 g m<sup>-1</sup>event<sup>-1</sup>) were held constant.

As expected, sand transport rates increased dramatically when the fraction of sand was increased from 5% to 20%, resulting in larger periphyton losses (Figure 6.10a, b). When the fraction of sand on the bed was 5%, sand transport rates were the lowest of all the test cases (N.B. including the model runs assessing the effects of upstream sand supply that are described in the next section). Specifically, there was no sand transported on riffles with stream power less than 70 W/m<sup>2</sup>. Consequently, high biomass occurred everywhere within the link (Figure 6.10b). When the fraction of sand was increased to 15%, sand was transported over the whole link near a threshold shown to dramatically reduce periphyton, but higher periphyton was retained on the larger substrates (64-180 g m<sup>-1</sup>event<sup>-1</sup>, Ch. 4). Sand transport rates greatly exceed this disturbance threshold when the fraction of sand was 20% or more. The highest sand transport rates occurred in Medium-HGRs when the fraction of sand on the bed exceeded 15%. Consequently, Medium-HGRs had low periphyton biomass. Low transport rates in Low-HGRs were

associated with low shear stresses (Figure 6.8c). In High-HGRs, shear stresses were at a maximum (Figure 6.8c) but sand transport rates were limited by the low initial sand supply (i.e. 10 g m<sup>-1</sup>event<sup>-1</sup>) from upstream in these runs. The downstream increase in sand transport rate in High-HGRs became more pronounced as the amount of sand available for transport at each riffle increased with the fraction of sand on the bed.





**Effect of upstream sand supply.** To examine the influence of initial upstream sand supply on the downlink distribution of periphyton biomass, we simulated an average summer spate condition (i.e. 0.85MAD) and varied the upstream supply from 1 to 2700 g

 $m^{-1}event^{-1}$ , bounding the reference rate of 10 g  $m^{-1}event^{-1}$  (Figure 6.10c,d). The change in periphyton biomass in these model runs was directly attributable to the sand supply, because the fraction of sand on the bed (15 %) and discharge were held constant.

High HGRs experienced the largest increase in sand transport rate (Figure 6.10c) and reduction in periphyton biomass (Figure 6.10d) for a given increase in upstream sand supply. The effects were less pronounced in Medium-HGR and negligible in Low-HGR riffles. The most abrupt decrease in biomass occurred between model runs simulating sand supply rates between 5 and 250 g m<sup>-1</sup>event<sup>-1</sup>. At a supply rate of 250 g m<sup>-1</sup>event<sup>-1</sup>, sand transport rates exceeded 100 g m<sup>-1</sup>event<sup>-1</sup> in High- and Medium-HGRs. Higher rates of sand supply caused sand to be transported further down the link, lowering biomass on some riffles in the upstream end of Low-HGRs. In general, the biomass on Low-HGR riffles did not vary much over large increases in simulated sand supply.

Our results illustrate the effects of sand supply limitation (e.g. below dams or lakes) and oversupply (e.g. quarry source, hill side soil erosion) on the spatial distribution of periphyton. Surprisingly, the sand transport rate increases downstream in High-HGRs for all but the highest supply condition tested (2700 g m<sup>-1</sup>event<sup>-1</sup>) indicating sand transport was supply limited below this high sand supply rate (see Section 6.3.2). As expected under lower (i.e. 10 to 500 g m<sup>-1</sup>event<sup>-1</sup>) sand supply conditions (e.g. below dams or lakes), periphyton biomass along High-HGRs decreases downstream as the sand transport rate increased. As expected under high (e.g. 2700 g m<sup>-1</sup>event<sup>-1</sup>) sand supply conditions (e.g. below an aggregate quarry), biomass increased downstream of the sediment source (i.e. top of the link) as sand transport rates diminished and sand was deposited in the channel (i.e. in Medium-HPG's). Regardless of the level of sand supply, periphyton biomass increased downstream in Low- and Medium-HGRs, as the flow competence and sand transport rates decreased below periphyton perturbation thresholds.

#### 6.4 Discussion

The results reflect the nonlinear relationships between substrate size, spate shear stress, saltating sand fluxes and post-spate periphyton biomass. Periphyton biomass decreased with both the intensity of sand transport at the channel bed and with how immersed the host-rock was within the layer of saltating sand. All these factors varied with the size of the bed material and the ability of the stream to do work.

# 6.4.1 The plan-scale periphyton habitat template: The geomorphic character of HGRs

The median grainsize on the SMR varied smoothly down the specific stream power gradient ( $SSP = 6-87 \text{ W/m}^2$ ) from cobble to coarse gravel, as observed on other rivers (Rice and Church, 1998). However, the sedimentary links were divisible into three channel types. Previous studies have used channel type (e.g. meandering, anabranching, braided) and descriptors of substrate stability (e.g. armoured, mobile) to describe hydrogeomorphic reaches (HGRs, Thoms and Parsons, 2003). All three Sainte Marguerite river channel types can be classified as "meandering" channels, based on their aspect ratios and bankfull SSP (Brookes, 1996; Burge, 2005). Brookes (1988) compared stream form, activity rate and engineering success with the amount of SSP for Danish and United Kingdom Streams and found: "stable stationary channels" had bankfull SSP's that ranged from 10 W/m<sup>2</sup> to 35 W/m<sup>2</sup> (e.g. c. Low-HGR), "*trainable* actively meandering channels" ranged from 35 W/m<sup>2</sup> to 60 W/m<sup>2</sup> (e.g. c. Medium-HGR), and "*untrainable* actively meandering channels", where bed and bank stabilization works fail through erosion (e.g. bank erosion and planform adjustment), ranged from 60  $W/m^2$  to 100  $W/m^2$ (e.g. High-HGR). Nanson and Knighton (1996) found that anabranching channels with SSP's exceeding 50W/m<sup>2</sup> were associated with channel avulsion, where flow takes a more direct path down the valley. Nanson and Croke (1992) found 50  $W/m^2$  to be the lowest SSP for "braided" channels. Braided channels are characteristically broad and shallow (w/d > 40), are prone to lateral migration through bank erosion, frequent avulsions and possess a straight braidplain. These studies suggest that channels with stream power SSP's > 50-60 W/m<sup>2</sup> are more likely to experience bank shifting and chute cutoffs, possess higher width to depth ratios, have prominent bars and a straighter planform overall. On the Sainte Marguerite river, riffles with a SSP greater than 50  $W/m^2$ were coarser textured, wider and shallower than riffles with lower SSP's. Further, the high SSP riffles were in straight reaches (i.e. Radius of curvature/bankfull width > 5) and

lacked sandy point bar deposits. Riffles with *SSP*'s less than 50 W/m<sup>2</sup> possessed tighter meander bends and had more sandy point bar deposits. Remarkably, the HPPM model predicted sand deposition on riffles with *SSP*'s less than 50 W/m<sup>2</sup> (Med- and Low-HGRs – Figures 6.9b, 6.9c - cf. point bar  $F_{sa}$ ) and sand erosion on riffles with greater *SSP*'s (High-HGRs – no point bars) for a very high-frequency spate flow (i.e. equalled or exceeded 48% of the year). The conformity between previous study results, our process model predictions, and the morphometric form analysis provide an element of validity to the HPPD and suggest important differences in form and process between channel types.

# 6.4.2 Linkages between HGRs and periphyton refuge for normal sand supply conditions.

The highest post-spate biomass (i.e. refuge) was found in the gravel dominated channel type with the lowest flow energy (Low-HGRs) for the modelled low-magnitude, high-frequency spate condition (i.e. 0.85MAD, Figure 6.8a, and 0.63MAD, Figure 6.6d). This high biomass was associated with the lowest sand transport rates, flow shear stress and conditioning velocity, as well as the highest degree of exposure for a given host-rock size (i.e. lowest  $D_{50}$ ). The large down link increase in biomass predicted by the HPPM for such a weak spate (chl*a* = 2-20 mg/m<sup>2</sup>) through Medium-HGRs and Low-HGRs was validated by field data and occurred because damaging conditions for periphtyon removal were lowest in low energy HGRs.

A slight upstream increase in biomass within High-HGRs was predicted (Figure 6.6d,  $chla = 1-4 \text{ mg/m}^2$ ) when the fraction of sand was held constant down the generic reference link in the HPPM. The biomass increased upstream within High-HGRs after the higher magnitude spate in 2003 (Figure 6.7d), however this trend was not observed in the small 2004 spate data because of the natural variability in the longitudinal distribution of the fraction of sand on the bed. The upstream increase in biomass in the HPPM simulations for both weak and moderate spates resulted from the sheltering effect of large substrates combined with the downstream increase in the sand transport rate associated with supply limitation at the head of the link. This model behaviour is consistent with sand transport measurements below dams (Salant et al., 2006a; Salant et al., 2006b).

## **6.4.3** Effects of channel morphology and initial sand supply on sand abrasion and periphyton biomass trends: HGR context within the sedimentary link

Apart from the data presented in our HPPM validation (section 6.3.2), we are unaware of additional field data with which to compare to our modeled downlink distributions of periphyton for low magnitude spates. However, studies reporting biomass patterns across gravel-cobble bed channels have noted high biomass on fine sediments (i.e. sand and smaller fractions) that are deposited in low velocity regions (Tett et al., 1978; Sand-Jensen, 1988; Coleman and Dahm, 1990; Cattaneo et al., 1997), and on larger host-rocks, presumably because these gravel-cobble sized clasts are more stable and located where higher velocities enhance growth (Hynes, 1970; Uehlinger, 1991; Meyers et al., 2007). Intermediate to these extremes in grainsize are sandy gravel beds. The variability in periphyton biomass is higher on sandy gravel than on either patches of clean gravel-cobbles or patches of sand (Tett et al., 1978). It is not clear if these biomassgrainsize associations developed from cross channel observations apply to downstream sedimentary link biomass patterns. If this assumption is true, then a link that grades from clean gravel, to sandy gravel, to pure sand, should have a concave upward distribution of periphyton biomass. Specifically, periphyton biomass may be high both at the downstream depositional end of a link (sand), where velocities are the lowest and sediments are the smallest, and at the upstream end of a link (clean gravel), where sediments are the largest. The sandy gravel in the middle of the link would be most susceptible to scour, yet exposed to moderate velocities for optimal growth. We did not test this gravel-to-pure-sand sedimentary link case with the HPPM model because we did not sample pure sand bed reaches with  $SSPs < 10 \text{ W/m}^2$ . However, in a cobble-to-gravel sedimentary link, the HPPM model showed that the downlink distribution of biomass was also concave upward with minimum biomass occurring in the middle of the sedimentary link.

This nonlinear longitudinal trend in biomass predicted by the HPPM was predominantly driven by the degree of exposure of a host-rock to saltating sand, represented by the immersion index that had a convex downward distribution along the sedimentary link. For example, where the spate shear stress is low (e.g.  $SSP < 20 \text{ W/m}^2$ ), no saltation occurred (Figure 6.9a, Immersion Index = 0). As the shear stress increased up the sedimentary link, sand began to saltate and the saltation heights progressively increased (equation (6.7)). This saltation height increased rapidly with distance up the sedimentary link, relative to the upstream increase in protrusion height of the host-rock (Figure 6.9a). Consequently, the immersion index (equation (6.6)) increased rapidly between Low- and Medium-HGRs leading to an upstream reduction in biomass. The immersion index peaked in Medium-HGRs. The immersion index then decreased in High-HGRs because host-rock protrusion height increased relative to the saltation height with distance upstream. Thus, periphyton residing on the top of High-HGR host-rocks extended above the saltation layer.

Like the immersion index, the sand transport rate had a convex parabolic distribution. This also contributes to down link biomass trends for the low-magnitude reference spate (Figure 6.8b). The sand transport rate during the small reference spate was high enough to cause some periphyton losses. The downstream increase in transport rate in High-HGRs resulted from the supply limitation at the upstream end of the reference link followed by a cumulative addition of sand supplied from bed erosion on each subsequent riffle downstream. Supply limitation occurs when the ability of the stream to transport sediment (e.g. sand) exceeds the sediment supply (Bravo-Espinosa et al., 2003; Curran and Wilcock, 2005). For example, at the head of our link, the shear stress exceeded the critical shear stress, so the first riffle transported the initial sand supply (e.g. 10 g  $m^{-1}$  event<sup>-1</sup>) and additional sand eroded from the bed (equation (6.1),  $Q_{s in}$ , Figure 6.9b, erosion). As the shear stress decreases relative to the critical shear stress going downstream (Figure 6.8c), less sand was eroded from each successive riffle until the ability of flow to entrain sand on the riffle surface became extremely low (equation (6.4), Figure 6.8c). Erosion from the bed of the riffle essentially stopped when the stress required to transport sand was higher than the flow shear stress. From this point where bed erosion ends, the sand that was in motion continued to be transported downstream, but at a diminishing rate (e.g. increasing deposition) that is a function of the conveyance capacity of the inter-riffle reach (Figure 6.9b). Specifically, the conveyance of the upstream reach is high when the difference in SSP between the upstream and

modeled riffle is small (equation (6.2)). Reach conveyance also increases with the degree of downstream fining (suggestive of a downstream decrease in critical shear stress). These HPPM model findings show that the order of the HGRs down a sedimentary link influences the downstream progression of sand during a spate and thus the longitudinal distribution of post-spate biomass. As Chessman et al. (2006) suggested, the larger scale context of the HGR is important to consider when assessing potential biotic responses based on internal HGR characteristics.

#### 6.4.4 Effects of channel morphology and sand supply on periphyton biomass

The range of conditions for fraction of sand on the bed tested (5% to 30%) was typical for gravel and cobble bed rivers (Osmundson et al., 2002; Kenworthy, 2006). In the upper Colorado river, the fraction of sand on the bed at the network scale (i.e.  $F_{sa}$ averaged over topological links) can range from <5% to >35% (Osmundson et al., 2002). On the Sainte Marguerite river, the fraction of sand on the bed at trap locations varied from 1.5-31% in unaltered section of the river but was as high as 51% in a long reach straightened and relocated 50 years ago, as described and modeled in Talbot and Lapointe (2001a; b).

Thomson et al. (2005) found that the passage of a sediment slug after a dam removal increased the amount of sand on the bed from 1-15% and was associated with a 25% lower algal biomass. In their study, periphyton was sampled only from larger 10-20 cm rocks, so reported biomass losses were likely conservative, assuming lower substrates were abraded more thoroughly. In the HPPM, an increase in the fraction of sand on the bed from 5% to 15% led to a 62-93% lower biomass. Periphyton biomass is very sensitive to sand availability. Periphyton biomass remained relatively high (> 20 mg/m<sup>2</sup>) over the entire link when the fraction of sand on the bed was only 5% (Figure 6.10b) while at 15% sand, only Low-HGRs retained any post-spate biomass exceeding 10 mg/m<sup>2</sup>. Considering that the spate discharge tested was equalled or exceeded 48% of the time annually, the high periphyton losses associated with small changes in the fraction of sand on the bed predicted by the HPPM suggest that sand loading to river systems poses a potentially severe limitation to biomass accumulation.

A downstream decrease in periphyton biomass has been observed below fine sediment sinks such as dams and lakes (Cattaneo, 1996; Jakob et al., 2003; Meyers et al., 2007). This periphyton perturbation pattern suggests a downstream increase in fine sediment abrasion based on the serial discontinuity concept (Ward and Stanford, 1983; Stanford and Ward, 2001). Our HPPM results illustrated this downstream decrease in biomass with increasing transport rate under supply limited conditions (e.g. Figures 6.10c, d, 10 g m<sup>-1</sup>event<sup>-1</sup>). However, the downstream decrease in particle size relative to the saltation height along the link was also instrumental in generating the pattern.

In contrast to this supply limited case, biomass increased down the entire sedimentary link at very high initial sand supply rates (e.g. Figures 6.10c, d, 2700 g m<sup>-</sup> <sup>1</sup>event<sup>-1</sup>). Such a transport limited case is expected below a point source of sandy sediment. Yamada and Nakamura, (2002) found biomass increased downstream of a quarry as the amount of silt trapped in periphyton decreased with distance from the quarry source. The anthropogenically modified reach immediately downstream of the quarry was wider than natural river sections. This unnatural and over-widened section of river had low velocities and trapped fine sediments, presumably buffering the downstream reach from detrimental effects. A direct comparison between the results of Yamada and Nakamura (2002) and ours is not feasible. However, the HPPM model behaviour predicts a similar longitudinal pattern in sand deposition and increased biomass as the one they inferred from silt accumulated in periphyton. Specifically, in HPPM terms, the transition from a natural channel into a channelized over-widened reach creates an abrupt downstream decrease in SSP with small longitudinal change in grainsize. These factors promote a rapid downstream increase in the rate of sand deposition (equation (6.1)). Thus, sand is stored in the over-widened channel and less sand is conveyed downstream to the unaltered reach. Consequently, the HPPM would predict a downstream decrease in abrasion losses. Periphyton biomass would increase downstream as observed by Yamada and Nakamura (2002).

#### 6.4.5 Model limitations, bias and confounding effects

The resistance of an algal community to scour differs with algal growth form, attachment mechanism and physiological condition (Azim et al., 2005; Francoeur and Biggs, 2006). To minimize these effects, we focused here on a predominantly diatom dominated community. The HPPM parameter values and runs presented here are specific to the benthos and sediment transport characteristics of the meso-oligotrophic Sainte Marguerite river and are based on saltation abrasion of a predominantly diatom dominated community. The HPPM may not be valid for sand bed (e.g.  $SSP < 10 \text{ W/m}^2$ ) systems or braided systems (e.g.  $SSP > 100 \text{ W/m}^2$ ), because these channel forms are outside the range of the geomorphic reference data. Data from low stream power riffles ( $SSP < 10 \text{ W/m}^2$ ) are required to more thoroughly validate the large increase in biomass predicted in channels below this SSP threshold.

The fraction of sand on the bed in the HPPM was assumed constant down a sedimentary link. This assumption is generally reasonable along boulder, cobble or gravel reaches, as along the Sainte Marguerite river it was violated only for sites that were geomorphically unstable, such as the 1960s channelized reach within the Meander Link. Osmudson et al. (2002) found no significant downstream differences in the fraction of sand (i.e. < 2 mm) in riffles over 375 km of the Colorado River.

In the HPPM, the fraction of sand on the bed ( $F_{sa}$ ) was not permitted to increase with the amount of sand deposited on the bed during a model run. This is reasonable given the short duration and limited transport totals during one low amplitude spate. If this feedback was permitted within the HPPM, then an increase in sand deposition would cause  $F_{sa}$  to increase and in-turn cause an increase the sand transport rate. However, the increase in sand transport rate decreases sand storage on the bed ( $F_{sa}$ ), which in-turn reduces the sand transport rate. Regardless of this negative feedback, the distance a sand wave propagated downstream may be underestimated in the current, simpler form of the HPPM. This model limitation could be overcome by budgeting surface material using a two fraction form of the Exner equation (e.g. see Hoey and Ferguson, 1994). In lieu of this solution, we estimated how the fraction of 1 mm sand would change for a range of sand storage rates (i.e.  $Q_{s_{in}} - Q_{s_{out}}$ , g m<sup>-1</sup>event<sup>-1</sup>) assuming a sediment density of 2650 kg/m<sup>3</sup> and 30% interstitial space between 44 mm gravel. By the estimate, the fraction of sand on the bed changes less than 0.5% if the deposition rate is less than 130 g m<sup>-1</sup>event<sup>-1</sup>. Consequently, our results regarding the reference case model run ( $F_{sa}$ = 15%,  $Q_{s_{in}}$  = 10 g m<sup>-1</sup>event<sup>-1</sup>) and half of our  $Q_{s_{in}}$  test cases are only marginally affected by the absence of a routine to update the fraction of sand on the bed. The highest deposition rate for our highest  $Q_{s_{in}}$  case tested (i.e. 2700 g m<sup>-1</sup>event<sup>-1</sup>) is 500 g m<sup>-1</sup>event<sup>-1</sup>. This deposition rate is estimated to increase the fraction of sand on the bed by 2%. As indicated by our simulation runs testing the effects of fraction of sand on the bed (Figure 6.10a), a 2% increase in  $F_{sa}$  has a larger effect (i.e. transporting sand further downstream) when the initial fraction of sand on the bed is low (e.g. < 15%). However, at  $F_{sa}$ = 20%, biomass down the entire link is low because transport rates exceed perturbation threshold. Consequently, a  $F_{sa}$  updating routine would yield no further insight into down link biomass trends when  $F_{sa} > 20\%$  for the spate condition tested.

Studies of periphyton refuge typically have focused on small spatial scales such as the shelter provided by the cracks in rocks (Bergey, 2005), in the lee of rocks (Francoeur and Biggs, 2006), on stable rocks or clusters of rocks (Francoeur et al., 1998) and across riffles (Ch. 4). Our analysis provides insight into link and planform scale refuge patterns. The HPPM considered only algae residing on top of host-rocks nested in riffles. Biomass on top of rocks is typically low relative to the lee side of rocks (Francoeur and Biggs, 2006). Consequently, the HPPM likely predicts minimum biomass values. Our results should also be considered within the reach context whereby in low nutrient river systems, periphyton biomass in riffles tends to be higher and more variable than in runs (Biggs et al., 1998; Osmundson et al., 2002).

### **6.5 Conclusions**

This study examined plan scale (Table 6.1, *sensu* Frothingham et al. (2002)) hydrogeomorphic reaches (HGRs) nested within sedimentary links and focuses on the effects of morphological form and substrate abrasion on longitudinal periphyton biomass. Our research tests eco-geomorphological theory, yet the HPPM model was designed to be adaptable to practical applications at the link or network scale. The transferability of the HPPM to river systems with a different nutrient regime requires using a version of saltation abrasion model for periphyton that includes pre-spate biomass (Ch 3, equation (6.11)) and an algal growth model to estimate this parameter (e.g. Doyle and Stanley, 2006). The sand transport submodel of the HPPM can be calibrated with data from a line of sand traps entering and leaving key nodes in the system (e.g. stream gauges, storm sewer outfalls, tributaries). Bucket type sand traps are easy and safe to install and reclaim during periods of low flow, and provide time integrated measurement of supply conditions (also see Wilcock, 2004). The periphyton sub-model can be validated using data collected at the sand trap locations. It is now feasible to collect most of the data required to validate the geomorphic sub-models at the network scale using remote sensing techniques (Carbonneau et al., 2005 ; Dollar et al., 2006; Warnaars et al., 2007).

The HPPM enabled a causal assessment of how channel form and sand transport dynamics potentially influence periphyton biomass under a fixed flow condition at the link and planform scale (i.e. HGRs). This sediment transport centred approach both contrasts and complements studies defining HGRs based on flow dynamics and channel pattern (Thoms and Parsons, 2003). For a generic boreal Canadian shield river, the HPPM results provided a quantitative validation of the hypothesis that the patchiness of post-spate periphyton biomass for a given spate magnitude varies significantly depending on the amount of fine sediment on the bed prior to the spate (Tett et al., 1978; Power and Stewart, 1987; Poff et al., 1997; Francoeur and Biggs, 2006). With further development, the HPPM may be used to assess large-scale and long-term spate related changes in periphyton biomass to help make informed river management decisions and design adaptive management solutions (see Uehlinger, 2000; Bouletreau et al., 2006; Doyle and Stanley, 2006; Schweizer, 2007).

The dominant biomass regulating processes varied between HGRs. Our HPPM results concur with theories that stress the associations between geomorphic form and function and ecological response at the planform scale (Montgomery, 1999; Church, 2002; Chessman et al., 2006). The HPPM results also illustrated how the geomorphic context affected the amount of sand arriving from upstream and thus the patchiness of

post-spate biomass. Future HPPM work will examine how abrupt transitions in HGRs (e.g. High- to Low-HGR), such as at tributary junctions, affect the distribution of periphyton biomass under various flow and sand supply conditions (e.g. Benda et al., 2004; Ferguson et al., 2006; Kiffney et al., 2006; Rice et al., 2006).

Our HPPM provided a physical basis and new insight regarding how post-spate biomass is distributed down a sedimentary link of diminishing grainsize. HPPM simulations indicated that the longitudinal pattern of biomass down a sedimentary link was nonlinear, as inferred from rock scale biomass associations reported in previous field studies. Link scale periphyton refuge was highest at the downstream end of the link for a low-magnitude spate (i.e. 0.85MAD) but highest at the upstream end for a highmagnitude spate (i.e. 3MAD). While still contentious, a cursory analysis of the data reported in previous studies suggest that network scale (Table 6.1, *sensu* Frothingham et al. (2002)) periphyton refuge (e.g. higher than average post-spate biomass retained in isolated tributaries) exists in the headwaters because the intensity of velocity conditions on riffles, the supply of fine sediment and fraction of sand stored on the channel bed increase down the network (Osmundson et al., 2002; Biggs and Kilroy, 2007). Future HPPM work will test the hypothesis that periphyton refuge is highest at the downstream end of sedimentary links that are at the upstream end of the drainage network (also see Young and Huryn, 1996).

### Chapter 7 Summary and Conclusions

This research program answered several fundamental questions regarding how periphyton is removed from the bed of a river by saltating sand, how channel morphology affects the transport of sand and distribution of post-spate periphyton, and how the amount of sand in the river affects the longitudinal distribution of post-spate periphyton biomass down sedimentary links. Our objectives were achieved through field based empirical measurements, *in situ* experimentation, and numerical modelling.

Studies of large scale (e.g. watershed) patterns in periphyton abundances have shown that the spatial distribution of biomass is influenced by small scale (e.g. rock) habitat variability, the time since the previous spate, the magnitude of the previous spate, and the spatial distribution of resources (e.g. nitrogen) required for growth. At much larger spatial scales, researchers have reported many obstacles to conducting research including: high sampling expense, logistical difficulties of obtaining concurrent measurements at 100's of locations, difficulties achieving adequate statistical power after controlling for covariates, and the unpredictability of the spate timing and magnitude (Cattaneo et al., 1993; Uehlinger et al., 1996). For example, during our first, major field monitoring program in 2003, periphyton data had to be collected from 5 reaches (35 cross sections, 2100 rocks) over 40 km of river, within the shortest time possible. Three highmagnitude untypical summer spates scoured the bed nearly clean prior to periphyton sampling. The only periphyton refuge was found on one riffle (of 35), at the downstream end of the most headward link. The variance in periphyton biomass at all other riffles was too low to develop a mechanistic understanding of how the large 2003 spates scoured the bed clean. Consequently, I targeted and monitored a small spate in 2004 and developed a numerical model to isolate the effects of morphology, flow and sand transport on post-spate biomass distribution.

The numerical model required the development of a submodel to describe the spate related environmental conditions that lead to periphyton loss, at the rock scale. A

saltation abrasion model for periphyton (PSAM) was developed conceptually based on an existing mechanistic model for bedrock erosion (Sklar and Dietrich, 2004). The model was tested with other covariates known to affect losses of periphyton, such as plucking by the shear force of water (Ch. 3). Periphyton was monitored in 2004 before and after a low-magnitude spate (0.6mean annual discharge, 0.6MAD) with a mean weekly summer recurrence. Our results indicate that saltation was the predominant mode of transport for sand (0.5-2mm) during the spate. Patches of bed with high periphyton biomass were divided from patches with low biomass, by a well established threshold for the initiation of sand entrainment (i.e. $W^* > 0.002$ , Wilcock and Kenworthy 2002). Low periphyton biomass (< 10 mg/m<sup>2</sup>) was found where sand transport rates exceeded 64-180 g m<sup>-1</sup> event<sup>-1</sup>, peak shear stresses were greater than 15 Pa and average baseflow velocities higher than 0.5 m/s. The 15 Pa threshold is approximately three times the stress required to initiate the transport of sand on a cobble bed.

For rocks exposed to high sand transport rates, the modified saltation abrasion model (PSAM) explained 56% to 59% of the variance in biomass. The sand transport rate had a strong negative effect on periphyton biomass and was a significant predictor in the SAMP model. This variation in sand transport rate was independent of baseflow velocity and peak spate shear stress. The immersion index I proposed was a significant predictor of biomass, and represented the extent to which the rock was contained within the saltation layer (i.e. where the number of sand grain impacts by transported sand is highest). The saltation abrasion model was successful in describing differences in rock scale biomass. The amount of periphyton retained after the spate increased with protrusion of the growth surface above the saltation layer.

The spatial distribution of periphyton refuge across 15 riffles during a lowmagnitude spate period was documented (Ch. 4). As hypothesized, refuge was found in an intermediate zone between the thalweg and the near shore zone (i.e. varial zone of frequent wetting and drying subject to desiccation stress) for periphyton, as Jowett (2003) hypothesized for the case of macroinvertebrates. Biomass increased away from the thalweg as sand transport rates decreased. In one reach however, biomass decreased again towards the edge of the low flow channel where a small secondary peak in sand
transport occurred, despite the laterally decreasing flow strength. In this reach, there was an increase in fraction of sand on the bed towards the channel edge, which increased the mobility of sand, contributing to this secondary peak in transport.

An *in situ* experiment was also conducted to determine if the empirical results were supported by direct observation of the sand abrasion process (Ch. 5). Our analysis showed that the periphyton losses occured at ~ 64 g m<sup>-1</sup> event<sup>-1</sup> as inferred from natural spate data, but also occurred as low as 9 g m<sup>-1</sup> event<sup>-1</sup> if the sand was coarse (0.5-2 mm vs 0.063-0.5) and predominantly saltating (i.e. vs. suspended). Substrates closer to the bed lost more periphyton than elevated substrates, confirming the hypothesis that refuge potential increases with elevation above the bed. At high rates of sand transport, post-spate periphyton biomass was low, regardless of the elevation above the bed, size of sand in motion or mode of transport (i.e. suspended or saltating). The results from Chapters 3-5 contribute to the body of knowledge regarding factors affecting post-spate periphyton biomass by adding documented proof of the importance of saltating sand to periphyton abrasion (Figure 7.1).



Figure 7.1 Diagram of local controls on periphyton biomass including saltation abrasion.

A hierarchical periphyton perturbation model (HPPM) was then developed to investigate the effects of sand supply and channel morphology on sedimentary link scale patterns in periphyton refuge (Ch. 6). The HPPM required the development of a rock scale sand transport submodel that accounts for the advection of sand from the upstream riffle (i.e. the overpassing phase of sand transport, see Ferguson et al., 1989). The new sand transport submodel explained 68% of the variance in low sand transport rates using 2004 data from the Sainte Marguerite River. The parameterized overpassing transport model showed that more deposition occurs between riffles when there is an abrupt downstream decrease in stream power, and a small downstream decrease in grain size between riffles. Deposition between riffles reduced (or eliminated) sand delivery to the downstream riffle. Thus the model findings showed that the reach scale channel morphology affected the supply of sand to a habitat patch. These results indicate that a riffles geomorphic context affects how protected the riffle surface is from the abrasive effects of sand, transported from upstream.

The HPPM also required developing a geomorphic model to characterize channel form from the rock scale, to the sedimentary link scale (i.e. the habitat template). The morphometric data used to parameterize the geomorphic sub models were collected on 35 riffles (and associated reach), within 5 reference links on the Sainte Marguerite river. These data were also classified into morphologically distinct planform scale units (hydrogeomorphic reaches - HGRs) based on specific stream power divisions selected using multivariate adaptive regression splines. Low-HGRs ( $10 \text{ W/m}^2 < \text{Specific Stream}$ Power -  $SSP < 30 \text{ W/m}^2$ ) had low gradient and sinuous reaches, with gravel-cobble bed riffles, and were typically located at the downstream end of links. Medium-HGRs (30  $W/m^2 < SSP < 60 W/m^2$ ) were positioned between Low-HGRs and High-HGRs, and possessed morphological properties of these adjacent channel types. High-HGRs (60  $W/m^2 < SSP < 80 W/m^2$ ) had high gradient and straight reaches, coarser bed material (cobble-boulder), and were typically located at the upstream end of the sedimentary sedimentary links. The SSP divisions that divided morphologically distinct HGRs also overlapped SSP thresholds reported in other river morphology classification studies (Brookes, 1996; Nanson and Knighton, 1996; Kondolf et al., 2003; Burge, 2005).

The HPPM model permitted a heuristic assessment of the influence of both sedimentary link morphology and sand supply on the spatial distribution of periphyton biomass at the link scale. I focused on the disturbance of a small spate (0.85MAD) that has an average recurrence period 4 times more frequent than the time required for periphyton to reach peak biomass on the Sainte Margarete river. Simulations showed that the longitudinal pattern of biomass down a sedimentary link did not simply decrease downstream with decreasing grainsize, under the assumption that smaller substrates are more mobile and therefore loose more periphyton during spates. Rather, biomass initially decreased with distance downstream from the top of the link. The downstream decrease in biomass continued until the location where riffles had a specific stream power (*SSP*) of 50 W/m<sup>2</sup>. Biomass then increased in the downstream direction to maximum values (10-40 mg/m<sup>2</sup>) on riffles with very low specific stream power (10 W/m<sup>2</sup>). The 50 W/m<sup>2</sup> threshold also divided straight channels with broad shallow cross sections (e.g. High-HGR) from sinuous channel with a more u-shaped cross section (e.g. Low- & Med-HGRs).

Low-HGR riffle rocks, located at the downstream end of the link, had the highest post-spate biomass (i.e. highest amount of refuge) because hydraulic stress and sand transport rates were low (Tables 7.1 and 7.2). Medium-HGR riffle rocks, located upstream of Low-HGR riffles, were the most susceptible to abrasion by sand because host-rocks were exposed to high rates of transport. High-HGR riffle rocks, located in the coarse upstream end of the link, were 'hidden' by large adjacent rocks (i.e. low exposure index), and protruded above the saltation layer providing some refuge (i.e. low immersion index). Biomass increased in an upstream direction in High-HGRs as bed material size increased, decreasing both the PSAM indices of 'exposure' and 'immersion'. The small amount of refuge provided by these High-HGR riffles was very susceptible to erosion by sand supplied to the upstream end of the link.

One of the most significant results from our HPPM investigation is that an increase of the fraction of sand on the bed from 5% to 20% led to an 8 fold decrease in biomass in all HGRs. This is significant because these findings apply to spates with an average weekly recurrence period. This suggests that the standing crop of periphyton in

**Table 7.1** Summary of differences in periphyton biomass and physical disturbance factors by channel type. Results from a small simulated spate (0.85MAD) using the hierarchical periphyton perturbation model.

	Low-HGR	Med-HGR	High-HGR	
	10 < <i>SSP</i> < 30	30 < <i>SSP</i> < 60	60 < <i>SSP</i> < 100	
Periphyton biomass	High	Low	Moderate	
Sand transport	Low	High	Moderate	
Exposure	Exposed	Mod. Exposed	Hidden	
Velocity	Low	Moderate	Moderate	
Refuge	High	Low	Low-Moderate	

**Table 7.2** Sensitivity of periphyton biomass to changes in sand supply on the bed  $(F_{sa})$ , sand delivery from upstream  $(Q_s)$  by channel type. Summary of simulation runs for a small simulated spate (0.85MAD) using the hierarchical periphyton perturbation model.

	Low-HGR	Med-HGR	High-HGR		
	10 < <i>SSP</i> < 30	30 < <i>SSP</i> < 60	60 < <i>SSP</i> < 100		
Periphtyon biomass sensitivity to $F_{sa}$	Low	High	Moderate		
Periphyton biomass sensitivity to Q <sub>s</sub>	Low	High	High		
Refuge	High	Low	Moderate		

the Sainte Marguerite river is highly susceptible to subtle changes in the amount of sand on the bed.

The HPPM model results showed that a downlink increase in biomass occurs with distance from a source of sediment (e.g. tributary, quarry, storm sewer) as suggested by (Yamada and Nakamura, 2002), and a downlink decrease in biomass occurs with distance from a sediment sink (e.g. lake or reservoir) as suggested by (Cattaneo, 1996; Jakob et al., 2003; Meyers et al., 2007). The linkage between longitudinal trends in biomass and sand supply has been developed through field studies that inferred transport activity from biomass patterns (i.e. the studies lack sand transport measurmements). The HPPM model

provided clear causal pathways linking the spatial distribution of periphyton biomass with sand supply.

Our results support proponents stressing linkages between biomass and channel type (Coleman and Dahm, 1990; Chessman et al., 2006; Meyers et al., 2007; Walters et al., 2007) but illustrate how position in the network relative to sediment sources should be considered. While the HPPM was validated by independent event data and a sensitivity analysis, further testing is required on other systems. The HPPM provides a modelling framework to test ecological theory, and evaluate how changing environmental conditions affect the spatial distribution of refuge and food availability, at a scale relevant to river managers. A dynamic form of the model should include accrual and autogenic sloughing processes (Uehlinger et al., 1996; Bouletreau et al., 2006; Schweizer, 2007), and substitution of empirical relations with mechanistic model components to simulate the negative feedback between bank erosion, width expansion and sand supply on the bed.

There is a great deal of interest in determining the ecological impact of hydrogeomorphological discontinuities in the fluvial system such as confluences (e.g. Benda et al., 2004; Ferguson et al., 2006; Kiffney et al., 2006; Rice et al., 2006). Researchers have shown that the hydro-geomorphological nature of these junctions is governed by network structure (Benda et al., 2004) and the relative supply of sediment and water (Ferguson et al., 2006). This dissertation addressed how periphyton biomass is distributed between channel confluences. However, the HPPM results inspire a series of hypotheses regarding expected longitudinal trends in biomass to be found at channel junctions that are based on the juxtaposition of different types of influent HGRs and diffluent HGR in the confluence (Figure 7.2).

What this study does not explain is how the periphyton disturbance thresholds in sand transport rate, shear stress and conditioning velocity reported here vary depending on the resistance of the periphyton community. While the empirical PSAM model explained biomass abundance in the field, laboratory testing of the dimensioned PSAM mechanistic model would provide a more thorough assessment of the process of saltation abrasion for periphyton. Parameterization of the PSAM in the flume would require

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**Figure 7.2** a) Downstream distribution of periphyton within a sedimentary link after a small spate modeled using the hierarchical periphyton distribution model (Ch. 6). In a drainage network, only a portion of this idealized link may be expressed between sediment sources such as tributaries. Different channel types are juxtaposed at confluences depending on the structure of the network (see Benda et al., 2004; Kiffney et al., 2006). Some of these channel type combinations are shown in confluences A-F as well as the hypothesized changes in periphyton biomass at these discontinuities based on Figure 7.2a. Differences in nutrients and temperature may override these hypothesized trends.

quantifying how resistant different periphyton communities are to abrasion by saltating sand. More specifically, we require measurement of the volume eroded per impact ( $V_{ip}$ , equation (3.2)) and the mat density ( $\rho_{mat}$ ) for different types of algal growth forms.

The sand transport model developed for the HPPM requires further validation against a broader range of field data, and comparison with conventional sediment routing models. Further work is encouraged regarding how sand is transported over a coarse bed of mixed sediments, and how turbulence affects the kinetic properties of sand grains within the saltation layer. The development of our mechanistic understanding of periphyton abrasion by mobile sediments, and advances in our ability to model these sediment fluxes within the drainage network, will enable a network scale HPPM to be developed to assess changes in periphyton (i.e. stores of carbon, nitrogen, and food) biomass resulting from land use and climate change on a broad range of riverine ecosystems.

This study did not address how the sedimentary climate near the streambed changes with spate magnitude. The "sedimentary climate" refers to the mix of grain sizes in motion and how they are being transported. This sedimentary climate is a fundamental characteristic of the habitat template that governs the structure of benthic communities through its influence on the selection of organisms with the appropriate adaptive strategies (behavioural, physiological and life history) for a given sediment transport regime (Poff and Ward 1990, Church 2000). It is possible to gain some insight into the sedimentary climate and most erosive grain size for a given spate by predicting bedrock erosion rates using the Saltation Abrasion Model (SAMB) of Sklar and Dietrich (2004) for a range of particle sizes (Figure 7.3). The SAMB model dictates that the erosion rate for exposed bedrock is the product of the volume of material eroded per impact and the rate of impact (Sklar and Dietrich, 2004). These two terms vary with grain size. As particle size increases for a fixed flow condition, the particle impact rate decreases with diminishing excess shear stress but the volume eroded per impact increases with particle mass. Based on the SAMB model, the product of these two counterbalancing factors resulted in a different particle size causing the maximum bedrock erosion for a given spate condition (e.g. represented by shear stress level, Figure 7.3). These calculations



**Figure 7.3** Bedrock erosion rate for different sizes of bed material (0.5 mm – 64 mm) as a function of shear stress predicted by the saltation-abrasion model (SAMB, equation (3.1)) of Sklar and Dietrich (2004), holding sediment supply, depth and median particle size constant. Also plotted are the reach average shear stress (vertical lines) for the experimental conditions and natural spate monitored in 2003 and 2004 (Event Text Box). The spate event frequencies are posted to illustrate that larger bed material becomes entrained during less frequent spates, but a greater percentage of fine material becomes suspended.

represent bedrock erosion by saltation, but the SAMB model results are not inconsistent with our observations of periphyton abrasion during our *in situ* experiment.

The SAMB model was used to illustrate how the sedimentary climate changes with larger, less frequently occurring discharge events. The average shear stress during discharge events was used to plot (Figure 7.3) the position of the spates monitored in 2003 and 2004 (Ch. 4) and the experimental conditions reported here. The small spate of 2004 (0.6MAD) has a mean return period of 7 days and its peak discharge is exceeded 48% of the time during the growing season (Ch. 4). During this spate, the SAMB model predicts the highest rate of erosion by 2 mm sand and a similar but lower rate for 1 mm

sand. Further, bed material smaller than 1 mm is in suspension and 8 mm gravel is at the threshold for motion. The hydraulic conditions tested during the experiment were 14 Pa which plots just above the 2004 spate. During the experiment, the SAMB predicts that 2 mm sand is the most efficient at eroding bedrock, and 8 mm gravel is mobile and eroding bedrock. One mm sand was at the threshold for suspension. In contrast, the much larger spate of 2003 (3MAD) filled 3/4 of the bankfull channel and was exceeded 0.7% of the growing season (Ch. 3). The average shear stress of riffles in four sedimentary links on the Saint Marguerite river (SMR) varied from 24 to 52 Pa during this spate. Over this range of shear stresses, 16 mm gravel were mobile and the most efficient sizes at eroding bedrock range from 2 mm sand at 24 Pa, to 8 mm gravel at 52 Pa. All sand less than 1 mm were transported in suspension at shear stresses exceeding 24 Pa. The SAMB model predicts that 2 mm sand was saltating and capable of eroding bedrock over the full range of spates from very frequent to bankfull conditions.

Greater than 40% of mobile sediment caught in the 608 sand traps during the spates monitored on the SMR were 0.5 to 2 mm sand for discharge events ranging from frequent spates to near bankfull events (Ch. 3). This high percentage of sand in the bedload is common for gravel/cobble bed rivers (Lisle, 1989; Stokseth, 1994; Lisle, 1995; Wilcock et al., 1996). Given the ubiquity of 0.5 to 2 mm sand in the bedload and ability of this coarse sand to scour substrates over the full range of spates that can occur during the growing season, this size fraction can be of primary importance in governing biomass of diatom-dominated periphyton communities in gravel-cobble bed rivers.

### **APPENDIX** A

### A.1 Measuring Saltation height.

Saltation heights are typically measured using high speed videography and image analysis (Lee et al., 2002) but this approach was not practically feasible at hundreds of locations during one spate. Consequently, steel spikes 0.3 m in length were painted (latex) and driven into the bed at every other sediment trap to measure the abrasion height due to the saltation load during the monitoring period (Figure 4.5b). The abraded section of paint on each nail was measured from the substrate insertion point to the top of the dulled paint.

#### A.2 Validation of saltation height submodel

The measured height of paint abrasion on steel spikes was regressed against a prediction of average saltation height made using the method of Sklar and Dietrich (2004):

$$Hs_{Sklar and Dietrich} = 1.44 \left(\frac{\tau^*}{\tau_c^* - 1}\right)^{0.5} D_s$$
 (A.1)

where,  $\tau^*$  is the shear stress at the spate peak, made dimensionless by the size of sand in motion ( $D_s = 2$  mm), and  $\tau_c^*$  is the dimensionless critical shear stress when sand motion is initiated. The dimensionless shear stress at the spate peak is given by:  $\tau^* = \tau/(S_g - 1)\rho g D_{sa}$ , where  $\tau$  is the shear stress given by equations (3.5) or (3.6),  $S_g$  is the specific gravity of sediment, and  $D_{sa}$  is the diameter of sand in transport.  $S_g = \rho_s/\rho_w$  and  $\rho$  is the density (kg/m<sup>3</sup>) of sediment ( $\rho_s$ ) and water ( $\rho_w$ ). The method of Wilcock and Kenworthy (2002) to determine critical shear stress for entrainment of mixed sand and gravel beds was used to calculate  $\tau_c^*$  (i.e. ~  $\tau_r^*$ ) at each rock. By their method,  $\tau_c^*$  decreases as the fraction of sand on the bed increases, and as particle becomes less hidden by the surrounding substrate.

The average saltation height was calculated at each abrasion pin location using equation (A.1) and  $\tau_c^*$  using Wilcock and Kenworthy (2002). Abrasion height measurements were the paint abrasion height was clearly identifiable by a definitive line

of scour (n = 20) were regressed against the average saltation height estimate. The average saltation height submodel estimate (equation (A.1)) explained 73% of the variance in group two measured steel pin abrasion heights (SE = 0.11, p < 0.001, n = 20). Consequently, equation (A.1) was used to calculate average saltation heights at all rock locations for the 24 August 2004 spate.

#### A.3 Abrasion height regression model

We required a best estimate of abrasion height (i.e. vs Sklar and Dietrich (2004) mean saltation height estimate) for our statistical analysis (Section 3.3.4) to investigate if abrasion height is a stronger predictor of post-spate biomass than average saltation height. For this objective, interpretability is secondary to how well *AH* is predicted. Independent predictor variables were selected based on saltation kinetics theory. Dimensionless forms of flow and sediment variables were preferred. The variables include: the fraction of sand on the bed ( $F_{sa}$ ), the flow Froude Number (*FR*), and the suspension criteria for 2 mm sand ( $SC_{2mm}$ ) and median protrusion height of a patch of 10 rocks ( $P_{50}$ ). The abrasion height (*AH*) is given by:

$$AH = 0.015 + 0.085P_{50} - 0.046F_{sa} + 0.051FR + 0.045SC_{2mm}$$
(A.2, 6.8)  
SE=0.007,  $R^2_{Adj} = 0.65$ ,  $p < 0.001$ ;  $n = 56$ .

using that same abrasion height measurement data used to assess the applicability of equation (A.1) to our field sites plus 36 additional data points. The paint abrasion height on these 36 abrasion pins was clearly identifiable but the scoured paint section graded more gradually into the unscoured paint section of the abrasion pin. Consequently, the measurement error is slightly larger on this larger data set. The four predictor variables in equation (A.2) explain 92% (p < 0.002; n = 20) of the variance in measured abrasion height data using the smaller data set.

# **APPENDIX B**

# **B.1** Summary of Boundary and Initial Conditions for HPPM model runs.

Table B.1 Summary of Boundary and Initial Conditions

Boundary Condition	Explanation	Reference Case
Specific Stream Power (SSP)	Specify a down link gradient of riffle cross sections ranging in stream power from 5-80 W/m <sup>2</sup> .	5-80 W/m <sup>2</sup>
Drainage Basin Area (DBA)	Specify position of link within the drainage basin using drainage basin area.	240 km <sup>2</sup>
Channel Shape Parameter	Specify degree of cross section asymmetry. (Ferguson, 2003)	0.24
Spate Discharge ( $Q_{spate}$ )	Specify test spate peak discharge	8.2 m <sup>3</sup> /s
Sand Discharge at upstream end of link $(Q_{s_in})$	Specify assumed sand input at the upstream end of the link: Guided by empirical relation between spate discharges vs. sand discharge from field data.	10 g m <sup>-1</sup> event <sup>-1</sup>
Fraction Sand on the Bed	Specify fixed fraction of sand on the bed.	15%
$(F_{sa})$	(Wilcock and Kenworthy, 2002)	

# **B.2** Summary of HPPM Model Parameters.

# Table B.2 Summary of Model Parameters

Parameter	Explanation				
Determine Ba	Determine Bankfull Channel Dimensions.				
1.1) Bankfull Discharge	Developed from Ste. Marguerite Data (Sainte-Marguerite Nord-Est Branch gauge 062803, 1100 km <sup>2</sup> prorated to 240 km <sup>2</sup> , 1976-2003)				
$(Q_{bfl})$	$Q_{bfl} = 0.52 DBA^{0.8}$				
	DBA =Drainage Basin Area				
1.2) Median	Developed from Ste. Marguerite Data (35 Cross Sections)				
Particle Size $(D_{50})$	$\log D_{50} = 0.762SSP - 0.363$				
	SSP = specific stream power				
	$SSP = \rho g Q_{bfl} S / W$				
1.3) Riffle Slope ( <i>S</i> )	$\frac{\rho g Q_{bfl} \frac{S}{SSP}}{\frac{14.747 Q_{bfl}^{0.514} S^{0.238}}{D_{50}^{0.142}}} = 1$				
	Given SSP, $Q_{bfl}$ , $D_{50}$ , Iteratively solve for S.				
1.4) Bankfull	Developed from Ste. Marguerite Data - Relation form from Griffiths (1981).				
vviðtn (W <sub>bfl</sub> )	$W_{\rm bfl} = \frac{14.747 * \rm Qbfl^{0.514} * S^{0.238}}{D_{50}^{0.142}}$				

1.5) Mannings <i>n</i>	(Limerinos, 1970).				
1.6) Bankfull Depth (D <sub>bfl</sub> )	Normal Depth calculation using $Q_{bfl}$ , area and perimeter of a compound channel (2 triangles, 1 rectangle), continuity of flow, mannings and Limerinos (1970). Solution made using "Solver" Excel, batched using Visual Basic.				
1.7) Banktop Depth (Q <sub>btp</sub> )	Normal Depth calculation using $Q_{btp}$ , area and perimeter of a compound channel (2 triangles, 1 rectangle), continuity of flow, Mannings and Strickler. Solution made using "Solver" EXCEL, batched using Visual Basic.				
1.8) Area (A)	Given <i>W</i> , <i>b</i> , and <i>D</i> calculate using compound channel configuration (2 triangles, 1 rectangle).				
1.9) Velocity $(V_{bfl})$	$V_{bfl} = \frac{Q_{bfl}}{A}$				
1.10) Channel Dimensions	$A = A_{Triangle1} + A_{Triangle2} + A_{Rectangle}$ Ferguson (2003) – For $W_i, A, b, A_{Triangle1} = A_{Triangle2}$				
Divide each c for each patcl	ross section into 10 patches. Calculate cross section grain size characteristics h. Calculate discharge dependent water surface slopes.				
2.1) Patch distance	$DP = \frac{W_{bfl}}{11} + DP_{pi-1}$				
across channel (DP)	DP <sub>pi-1</sub> =distance of previous patch				
2.2) Bankfull depth at patch i $(d_{bfl_Pi})$	$d_{bfl_Pi} = if DP \le W_{T1}then S_{lat\_bed\_Tr1}DP \ else DP - bW_{bfl}S_{lat\_bed\_Tr2} + d_{rect}$ where, $W_{T1}$ is the width of triangle 1, $S_{lat\_bed}$ is the lateral bed slope of triangles one $Tr1$ ) and two ( $Tr2$ ), and $d_{rect}$ is the depth of the rectangle.				
2.3) Cross Section Asymmetry $(A_{cx}^*)$	$A_{cx}^{*} = \frac{A_{Large} - A_{small}}{A_{ttl}}$ Ref: Knighton (1987), Pg 106, Figure 4.6a.				
2.4) Lateral Sorting Gradient ( <i>LSG</i> )	Developed from field data $LSG = 0.08623 + 0.2671D_{50}100 - 0.00033DBA$ $DBA = Drainage Basin Area = km^2$				
2.5) <i>D</i> <sub>50_<i>pi</i></sub> Patch	Assume $D_{50_{cx}}$ applies to the centre of cross section and apply lateral sorting gradient.				
2.6) Fraction Sand – Lateral Gradient	$F_{sa\_i} = \overline{F_{sa\_cx}}(0.904 + 0.678DFT)$ Where $F_{sa\_i}$ is the fraction of sand at location $i$ , $\overline{F_{sa\_cx}}$ is the mean cross section fraction of sand, and $DFT$ is dimensionless distance from the thalweg. $R^2 = 0.5$ , $F_{(1,191)} = 185$ , p=0.000				
2.7) Ratio of August low flow to spring bankfull	$S_{rat=\frac{S_{low}}{S_{bfl}}}$ where, $S_{low} = 0.00052 + 0.72433S_{riffle}$				

slope (S <sub>rat</sub> )	$S_{bfl} = 0.001874 + 0.44895S_{riffle}$					
	where $S_{low}$ is water surface slope at base flow, $S_{bfl}$ is water surface slope at bankfull, and $S_{riffle}$ is given in Table B.2, Section 1.3.					
2.8) Baseflow Slope	$S_{baseflow} = S_{riffle} \left( \frac{S_{base}}{S_{bfl}} \right)$					
2.9) Slope at test depth	$S_{d\_test} = S_{baseflow} + \left(\frac{d_{test}}{d_{bfl}}\right) \left(S_{riffle} - S_{low}\right)$					
Determine hy velocity at bas	draulic and sand transport conditions at test stage. Calculate conditioning seflow.					
3.1) Test Depth at patch <i>i</i>	Normal Depth calculation using test discharge, bankfull channel characteristics, continuity of flow, mannings and Limerinos (1970). Subtract stage for test discharge from bed elevation.					
3.2) Check	Velocity at patch $i$ - Mannings and Limerinos (1970) with test depth at patch i.					
Q at test depth for $CX_i$	Area of panel between patch $i$ and $i + 1 = \overline{d}w$					
	$Q_{pi} = A_{pi} V_{ip}$ ,					
	$Q_{pi} = Q$ at patch <i>i</i>					
	$Q_{TD\_cx_i} = \sum Q_{pi}$					
	$Q_{TD_cx_i} = Q$ at test depth for cross section <i>i</i>					
3.3) Shear	$\tau_{Pi} = 2.932 + 0.510\tau_{DuBoys} + 1.171RR - 2.432DFT$					
patch I ( $\tau_i$ )	$(R^2 = 0.68 R^2_{adj} = 0.66 SE = 0.22 Pa n = 50)$					
	where:					
	$\tau_{\rm DuBoys} = \rho g D_{\rm pi} S,$					
	<i>RR</i> = relative roughness = rock b axis/flow depth					
	DFT= distance from the deepest part of the channel/active channel width					
3.4) Shear	$\tau_{avg\_cx_i} = \overline{\tau_{\iota\_cx_\iota}}$					
depth for $CX_i$	$\tau_{\max\_cx_i} = \max\left(\tau_{i\_cx_i}\right)$					
3.5) Sand Transport at patch I $(ST_i)$	Overpass compensating sand transport model (Luce et al., 2008).					
	$ST_{i} = (5.76\phi^{4.4})_{rock/patch} \left( Q_{sa_{in}} \left( \frac{SSP_{below}}{SSP_{above}} \right)^{2} \left( \frac{D_{us}}{D_{riffle}} \right)^{\frac{1}{2}} \right)_{reach} R^{2} = 0.68$					
	where,					
	$\phi = \frac{\tau_{i}}{\tau_{crt}},$					
	where $\tau_{crt}$ is given by Wilcock and Kenworthy (2002) for 2 mm sand, $Q_{sa_{in}}$ = mean sediment transport rate of upstream riffle, $SSP_{above}$ = upstream riffle stream power, $SSP_{below}$ = stream power at subject riffle, $D_{riffle} = D_{50}$ of subject riffle, $D_{us} = D_{50}$ of					

	upstream riffle.		
3.6) $ST_i$ at test depth for $CX_i$	$\overline{ST_{cx}} = mean(ST_i)$ $ST_{cx_max} = max(ST_i)$		
3.7) Conditioning Velocity	Mannings and Limerinos (1970) with assumed growth stage of 0.34 <i>Bfl stage</i> – based on field data.		
Determine pe periphyton.	riphyton biomass after test flow using the saltation abrasion model for		
4.1) Post-	Periphyton Saltation Abrasion Model (PSAM) from Chapter 3		
Spate Periphyton at patch $i$ $(R_{Pi})$	$PR = f(CV_i, \mathcal{T}_i, ST_i, Prot_i)$		
PSAM Validation2.syc	$log RP_{i} = 2.488 - 0.412 log ST_{i} - 1.486 log \left(0.5 + \frac{SH}{Prot_{i}}\right) - 1.776 CVi^{0.5} - 7.693 AH_{2mm} - 0.472 log \frac{Prot_{i}}{P_{50i}}$		
	where:		
	$AH_{2mm}$ = abrasion height for 2 mm sand = equation 6.8 , $Prot_i = 0.55D_{50pi}$		
Plot cross section average periphyton biomass and disturbance conditions as a function of specific stream power.			
4.2) Mean <i>RP</i> at test depth for <i>CX<sub>i</sub></i>	$\overline{RP_i} = mean(RP_i)$		

# **B.3** Link dimension assumptions.

**Table B.3** Link dimension relations (used for display purposes only).

Link Length (LL)	(Benda et al., 2004). $\log LL = 0.81 \log DBA + 1.30$
Cross Section Location on Link (IRL)	Assume six channel widths between riffles.
	$IRL = SD + 6W_{bfl}$
	where <i>SD</i> is distance upstream and $W_{bfl}$ is bankfull stream width.
Riffle Elevation (RE)	Arbitrary elevation selected at top of reach and subsequent elevations determined from successive riffle slopes.
	$RE = E_{us_r} - \frac{S_{us_cx} + S_{ds_cx}}{2} \left( SD_{d/s \ cx} - SD_{u/s_cx} \right)$
	where, <i>E</i> is elevation, <i>S</i> is slope, <i>SD</i> is distance upstream and the subscripts <i>r</i> is riffle, $cx$ is cross section, $us$ is upstream and $ds$ is downstream.

### **APPENDIX C**

#### C.1 Sand Transport Sub-Model

There are three phases of sediment transport including the overpassing phase, size selective phase, and fully mobile phase (Ashworth and Ferguson, 1989). During the overpassing phase, sand advected from upstream is transported over a static local bed. Size selective transport occurs when only some of the clasts on the local bed are mobile. Full mobility occurs when all the material on the local bed are in motion. The overpassing phase is likely to occur during small frequent spates, shown to be capable of abrading periphyton by mobile sand. Traditional sediment transport equations are capable of representing conditions of partial and full mobility but cannot adequately model the overpassing phase of transport. During the 2004 small summer spate, we observed sand transport at locations where the excess shear stress was not high enough to entrain sand and noted that these cross sections were located downstream of higher energy riffles where sand transport did occur. Consequently, we developed a sediment transport function that incorporates sediment routing from upstream, based on conveyance characteristics of the inter-riffle reach, with a local patch scale prediction provided by the sediment transport equation of Wilcock and Kenworthy (2002). A full account of the model development is given in (Luce et al., 2008) and summarized below.

#### **C.2 Model Development**

#### C.2.1 Patch Scale Sand Transport

Sediment transport functions that are based on the bulk properties of flow are typically in the form:

$$Q_{sa} = \alpha \phi^{\beta} \tag{C.1}$$

where,  $\phi$  is excess shear stress,  $\alpha$  and  $\beta$  are fitted constants. The excess shear stress is given by:

$$\phi = \frac{\tau}{\tau_{crt}} \qquad (C.2)$$

where  $\tau$  is the shear stress during the event and  $\tau_{crt}$  is the critical shear stress. The total shear stress is given by DuBoys as:

$$\tau = \rho g dS \tag{C.3}$$

where,  $\rho$  is the density of water (kg/m<sup>3</sup>), is *g* the acceleration due to gravity (m/s<sup>2</sup>), *d* is the flow depth (m), and *S* is the energy grade line but often assumed to be the local water surface slope (m/m).

Application of bedload transport formulae to mixed grain sizes requires the consideration of the degree of hiding of the grain amongst the adjacent bed particles. If a grain is larger than surrounding bed material, then it is more exposed to flow and is more easily moved than a small grain surrounded by larger rocks. Wilcock and Kenworthy, (2002) presented a two fraction model where the effect of sand supply on the bed is also considered in the determination of resisting stress. The authors found that the critical shear stress for sand (and for gravel) decreased with increasing fraction of sand on the bed. This results in sediment movement at lower shear stresses when higher amounts of sand are present on the bed (Figure C.1).



**Figure C.1** Graph showing the reduction of dimensionless reference shear stress for sand with increasing sand content on the bed (Adapted from Wilcock and Kenworthy, 2002)

Wilcock and Kenworthy, (2002) used both field and flume data to fit their sediment transport model which is presented below and illustrated in Figure C.2:

$$W_i^* = \begin{cases} 0.002\phi^{0.75} & \text{for } \phi > 1.35 \quad (C.4, 2.4) \\ 14\left(1 - \frac{0.894}{\phi^{0.5}}\right)^{4.5} & \text{for } \phi \ge 1.35 \quad (C.5, 2.5) \end{cases}$$

where,  $W_i^*$  is the dimensionless sediment transport rate for size fraction *i* and:

$$W_i^* = \frac{(s_g - 1)gq_{bi}}{F_i u_*^3} \tag{C.6}$$

where,  $S_g$  is the specific gravity of sediment,  $q_{bi}$  is the volumetric transport rate per unit width of size *i*,  $F_i$  is the proportion of size *i* on the bed surface, and  $u_*$  is the shear velocity  $u_* = \sqrt{\tau/\rho}$ .

In their two fraction model, different critical shear stresses are determined for the gravel and sand portion of the bed. In our study, we are concerned with sand transport where  $\tau_{crt} = \tau_{rsa}$ , a reference shear stress for the initial movement of a very small quantity of sand. The reference shear stress for sand is given by:

$$\tau_{rsa} = \tau_{rsa}^* (S_g - 1) \rho g D_{sa} \tag{C.7}$$

where,  $\tau_{rsa}^*$  is the dimensionless critical shear stress for sand,  $S_g$  is the specific gravity of sediment, and  $D_{sa}$  is the diameter of sand in transport (m). Where  $S_g = \rho_s / \rho$  and  $\rho_s$  is the density of sediment (kg/m<sup>3</sup>). The dimensionless critical shear stress for sand is given by the equation below and illustrated in Figure C1:

$$\tau_{rsa}^* = (\tau_{rsa}^*)_1 + ((\tau_{rsa}^*)_0 - (\tau_{rsa}^*)_1)e^{-14F_{sa}}$$
(C.8)

where,  $(\tau_{rsa}^*)_1 = 0.065$ ,  $F_{sa} =$  Fraction of sand on bed, and:

$$(\tau_{rsa}^*)_0 = \alpha \left(\tau_{rg}^*\right)_0 \left(\frac{D_g}{D_s}\right) \tag{C.9}$$

where,  $D_g$  = Median particle size of patch,  $D_s$  = Diameter of sand in transport, and  $(\tau_{rg}^*)_0 = 0.035$ .



**Figure C. 2** Dimensionless sediment transport rate vs. excess stress (Adapted from Wilcock and Kenworthy, 2002).

### **C.2.1 Reach Scale Transport Relation**

Wilcock (2004) used a proportionality developed by Henderson, (1966) to assess the influence of changing sediment supply on the stability of reconstructed reaches. The approach quantifies the sediment balance of Lane (1955) combining the Einstein-Brown transport law, Chezy flow resistance law, and the conservation of momentum and mass into the following proportionality:

$$\frac{q_s}{q} \propto \frac{qS^2}{D^{\frac{3}{2}}} \tag{C.10}$$

where,  $q_s$  is the sediment transport rate, q is water discharge, S is channel slope, and D is sediment grain size. Rearranging equation (C.10) in terms of  $q_s$  gives:

$$q_s \propto \frac{q^2 S^2}{D^{\frac{3}{2}}} \qquad (\text{C.11})$$

To determine the downstream influence of changing  $q_s$ , equation (C.11) can be written twice, once for each an upstream and downstream reach. The ratio of this proportionality gives:

$$\frac{q_{s2}}{q_{s1}} \propto \left(\frac{q_2 S_2}{q_1 S_1}\right)^2 \left(\frac{D_1}{D_2}\right)^{\frac{3}{2}}$$
 (C.12)

where, the subscripts 1 and 2, refer to the upstream reach and downstream reach respectively (Figure C.3). Rearranging equation (C.12) in terms of the downstream receiving reach and substituting specific stream power ( $\omega = \lambda q S / W_{unit}$ ) for qS gives:

$$q_{s_i} \propto q_{s_i-1} \left(\frac{\omega_{i+1}}{\omega_i}\right)^2 \left(\frac{D_{i-1}}{D_i}\right)^{\frac{3}{2}}$$
(C.13)

The  $q_{s_i}$ -1term indicates that the sediment transport rate across a downstream riffle is positively related to the quantity of sediment delivered from the upstream riffle. The latter two terms of equation (C.13) are indicative of the conveyance capacity between these riffles. The specific stream power and particle size ratios counter-balance each other. Specifically, a downstream decrease in grain size increases the transport rate, but a downstream decrease in specific stream power decreases the transport rate. This model conceptually resembles the excess shear stress model in equation (C.1) because sediment transport rate decreases with declining driving force (i.e. downstream decrease in specific stream power) but increases with lower resisting force (e.g. downstream decrease in particle size, enabling less hiding on a finer bed which results in lower critical shear stress).

#### C.2.3 Network Scale Transport Relation.

Tributaries supply q and  $q_s$ , often delivering different bed load grain sizes to the mainstream (Fig. B3, Benda et al., 2004; Ferguson et al., 2006). The degree to which the tributary affects sediment transport in the riffle(s) immediately downstream are hypothesized to follow the proportionality:

$$\frac{q_{s\_main}}{q_{s\_trib}} \propto \left(\frac{q_{main}}{q_{trib}}\right)^2 \left(\frac{S_{main}}{S_{trib}}\right)^2 \left(\frac{D_{trib}}{D_{main}}\right)^{\frac{3}{2}}$$
(C.14)



**Figure C.3** Three connected inter-riffle reaches and an adjoining tributary. Definition of key sediment transport parameters hypothesized to modify local sediment transport rates.

When equation (C.14) is written in terms of the effect of the tributary on mainstream sediment transport the proportionality takes the form:

$$q_{s\_main} \propto q_{s\_trib} \left(\frac{\omega_{main}}{\omega_{trib}}\right)^2 \left(\frac{D_{trib}}{D_{main}}\right)^{\frac{3}{2}}$$
 (C.15)

## **C.3** The Combined Relation

The sediment transport rate at a habitat patch/rock location should be affected by routing down the main stream and delivery from lateral sources such that:

$$(\alpha \phi^{\beta})_{patch} \left(q_{s\_us\_riffle} \left(\frac{\omega_{below}}{\omega_{above}}\right)^{2} \left(\frac{D_{us}}{D_{ds}}\right)^{\frac{3}{2}}\right)_{Reach} \left(q_{s\_trib} \left(\frac{\omega_{main}}{\omega_{trib}}\right)^{2} \left(\frac{D_{trib}}{D_{main}}\right)^{\frac{3}{2}}\right)_{Network} (C.16)$$

We tested the patch and reach components of this hypothesis using nonlinear regression and field data that captured sand routing behaviour down two sedimentary links of river during a small spate which occurred in 2004. The results are presented in Section 6.2.2.

See WRR\_Technical\_Note.doc

### **APPENDIX D**

#### **D.1 PSAM Models without pre-spate biomass**

We tested linear models that did not include pre-spate biomass because this measure is rarely available. The nonlinear regression form of our model is the most direct expression of the mechanistic form of the PSAM model (equation (6.2)). Not including pre-spate biomass results in a less complete specification of the system yet it allows us to explore if the predictive power of conditioning velocity increased if pre-spate biomass is removed (i.e. Does conditioning velocity share variance with a growth related parameter?). We used linear models for this test because this type of model (linear, linear mixed effects) is more statistically robust than nonlinear models yet there was close agreement of predictions from the nonlinear and linear regression models in section 3.4.

Table D.1 contains the best linear models excluding pre-spate biomass according to the same cumulative and sequential addition of the immersion index (3a), the exposure index (3b), and the abrasion height (3c). Unlike the models that included pre-spate

**Table D.1** Models 2a, 2b, 2c (Ch. 3) with pre-spate biomass excluded. The beta values correspond to the expanded model:  $PB_{T2} = \alpha + \beta_1 PB_{T1} + \beta_2 V_{water} + \beta_3 I_{r\_sand\_t} + \beta_4 F_{ep} + \beta_5 AH + \beta_6 \tau_{spate\_peak} + e^*$  (eq. (3.4) base); where,  $PB_{T2}$  and  $PB_{T1}$  are post-and pre-spate biomass respectively,  $V_{water}$  is conditioning velocity,  $I_{r\_sand\_t}$  is sand transport rate, and  $F_{ep}$  is either the exposure index (*HI*, i.e. eq. (3.7)), immersion index (*II*, i.e. eq. (3.8)). Beta values are standardized and  $R^2$  is adjusted.

Model	Model	R <sup>2</sup>	Pre-spate	Conditioning	Sand	Immersion	Exposure	Abrasion	Peak spate
	Туре		biomass	velocity	transport	Index	Index	Height	shear stress
			(β1)	(β₂)	(β₃)	(β <sub>411</sub> )	(β <sub>4HI</sub> )	(β <sub>5</sub> )	(β <sub>6</sub> )
3a	RE-G	0.44	Х	-0.43***	-0.21***	Х	Х	Х	х
3b	RE-G	0.46	х	-0.55***	-0.28***	Х	-0.15**	Х	х
3c	LM	0.52	x	-0.40***	-0.29***	-0.23	-0.26***	-0.13	Х

X' indicates that the variable was not entered as a predictor; \*p<0.1; \*\*p<0.01; \*\*\*p<0.001

biomass (section 3.4.2 and Table 3.5), the effect of conditioning velocity persists even when abrasion height is included in the model. The between cross section heterogeneity was larger in model 3c than what was observed in model 2c, but the heterogeneity was not significantly large enough to require the use of a random effects model for prediction (e.g. could use LM vs. Re\_G). The adjusted percentage of variance explained by model 3c is 52%, showing the decreased (but still significant) explanatory power of a model that does not include pre-spate biomass.

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