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Sand aggradation alters biofilm standing crop and metabolism in a low-gradient Lake Superior tributary

Amy M. Marcarelli [a,*], Casey J Huckins [a], Susan L. Eggert [b]

[a] Department of Biological Sciences, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA
[b] USDA Forest Service, Northern Research Station, 1831 Highway 169 East, Grand Rapids, MN 55744, USA

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Sediment deposition changes the physical characteristics of river beds, and may alter the production and/or processing of allochthonous and autochthonous organic matter, with potential consequences for stream food webs. We conducted a comparative study of biofilm standing crop and metabolism in the Salmon Trout River, a tributary of Lake Superior where watershed disturbances have led to 3-fold increases in streambed fine sediments, predominately sand, in the past decade. We compared biofilm standing crop and metabolism rates using light–dark chambers in reaches where substrate consisted of predominately exposed rock or sand substrates. Biofilm chlorophyll *a* was 4.2-fold greater on rock substrates, but ash-free dry mass was 8-fold greater on sand substrates. Rates of gross primary production were 2 to 25-fold greater on rock versus sand substrates, and differences persisted whether rates were scaled for area or biofilm standing crop. In contrast, rates of respiration were similar on rock and sand substrates when scaled per unit area but 7–13 times lower on sand when scaled for biofilm standing crop. Together, these results suggest that sand aggradation in this river alters organic matter processing during the summer from net production to net consumption and storage of organic matter. Sand aggradation may alter the availability and processing of both allochthonous and autochthonous food resources in this forested river, with potential far-reaching impacts on the food web.

Introduction

Natural and anthropogenic disturbances in river ecosystems can alter the physical characteristics of the stream bed and channel, particularly when they lead to an increase in sediment delivery and aggradation. Geomorphic and climatic processes like landslides, storm flows, and glaciation deliver sediments to rivers, where they are distributed and dispersed via hydrologic processes (Leopold et al., 1964; Waters, 1995; Knighton, 1998). However, human activities including deforestation, agricultural development, livestock grazing and road building have increased sediment loads to freshwater habitats (Brown et al., 2013; Hecky et al., 2003; Quinn et al., 1997) and sedimentation is a leading cause of stream ecosystem impairment across the United States and globally (EPA, 2009; Millennium Ecosystem Assessment, 2005). The extent and severity of sediment delivery and aggradation vary depending on the geologic history and geomorphic setting of the watershed (Leopold et al., 1964; Wood and Armitage, 1997). For example, in the upper Great Lakes region, low stream gradients, low volumes of large wood debris and an abundance of glacial sands and tills have created a setting where stream channels naturally tend to have small-sized substrates that are redistributed in a shifting mosaic of sand and cobble substrates (Alexander and Hansen, 1986; Cordova et al., 2007; Yanoviak and McCafferty, 1996). Historic and current logging and road building activities have accelerated sediment delivery, leading to sand aggradation and negative ecological impacts in streams throughout the upper Midwestern US (Nerbonne and Vondracek, 2001; Merten et al., 2010; VanDusen et al., 2005).

Although there is strong evidence that sand aggradation may negatively impact stream fishes and macroinvertebrates (Waters, 1995; Wood and Armitage, 1997), we know less about the mechanisms by which it may affect ecosystem processes. Sand deposited onto streambeds can hinder the movement of water, dissolved gases, and dissolved and particulate organic matter (Brunke and Gonser, 1997; Jones et al., 2015; Nogaro et al., 2010), potentially altering rates of microbially-driven processes like gross primary production (GPP) and respiration (R). Fine sediments are more prone to movement and disturbance than gravel or cobble (Knighton, 1998) and can be in constant motion even under low-flow conditions (Uehlinger et al., 2002; Verdonschot, 2001). This structural instability reduces standing crops of biofilms (Myers et al., 2007), which are composed of diverse microbial assemblages of algae, bacteria, and fungi. Sand substrates have been shown to have low rates of GPP (Atkinson et al., 2008; Hoellein et al., 2009), but it is unclear whether this occurs because of low standing crops of the autotrophs responsible for primary production or because of low photosynthetic activity per unit standing crop. On the other

* Corresponding author. Tel.: +1 906 487 2867; fax: +1 906 487 3167.
E-mail address: ammarcar@mtu.edu (A.M. Marcarelli).

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hand, sand appears to have less severe effects on R (Atkinson et al., 2008; Uehlinger et al., 2002). Overall, there is uncertainty regarding how sand aggradation in streams may alter the balance between allochthonous and autochthonous resources by altering biofilm standing crops, metabolic activity, or both.

The objective of this study was to quantify the effects of sand aggradation on stream biofilms and metabolism (balance between GPP and R) in the Salmon Trout River, Marquette County, Michigan. Although much of the river corridor is on protected private lands, portions of the Salmon Trout River watershed have a history of anthropogenic disturbance including logging, road building, and fish harvest (Flaspohler and Meine, 2006; Salmon Trout River Technical Advisory Group, 2007). Recent observations suggest that fine sediment aggradation in the river has increased over the past 15 years, burying natural rock substrate under plumes of sand, particularly in downstream reaches of the river (C.J Huckins, personal observation; Fig. 1). The Salmon Trout River is regionally important because it hosts a critically important and verified remnant population of adfluvial migratory brook trout, known as "Coasters", on the south shore of Lake Superior (Huckins and Baker, 2008; Huckins et al., 2008; Scribner et al., 2012). Understanding how sand aggradation alters rates of metabolism will shed light on resulting patterns of energy flow to juvenile coasters and other resident and migratory fishes. We hypothesized that biofilm standing crop (chlorophyll *a*, a surrogate for algal biomass, and ash-free dry mass or AFDM, which includes all benthic microbes and fungi as well as dead organic matter) would be lower on substrates in reaches dominated by sand compared to those dominated by rocks because of the smaller particle size and higher mobility of sand versus rock substrates. In turn, we hypothesized that rates of GPP and R would be lower in sand-dominated reaches versus rock-dominated reaches due to lower biofilm standing crops and/or lower production rates per unit standing crop.

Methods

The Salmon Trout River watershed is located in northwest Marquette County in the Upper Peninsula of Michigan (46.85° –87.80°). The headwaters of the Salmon Trout lie in the Yellow Dog Plain about 16 km south of Lake Superior and 245 m above the elevation of Lake Superior (Bullen, 1986). The watershed drains approximately 127 km^2 of mostly forested land and forms a riparian corridor through mature hardwood and mixed conifer forest. We conducted a comparative survey of biological and physical attributes in two different segments of the Salmon Trout River (Fig. 2): a downstream segment where in places >1 m of sand has aggraded within the past decade (Fig. 1; C.J Huckins, personal observation), and an upstream segment with a more natural mosaic of sand-dominated and rock-dominated reaches. Canopy cover was similar between these two segments (33 ± 25% (mean ± SD) at the upstream segment and 24 ± 9% at the downstream segment; Coble, 2015). Within each segment we selected two reaches (Fig. 2): one dominated by fine substrates (sand) and the other dominated by exposed rock substrates (rock). Study reach boundaries were identified to include river reaches with relatively uniform substrate, which resulted in reaches with an average length of 21.4 m (Table 1).

Stream physical habitat and water chemistry

To characterize the streambed sediments in each study reach, we conducted detailed pebble counts (Wolman, 1954) of 92–200 particles in each study reach (126 ± 43, mean ± SD) and calculated the median particle size (D_{50}) and the particle size at which 84% of the material was smaller (D_{84}). At three independent locations within each reach we also estimated the percent fine (<2 mm particle size) composition of riffle substrates using bulk measurement techniques based on volumetric displacement (Hames et al., 1996). We established 3 transects (upstream, middle, downstream) within each study reach to measure wetted width, water depth, sediment depth, and discharge. At 5 equally-spaced locations on each transect we measured water depth using a wading rod, sediment depth using a metered probe, and water velocity at 0.6 of the total depth using a Flo-Mate flow meter and top-setting wading rod (Hach/Marsh–McBirney, Frederick, Maryland). Discharge was calculated for each transect using water depth, velocity and width measurements. All measurements were averaged among transects to generate a reach-level estimate of each characteristic. These physical habitat measurements were repeated on two occasions during the sampling period (June and July 2010; Table 2), but did not differ between dates so were averaged to produce a single value to describe each study reach. Discharge was also measured along a single transect within each

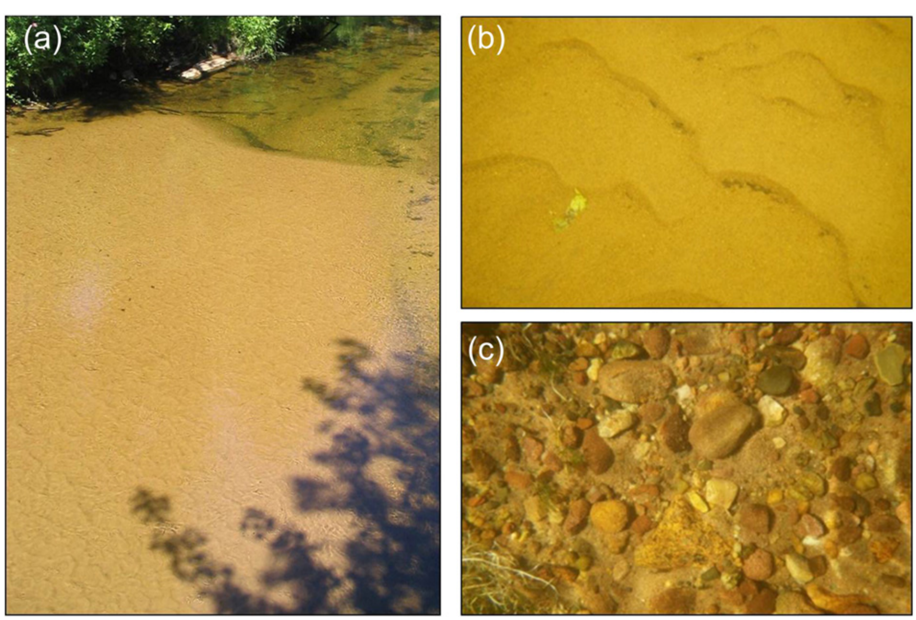

Fig. 1. (a) Plume of sand burying the stream bed just upstream of the downstream sand study reach (image by C.J Huckins, July 2007). (b) Example of sand substrate sampled in the downstream sand study reach (image by A.M. Marcarelli, Sept 2010). (c) Example of rock substrate sampled in the upstream rock study reach (image by S.L. Eggert, Sept 2010).