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

ABSTRACT

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, predominantly 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.

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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).

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
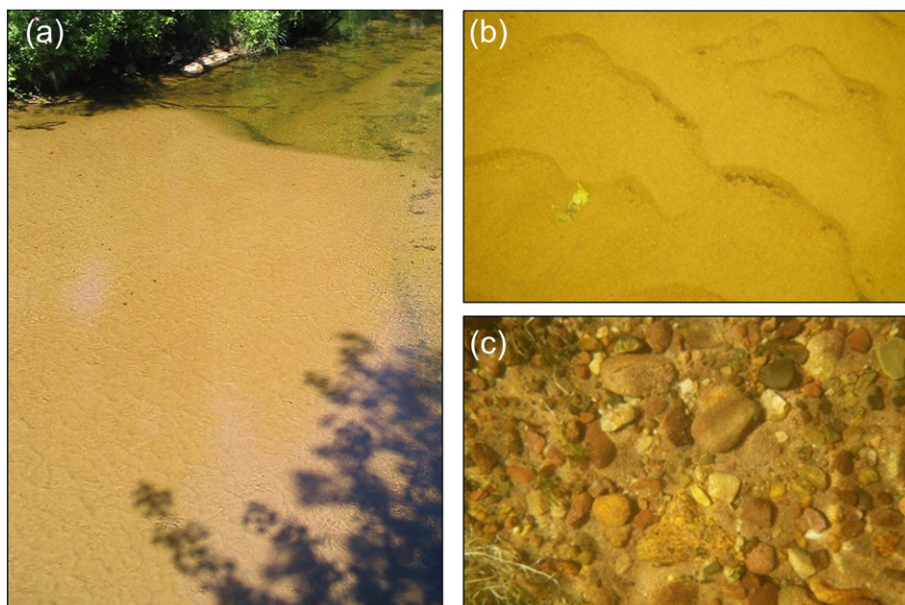
Fig. 1. (a) Plume of sand burying the stream bed just upstream of the downstream sand study reach (image by C.J Huckins, July 2007). (b) Example of sand substrate sampled in the downstream sand study reach (image by A.M. Marcarelli, Sept 2010). (c) Example of rock substrate sampled in the upstream rock study reach (image by S.L. Eggert, Sept 2010).
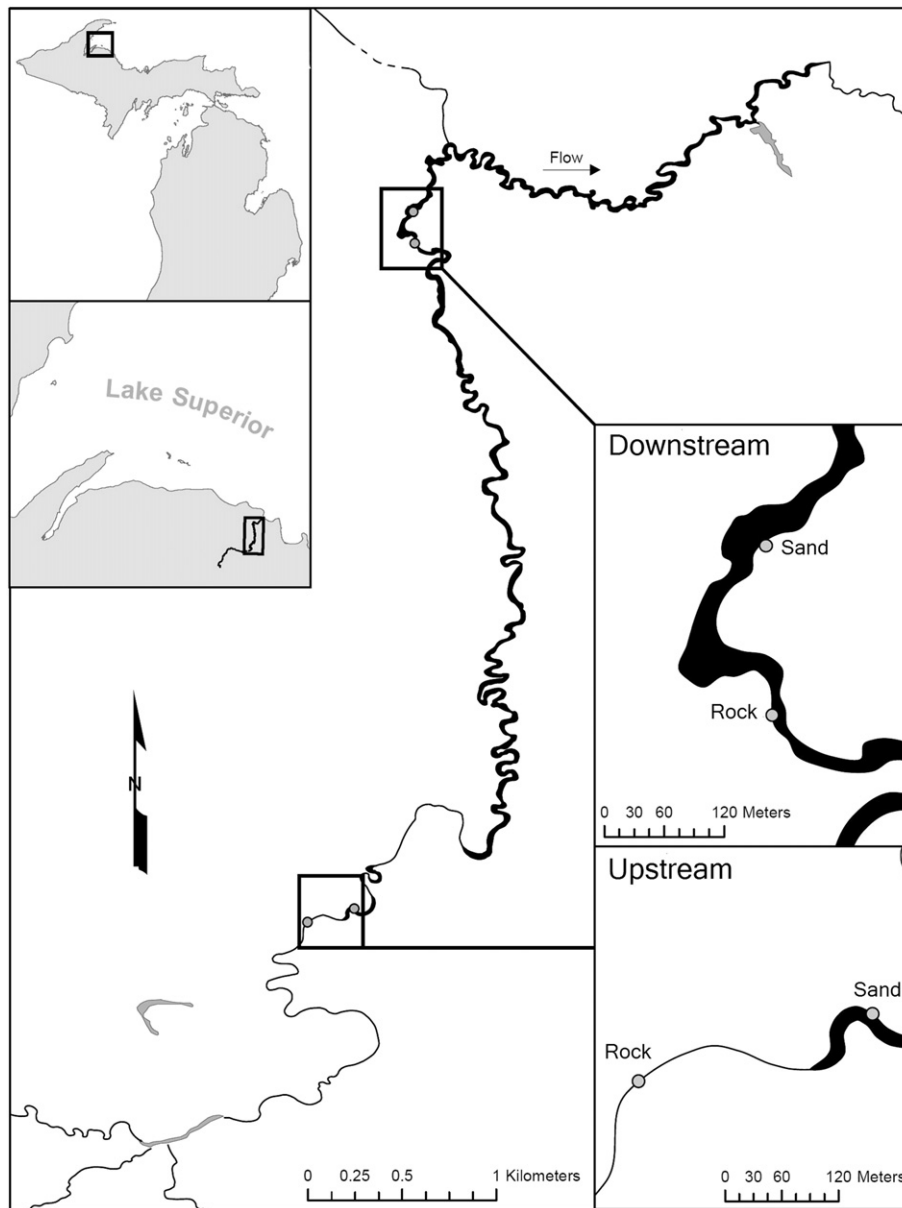
Fig. 2. Map of the study segments and reaches in the Salmon Trout River. Top left inset shows the location of the study area relative to the state of Michigan, bottom left inset shows the location of the study river along the south shore of Lake Superior. Boxes show the location of the upstream and downstream study segments along the mainstem Salmon Trout River; with the bottom right insets showing the location of the sand and rock study reaches within each segment. Note that the width of the river channel is not drawn to scale.

study reach on every date when biofilm standing crop and/or metabolism were measured.

Although we did not predict that sediment conditions would alter nutrient concentrations among the study reaches, we collected background nutrient data to confirm that nutrient variation was not causing observed biofilm and metabolism responses. On each sampling date (Table 2), we used a YSI 6920 V2 sonde (YSI Incorporated, Yellow Springs, Ohio) to measure water temperature, dissolved oxygen (DO_2), conductivity, pH, and turbidity in each of the identified study reaches. We also collected 0.45 μm membrane-filtered water samples for analysis of ammonium-nitrogen (ammonium-N) using fluorometric analysis (Holmes et al., 1999; following modifications of Taylor et al., 2007) with an AquaFluor® handheld fluorometer (Turner Designs, Sunnyvale, California), nitrate-N using an ICS-900 Ion Chromatograph (Dionex, Sunnyvale, California), soluble reactive phosphorus (SRP) via the ascorbic acid colorimetric method (APHA, 2005), and dissolved organic carbon (DOC)/total dissolved nitrogen (TDN) using a TOC-5000A analyzer (Shimadzu Scientific Instruments, Columbia,

Maryland). We also collected unfiltered water samples for analysis of total phosphorus (TP) via ammonium persulfate digestion followed by ascorbic acid analysis as for SRP (APHA, 2005)

Biofilm standing crops

We sampled biofilm standing crops monthly between May and October 2010 (Table 2). Samples were collected at 3–6 locations within each reach and averaged to estimate mean standing crop within each reach on each date. Rock biofilms (encountered only in rock-dominated reaches) were scrubbed with a small brush from 3 rocks haphazardly collected from each location and combined into approximately 250 mL of water, from which subsamples of the resultant slurry were filtered onto pre-combusted 0.7 μm glass fiber filters. Rock area was determined by tracing the planar rock area onto paper, weighing the cutout, and applying a paper weight-to-surface area regression (Bergey and Getty, 2006). Sand biofilms (encountered only in sand-dominated reaches) were collected by inserting a 2.6-cm diameter

Table 1
Physical and chemical characteristics (means ± SD), averaged across all sampling dates for each site.

Parameter	Downstream		Upstream	
	Rock	Sand	Rock	Sand
Reach length (m)	25.4	19.1	24.3	16.5
Wetted width (m)	7.9 ± 0.03	10.1 ± 0.34	7.7 ± 0.52	9.4 ± 0.05
Depth (m)	0.252 ± 0.000	0.361 ± 0.033	0.330 ± 0.008	0.602 ± 0.002
D_{50} (mm)	26.5 ± 3.5	0.8 ± 0.4	16.5 ± 2.1	1.0 ± 0.0
D_{84} (mm)	66.5 ± 5.0	1.0 ± 0.7	23.0 ± 2.8	20.5 ± 14.9
Sand depth (cm)	2.8 ± 0.7	38.8 ± 4.1	5.3 ± 0.4	14.8 ± 0.2
Streambed fines (%)	34.7 ± 30.0	98.0 ± 1.2	29.0 ± 5.0	75.2 ± 41.9
Discharge (m^3/s)	0.990 ± 0.010	0.937 ± 0.103	0.913 ± 0.065	0.865 ± 0.039
Mean water temp (°C)	12.5 ± 4.6	12.4 ± 4.6	11.8 ± 5.0	11.5 ± 5.0
Conductivity (µS/cm)	132 ± 12.1	131 ± 11.1	132 ± 11.2	132 ± 11.2
Dissolved O_2 (mg/L)	10.6 ± 1.2	10.4 ± 1.4	11.6 ± 1.2	11.3 ± 1.2
Turbidity (NTU)	0.1 ± 1.2	0.5 ± 1.5	0.1 ± 1.5	0.6 ± 1.9
NH_4-N (µg/L)	6.73 ± 1.57	9.66 ± 4.26	7.62 ± 2.75	7.57 ± 2.91
NO_3-N (µg/L)	37.3 ± 18.8	37.1 ± 24.4	41.4 ± 20.2	48.2 ± 27.4
TDN (µg/L)	159 ± 23.2	174 ± 40.2	178 ± 33.5	178 ± 44.3
SRP (µg/L)	3.39 ± 1.04	3.47 ± 0.49	4.52 ± 2.31	4.57 ± 0.88
TP (µg/L)	5.22 ± 3.92	4.53 ± 1.62	4.83 ± 2.83	4.59 ± 2.74
DOC (mg/L)	4.27 ± 0.75	4.69 ± 1.00	4.68 ± 0.75	4.64 ± 1.13

polyethylene tube into the sand, then transferring the top 0.5-cm of material in the core into a 50-mL centrifuge tube for storage. We kept only the top 0.5 cm to focus measurements on the portion of the substrate most likely to be hospitable for microbes capable of photosynthesis and thus analogous to the rock biofilm samples. All samples were placed on ice and frozen within 1–2 h of collection. In the lab, chlorophyll *a* was extracted from samples using 95% ethanol and analyzed spectrophotometrically using standard methods (APHA, 2005). Ash-free dry mass was measured by drying at 60 °C, weighing, combusting at 550 °C, rewetting, drying and reweighing to obtain ash-free dry mass per m^2 (APHA, 2005).

Ecosystem metabolism

Net primary production (NPP) and R were quantified in July, August and September 2010 (Table 2). We measured metabolism in recirculating light–dark chambers (15.5 × 15.5 × 6 cm, approx. 1.5 L volume; Cuffney et al., 1990), which measure rates on small areas (approx. 0.02 m^2) of benthic substrates. For each reach on each date, we measured rates in 3 light and 3 dark chambers; measurements in light chambers represent NPP, which includes oxygen generated by GPP and consumed via R by both autotrophs and heterotrophs. Dark chambers exclude GPP, so represent R alone. GPP was estimated by averaging R for the 3 dark chambers in each reach and adding that

Table 2
Schedule of parameters sampled in each month over the duration of summer 2010 for this study. X indicates that the parameter was sampled on that date, – indicates it was not sampled.

	May	June	July	August	September	October	November
Physical habitat	–	X	X	–	–	–	–
Water chemistry	X	X	X	X	X	X	X
Biofilm standing crop	X[a]	–[b]	X	X	X	X	–
Ecosystem metabolism	–	–	X	X	X	–	–

[a] Samples were only analyzed for chlorophyll *a*, not ash-free dry mass (AFDM), so no AFDM data shown in Fig. 3.
[b] Samples were collected but lost in storage, so no June data reported for chlorophyll *a* or AFDM in Fig. 3.

mean to each of the 3 NPP values. Because we were interested in autotrophic versus heterotrophic processes as they related to changes in standing crops of biofilms, we focused on GPP and R estimates in our analyses.

To estimate metabolism rates on each date, chambers were filled with similar surface areas of rock or sand obtained from the study reaches. Rocks were haphazardly collected from the study reach and oriented in the chambers so that they experienced similar flow direction as they had in the stream. Sand substrates were collected using 155.25 cm^2 aluminum boxes with removable bottoms; the bottom was removed from the boxes, which were then inserted into the sediments to a depth of ca. 1.5 cm (range 0.9 to 2.3 cm), and then the bottom was slid under to collect an intact core of sand substrates and associated organic material. Chambers were sealed and allowed to incubate for 1 hour fully submerged in the stream to maintain temperatures similar to stream water, and water velocity in the chambers was 0.14–0.17 m/s. Oxygen concentrations were measured in the stream water adjacent the chamber at the time of initial closure and in water in the chamber at the end of the incubation period using Winkler titrations (APHA, 2005). Chambers with rock and sand substrates were incubated in the same location within each segment to minimize differences due to minor reach-scale differences in canopy cover and light availability. Metabolism rates were estimated as the change in oxygen concentrations, corrected for the incubation duration and the surface area of the substrate in each chamber. We also collected the substrates for estimation of biofilm standing crop. For rocks, we scrubbed biofilms from all of the rocks contained in a chamber into a single slurry, then sampled for chlorophyll *a* as described above. For sand we collected the entire sand core incubated in the chamber, then measured AFDM standing crop on the entire sample. We calculated metabolism rates as change in oxygen concentration per unit of standing crop measured on the substrates incubated in the chambers over the duration of the incubation.

Statistical analyses

We compared stream physical characteristics, biofilm standing crops and metabolism rates among study reaches using analysis of variance (ANOVA). Sediment characteristics (D_{50}, D_{84}, sand depth and percent fine substrates) were compared between rock and sand reaches using one-way ANOVA, with reaches nested within the two study segments (upstream and downstream) as a random factor. Biofilm standing crops, area-scaled and biomass-scaled metabolism rates were compared between rock and sand (referred to as "substrate" effect below) and among sampling dates ("date") using repeated measures ANOVA (RM-ANOVA), with reaches as the repeated factor and with a random factor accounting for reaches nested within the two study segments. All analyses were conducted using PROC MIXED in SAS version 9.2 (SAS Institute, Inc., Cary, North Carolina), and significance was considered at $\alpha = 0.10$ due to low replication ($n = 2$ for each treatment). Chlorophyll *a*, AFDM and biomass-scaled GPP were log-transformed to meet assumptions of normal residual distribution and constant variance (Oehlert, 2000); all other variables did not require transformation to meet these ANOVA assumptions.

Results

Stream physical habitat and water chemistry

Reaches with rock substrates tended to be shallower and narrower than those with sand substrates (Table 1), likely because sand aggradation can lead to alluvial bank erosion and cause streams to widen (Montgomery and Buffington, 1998). Discharge across all study sites and dates ranged from 0.865 to 0.990 m^3/s, and was slightly greater in the downstream compared to the upstream segments but did not differ

between rock and sand reaches nested within each study segment (Table 1).

Sediment sampling confirmed the visual observations that streambed characteristics differed greatly between the sand and rock study reaches (Fig. 1). D_{50} was 25 times smaller (one-way ANOVA $F_{1, 2} = 17.0$, $p = 0.05$), and percent fine substrate was 2.7 times higher in sand compared to rock reaches ($F_{1, 2} = 21.7$, $p = 0.04$; Table 1). Although D_{84} was also smaller and sand depth was deeper in sand versus rock study reaches (Table 1), neither of these differences was significant ($p = 0.20$ for both). These results confirmed the study design and subsequent comparison of differences in biofilm standing crop and metabolism based on different substrate characteristics in the study reaches.

We observed no systematic differences in water chemistry between the sand and rock study reaches (Table 1). Conductivity, turbidity, ammonium-N, nitrate-N, TDN, SRP, TP and DOC were similar among all sites and study dates. Water temperature tended to be higher and DO_2 tended to be lower at the downstream versus the upstream segment, but these differences were likely due to sampling at different times of day rather than between-segment differences.

Biofilm standing crop

Chlorophyll *a* concentrations were 4.2-fold greater on rock than on sand substrates on average across all study dates (Fig. 3a), supporting our hypothesis, but the differences were much greater between rock
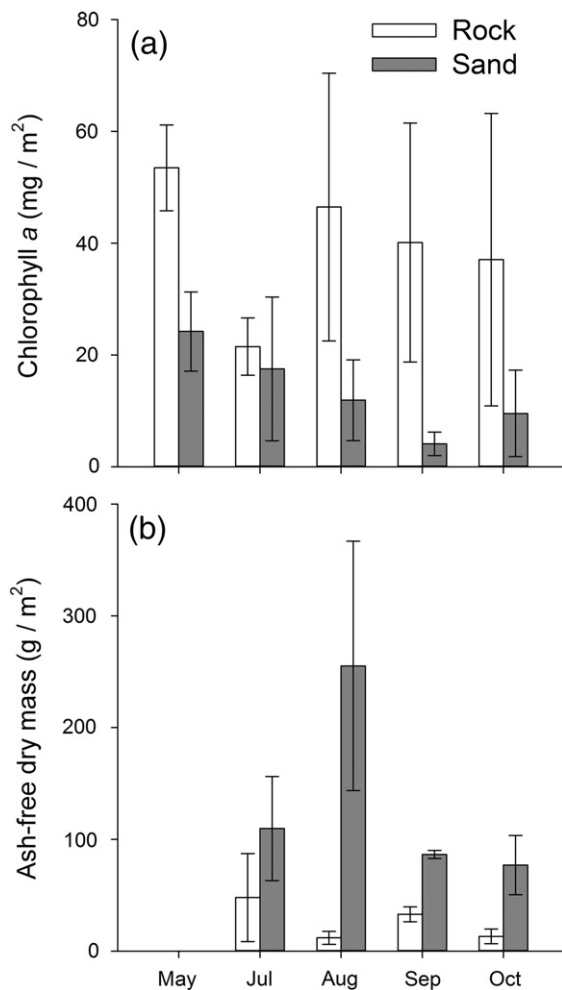

Fig. 3. (a) Chlorophyll *a* and (b) ash-free dry mass standing crops measured for rock and sand substrates. Ash-free dry mass was not measured in May, resulting in 4 sampling dates compared to 5 for chlorophyll *a*. Error bars ± 1 SE, n = 2 for each bar.

and sand reaches in the downstream segment than in the upstream segment. As a result, there was no significant effect of substrate or substrate × date interaction in the RM-ANOVA ($p > 0.2$ for both); there was a significant effect of date alone ($F_{4, 8} = 3.3$, $p = 0.07$). Contrary to our hypothesis, AFDM was 8.0-fold larger on sand substrates versus rock substrates averaged across all study dates (Fig. 3b; substrate $F_{1, 2} = 8.4$, $p = 0.10$). There was no significant main effect among dates ($p = 0.45$) or interaction between substrate and date ($p = 0.14$).

Metabolism

Consistent with our hypotheses, rates of GPP were 3–25-fold greater on rock versus sand substrates across all 3 sampling dates (Fig. 4). This difference persisted whether rates were scaled per unit area (substrate $F_{1, 2} = 27.6$, $p = 0.03$; substrate × date $F_{2, 4} = 5.8$, $p = 0.06$) or per chlorophyll *a* standing crop (substrate $F_{2, 4} = 37.6$, $p = 0.03$). This suggests that GPP was lower in sand reaches due to both lower metabolic activity as well as lower standing crops of primary producers on sand substrates. On the other hand, R was not significantly lower in sand versus rock reaches when scaled per unit area (substrate and substrate × date interactions $p > 0.4$); there was a significant effect of date ($F_{2, 4} = 7.0$, $p = 0.05$). However, when scaled per unit AFDM, R was 7–13-fold lower on sand substrates compared to rock substrates ($F_{1, 2} = 6475.2$, $p < 0.001$); there were no significant effects of date or interaction between date and substrate ($p > 0.12$). This suggests that R rates were similar when scaled per unit area because of the larger standing crops of AFDM associated with sand versus rock substrates, but that rates of respiratory activity were much lower in association with sand versus rock substrates.

Discussion

Sand aggradation in the Salmon Trout River affects biofilm metabolism both by altering the standing crops of living and dead organic matter, and also by changing the rates of metabolic activity per unit standing crop. We found that standing crops of AFDM were 8-fold greater in reaches dominated by sand, but that rates of R scaled per unit AFDM were 7–13 fold lower, resulting in similar rates of R when scaled per area on rock and sand substrates. Sand aggradation also decreased rates of GPP in the Salmon Trout River, however in contrast to R, this was due to decreases in both the standing crop of primary producers as well as rates of GPP per unit chlorophyll *a*. The GPP rates we measured on rock and sand substrates were an order of magnitude higher than those measured on similar substrates in other regional streams by Hoellein et al., (2009); however, the small, closed canopy streams they studied had chlorophyll *a* standing crops at least an order of magnitude lower than those we observed in the 4th-order Salmon Trout River. Overall, daytime GPP:R ratios in the Salmon Trout averaged 1.6 ± 0.3 (mean ± SE) on rock substrates versus 0.1 ± 0.1 on sand substrates.

Others have shown that rivers with streambeds dominated by sand substrates can have lower rates of GPP and GPP:R ratios, however in those cases the mechanism for these lower rates has been primarily attributed to low standing crops of primary producers (Atkinson et al., 2008; Biggs et al., 1999; Uehlinger and Naegeli, 1998). Small standing crops of primary producers could be due to the mobile and disturbance-prone nature of sand particles, which provide poor substrate for diatom attachment or development of three-dimensional biofilm structure (Cox, 1988; Krejci and Lowe, 1986; Miller et al., 1987). Fine sediments may also be more prone to flow-related disturbance (Biggs et al., 1999); the Salmon Trout River experiences a large flood pulse associated with spring snowmelt as well as a series of summer spates that likely contributed to the month-to-month as well as between reach differences we observed in chlorophyll a and AFDM standing crops. Others have attributed low standing crops of primary
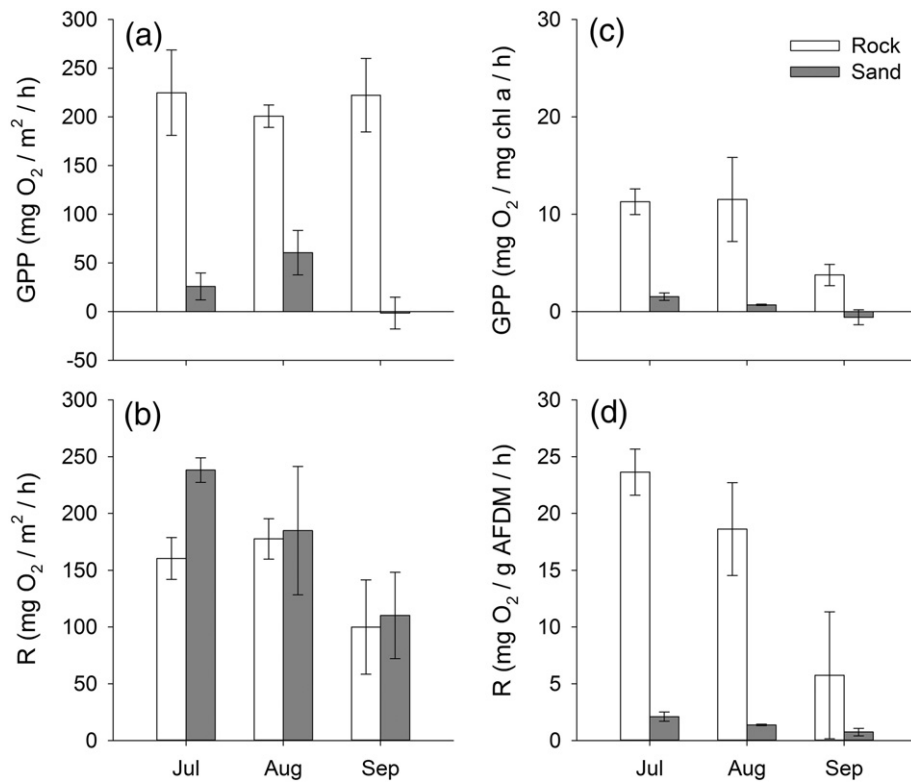
Fig. 4. (a) Gross primary production (GPP) and (b) respiration (R) scaled per unit of benthic area and (c, d) per unit of standing crop on 3 different dates. Error bars ± 1 SE, $n = 2$ for each bar.

producers to increases in turbidity associated with sand deposition that reduce light penetration to the benthos (Yamada and Nakamura, 2002); however, in our study we did not observe any large differences in turbidity among the study reaches (Table 1).

It has been suggested that R may be more resilient to sediment instability and disturbance than GPP (Atkinson et al., 2008; Uehlinger et al., 2002), however it should be noted that these studies measured metabolism using open-channel methods, which incorporate respiration from near riparian and hyporheic zones that may be less susceptible to in-channel disturbance. Although we observed GPP:R ratios greater than 1 on the rock substrates during the day, open water, 24-h ecosystem metabolism estimates from this river and others in the region suggest that GPP:R is likely <1 throughout much or all of the year (Burtner et al., 2011; Levi et al., 2013; A.M. Marcarelli, unpublished data), suggesting that R may be much higher than suggested during our short-duration, surface-focused measurements in chambers. Several methodological artifacts associated with our chambers may also have led to measurements of lower R rates than those that may occur under natural conditions. For example, in rock reaches, we selected for surficial rock biofilms but excluded AFDM and biofilms in interstitial spaces, where substantial respiration is likely to occur. On the other hand, because the aluminum boxes in which we collected sand sediments for incubation did not allow interstitial flow, we did not likely account for all of the R within the sand during our short incubations. Regardless of these methodological and spatial scaling issues, our results suggest that shifting daytime GPP:R on streambed sediments in the Salmon Trout River is due to changes in rates of both GPP and R, both of which showed substantial differences between rock and sand substrates.

Our results suggest that R is much less efficient on sand substrates in the Salmon Trout River, resulting in storage of organic matter as evidenced by the 8-fold greater AFDM standing crops we observed in sand versus rock reaches. A suite of microbial and macroinvertebrate consumers process organic matter in streams, any or all of which may

be affected by sediment deposition. Sand deposition as low as 20% fine sediment covering the streambed has been linked to decreased abundance of sensitive Ephemeroptera, Plecoptera, and Trichoptera macroinvertebrate taxa (Burdon et al., 2013) and a shift towards burrowing taxa (Suttle et al., 2004) and collector gatherers (Yamamuro and Lamberti, 2007). Scraper biomass in our study reaches was 4.7–10.9 times greater in rock versus sand reaches (S.L. Eggert, unpublished data); it is particularly notable that biofilm standing crops were greater on rock substrates despite likely experiencing higher grazing pressure than sand substrates. Changes in macroinvertebrate assemblages with sand deposition may be caused by altered habitat availability (Burdon et al., 2013), increased bed mobility and disturbance frequency (Cobb et al., 1992), and/or or by the availability of allochthonous or autochthonous resources (Death and Zimmermann, 2005; Yamamuro and Lamberti, 2007). Sand can decrease invertebrate processing rates of organic matter by restricting access to substrates. For example, Navel et al., (2010) found that the consumption of leaf litter buried in river sediments by shredders was strongly influenced by porosity, and Scott and Zhang (2012) showed that burial of leaves in a sandy, low-gradient stream reduced colonization by collector gatherers. The effect of sediment deposition and aggradation on microbial decomposition is less clear; Romani and Sabater (2001) found that microbial communities living in sand substrates had lower biomass but were more efficient at processing allochthonous material than those on rock substrates, and Nogaro et al., (2010) reported that microbial abundance and activity could either increase or decrease as sediment increased in hyporheic zones, depending on residence time of water within the sediments. Finally, there is evidence that sand aggradation may shift the mechanism of decomposition from microbial processing to physical abrasion and grinding by moving sediments (Spänhoff et al., 2007). Burial as well as physical processing of organic matter could act together to limit the availability and transfer of allochthonous organic matter into the food web of the Salmon Trout River.

A reduction in GPP, R, algal standing crops and biologically-driven decomposition in association with sand aggradation in the Salmon Trout River is likely to have far-reaching food web and ecosystem consequences. Forested stream and river ecosystems are fueled by organic matter from both terrestrial and autochthonous sources (Marcarelli et al., 2011), with terrestrial organic matter fueling the majority of microbial production and respiration (Hall et al., 2000; Marcarelli et al., 2011) as well as secondary production of macroinvertebrates (Hall et al., 2000; Wallace et al., 1997). However, even in forested streams algae can be an important food resource for stream invertebrates (Fuller et al., 1986), and fuel the production of grazing-specialized species (Mayer and Likens, 1987). Additionally, biofilms on wood and microbes on coarse organic matter can both be key food resources for many stream detritivores (Eggert and Wallace, 2007; Hall et al., 2000). Because sand aggradation in the Salmon Trout River reduces rates of production and decomposition of both allochthonous and autochthonous food resources, it may have large consequences for macroinvertebrate production, which may then transmit up the food web to influence the production of both juvenile migratory and resident fish (Wallace et al., 1997; Wipfli and Baxter, 2010). Sand aggradation could be an additional stressor for the regionally important Coaster brook trout population in the Salmon Trout River by decreasing food availability and increasing competitive interactions among juvenile salmonids for limited prey resources. For example, Suttle et al., (2004) demonstrated steep and linear decreases in growth of juvenile steelhead trout due to decreased prey availability as substrate embeddedness increased.

Sand deposition and aggradation is a source of stream impairment that is recognized as important at regional (VanDusen et al., 2005), national (EPA, 2009), and global scales (Millennium Ecosystem Assessment, 2005). Therefore, a variety of stream restoration activities have been tested and implemented with the goal of reducing sediment load and/or streambed embeddedness. A few of these practices include the addition of sediment traps (Alexander and Hansen, 1983; Hoellein et al., 2012; Moerke et al., 2004), installation of erosion structures (Roni et al., 2008), or "cleaning" streambed sediments with hydraulic pumps (Meyer et al., 2008; Sepulveda et al., 2014). Although these restoration activities are typically undertaken with the intention of improving the spawning and rearing habitat of target fish species (Roni et al., 2008), our results suggest that sediment reduction activities may also benefit these species by increasing the availability of basal resources to the food web. Monitoring stream metabolism and other ecosystem processes may provide additional insight into the mechanism of fisheries responses to restoration activities undertaken with the goal of reducing sedimentation impacts on stream ecosystems and food webs. However, practitioners must be careful to consider such metabolism rates along with standing crops to understand whether changes in process rates are due to changes in organic matter storage versus rates of microbial and biofilm activity.

Acknowledgements

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