

Research

Consumer movement dynamics as hidden drivers of stream habitat structure: suckers as ecosystem engineers on the night shift

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Ecosystem engineering can control the spatial and temporal distribution of resources and movement by engineering organisms within an ecosystem can mobilize resources across boundaries and distribute engineering effects. Movement patterns of fishes can cause physical changes to aquatic habitats through nesting or feeding, both of which often vary in space and time. Here we present evidence of ecosystem engineering by the Sonora sucker *Catostomus insignis*, a dominant fish in streams of the southwestern United States, and show how cryptic nocturnal movement patterns and bioturbation activities control heterogeneity in benthic substrates, and in sediment and carbon export. Sonora suckers exhibit distinct diel movement patterns, spending daylight hours in refuge habitats (typically deep pools) while moving into shallow habitats at night to feed. Feeding by suckers creates substantial disturbance in soft sediments that are patchy in space and time. These disturbances moved up to $2.4 \times 10^4 \text{ cm}^3$ of sediment per square meter per week in locations that are up to hundreds of meters away from sucker daytime refuges. The diel cycles in feeding activity (i.e. nocturnal digging in benthic substrates) caused nighttime pulses in suspended sediment that comprised up to 32% of the daily suspended load and organic matter transport of a stream reach. During the daytime, this particulate transport settles in habitats beyond the location of the initial disturbance, thus redistributing both sediment and organic matter. Our data indicate that cryptic movement by ecosystem engineers can distribute their effects in space and time generating heterogeneity in resources and suggest that habitat modifications restricting consumer movement may alter the impact of engineering activities.

Keywords: bioturbation, *Catostomus insignis*, ecosystem engineer, heterogeneity, movement, organic matter export, Sonora sucker

Introduction

A wide variety of organisms may contribute to environmental heterogeneity, and ecosystem engineers (Jones et al. 1994, 1997, Coleman and Williams 2002, Wright and Jones 2006, Berke 2010, Albertson et al. 2015, Wilkes et al. 2019) are particularly likely to change the spatial and temporal distribution of resources within ecosystems

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by creating or altering local habitat structures, bioturbating substrate (Cooper et al. 2016), or by transforming the chemical and light environment (Berke 2010). Patchy distribution of resources in space may modify the distribution of organisms within stream ecosystems (Bernstein et al. 1991) and the patchy distribution of organisms can create nutrient recycling hotspots (McIntyre et al. 2008, Francis and Côté 2018), with major consequences if the dominant species are lost (McIntyre et al. 2007). Environmental heterogeneity has been shown to consistently increase species richness across a variety of systems and habitats (Ortega et al. 2018). By creating patches that differ in critical ways (e.g. nutrients, physical structures or disturbance) from the surrounding habitat, engineering taxa can change landscape-level patterns such as primary and secondary productivity or species richness.

There is substantial evidence that animals can engineer terrestrial, marine and freshwater ecosystems (Jones et al. 1994, 1997, Coleman and Williams 2002, Crooks 2002, Reichman and Seabloom 2002, Moore 2006, Wright and Jones 2006, Berke 2010, Vu et al. 2017), but relatively little attention has been given to how movements of engineering taxa may modulate effects on ecosystem parameters (Flecker et al. 2010, Rice et al. 2019) and generate heterogeneity (Townsend and Fonseca 1998). A well-studied example of ecosystem engineering is migratory salmonids, which create strong disturbances in benthic sediments as they dig redds (nests) and additionally provide a seasonal resource subsidy in the form of marine-derived nutrients through excretion and egestion, as well as their carcasses (Gende et al. 2002, Claeson et al. 2006, Hasson et al. 2008, Tiegs et al. 2009, Wheeler et al. 2018). The strength of these engineering impacts has been attributed to variation in fish biomass and physical characteristics of the stream, and has typically been described as an annual seasonal dynamic that fades when the organisms die or depart (Flecker 1996, Janetski et al. 2009). This seasonal perspective is appropriate where the nature of the engineering activity is constrained; most migratory salmonids (except steelhead) typically excavate a limited number of redds (usually 1; Gallagher and Gallagher 2005) and so the potential for sediment disturbance will be dictated by overall biomass in the spawning location. Engineering taxa, particularly those whose engineering activities are relatively unconstrained (e.g. foraging or burrowing), may engineer multiple locations on many occasions and are often common, if not dominant, taxa in a variety of systems (VanBlaricom 1982, Coleman and Williams 2002, Reichman and Seabloom 2002, Harvey et al. 2014, Rice et al. 2016, 2019, Pledger et al. 2017). These taxa are likely to exhibit movements on shorter time scales and over more limited spatial areas; thus we expect that some ecosystem-level effects may be heterogeneous and will be determined by the rate at which engineers colonize or abandon habitats (e.g. crabs, Martinetto et al. 2005; beavers Wright 2009), rather than density alone. Movement patterns of ecosystem engineers may modify the size and distribution of habitat patches, dictate the level of connectedness between habitat patches, and link processes over larger spatiotemporal

scales (Statzner et al. 2003, Albertson et al. 2015, Rice et al. 2019).

Moore's (2006) conceptual framework suggests that the importance of ecosystem engineers is controlled by body size, density and engineering behavior, filtered through the abiotic environmental context. Although the direct effects of an ecosystem engineer will typically occur where the engineer acts (e.g. sediment disturbance), in flowing waters downstream transport (e.g. sediment or nutrients) may extend those impacts beyond the site. The timing, frequency and ability of engineering organisms to move within a landscape has the potential to dramatically impact the scope and importance of these engineering actions as well as to introduce heterogeneity.

Due to their linear nature, stream systems are often directly fragmented by natural (e.g. drought) and anthropogenic factors (Neeson et al. 2015, Grill et al. 2019). Thus, we argue that the ecosystem engineering conceptual framework should also include the timing or frequency (annual versus diel) of movement of the engineering organisms. Movements at fine spatial and temporal scales may alter patterns of heterogeneity within an ecosystem in ways that are not directly related to the engineering behavior itself.

We explored the role of movement in generating heterogeneity through ecosystem engineering by investigating the role of Sonora suckers *Catostomus insignis* in a large, semi-arid watershed in the southwestern United States. Including movement as a potentially critical modifying factor in an update to Moore's (2006) conceptual model (Fig. 1), we predicted that movement patterns (e.g. between daytime refuges and nocturnal feeding grounds, and larger-scale seasonal movements among habitats) drive the variation in timing and distribution of fish effects in the ecosystem, as well as generate pulsed indirect effects. We hypothesized that feeding by fish creates local patch-scale variation in substrate disturbance

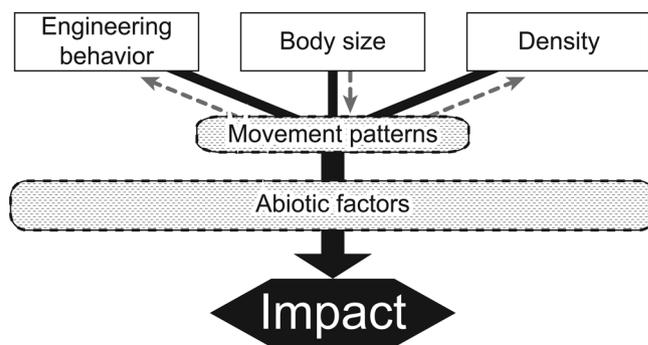


Figure 1. Update of Moore's (2006) conceptual model of the factors influencing the impact of ecosystem engineers. White boxes indicate key features of engineers likely to influence their impact, hashed boxes indicate filters that modify the total impact. Dashed gray arrows indicate feedbacks between movement and features of engineering organisms. Movements of engineering organisms may fundamentally modify the magnitude, duration and frequency of their impacts in ways that are independent of the engineering behavior itself.

(controlled by visitation frequency) and modifies both the magnitude and periodicity of downstream export of sediment and carbon, particularly during periods of low stream flow. To understand how within-stream-reach movement can modify the ecosystem-level effects of fish feeding, we monitored the movement of individual fish on several spatial and temporal scales and combined these measurements with a series of observational studies of sediment disturbance and organic matter flux from the stream ecosystem generated by engineering activities.

Material and methods

Study species and location

Catostomus insignis occurs in a broad range of streams throughout the southwestern United States (Minckley 1973), feeding on invertebrates and detritus (Clarkson and Minckley 1988). It is abundant during the day in deeper pools with restricted flow and fine substrates where it is often found in large aggregations (>30 individuals per pool; Booth et al. 2013). *Catostomus insignis* is described as a pool-dwelling fish (Minckley 1973); however, recent data show that suckers forage widely over the entire stream including extremely shallow areas during low light periods (night or high turbidity, i.e. cryptic movements, Booth et al. 2013). Individual fish dig holes while feeding on invertebrates in soft sediments (i.e. sand, silt, gravel) resulting in roughly cylindrical divots in the streambed (Supplementary material Appendix 1 Fig. A1), which range in size from 1 cm wide and 0.4 cm deep to 40 cm wide and 6.8 cm deep. Sonora suckers also feed on hard substrates, moving unconsolidated particles (pebbles to small cobbles) as they forage for invertebrates.

Our study site at the Heartbar Wildlife area was located near the confluence of the West and Middle Forks of the Gila River in western New Mexico, USA. *Catostomus insignis* typically represents the majority of fish biomass in this section of the upper Gila River (Whitney et al. 2015).

Timing and extent of fish movement

We assessed movement patterns of suckers using PIT (passive integrated transponder) tags and a combination of a mobile antenna and stationary antenna array. Our methods are described in detail by Booth et al. (2013, 2014). Briefly, fish were captured and uniquely numbered, half-duplex PIT tags were implanted in the body cavity of the fish. Tagged fish were released in the same location where they were captured. We tagged 450 *C. insignis* within a 1.8 km reach of the West Fork Gila River from 2008 to 2010 (May–July). We mapped the tagging reach, characterized habitat (e.g. pools, riffles, runs) and substrate types, and created a GIS map in Manifold 8.0.

Implanted PIT tags were detected using either stationary antennas that continuously recorded the passage of tagged fish past fixed points in the stream, or a portable antenna that

was moved within the stream to scan habitats for tagged fish. We collected weekly position data using the portable antenna within a 2–4 km reach during May through July 2008–2010. In 2009 and 2010, we installed eight continuously recording stationary PIT antennas to detail ‘habitat-scale’ fish movements (Fig. 2). We collected 65 days of data during 2009 and 28 days during 2010. An estimated 25–50% of the *C. insignis* population within the full 1.8 km study reach contained PIT tags during the study period; in the stationary antenna reach (Fig. 2), the tagged population ranged between 16–42 (2009) and 8–25 (2010) individuals, though the individuals composing the population changed over time (Booth et al. 2013).

Ecosystem variables

Daily discharge has been recorded on the lower Gila River (downstream approx. 80 km, USGS gauge no. 09430500) from 1927 to the present. In the stationary antenna reach during the 2010 season, we recorded water level every 5 min using water level loggers and developed a rating curve during the sampling period to estimate discharge (Gore 2007) and correlated local flow with values from the long-term USGS gage site.

Divot distribution

To estimate the overall distribution of feeding divots, we performed weekly surveys (June–July 2009) within the 1.8 km in length focal stream reach. In each habitat that contained sand and silt patches (Fig. 2), we estimated divot density along two transects. For each transect, in each of four 0.25 m² quadrats we counted all divots, measured the diameter and depth of four representative divots, estimated the volume of sand displaced (approximated as a cylinder), and computed total sediment moved as the average divot volume multiplied by the total number of divots. We estimated the minimum distance to major fish refuge sites (locations with consistently >10 individuals detected) using the GIS map (Fig. 2). In addition to the distribution of feeding divots, we also estimated daily rates of divot formation in three habitats by smoothing the surface of the stream bed with a rake and returning daily from 7 July to 11 July 2008 to quantify the size and number of divots formed using the same transect method.

Consequences of divot formation

Due to the high prevalence of divots and the high frequency of their creation (i.e. new divots on top of old divots, so that it was unclear when a patch of habitat had last been disturbed and the majority of the bed appeared disturbed), it was not possible to estimate directly how divoted sediments differed from those that were undisturbed. Instead, we estimated how divots change organic matter retention and invertebrate abundance in the streambed using artificially-created divots made from 120 ml specimen cups (0.02 m² orifice, generally similar in shape and diameter to natural divots; cups are 5–20%

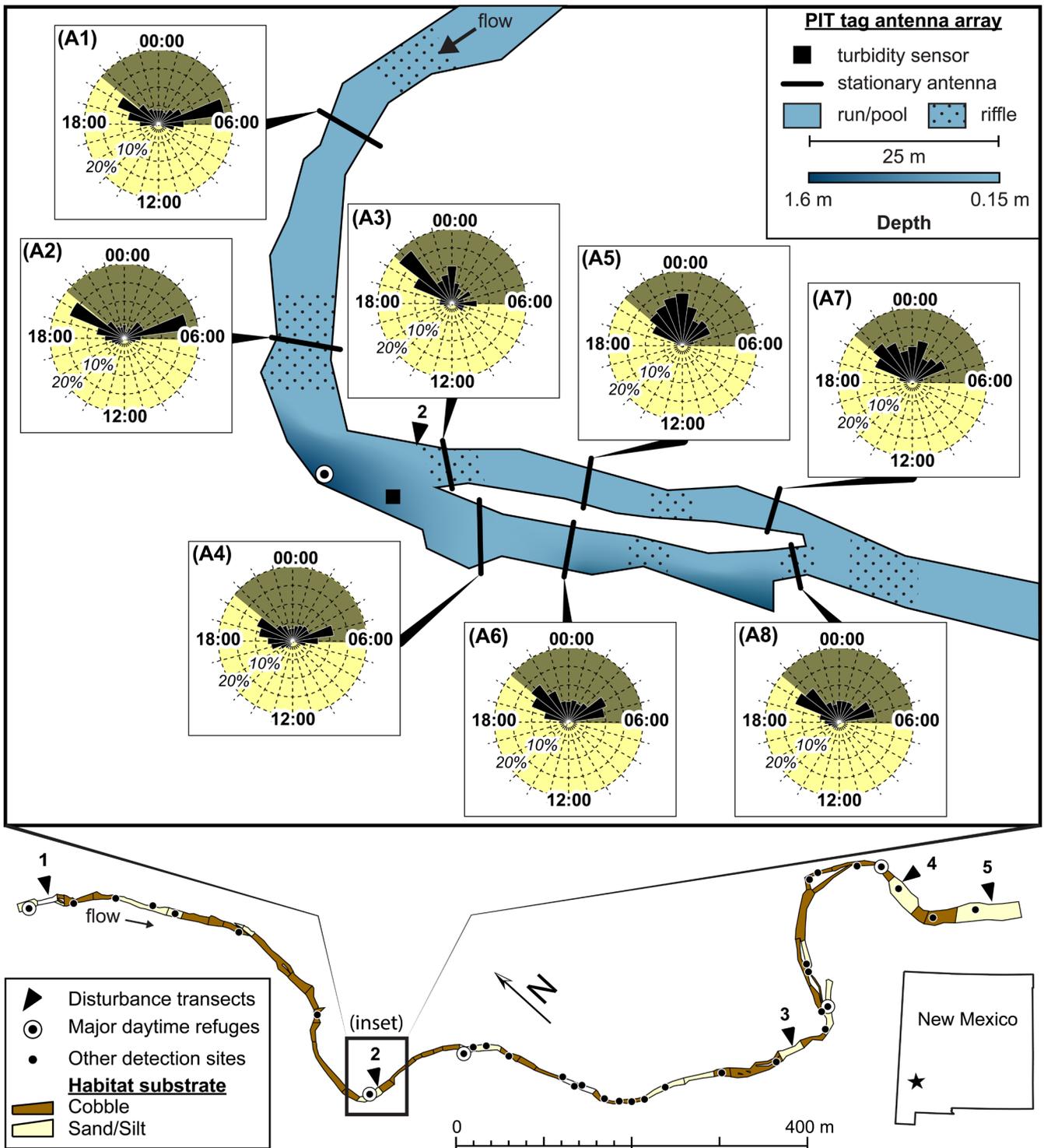


Figure 2. Map of the study site, including locations of 2009 disturbance transects, major (average of >10 individuals/survey) and minor daytime refuges, and the distribution of substrate types. Shading intensity indicates water depth. Inset shows the 2010 stationary antenna array, and turbidity sensor. Black bars on clock graphs A1–A8 show the proportion of tag detections for each one hour period at each stationary antenna during the study period; gray shading indicates average dusk to dawn hours, yellow indicate daylight during study period. Antennas A5 and A7 are located in a shallow run where the entry/exit riffles became too shallow for fish to pass during low flow periods. Increased detections at dawn and dusk are tagged fish entering or exiting the refuge pool. Tagged fish are detected only when within approximately 0.5–1 m of each stationary antenna.

deeper than natural and the downstream wall of the cups is more vertical). At each of three sites in 2010, 20 cups were embedded in the sediment so the opening was flush with the bed surface in a four by five array, with five cups collected at each sampling interval of 1, 3, 5 and 10 days. On day five, five replicate ambient 'no divot' sediment samples were collected at each site by quickly scooping sediment in specimen cup. Samples were frozen for storage, thawed and filtered through 1 mm, 250 μm and 45 μm mesh filters. The 1 mm and 250 μm fractions were sorted under a dissecting microscope removing all invertebrates, then all fractions were combusted using standard protocols to measure organic matter content (Wallace et al. 2006, Hutchens et al. 2017). Invertebrate taxa were identified to major taxonomic groupings (family) and dried and weighed to determine biomass.

Disturbance transects

To estimate how variation in fish visitation generates heterogeneity in disturbance over space and time, we set up transects perpendicular to stream flow (width 5.5–13 m) at five locations distributed throughout our 1.8 km study reach (Fig. 2), selected to represent the range of fine substrate habitats present in the river. Eight to eleven quadrats (0.25 m²) were evenly distributed along each transect, approximately every 0.5–1 m. Within each quadrat, five bicolored and uniquely numbered 22 mm diameter flat metal washers were placed flat on the substrate surface in a cross orientation centered in the quadrat, with washers placed approximately 10–15 cm apart. We scored disturbance each morning by recording, as points, if each washer had been moved (1 pt), flipped over (1 pt), buried with sediment (1 pt) or was now in a divot (1 pt); total disturbance was the sum of all washers in the quadrat (4 pts/washer \times 5 washers = max 20 pts). After scoring, washers were reset or replaced with minimal disruption of the sediment. We did not observe scores higher than 12 because it was unlikely that all washers experienced each of the four disturbance categories. We monitored disturbance transects daily during two periods (6–16 June and 12–26 July 2009). A flash flood event on 25 June 2009 ended the first study period, and deposited approximately 1–2 cm of fine sediment and coarse organic matter over most benthic surfaces. Return time was calculated as the average time between scored disturbances within a study period. Frequency of high disturbance was calculated as the number of disturbances with scores greater than four divided by the total number of observations. Our approach to analyzing the frequency of disturbance was similar to that of more recent works (Marquis and Roy 2012, Pledger et al. 2017) which employed vertically oriented washers in coarser gravel and cobble substrates to identify the depth of disturbance and bed movement. To quantify spatial autocorrelation, Moran's I was calculated in program R (<www.r-project.org>) by computing an inverse distance matrix for each transect, and then using the Moran.I function from the 'ape' library.

Suspended sediment and turbidity

To estimate the degree to which suspended load and carbon export were related to fish bioturbation, we collected bulk water samples (approximately 10 l) every 3 h for 24 h from one site on three dates (stationary antenna reach, 2009), three sites on two dates (upstream, stationary antenna reach and downstream location, 2009), and one site on two dates (stationary antenna reach, 2010). Turbidity was recorded every five minutes within the stationary antenna reach during the 2010 season using a self-cleaning turbidity probe (YSI 6136) mounted on a sonde located within our stationary antenna array. We used the 2010 bulk water samples to relate turbidity values to suspended load and carbon export. Three replicate samples were filtered on pre-ashed filters, immediately frozen, and processed using standard methods for ash-free dry mass (AFDM) (Wallace et al. 2006, Hutchens et al. 2017). We regressed average turbidity against our measured suspended load, and used the regression equations to estimate suspended load ($\text{DM mg l}^{-1} = 0.00277 + 0.00063 \times \text{turbidity NTU}$; $R^2 = 0.55$) and carbon export ($\text{AFDM mg l}^{-1} = 0.00073 + 0.12957 \times \text{DM mg l}^{-1}$; $R^2 = 0.60$) for each turbidity record, multiplied by the discharge at that point. We used the average turbidity value for the hour prior to bulk sampling when developing regression equations to account for short-term turbidity spikes.

To link fish activity to turbidity measures, we used detections from the four antennas directly adjacent to the pool where our turbidity monitoring equipment was located, an approach similar to that subsequently employed by others (Cooper et al. 2016, Rice et al. 2016) to link cryptic activity of invasive crayfish to diel turbidity cycles. Fish activity was the number of unique individuals detected within the antenna array during the one-hour period prior to each turbidity record (5 min intervals). Individual fish were only tabulated once per rolling interval, and in this context we treat activity as an index of the population of tagged fish entering or exiting the shallow foraging area. The spatial occurrence of antenna detections (Fig. 2) and visual observations of fish activity indicated that fish typically remained out in shallow water once they had left the refuge pool and passed the antenna array.

We calculated daily sediment loads for 24 h periods starting at 15:30 h, when the typical daily minimum suspended sediment value occurred. We calculated the total amount of sediment passing by a single point (using the turbidity-sediment regression and discharge) for each 5 min interval, and summed all values for each 24 h period. Baseline suspended load was calculated as the minimum turbidity value for the day, extrapolated to the entire 24 h period. During normal base flow (no storm event), fish were the primary influence on short-term changes in suspended load, so that any increase from the daily minimum value was due to fish activity. The suspended load due to fish was calculated as the difference of the total and the baseline sediment load. Time lags (the time between the peak of fish activity and turbidity) were calculated using the time series platform in JMP 8 (SAS Inst.),

using the number of time steps (k) that maximized the correlation between the two curves. Each sampling period was fit separately. Cross correlation values larger than $1.96/\sqrt{k}$ in magnitude were considered significantly different from zero (Cryer and Chan 2008).

Results

Timing and extent of fish movement

Timing of movement was strongly biased toward low light periods, with more than 88% of nearly 2.16×10^5 detections in the stationary antenna arrays occurring between 19:00 and 06:00 h (Fig. 2). Fish passage through the antenna array typically peaked between 20:00 and 21:00 as fish left the pool for shallow water and again between 03:00 and 04:00, when fish returned to the pool (Fig. 2). The timing of fish movement was consistent from day to day and among years, except during brief periods of turbid flow caused by flash floods, when fish immediately became active and remained active during daylight until waters cleared.

Of the 450 fish originally tagged, 420 were detected at least once, and 377 more than once. Fish regularly moved among daytime refuge habitats. Based on scans of the 4 km reach, more than 73% of the 377 fish were detected in at least one additional refuge site (mean 2.5, range 1–9 locations). The remaining fish, observed during the day only in the refuge site of their initial tagging, were detected in stationary antennas in shallow habitats adjacent to their home refuge. Total movement distances during the study period ranged from 12 to 5400 m, with a mean of 628 m and median of 376 m. Some refuge sites consistently held substantially more fish (average number of individuals >10, major refuge sites, Fig. 2) than other sites which had few fish or in which fish were only present sporadically (other detection sites, Fig. 2). Shallow riffles in some reaches restricted or prevented fish movement as flows receded during the course of the season. Following a spate on 25 June 2009, 80% of tagged fish (48 out of 66 individuals) that had been observed in a major refuge site located approximately 100 m downstream of disturbance transect 3 (Fig. 1), moved to other refuge sites (>300 m upstream, 38 individuals; >100 m downstream, 10 individuals). New individuals slowly repopulated the refuge habitat from both upstream (11 individuals) and downstream reaches (two individuals) and nearby small refuge habitats, but fewer total tagged fish were observed after the spate.

Divot distribution

Divots were widely distributed throughout all soft-bottom sediments within the river, provided there was access from the main channel of the river, and divots appeared in newly inundated areas soon after flood events. Weekly measures of the volume of sediments displaced by divot formation in soft bottom habitats showed substantial variation within a site, but no correlation with distance to a major daytime refuge

site ($R^2 < 0.01$, $p = 0.06$; Fig. 3a). Divot density was also variable among sites and sample dates (Supplementary material Appendix 2 Table A1). Percent cover of divots ranged from 0 to 100% of the bottom, with the volume of sediment moved ranging between 0 and $2.4 \times 10^4 \text{ cm}^3 \text{ m}^{-2}$. Sites further away from fish refuges had significantly higher coefficients of variation (CV) in sediment volume moved due to greater variation within the site and over time than locations close to fish refuges ($R^2 = 0.30$, $p = 0.028$; Fig. 3b). Rates of divot formation averaged 260 ± 220 (mean \pm SD, range 40–840) $\text{cm}^3 \text{ m}^{-2} \text{ day}^{-1}$. Given these rates of divot formation and typical percent cover (mean 28%, 95% confidence interval 26–30%), fish disturbance resulted in bioturbation of the top 2.5 cm of soft sediment habitats in the streambed approximately every 3–4 days.

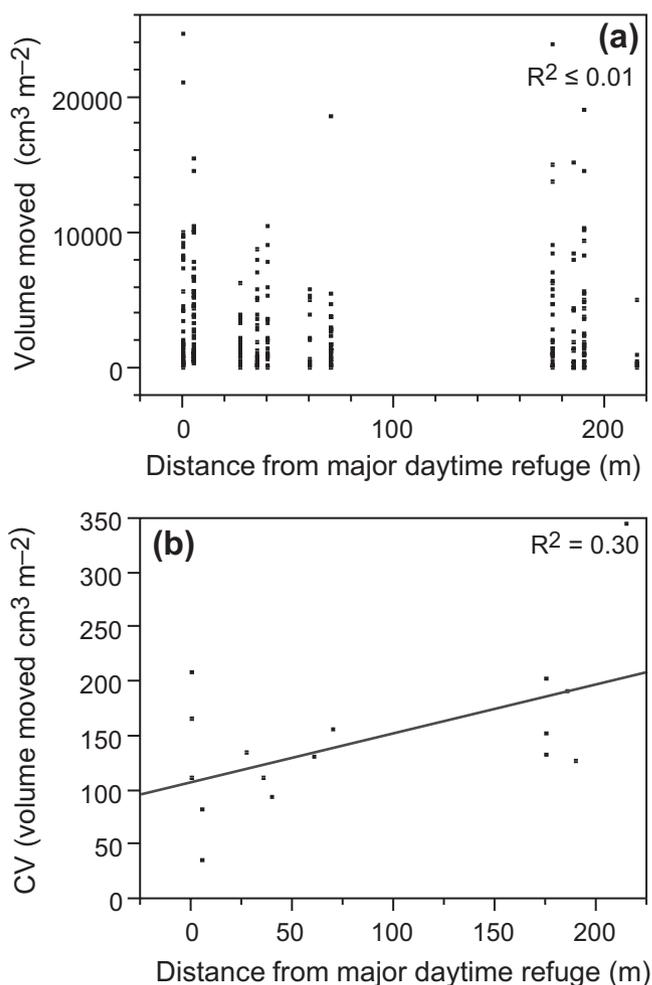


Figure 3. Sediment disturbance with respect to distance from a major daytime refuge habitat (Fig. 2). (a) Each point represents a quadrat-level estimate of sediment volume moved at each divot survey site over the 2009 sampling period. The volume of sediment moved by fish was not related to the distance from major daytime refuges. (b) CV values were calculated for each sample site and incorporate variation in time and among the quadrats within each site.

Consequences of divot formation

Once divots were formed, they were relatively long-lived (days–weeks), and typically filled with sediment again only due to new, adjacent, feeding activity. In general, artificial divots trapped coarse particulate organic matter (CPOM; >1 mm), such as leaves and twigs, but the overall amount was variable among sites. Within one day, artificial divots trapped $13.6 \pm 7.9 \text{ g m}^{-2}$ (mean \pm SD) of CPOM, and by day three CPOM increased to $37.9 \pm 29.0 \text{ g m}^{-2}$ (mean \pm SD). Within artificial divots, CPOM was often buried by sand and gravel pushed into the divots by adjacent fish feeding. Little to no organic matter was observed on the surface of neighboring sediment, indicating that organic matter found buried in sediment may be a result of feeding activities. As no historically undivoted sediments were available for sampling, it was not possible to definitively distinguish the source of organic matter within the sediment matrix. Artificial divots contained similar amounts of organic matter to ambient ‘no divot’ neighboring sediments, but proportionally contained significantly more organic matter per unit dry mass (Fig. 4a; ANOVA $F_{1,21}=66.17$, $p < 0.001$). We observed significantly greater biomass of invertebrates in artificial divots than in samples from ambient ‘no divot’ areas (Fig. 4b; ANOVA $F_{3,19}=6.17$, $p=0.004$). In addition, divots contained (Fig. 4c) significantly more mayflies (ANOVA $F_{3,19}=20.49$, $p < 0.0001$) and elmid beetle larvae (ANOVA $F_{3,19}=4.65$,

$p=0.0134$) than ambient ‘no divot’ sediment, which primarily contained dipteran larvae (chironomids) (ANOVA $F_{3,19}=17.18$, $p < 0.0001$).

Fish-related disturbance frequency

Relative disturbance by suckers, as measured by change in orientation of washers distributed on the sediment surface, was highly variable from day to day and among transects (Table 1, Fig. 5), however some transects (transect 1 and 4) had substantially more disturbance than others (transect 2, 3 and 5). Transect 2 (ANOVA $F_{1,21}=16.01$, $p=0.0006$) and transect 3 (ANOVA $F_{1,21}=43.71$, $p < 0.0001$) experienced significantly less disturbance in July (the post-flood period). Disturbance return time (average time between disturbances within a sampling period, Fig. 5) ranged between one day (disturbed daily) and eight days for June, and 1–15 days for July. Average frequency of high disturbance (number of quadrat scores >4 divided by total number of disturbances, Fig. 5) was lower after the flood event in late June for transects 2 and 3, increased in transect 5, and was similar pre- and post-flooding for transects 1 and 4. In transect 3, return times greatly increased and disturbance magnitude decreased following the flood, coincident with many fish departing the nearby refuge habitats. Moran’s I values, a measure of spatial autocorrelation (i.e. the degree to which disturbance to the streambed was grouped), were typically negative for transects 1, 2 and

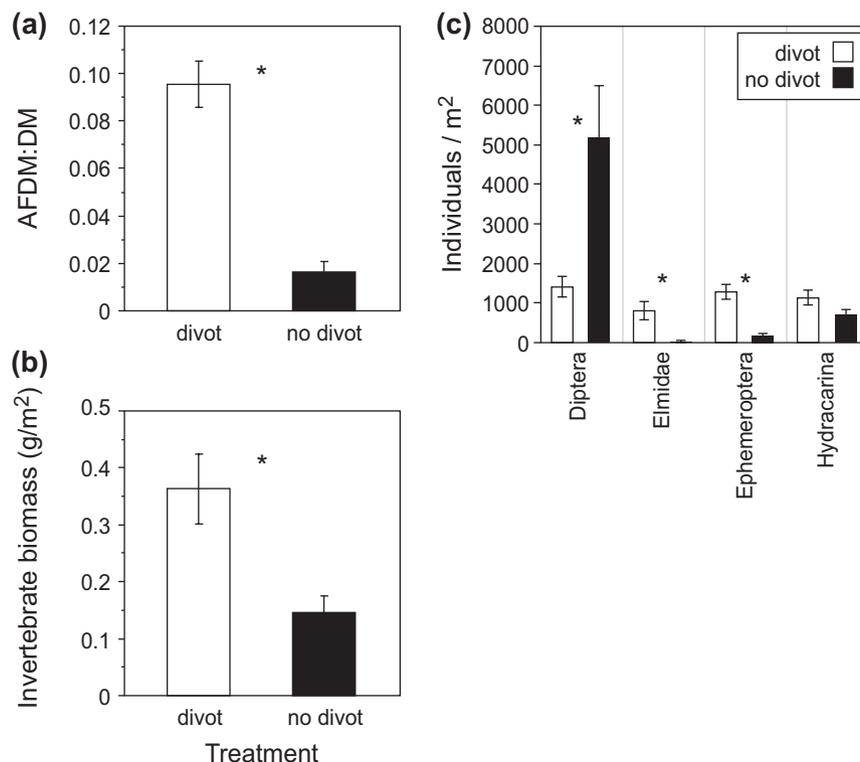


Figure 4. The consequences of divot formation for (a) organic matter retention, shown as the ratio of ash-free dry mass (AFDM) to total dry mass (DM), (b) macroinvertebrate biomass and (c) dominant macroinvertebrate taxa. Data represent means \pm SE from samples collected on day five from artificial divots and ‘no divot’ ambient sediment. Significant differences at $p < 0.05$ are denoted with an *.

Table 1. Mean relative disturbance values and Moran's I for disturbances for June and July sample periods. Negative Moran's I values were not significant ($\alpha=0.05$), indicating a random dispersion pattern of disturbance, while positive values typically were significant, indicating clustering of like disturbance values (significant Moran's I values are indicated shown in Fig. 5).

Transect	June		July	
	Relative disturbance Mean \pm SD	Moran's I Mean \pm SD	Relative disturbance Mean \pm SD	Moran's I Mean \pm SD
1	31 \pm 9	-0.13 \pm 0.09	30 \pm 14	-0.13 \pm 0.08
2	17 \pm 11	-0.04 \pm 0.15	6 \pm 3	-0.08 \pm 0.06
3	15 \pm 7	0.04 \pm 0.14	3 \pm 2	-0.05 \pm 0.07
4	32 \pm 9	0.10 \pm 0.18	29 \pm 10	0.23 \pm 0.07
5	10 \pm 6	-0.07 \pm 0.09	8 \pm 6	-0.13 \pm 0.07

5 (Table 1); however, values were not significant ($\alpha=0.05$), suggesting that disturbances were randomly distributed and not spatially autocorrelated. In contrast, transects 3 (June) and 4 (both sample periods) displayed significant, positive Moran's I values (Fig. 5), indicating spatial autocorrelation. In sites with high correlation, the majority of disturbance occurred in less compacted, deeper, and higher flow portions of the transect.

Effects on suspended sediments

Turbidity in the water column was greater at night than during the day (Fig. 6), and was significantly cross-correlated with the timing of fish activity, with a time lag ranging from 1:10 to 2:45 (Table 2). Although other factors may contribute to suspended sediment loads, we did not observe other organisms with high nocturnal activity in the study area or correlated patterns in discharge or algal sloughing (Booth unpubl.). There was relatively little variation in daily discharge during the study period (normally $\pm 10\%$ of mean discharge) and the daily variation in discharge (due to riparian evapotranspiration) typically had weak explanatory power (typical $R^2 < 0.10$) for changes in turbidity values. Three dates showed strong positive correlation ($R^2 > 0.51$, $p < 0.001$) with discharge, likely due to increased sediment input from precipitation events on those dates. We did not include these dates in our suspended load and carbon export analyses because for those dates we were not able to disentangle discharge effects from those of fish activity.

Overall, there was a decrease in discharge from 2.4 to 0.4 $m^3 s^{-1}$ from June to July, with a correlated decrease in average daily turbidity (ANOVA $F_{1,7302} = 8270$, $p < 0.0001$, $R^2 = 0.53$). We used this linear fit to subtract the effect of changes in discharge from turbidity and estimate the contribution of fish independent of discharge. Fish activity consistently contributed to the dry mass and organic matter in the suspended load (Table 2). As discharge decreased, the relative importance of fish activity grew, with the proportion of dry mass moved at night due to fish increasing from 20 to 32%. Decreases in turbidity levels during the daylight hours were due to settling of suspended particles, which formed a fresh layer of deposition over the streambed every day. Diel bulk seston sampling from 2009 to 2010 produced similar results to our turbidity records in different locations within

the study reach, with peaks in suspended load higher between sunset and sunrise (Supplementary material Appendix 3 Fig. A2).

In order to understand the overall importance of turbidity induced by fish-feeding activity, we calculated the proportion of time that flows were low enough to observe a substantial fish effect. Based on the historical discharge record for Gila River from 1928 to 2010, we estimate that about 75% of average daily discharge values were equal or lower than 2.4 $m^3 s^{-1}$ (the highest average discharge where turbidity measures were taken in this study). At this level of discharge, we estimate that at least 20% of suspended sediment dry mass and organic matter export is due to fish activity, and at lower discharge values, fish play a greater role in sediment export (Table 2).

Discussion

Sonora suckers are important ecosystem engineers in the Gila River with effects that vary simultaneously in time and space with their movement behavior acting as a modifier of engineering processes (Fig. 1). They substantially modify the physical structure of benthic sediments, generate heterogeneity in disturbance of the streambed, increase the magnitude of sediment and organic matter resuspension, settling and export, and influence the distribution and density of aquatic insects. Variability in movement patterns drive the frequency and spatial extent of their effects and the periodicity of fish activity creates pulses of sediment export and settling. The relative importance of the engineering activity is muted under the harsh environmental conditions of high flow, as predicted by a conceptual model (Moore 2006), but is substantial when conditions are more benign (Albertson et al. 2015).

In both terrestrial and aquatic systems, engineering activities that increase heterogeneity in the landscape appear to influence overall landscape-scale species richness by creating habitat that differs in a key metric (e.g. complexity, nutrients or disturbance) from unmodified habitat (Tardiff and Stanford 1998, Bruun et al. 2005, Moore 2006, Pringle 2008, Wright 2009). In both marine and freshwater aquatic systems, disturbance magnitude and frequency may influence the structure of the macroinvertebrate community in soft bottom sediments, both due to direct consumption (Williams et al. 2003)

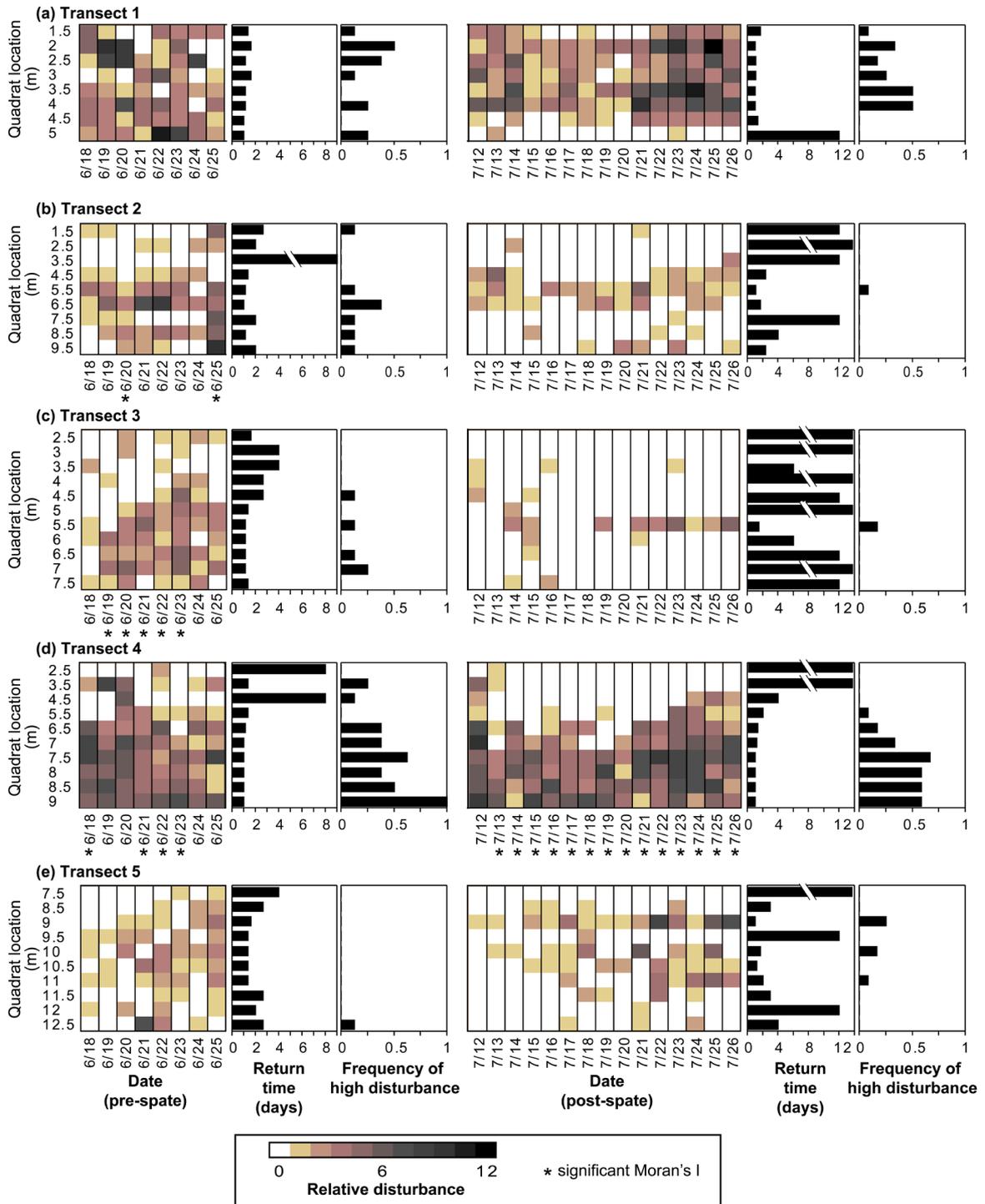


Figure 5. (a–e) Patterns of spatial and temporal distribution of fish disturbance (i.e. divot creation) along monitoring transects quantified using washer transects. Each column represents the distribution of sediment disturbance along the monitoring transect for each date and each shaded rectangle represents a quadrat along the transect. Darker shades represent higher levels of disturbance. Return time is the average time between disturbance events of any magnitude for each quadrat and broken bars indicate that the time between disturbances was longer than the monitoring period. Note that the scale of return time differs between pre-spate and post-spate monitoring. Frequency of high disturbance is the number of disturbances >4 divided by the total number of observation dates. Dates which had positive, significant Moran's I values, indicating nonrandom disturbance, are denoted with an * at the bottom of the column. The June and July sampling regimes were separated by a significant flooding event on 25 June. Following the spate, 80% of tagged fish that had been observed in a major refuge site about 100 m downstream of disturbance transect 3 (c) moved to more distant refuge sites up and downstream. New individuals slowly repopulated the refuge habitat from adjacent reaches, but fewer total tagged fish were observed after the spate.

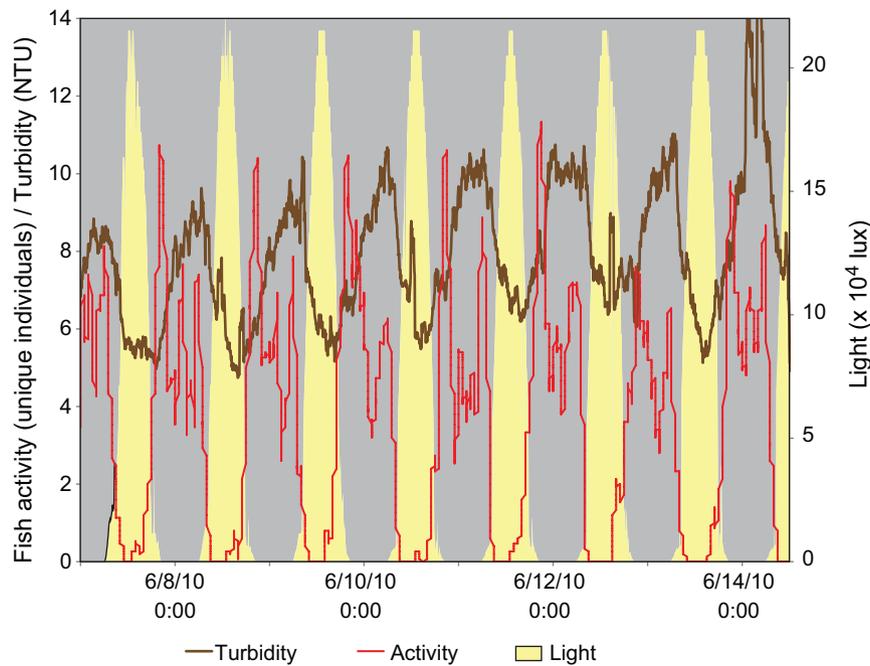


Figure 6. Diel pattern of fish activity, turbidity and incident sunlight. Turbidity and fish activity values are smoothed, 1 h rolling averages and shaded grey areas indicate evening periods when incident sunlight was not detected by sensors adjacent to the stream.

and by the creation of new habitats through the formation of microdepositional zones (VanBlaricom 1982, Hall 1994) such as the divots that *Catostomus insignis* make while feeding. Such depressions can be common features in aquatic systems and generated by a wide variety of organisms (Gregory et al. 1979, Townsend and Fonseca 1998, Coleman and Williams 2002, Meysman et al. 2006, O’Shea et al. 2012, Takeuchi and Tamaki 2014, Polvi and Sarneel 2018). In our study system, these divots rapidly trap organic matter and transform a smooth sand/silt streambed into a complicated honeycomb of pockets and microplateaus. The formation of divots causes substantial disturbance to the streambed, with the magnitude of the average disturbance equivalent to turnover of the top 2 cm of the stream bottom every 3–4 days, and creates a temporally and spatially varying mosaic of disturbed and undisturbed habitat patches over time. This heterogeneity has consequences for other organisms (Wilkes et al. 2019) including taxa that are prey of the foraging suckers: our divot surrogates were rapidly colonized by invertebrate taxa rarely found in adjacent undivoted sediment or generally in sand/silt habitats. Although we cannot isolate the potential impact artificial nature of the divot surrogates (i.e. burrowing taxa could not colonize through the sediment due to the container), the taxa found in divots, primarily composed of mayflies and elmids larvae, appeared to respond to the physical structure of the divot, where organic matter rapidly accumulated (hours–days). While it was not clear whether insects sought out the divots or were captured by the flow dynamics created by the divot, in marine systems, benthic infauna actively colonize divots created by foraging rays due to the concentration of otherwise relatively dispersed food resources (organic matter)

found there (VanBlaricom 1982). Although taxa differed in the timing of their colonization trajectories (e.g. Hydracarina abundance was maximum on day 1, but declined over time, while other, primarily mayflies and elmids increased, but at different rates; Booth unpubl.), invertebrate densities quickly increased within days to the presence of divots – indicating that variation in age and time to between disturbances will have biologically-relevant impacts to other taxa. Our observations of foraging fish did not indicate a clear preference for returning to a colonized divot over the undisturbed streambed, but suckers did regularly forage in previously created divots. This behavior of suckers may be a fortuitous, if not necessarily intentional, form of ‘farming’ – creating habitat that is colonized by their prey. In estuary habitats, burrow construction and associated bioturbation by burrowing crabs facilitates fish predation on benthic prey (Martinetto et al. 2005); likewise, suckers might also benefit from foraging in old divots.

Suckers primarily use pools as refuges during the day and the density of individuals varies daily (Booth et al. 2014), which may be a common phenomenon for stream fishes given changes in habitat preferences on a diel basis (Copp et al. 2005, Salas and Snyder 2010). These changes in density are the result of movements between refuges on a diel basis (Booth et al. 2013) as fish forage in shallow riffles and runs during the night. Part of the consequence of this regular movement among habitats was that the overall presence of divots (which are relatively long-lived, from days to weeks) was not related to the distance from refuge habitat, at least at the refuge spacing present in the Gila River. However, we did observe a dramatic reduction in disturbance magnitude

Table 2. Sediment and organic matter export through a cross section of the Gila River. Dry mass (DM) was calculated from turbidity values and organic matter (AFDM) was calculated from DM for each 24-h period beginning at 15:30. Table values represent means \pm SE for all days within the period. Lag times were calculated from cross correlation analysis and represent the time shift that maximizes the correlation between fish activity and turbidity curves. All cross correlation values were significantly different from zero based on the criteria of Cryer and Chan (2008). Fish activity was calculated as the proportion of 5-min intervals during the reporting period where fish were detected in stationary antennas.

Period	Lag time (h:min)	Cross correlation	Average discharge ($\text{m}^3 \text{s}^{-1}$)	Proportion of time fish active	DM (kg day^{-1})	DM by fish (kg day^{-1})	DM proportion due to fish	AFDM (kg day^{-1})	AFDM by fish (kg day^{-1})
1–3 June 2010	2:00	0.41	2.4	0.41	1953 \pm 46	382 \pm 37	0.20 \pm 0.01	253 \pm 6	49 \pm 5
4–14 June 2010	2:30	0.53	1.3	0.63	1025 \pm 126	279 \pm 31	0.27 \pm 0.01	133 \pm 16	36 \pm 4
16–21 June 2010	2:45	0.64	0.5	0.44	258 \pm 22	82 \pm 12	0.32 \pm 0.02	34 \pm 3	11 \pm 2
23 June–1 July 2010	1:10	0.41	0.4	0.48	168 \pm 18	53 \pm 8	0.32 \pm 0.02	22 \pm 2	7 \pm 1

and lower return frequency in a disturbance transect coincident with a large proportion of the fish population moving >300 m upstream following a spate (Fig. 5c). If the spacing between refuge habitats were to exceed typical home ranges observed (e.g. >250 m), divot structures in distant habitats may become less abundant, while local disturbance may be exacerbated (Statzner et al. 1996, Mathers et al. 2019). However, we suspect that the size of individual home ranges may be at least partially dictated by the availability of food, spacing of refuges and the density of fish within the refuge (Hansen and Closs 2005), so it is unlikely that engineering impacts in natural systems will be limited by distance, except in circumstances where movement potential is restricted.

Despite the presence of divots in habitats distant from refuge sites, the further a foraging habitat was from a refuge, the more variable effects were over space and time. As fish move between habitats, short-term population size within these habitats changes (Booth et al. 2013), likely influencing the frequency and intensity of disturbance to benthic substrates, and generating patches of varying disturbance age. In some habitats, most of the stream bottom was disturbed every night, although only a subset of patches experienced heavy disturbance in a given 24-h period, similar to that observed in a gravel bed river (Pledger et al. 2017). Other locations were frequently disturbed, but rarely very heavily, and experienced very different disturbance regimes before and after flooding. Although our data do not directly tie variation in fish abundance to the magnitude of the sediment disturbance, we infer that movements among habitats partially explain the heterogeneity in magnitude and frequency of divot formation in the streambed. Bioturbation changes sediment structure (Scheffer et al. 2003, Meysman et al. 2006), oxygenate sediments (Olivera Junior et al. 2018), preventing anoxic conditions (Ritvo et al. 2004) and modifying oxidation–reduction dependent biogeochemical processes (Laverock et al. 2011), while burying or re-exposing particulate organic matter and algal biofilms. Divot formation may also disturb sand and sediment biofilm communities, potentially selecting for taxa that are resistant to burial, creating a heterogeneous array of algal patches, and destabilizing sediments (Peterson 1996).

Flecker and Taylor (2004) observed that the effect of the abundance of an ecosystem engineer on heterogeneity follows a hump-shaped distribution, with high or low abundance leading to homogenization of resources, and moderate densities to heterogeneous distributions. Despite high numbers of large fish in the refuge habitats in the focal antenna reach (up to 65 individuals >25 cm total length within a 24 h period in 2009), we observed heterogeneous patterns of disturbance along our transects in the Gila River. We expect that movement accounts for this heterogeneity, because nightly foraging trips into shallow habitat distribute the high density of individuals over a much broader area, thus moderating the functional density of fish in the river. As a result, it is likely that refuge pools can sustain higher than expected fish densities because much of the foraging actually occurs outside of the refuge habitat except during rare periods when movements are restricted by low flows or physical barriers.

Under low flow conditions, suckers greatly reduce their entry into shallow habitats (Booth et al. 2013), potentially limiting movement to otherwise useable habitats (e.g. shallow riffles prevent passage between refuge pools and shallow foraging habitat). We expect (and anecdotally observed in pool habitats isolated during low flows) that when fish are precluded from moving into shallow foraging habitat, disturbance to the streambed becomes more homogeneous and of higher magnitude in refuge habitats and absent in shallow foraging habitats. Similarly dramatic patterns have been observed in other systems (Power et al. 1985, 1988), where reduced or lack of movement among habitats results in state changes. Although the seasonal reductions in flow observed in this study were part of the historical dynamics of the upper Gila River, in this and many other stream systems, climate change (Jaeger et al. 2014) and water extractions for human use may artificially decrease stream flow and impair functional hydraulic connectivity. Reductions in flow will strongly influence both overall movement rates between refuges and shallow habitats, and consequently the magnitude, distribution and heterogeneity of engineering impacts to the stream bottom.

As landscapes become fragmented, organisms are likely to be constrained in their ability to move (Comte and Olden 2018). Many engineering taxa are mobile and changes to habitats that limit or enhance their mobility may alter the modifying role of movement (Fig. 1) by accentuating or attenuating the engineering impacts on the system as a whole. For example, migratory engineers like salmon may move upstream until they reach a passage barrier, which can result in unnaturally high spawner densities and superimposition of spawning redds downstream of barriers (Ligon et al. 1995) – resulting both in high mortality for their offspring as well as homogenizing and increasing the magnitude of the engineering impact. Fragmentation can also change both the location and nature of movement behaviors (Graham et al. 2009), which may modify the amount and distribution of engineering activities, potentially altering the impact of an engineer from generating heterogeneity in the landscape to homogenizing landscape characteristics through high disturbance magnitude or frequency.

Direct disturbance to the sediment by foraging fish was patchy over space and time. In contrast, indirect effects of these engineering activities, such as sediment resuspension and settling, was more consistent and predictable, with sediment deposition occurring in the entire ecosystem on a 24-h cycle. We found that elevated sucker movement occurred during periods of low light, generating pulses of sediment movement downstream during the night that rapidly settled out during the day, similar to those observed for crayfish in other systems (Cooper et al. 2016). These pulses of sediment may have, in turn, had consequences for the timing and feeding activity by filter-feeding insects (e.g. simuliids, Hart and Latta 1986) and deposit-feeding insects. We observed 1–5 mm of sediment settling on benthic substrates per day, distributed throughout the stream (including areas

where fish do not feed) and it is likely that this degree of deposition will influence growth of periphyton and the composition of biofilms on benthic substrates (Peterson 1996). Sediment export due to fish activity made up a substantial proportion of the sediment transport from the stream reach as a whole. This is consistent with findings in experimental streams, where fish have been shown to regulate dynamics of downstream sediment transport (Statzner et al. 2003), in rivers (Rice et al. 2019), as well as work in aquaculture and shallow lake systems, where benthic feeding carp generate elevated suspended sediment loads (Breukelaar et al. 1994, Ritvo et al. 2004, Matsuzaki et al. 2009).

A variety of vertebrate and invertebrate taxa can influence sediment export from aquatic systems (Pringle et al. 1993, Zanetell and Peckarsky 1996, Statzner et al. 2000, Meysman et al. 2006, Moore et al. 2007, Tiegs et al. 2009). Sediment movement by organisms may be important in a variety of aquatic ecosystems, particularly as the activity of organisms will, in general, generate patterns of disturbance substantially different than those from abiotic forces (Statzner et al. 2003, Albertson et al. 2015, Rice et al. 2016, Pledger et al. 2017) and redistribution of sediment may also transport and release sediment-bound nutrients, like phosphorus (Nowlin et al. 2005). However, as predicted by Moore's (2006) conceptual model, the degree to which this sediment transport is relevant is dependent on abiotic conditions. In our system, we expect that the overall sediment export caused by suckers is relatively low compared with that during flood events (which are often highly turbid due to overland flow; Statzner et al. 2003) and high flows during winter snowmelt, however, the effects of consistent sediment pulses are quite strong during low flow periods and may be important at a watershed scale (Rice et al. 2019). Based on the historical discharge record, we estimate that about 75% of the time, flows in the Gila are within the discharge range for which fish provide greater than 20% of the suspended sediment export. So while organism-generated sediment export may not be the single greatest contributor to the sediment and carbon budget in this system, it represents a consistent movement of inorganic particles and organic matter similar to other systems (Cooper et al. 2016, Rice et al. 2016), as well as a major source of the particulate deposition and accumulation on the stream bottom.

Our update to Moore's (2006) conceptual framework (Fig. 1) suggests that movement patterns of ecosystem engineers act as an additional 'filter' and feedback on the effects of density, engineering behavior and possibly body size, in combination with the abiotic factors disturbing the system. Particularly for engineering taxa that consistently modify their habitat (e.g. foraging rather than single spawning bouts), movement (or lack thereof) may alter the extent and magnitude of the impacts, partially independent of density. Our work indicates that changes to spatial connectivity that restrict movement may strongly influence pattern, magnitude and overall role of organisms in engineering ecosystems.

Speculation

Cryptic movements are by nature difficult to observe, but may substantially modify the role of engineers. We observed some fish using only a single daytime refuge habitat, yet regularly moving into surrounding habitats to forage. By understanding the diel movements, we were able to connect these engineers to impacts in distant parts of the stream where we never observed them during the day. We suspect that cryptic movements resulting from predator avoidance (Pettersson and Brönmark 1993, Reeb et al. 1995), coupled with strong engineering impacts, are likely to result in similar magnitude diel effects in other aquatic systems.

We wonder about the degree to which suckers are 'farming' their habitat. Fish acquire food out of the sediment as they dig depressions, but the extent to which they actively seek out and benefit from previously dug depressions remains unclear. We know that fish feed in and expand previous divots at least some of the time. Within 24 h, divots contained invertebrate biomass equivalent to adjacent undivoted habitat, and within five days had double the biomass – suggesting that returning later to feed could be quite beneficial. However, divots were also ubiquitous – so returning to feed in divots may simply be a density dependent occurrence.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.qv9s4mw9h>> (Booth et al. 2019).

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Supplementary material (available online as Appendix oik-06396 at <www.oikosjournal.org/appendix/oik-06396>).
Appendix 1.