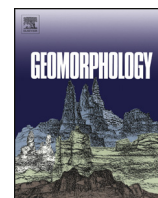




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The influence of channel bed disturbance on benthic Chlorophyll *a*: A high resolution perspective

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ABSTRACT

This study explores how spatial dynamics and frequency of bed mobility events in a headwater stream affect the spatial and temporal variability in stream benthic algal abundance and ultimately the resilience of benthic algae to stream scouring events of different magnitudes. We characterized spatial variability in sediment transport for nine separate flow events (0.1–1.7 of bankfull flow), coupling high resolution (<0.1 m²) two-dimensional shear stress values with detailed measurements of the channel substrate. The stream bed was categorized into regions of high and low disturbance based on potential mobility of different grain sizes. High resolution (<0.25 m²), in situ measurements of benthic Chlorophyll-*a* concentrations (Chl-*a*) were taken on 18 sampling dates before and after high flow events in regions of the streambed with contrasting disturbance to understand how benthic algal communities respond to sediment transport disturbance through space and time. According to the modeling results, the percentage of the channel likely to be disturbed varied greatly across the different flows and considered grain sizes between 7.7 and 70.4% for the lowest and highest flow events respectively. Mean shear stress in the channel bed across all sampling dates explained 49% of the variance in Chl-*a*. Over the 18 sampling dates – encompassing post-disturbance impacts and subsequent recovery – Chl-*a* differed between disturbance level categories defined based on the relative movement of the median grain size on 14 occasions. However, low disturbance locations were not always associated with higher Chl-*a*. The algal Chl-*a* biomass at any given time was a function of the stage of algal recovery following a high flow event and the magnitude of the disturbance itself – impacting algal loss during the event. Resistance of the algal communities to bed disturbance and resilience to recovery following a flow event varied spatially. Areas with low shear stress were less susceptible to scour during moderate disturbance events but were slower to recover when scour occurred. In contrast, high shear stress areas responded rapidly to flood events with rapid declines, but also recovered more quickly and appeared to have high potential for maximum accrual within our study reach. Ultimately, timing along with the inverse relationship between resiliency and disturbance frequency highlights the complexity of these processes and the importance of studying the interactions between geomorphic and ecological processes with high resolution across spatial and temporal scales.

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1. Introduction

The process of sediment transport and deposition is a fundamental organizing feature in fluvial systems that sets the physical habitat template of stream environments. Indeed, bed mobility is widely recognized as a key organizing feature for ecosystem processes and biota in streams (Peckarsky et al., 2014). Bed mobility and substrate scour that occurs during sediment transport and deposition are particularly important abiotic processes for stream primary production because they have

the potential to remove benthic algae and reset the succession of stream periphyton communities (Fisher et al., 1982; Biggs et al., 1999). Given the role of instream primary production in supporting aquatic biota and controlling stream nutrient dynamic, the resilience of stream primary producers – their capacity to withstand and recover from disturbance events (Holling, 1973; Bone et al., 2016) – is an important stream characteristic.

In systems with low substrate stability throughout a reach and during large discharge events when nearly all of the bed is mobile, abrasion caused by small particles combined with the molar movement of large particles scrapes away most of the existing benthic algae (Dodds et al., 1996; Rosenfeld and Hudson, 1997; Uehlinger, 2000; Uehlinger et al., 2003; Uehlinger, 2006; Hoellein et al., 2007; Atkinson et al., 2008;

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Holtgrieve et al., 2010; Luce et al., 2010; Segura et al., 2011; Gerull et al., 2012). For these large events that fully reset the system in regard to benthic algal communities, an assessment of resilience necessarily focuses the recovery of streambed algal standing stocks to pre-event levels (i.e., engineering resilience). In this context, recovery rates are key to understanding the temporal dynamics of stream primary production as well as nutrient demand and food resources for secondary production. During more moderate discharge events or when considering ecosystem processes over time scales that encompass low-flow conditions, considering stream resilience as a combination of recovery and the potential to maintain ecosystem function (i.e., ecological resilience) may be more appropriate (Holling, 1973; Hodgson et al., 2015; Bone et al., 2016). In this study, we use a two-dimensional hydraulic model to estimate stream bed mobility and repeated high resolution assessments of stream benthic algal standing stocks in a western Oregon stream to assess potential ecological and engineering resilience of stream primary producers to moderate and large extent sediment transport events.

High flow disturbances can remove benthic algae through (i) dislodging or breaking algae from its hold on a substrate through the elevated shear stress caused by increased water velocity, (ii) abrasion by mobilized sediments that scours and breaks algae off from its substrate, and (iii) molar action of tumbling gravel/cobble substrata upon which algae grow that scrapes the algae from substrates (Francoeur and Biggs, 2006). Although the importance of these processes has been recognized for decades in a broad sense (Resh et al., 1988; Reice et al., 1990; Biggs et al., 1999; Hart et al., 2013) most work quantifying mobility of the bed in relation to primary production and algal biomass has represented the flow field in one dimension. That is, assuming that the distribution of the flow field is uniform or that substrate mobilizes homogeneously across entire reaches or cross sections. This one-dimensional perspective misses for instance the potential to identify low mobility sections of a stream where scour may be more limited thereby allowing for persistence of benthic primary producers (Pitlick and Wilcock, 2013). We lack a clear conceptual framework that considers bed mobility events on two dimensions – with associated effects on stream ecosystem resilience. Part of the difficulty in developing this framework lies in the fact that benthic periphyton removal processes (i–iii above) are temporally and spatially variable. For example, while changes in sediment supply often vary at the basin or subbasin scale, discharge and channel morphology often vary at the reach scale; and shear stress and grain size distributions (GSD) in the channel bed vary at the patch scale. Considering the patch scale in particular, at this spatial resolution, different locations in the stream may undergo contrasting geomorphic processes simultaneously during a high flow event where active movement of bed material may occur in one spot while other spots are completely stable (Segura and Pitlick, 2015). This leads to spatially variable responses of benthic communities to increasing discharge within a reach (Biggs and Stokseth, 1996; Uehlinger et al., 2003). Early studies that evaluated the magnitude of scouring disturbance to benthic algal communities were based on peak discharge (Fisher et al., 1982; Biggs and Close, 1989; Segura et al., 2011; Townsend and Douglas, 2014) or one-dimensional models of sediment transport (Uehlinger et al., 1996; Biggs et al., 1999). These studies therefore overlook the potential for spatial changes in transport intensity during an individual event (Lisle et al., 2000; Stewart et al., 2005; May et al., 2009; McDonald et al., 2010; Legleiter et al., 2011; Segura et al., 2011; Segura and Pitlick, 2015), which could contribute to other factors that create spatial variability in benthic algae on the stream benthos (Stevenson, 1990; Jowett and Biggs, 1997; Biggs et al., 1999; Francoeur and Biggs, 2006; Townsend and Douglas, 2014). Algal abundances can vary at different spatial and temporal scales because of differences in scour, grazing pressure, light availability, and nutrient concentrations in the surrounding water. Variability in algal biomass can manifest at local scales across an individual sediment particle (Sekar et al., 1999; Kanavillil et al., 2015), at the patch scale among different sediment particles (Cattaneo et al., 1997), at the habitat unit scale of the stream bed

associated with different morphologies such as riffles and pools (Cardinale et al., 2002; Segura et al., 2011; Luce et al., 2013), and broadly across stream reaches and among streams (Bernot et al., 2010). Patchiness in algal biomass prior to a disturbance and patchiness in bed mobility and scouring processes within a reach together will affect the amount of biomass lost during high flow events; and the magnitude of biomass reduction caused by an individual high flow in turn influences how the community will recover after the disturbance has occurred (Biggs and Close, 1989; Peterson et al., 1994; Biggs et al., 1998; Snell et al., 2014; Coundoul et al., 2015). However, capturing the background heterogeneity in Chlorophyll *a* (Chl-*a*) abundance and deciphering the influence of variable scour from other factors that affect spatial variability in benthic algal standing stocks is challenging. Common sampling protocols assess few (i.e., <30) sediment particles that are selected at random through a reach (Biggs and Close, 1989; Davie and Mitrovic, 2014; Townsend and Douglas, 2014), at transects across a reach (Biggs et al., 1999; Townsend and Padovan, 2005), at patches (Segura et al., 2011), or in other systematic sampling schemes. In the few studies to date where spatial variability in sediment transport disturbance to benthic algae has been investigated, the experiments were conducted in streams with snowmelt flow regimes that experienced only one large mobilization event per year that fully reset the system. This limited the possibility to investigate the response and recovery of benthic algae to multiple disturbance events of different magnitudes (Segura et al., 2011). In this study, we use a novel Chl-*a* assessment method that allows for frequent in situ estimates of benthic algal standing stocks to overcome issues of spatial and temporal resolution in quantifying the response of benthic algae to multiple high flow events in a rain-dominated system.

The objective of this study was to evaluate resilience of stream benthic algal abundance to high flow events. We consider the spatial dynamics of disturbance and the potential for low shear stress areas to provide refuge habitat for benthic algae and the recovery of benthic algae following moderate and high flow disturbance events. We apply a two-dimensional (2D) shear stress model that encompasses a wide range of flows ($0.2Q_{bf}$ to $>Q_{bf}$) to determine the influence of sediment mobility on scour across the streambed and to assess recovery of benthic Chl-*a* at high spatial resolution ($<0.25 \text{ m}^2$) that can encompass areas with low and high shear stress. Understanding how the magnitude of high flow and bed scouring event disturbances affect primary production across two dimensions is important for a wide range of environmental management applications including setting meaningful environmental flow targets (Osmundson et al., 2002; Davie and Mitrovic, 2014), restoring natural processes through river rehabilitation projects (Murdock et al., 2004; Lake et al., 2007; Stanley et al., 2010), or quantifying river metabolic and production rates relevant to higher trophic levels.

2. Study site and methods

2.1. Study site

This study was conducted in a cobble-gravel bed reach of Oak Creek, Oregon (Fig. 1). The forested catchment drains 7 km^2 underlain by basaltic lithology (Milhous, 1973; O'Connor et al., 2014) in a region with Mediterranean climate characterized by wet winters and cool/mild summers. The study reach has a pool-riffle sequence in the upstream end and a relatively straight section in the downstream section. The reach is located directly upstream from a historic sediment transport sampling facility where bedload samples were collected between 1969 and 1973 (Milhous, 1973) and which currently provides a square cement weir where an accurate discharge to stage height relationship can be built. The bankfull dimensions of the study reach channel are 6 m in width and 0.46 m in depth. The reach average slope is 0.014 m/m , and the bankfull discharge (Q_{bf}) is $3.4 \text{ m}^3/\text{s}$ (Milhous, 1973). Elevations within the basin range from 143 to 664 m (Paustian and Beschta, 1979). The basin is located in the McDonald-Dunn Forest,

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