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ESTIMATING FISH HABITAT SELECTION AND MONITORING STREAM HABITAT QUALITY REQUIRES MORE THAN SIMPLY COUNTING FISH

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ESTIMATING FISH HABITAT SELECTION AND MONITORING STREAM HABITAT QUALITY REQUIRES MORE THAN SIMPLY COUNTING FISH

By

Anthony D. Matthys

A DISSERTATION

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This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Biological Sciences.

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Table of Contents

Preface

I led all aspects of the research contained in this dissertation, namely study design, data collection, data analysis and interpretation, and writing. Portions of this dissertation have been written as articles which will be submitted for publication to peer-reviewed journals. Chapter 1 will be submitted as part of a larger manuscript to a scientific journal to be determined at a later date. The research detailed in Chapter 1 was performed in collaboration with Casey Huckins who acquired funding to the restoration, helped in the collection of data and writing the manuscript. Chapter 2 will be submitted as an article to *Transactions of the American Fisheries Society* and was also written in collaboration with Casey Huckins who contributed to the study design, data collection, funding and writing of the manuscript. Chapter 3 was also coauthored by Casey Huckins who aided in the study design, and writing of the manuscript. We plan to submit this chapter as an article to the *North American Journal of Fishery Management.* Casey Huckins also contributed to Chapter 4 by aiding in the acquisition of funding, the study design, and the writing of the manuscript. We do not currently plan on submitting this chapter for publication, but reserve the right to publish the chapter in the future.

Finally a note on style, I have followed American Fisheries Society (AFS) naming conventions throughout my dissertation, because I intend to submit the majority of this dissertation to AFS journals. Following AFS conventions common names are capitalized, e.g. Brook Trout, however subspecies or life history variants are not, e.g. coasters.

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I would like to acknowledge my committee members for their support and assistance throughout my research. I especially thank my advisor Casey Huckins for his tireless support and guidance through my graduate education. I appreciate Amy Marcarelli's efforts to help catalyze and sustain the various reading and writing groups that have enriched my education at Michigan Tech. I would also like to recognize Amy Schrank and Chris Webster for their helpful comments that have helped me improve and reevaluate my research.

This research could never have been accomplished without all the hard work from the many field technicians who assisted our sampling. I would specifically like to recognize Emily Matthys, Brian Danhoff, Cameron Goble, and Cassie Matthys who volunteered during various portions of this work.

Finally I would like to thank my friends and family for their constant generosity and support. Thank you to my wife Emily, her help and support throughout my graduate career has been invaluable; I would not have gotten through this without her. To my parents, thank you for always stepping in and helping whenever or wherever the need arose.

Abstract

Identifying techniques to more easily monitor, assess and manipulate habitat quality will improve the assessment of habitat restoration and the management of native fish species. We utilized a relatively novel tool the Sand Wand^{TM} (Streamside Environmental, Findley,Ohio) to manipulate stream substrates by removing sand. After the removal we observed a 34% reduction in the area of the streambed covered by sand, and a decrease from 44% fine sediment within the streambed matrix before the manipulation to 20% post restoration (Chapter 1). In rivers that are heavily aggraded by fine sediments, a large reduction in fine sediments is likely to measurably increase habitat quality for Brook Trout (*Salvelinus fontinalis*) and sculpin (*Cottus* spp). We tested how reliably these changes in habitat quality could be inferred using three different metrics that had been used to infer habitat quality in the literature (Chapter 2). We found that immigration most reliable reproduced the assumed changes in habitat quality that resulted from our manipulation. We also found that density, a metric commonly used to assess restorations did not reliable infer changes in habitat quality at this spatial scale. When this metric was applied to other sites in the same river, we observed that in sandy sites native fish appeared to be attracted to exposed cobble, but this relationship did not hold in less sandy sites. We also observed that in at least some systems densities vary greatly over short time scales making measuring density more difficult. Abundances varied from 10-39 individuals over the course of 7 days (Chapter 3). This variation can result in low power if not properly accounted for within sampling designs. Finally, we experimentally tested the attractiveness of artificial boulders in different habitat contexts (Chapter 4). Based on previous observations we expected that boulders added to sandy sites to be more often occupied than boulders in rocky sites. This hypothesis was not supported. We observed very few fish in sandy sites and did not

observe an increase in occupancy after the boulder addition. As a whole the work detailed here deepens our understanding of how to monitor and assess restoration and how native fish select and use habitats.

Introduction

Romesburg (1981) warned wildlife scientists that without stringent quality control, a conceptual crash is unavoidable; resulting in a field of study that has to winnow through its past work to differentiate quality work from unreliable knowledge. Stream ecologists working on questions related to fish habitat quality and selection in rivers may be headed toward a conceptual crash due to the lack of a common conceptual model of habitat use and agreed upon terms to describe the associated key ideas and relationships. The use of a common conceptual model and language forms the heart of a schema (DiMaggio 1997), and using a common schema fosters more efficient communication within a field (Schimel 2012). Hall et al. (1997) literally pleaded for standardized definitions of habitat, habitat use, habitat selection, and habitat quality. Even though nearly 20 years has passed since Hall's review, I believe that more needs to be done to standardize our conception and use of these terms. This review will lay out a conceptual model of habitat use and suggested definitions of important terms.

The conceptual model of habitat use I am adopting was first proposed by Sale (1969) to describe a mechanism for similar patterns of habitat use by reef fish in a highly dynamic landscape. Mcmahon and Matter (2006) expanded on the Sale (1969) model to include emigration and dispersal. While these models informed the model I describe in this chapter, they are both mechanistic models used to describe a specific behavior (e.g., exploration or dispersal). The conceptual model I lay out here describes the relationship between the landscape, the fish, and the ecological drivers that result in habitat use. It also explicitly incorporates social interactions which are known to influence the distribution of individuals through territoriality and other social interactions (Nakano 1995; Winker et al. 1995) the importance of which is described later in this chapter.

The basic input into this conceptual model is the biological and physical characteristics within the landscape (Figure 0.1). The landscape contains within it a matrix of individual habitats; i.e., distinctive sets of physical and biological factors that affect an individual's survival and reproduction (adapted from Block and Brennan 1993). Individuals use habitats to obtain the resources needed to complete their life history (Block and Brennan 1993). Habitats within a landscape vary both spatially and temporally (Townsend and Hildrew 1994). Habitat quality is determined by the cumulative effect on fitness realized through use of a given habitat.

The actual quality of a habitat is likely unknown to individuals because organisms likely cannot perceive fitness consequences directly. For example, it seems impossible for an organism to perceive that use of Habitat A will likely result in X more offspring on average than Habitat B. Instead, organisms perceive various biological and physical characteristics such as predators or shelter within a habitat (Perception, Figure 0.1). These perceptions of the landscape are input into habitat selection (Figure 0.1), a hierarchy of behavioral processes that result in attempted use of the habitat or continued searching behavior (Jones 2001). This perception and subsequent habitat selection has likely been altered by natural selection because the outcome of habitat selection has fitness consequences. The importance of perception to habitat selection was experimentally illustrated by Gowan (2006), where they installed gates in a small stream to provide areas of high water velocity and feeders to manipulate food supply as part of habitat quality. They found that fish only used the feeders when they were paired with the cue of high water velocity. This illustrates how habitat quality can increased, due to the increase of food from the feeders in this case, but individuals will only take advantage of these changes when provided with the appropriate perceptions, like the high water velocity from the gates.

In addition to perceiving characteristics of habitat that correlate to high habitat quality, many organisms also perceive the social availability of habitat (Availability, Figure 0.1). Many species exhibit territorial behaviors that can prohibit the use of a habitat by a new immigrant (Fausch and White 1986; Grant 1990; Nakano and Furukawa-Tanaka 1994). Sometimes availability can be assessed directly through immediate observation; i.e., large size discrepancies. Other times organisms can directly assess availability by challenging the current occupant. Availability can also be assessed indirectly through transitive inference; if Fish A can displace Fish B, and Fish B can displace Fish C, the Fish A can displace Fish C. Brook trout have displayed the ability to perform this transitive inference has been shown in relatively simple social hierarchies in laboratory settings (White and Gowan 2012), but many habitats in the wild contain much more complicated social hierarchies (Katano 1990; Nakano and Furukawa-Tanaka 1994). In these more complicated hierarchies, the social availability of a habitat is likely much harder to assess, leading to an additional filter between selecting a habitat and actually using a habitat. For instance, a habitat may have resources that are attractive to immigrants, but the complex social hierarchy present in the habitat prevents many immigrants from actually using the habitat, resulting in high turnover.

The result of these various processes is habitat use. Individuals can use habitats to feed, to find refuge from predators or environmental risks, for reproduction, or as a dispersal path connecting various habitats. Deepening our understanding of how individual organisms use a given habitat will improve our understanding of the relationship between organisms and their environment. Furthermore, if we can identify characteristics of high quality habitats, and the cues that trigger habitat selection, we can tailor management to specific target organisms. For example, restoration activities could be designed to target a single species in a community and be successful at increasing that species' growth rate, or they could be an ecological trap to target and reduce an invasive species' population.

The model I present here provides the opportunity to measure or infer habitat quality in three different ways: Measuring habitat quality directly, inferring habitat quality through habitat selection and inferring habitat quality through habitat use (Figure 0.1). Each of these measures has its own set of assumptions, strengths and weaknesses. When designing a monitoring regime or an experiment, it is necessary to consider which of these metrics is being used, and if the assumptions and requirements of each metric match the planned sampling regime.

Measuring habitat quality directly would involve determining the fitness benefit garnered through use of a habitat (Figure 0.1). On large spatial scales, there exists many tools to estimate habitat quality directly by estimating the vital rates of the species of concern (Frederiksen et al. 2014). However, this approach requires that the individuals ideally spend their entire lives within the study site or that it is possible to partition the effects the proportional use of a habitat has on the fitness. The more of an individual's life history is spent outside the site, the higher the risk that positive or negative fitness effects will be improperly attributed to the study site. At smaller study site sizes (i.e., 100's of meters), such as the size of many restorations and smaller than the lifetime ranges of many fish, measuring the actual habitat quality directly in the field requires spatial tracking of individuals to compile a comprehensive list of the habitats used and their influence on the individual's fitness. The contribution of each habitat then needs to be teased out of this dataset. This would provide a single sample of habitat quality; many samples would likely be required to accurately estimate habitat quality. Therefore, accurately estimating habitat quality directly at small spatial scales directly is a herculean task that it is likely practically impossible.

However, this does not mean investigating habitat quality at small spatial scales is fruitless. Measuring components that likely affect fitness such as net energy intake, predation risk or survival may provide important insights to habitat quality, even if the ultimate effect on fitness in unknown. The use of N-mixture models can allow the estimation of annual survival rates over small scales using without tracking individuals (Kanno et al. 2014b). Investigating relative differences in these metrics can provide further insight into changes in relative quality. In this study we decided not to proceed using these metrics because they are still difficult and expensive to measure, and the relationship between energetics, risk and fitness is not always straightforward (Lima and Bednekoff 1999).

Even if habitat quality of relatively short reaches cannot be directly measured, in experimental manipulations it may not always be necessary to know the exact magnitude of the change, only the direction and that the magnitude is large enough to likely have effects. As an example of this approach In Chapter 1 we detail a method to manipulate the habitat quality within sandy rivers by hydraulically removing fine sediments. This manipulation likely increases habitat quality because homogenously sandy streams are poor quality habitat for salmonids (See chapter 2 for review of the relationship between sand and habitat quality).

Further, theoretical explorations of habitat quality through simulations, where habitat quality is perfectly known or clearly defined, can also lead to valuable insights. One example was Railsback et al. (2003), who modeled a ‘river’ consisting of a matrix of habitats of known quality, into which they released virtual trout, i.e. a model of trout behavior that could replicate patterns of habitat use observed in real trout populations (Railsback et al. 2002). They found that abundances of these virtual trout, whose movement was governed by rules shown to reproduce patterns of habitat use observed in real populations, did not correlate to the perfectly known habitat quality of the simulated river.

Habitat selection can also been used to infer habitat quality (Figure 0.1), even though the exact decision processes that occur in the central nervous systems of organisms that weigh and choose between habitats are unknowable. We cannot know what individuals actually perceive and how exactly they process this information (Nagel 1974); as this would require humans to experience the world as would the organism of focus, for example, a bat, fish or elk, and this is likely impossible. However, this is a philosophical distinction. The outcome of habitat selection can be measured, modeled and predicted and models that predict habitat selection can be built (for example: Railsback et al. 1999), which allow the use of habitat selection to make inferences regarding habitat quality.

In order for habitat selection to provide reliable inferences of habitat quality there must be a relationship between habitat quality and habitat selection. We expect highly selected habitats to be high quality, since using a habitat impacts fitness. Maximizing the use of high quality habitats constitutes a selection pressure that should cause populations of organisms to evolve the ability to select high quality habitat (Fretwell 1972). Therefore we can infer that highly selected habitats are also typically relatively high quality habitats. This process requires a reliable and accurate metric of habitat quality, many metrics exist and selecting the appropriate metric will determine the ability to accurately infer habitat quality (Winker et al. 1995; Belanger and Rodriguez 2002). In chapter 2 we tested the ability of different metrics of habitat selection to mirror changes in habitat quality at a given spatial scale, and we provide an example of how using an appropriate metric of habitat quality can be used to identify physical characteristics that appear to serve as cues of high quality habitat.

Habitat use can also be used to infer habitat quality especially in the assessment and monitoring of restorations (Figure 0.1). Sometimes the assessment of habitat use involves careful observation of individuals to determine how they are using a habitat (e.g. Heerhartz and Toft 2015). However more often the abundance or density of individuals within a habitat is used a metric of habitat use to infer habitat quality (Stewart et al. 2009; Koljonen et al. 2013). This metric assumes that that the more individuals using a habitat the higher the quality. This metric of habitat quality is easy to understand, and is relatively easy to measure. Using density based metrics of habitat use to infer quality has long been criticized (Wiens and Rotenberry 1981; Winker et al. 1995), but it is still a relatively common metric when monitoring and assessing restorations (see e.g., Stewart et al. 2009). We tested the relative ability of density to mirror changes in habitat resulting from a restoration project that we are confident changed habitat quality (Chapter 2). These results led us to further investigate an existing data set which illustrated how precisely measuring density at reach and local habitat scales can be difficult due to short term movements in Chapter 3. We also used underwater cameras to determine habitat use (presence/absence) at very small spatial scales (~1 m^2) to test if the attractiveness of a boulder was influenced by the surrounding sediment regime in Chapter 4.

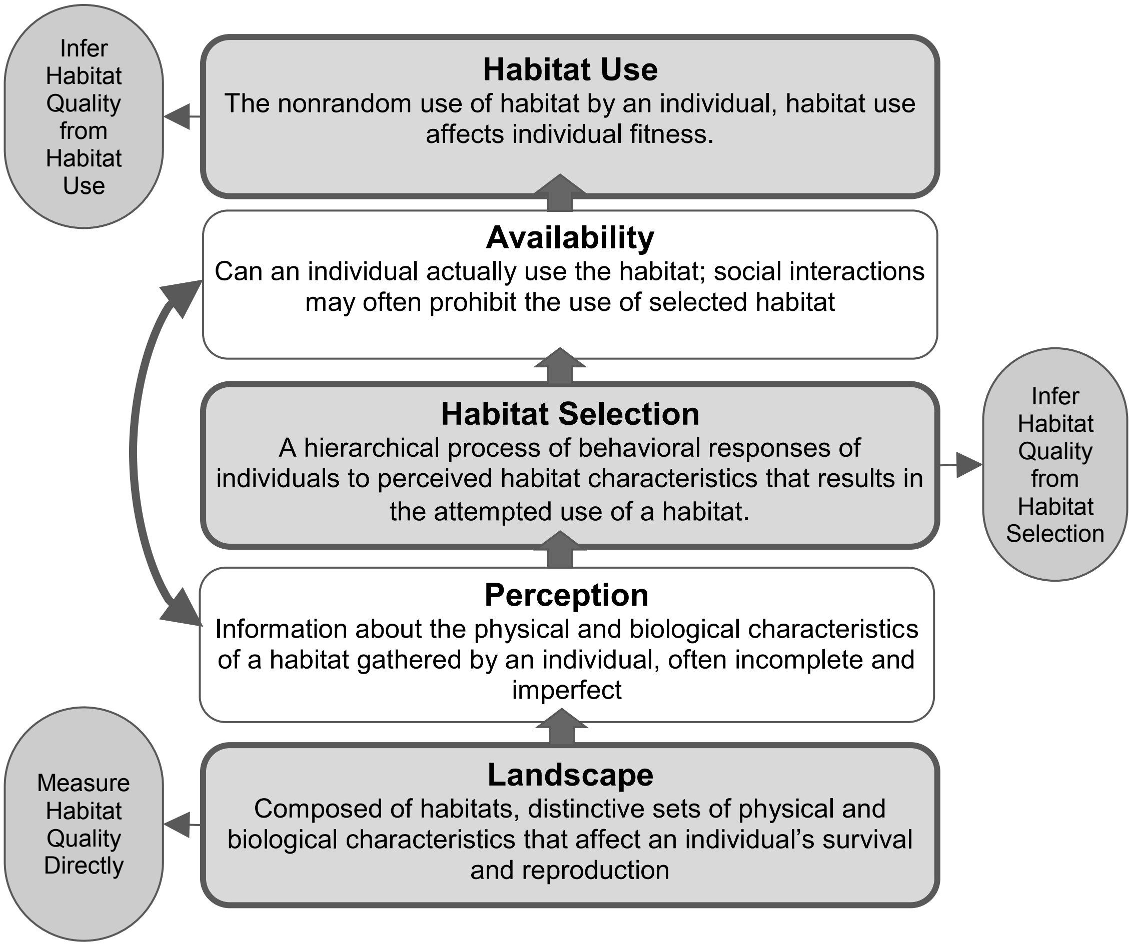

Figure 0.1. A conceptual model individual habitat use. Bold gray boxes represent ecological phenomenon that can be measured and ultimately used measure or infer habitat quality. White boxes represent filters that may limit the selection or use of a given habitat. The arrow represents how some aspects of availability can be perceived, but not all resulting in availability filtering both habitat selection and habitat use.

Chapter 1: The Effectiveness of the Sand Wand Sediment Removal Tool and Recommended Applications[1]

Abstract:

The ability to actively and selectively remove fine substrates from rivers would allow for the fine scale manipulation of habitats and highly targeted restorations within streams. We tested the ability of a Sand WandTM (Streamside Environmental, Findlay Ohio), a highly portable hydraulic dredge, to restore an aggraded spawning site within spawning gravels in the Salmon Trout River, Marquette County, Michigan, by reducing fine sediments in the streambed. We found that immediately after operating the dredge, the area of exposed cobbles increased 34% in the restoration site. The median pebble size increased from <2mm to 13mm, although the d16 and d84 were unaffected. Embeddedness in the restoration site decreased from 84.7% to 65.3%. Further, the percentage of interstitial fine sediments, measured through bulk samples in the restoration site, declined from 44% to 20%. Similar decreases in fine sediments were not observed in nearby reference reaches. This led us to conclude that a Sand Wand restoration can expose cobbles and alter streambed pebble distributions, as well as decrease the amount of interstitial fine sediments. Excess sedimentation is a widespread problem and the Sand Wand may be an useful tool to maintain spawning sediments while watershed scale sedimentation restorations are enacted and take effect. Further, the Sand Wand may be a useful tool to restore streams that are inaccessible to heavy equipment due to its portability. The high level of operator control also allows for fine scale experimental manipulations.

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[1] The material in this chapter is planned for submission.

Introduction

Alterations to a river's streambed sediment composition can lead to a regime shift in river morphology that is not easily reversed (Brooks and Brierley 2004). Nevertheless, reversing or at least mitigating the effects of an altered sediment regime is the goal of many restoration efforts (Palmer et al. 2014b). Addressing an altered sediment regime within a watershed requires an inherently large temporal and spatial scale. Due to the interconnectedness within rivers problems tend to not be local, but rather to spread throughout the river (Kearsley et al. 1994). Further once a sediment regime has been sufficiently altered it often cannot be quickly reversed (Jackson et al. 2005). While these long- and large-scale projects are implemented, populations of species targeted for improvement within the watershed may not respond. For example, Bouwes et al. (2016) described restoration efforts in Asotin Creek, Washington that changed farming practices and reduced sediment input into the stream during the 1990's, but the endangered Cutthroat Trout have yet to recover by 2009. Even though the main source of environmental degradation had been addressed, habitat within the river was still degraded. In order to jump-start the recovery of the Cutthroat Trout, managers utilized a large woody debris addition to increase scour and improve habitat quality. This type of local, active interventions, targeted at key habitats features or focal species may help protect populations while a large scale long term solution is put into place. They are not a solution to the larger management problem, but may mitigate the damage of the larger problem while a solution is being pursued (Palmer et al. 2014a).

Parts of the Salmon Trout River, Marquette County, Michigan have experienced significant fine sediment aggradation due to land use changes (Casey Huckins personal observation). However, land use changes and road crossings and maintenance appear have resulted in increased aggradation of fine sediments (Casey Huckins unpublished data). Increased fine sediment generally harms salmonid populations, especially through the destruction of spawning habitat (Wood and Armitage 1997b). Fine sediment on spawning redds can entomb eggs leading to decreased emergence (Curry and Macneill 2004) This degradation within the Salmon Trout is of particular concern because the river contains a naturally reproducing remnant population of coaster Brook Trout (*Salvelinus fontinalis*) on the South shore of Lake Superior. Coaster brook trout are adfluvial brook trout, which were once common throughout Lake Superior, but are now limited to a handful of scattered populations (Newman et al. 1997; Huckins et al. 2008; Schreiner et al. 2008). The population in the Salmon Trout River is small (Huckins and Baker 2008), and much of the annual spawning activity historically occurred at a single spawning site (Huckins unpublished data). We were concerned that this main spawning site could act as an ecological trap due to sediment aggradation (e.g., Battin 2004). This site attracts spawning activity, likely due to the presence of ground water inputs to the stream (Van Grinsven et al. 2012). Even through the spawning site is completely covered in fine sediment we still observe spawning behaviors like redd digging and spawning (Huckins unpublished data). After post-spawning departure by the adults, the redds are quickly buried by aggregation of sand (Huckins personal observation), which likely entombs eggs, and may further limit recruitment of the already small coaster brook trout population.

Restoring the Salmon Trout River will likely require watershed scale interventions to reduce sediment inputs and eventually clear sediment from the lower reaches of the river, where coasters spawn. Stakeholders are currently working to draft a holistic restoration plan, but no holistic restoration projects are currently in place. To mitigate the impacts of this aggradation while more holistic preventative and remediating solutions are put into place, we conducted a small scale targeted restoration using Sand Wand^{tm} (Streamside Environmental$_{LLC}$, Findley, Ohio) to remove fine sediments from the main spawning site of coaster brook trout and we assessed the ability of this technique to expose coarse sediments. We hypothesized that after restoration there would be a decrease in the area covered by fine sand, a shift in the size distribution of toward larger class sizes, a decrease in interstitial fine sediments, and a narrowing of the stream channel.

Methods

Site Description

The Salmon Trout River is located in Marquette County, Michigan, and is largely contained within the landholdings of a single private landowner. The watershed is 94% forested and largely undeveloped (2011 National Land Cover Database). We selected the location of a 33m restoration reach based on spatial distribution of current and historic coaster brook trout spawning activity in the lower Salmon Trout River (Huckins personal observation, Van Grinsven et al. 2012). Additionally we sampled two nearly contiguous 30m reference reaches, one upstream of the restoration the other downstream; Figure 1.1 shows the spatial relationship of the sites.

Sediment Removal

The restoration consisted of an active fine sediment removal using a Sand Wand$_{TM}$ (StreamSide Environmental$_{LLC}$)to hydraulically mobilize fine sediments, and then pump a slurry of fine sediments into an upland forest. The water from the slurry infiltrated into the forest floor leaving the removed sand outside the river floodplain where there was no evidence of overland flow that could transport removed sediments back to the river. Additionally in the years after the restoration, we observed vegetation growing through removed sediments, further stabilizing the pile (personal observation).

We observed an annual aggradation pattern within the restoration site where some fine sediments were removed from the site during spring high water events, then the site slowly aggraded with fine sediments during typical summer base flows. We removed sediments in late spring as the river was just returning to base flow, after spring floods, which we predicted would maximize the effectiveness of the restoration since spring floods would have mobilized and transported some of the aggraded sand. With reduced aggraded fines we were able to allocate more time to removing interstitial sand and reducing the embeddedness within a larger area of spawning substrates. We deployed active sediment collectors (Streamside Environmental$_{LLC}$, Findley, Ohio) upstream of the restoration site to intercept and collect fine sediment bedflow, so that it could be pumped out of the floodplain. These collectors operated throughout the summer and fall of 2013, until operation of the collectors ceased in winter 2013 to protect the pumps from freezing.

Data Collection

We quantified changes in habitat over the course of the study by surveying transects spaced every 3m along each site following Harrelson et al. (1994). At each transect a measuring tape was stretched across the river from terrace to terrace. Data were collected at points where changes in elevation were detected visually along the transect. On average 14 points (Range: 8-29) were taken within the wetted width along each transect. At each point we measured stream depth using a meter stick, water velocity using a Marsh-McBirney flow meter, and a visual estimate of embeddedness. Additionally if the point was uniformly covered in sand, sand depth was measured using a metered probe. We estimated the distribution of pebbles on the streambed surface using Wolman style pebble counts. Within each site we walked a zig-zag path between the wetted edges of the stream in an upstream direction and haphazardly collected between 99 and 116 pebbles and measured them to the nearest millimeter using calipers. We tested for differences in pebble distribution between samples with pairwise 2-sample Kolmogorov Smirnov tests. Interstitial sediment was estimated using a bulk shovel method (Hames 1996). A bulk sample consisted of single shovel of streambed sediment collected from behind a stilling well to reduce loss of fines. Within each site, 2-3 bulk samples were taken from the center 2/3rds of the stream at the 3m, 15m and 27m. Bulk samples were placed in plastic bags and taken to the lab where they were oven dried at 60°C for approximately 24 hours before they were seived. We used a 10 sieve stack to separate streambed particles into Wentworth size categories of cobbles (>63.5mm, 2.5in), two sizes of pebbles (>15.875mm, ⅝ in; >4mm), and fines <2 mm. Sand and other fines were further divided using a 1mm, 0.5mm, 0.25mm, 0.125mm, 0.063mm sieves and a catch pan.

Results

The size distribution and embeddedness of stream sediments within the restoration site were changed by the sand-removal restoration, but similar changes were not observed at the unrestored reference sites. The area of exposed cobbles, pebbles, and gravels (i.e. 0 mm sand depth), was 34% greater in the restoration site immediately following the restoration (Figure

1.1). The area of exposed cobbles decreased 34% in the downstream reference site, and was unchanged within the unrestored portion of the upstream reference. In the restoration site, the median pebble size (d_{50}) increased from sand <2mm pre-restoration to 13mm, but d_{16} and d_{84} were unchanged (Figure 1.2, Table 1.1). We did not observe any changes in pebble size distribution in the reference reaches (Figure 1.2, Table 1.1). The cumulative distributions of pebbles at the restoration site clearly reveal the predominance of fine sediments in the years preceding (2012) and following the restoration (2014) (Figure 1.2). The spring discharges in 2013 significantly shifted the distribution toward larger substrates (D=0.344, p=<0.001) and the sand removal further shifted the distribution toward larger substrates (D=0.492, p=<0.001) (Figure 1.2, Table 1.2). We found the restoration decreased the cumulative percentage of sand from 60% of samples immediately before the restoration to 45% immediately after the restoration (Figure 1.2). After the restoration we observed more pebbles between 2 and 25 mm (Figure 1.2), but the distributions of pebbles greater than 25mm were similar pre and post restoration in 2013 and there was not a significant difference between the two distributions (D=0.149, p=0.19) (Figure 1.2, Table 1.2). These patterns were not observed in the reference sites; there was an increase in fine sediments in both of the reference sites immediately after the restoration (Figure 1.2).

The amount of interstitial fine sediment in the restoration site decreased following restoration measured quantified visually (Table 1.3) and as bulk substrate samples (Figure 1.3). Embeddedness decreased from 84.7% to 65.3% within the restoration site immediately following the restoration; the embeddedness within the downstream reference site and unrestored portions of the upstream reference were unchanged (Table 1.2). The percentage of sediments smaller than 2 mm in the restoration site decreased from an average of 44% before the restoration to 20% after the restoration (Figure 1.3), whereas, the percentage of fine substrates increased in the downstream reference from 64% to 77% and decreased slightly from 84% to 75% in the upstream reference (Figures 1.4 and 1.5).

We expected width to depth ratios to vary across sites as a function of fine sediment removal during our restoration activities; however, we did not detect such changes in the channel morphology due to the restoration(Figure 1.7). There was a large difference in the width to depth ratio from year to year. In 2013, the width to depth ratio was much lower than in 2012, for example the 75th percentile of the pre restoration 2013 width to depth ratio distribution of the restoration site was 10.99, and the 25th percentile of the 2012 width to depth ratio distribution was 13.9. By 2014, the median width to depth ratio of the restoration site had increased to 13.00, but had not reached the median ratio observed in 2012 of 15.20. This pattern of a decrease in width to depth ratio follow by an increase in 2014 was also observed in the downstream and upstream reference sites (Figure 1.7). Water velocity showed temporal pattern similar to substrates for all three sites over time, including a decrease in 2013, followed by a slight increase after the restoration and then a larger increase in 2014 to levels similar to 2012 (Figure 1.8).

Discussion

The Sand Wand restoration succeeded in reducing the area covered by sand as well as the percentage of fine sediments in the restoration site. Our estimate of a 33% increase in the area of exposed substrate in the restoration site after the restoration is highly conservative. It only includes the area on the interpolated surface where sand depth was 0mm. However, due to the nature of the restoration there was a very sudden transition between exposed unembedded cobbles and the unrestored edge of the stream. However, this rapid transition is not represented on the maps due to the interpolation, leading to a likely underestimation of the areas of exposed cobbles. The restoration site returned to a sand covered state in 2014 (Figure 1.1), because we shut down the upstream sediment collectors in November 2013 to protect them from freeze damage during the winter. Although the sand cover was about as extensive as it was in 2012 before the restoration, it was not as deep, suggesting that the restoration did have some longer term effects, even 9 months after active collector operation was halted.

Our results are similar to Sepulveda et al. (2014), who also used a Sand Wand to remove fine sediments from a stream in Idaho. They observed an increase in median pebble size (4.0mm to 8.0 mm), and a decrease in the percentage of fine sediment (80% to 50%), after restoration. Our restoration was more successful at reducing the proportion of fine sediment. This was likely due to our focus on removing interstitial sands from spawning gravels, whereas Sepulveda (2014) only removed fine sediment until gravels were visible. This focus become apparent when considering the pebble count data, the distribution of pebbles >25mm were very similar before and after the restoration, suggesting that many of these larger clast sizes were already exposed by the spring floods (Figure 1.2). However the restoration reduced the prevalence of sand (pebbles <2mm) and increased the number of pebbles between 3mm and 25mm (Figure 2), which leads us to conclude that much of the sand removed was likely interstitial sand that was embedding the larger clasts. We therefore are confident in our conclusion that a Sand Wand restoration is capable of removing fine sediments and exposing buried cobbles.

The strength of this approach is enhanced by its portability and immediacy. The Sand Wand system does not require heavy equipment; instead it can be transported in a truck, or all-terrain vehicles. This portability increases the number of streams that can be restored. In

Michigan, most sediment interventions have consisted of digging sediment traps (Alexander and Allan 2006; Zorn and Wills 2012). While this can be an effective means to intercept fine sediment bed flow, thus increasing downstream scour, it requires the use of heavy equipment (Hansen et al. 1983). This limits where sediment traps can be dug, and thus may not be practical when the degraded spawning habitat is not near an upstream road crossing. A further benefit of the Sand Wand is that its direct effects are immediate and intentional. The operators can control the locations where sediment is removed from and the removal of fine sediments is immediate. Other measures like reducing sediment inputs or incepting bed flows through sand traps require time for the river to scour out fine sediments and lack the immediacy and control of the Sand Wand.

Directed small scale removal of fine sediments as in this study shows promise as part of an integrated management plan to protect key habitats such as spawning sites while watershed scale restoration projects are conducted to control the source of the fine sediments and the larger-scale disturbances. These larger scale restorations should target restoration of the river processes, like erosion and deposition that form and create high quality salmonid habitat (Beechie and Bolton 1999). We argue that the Sand Wand is well suited to smaller scale targeted restorations designed to mitigate fine sediment aggradation. Additionally because the Sand Wand’s portability and immediacy, it could be useful to respond acute sediments inputs like road washouts. The Sand Wand could be used to remove much of the input before it is dispersed downstream. Finally the control of the Sand Wand provides unique opportunities to design ecological experiments to better understand the impact of fine sediments on the ecosystem.

The ability to manipulate the sediment cover in stream reaches opens the door to experiments designed to test hierarchical landscape effects of aggradation and the relationship between aggradation and habitat quality. In chapter 2, we describe how the changes in streambed aggradation described here were used to test the accuracy various metrics of habitat quality.

Table 1.1. Size of the 16th percentile (d_{16}), 50th percentile (d_{50}), and 84th percentile (d_{84}) of pebbles within the restoration site and reference sites each year of the restoration. Pebble distributions were estimated using 100 count Wolman-style pebble counts. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

d16

Site	Pre 2012	Pre 2013	Post 2013	Post 2014
DSREF	0.01	2	2	2
REST	0.01	2	2	2
UPREF	0.1	2	2	2

d50

	Pre 2012	Pre 2013	Post 2013	Post 2014
DSREF	2	2	2	2
REST	2	2	13	2
UPREF	2	2	2	2

d84

	Pre 2012	Pre 2013	Post 2013	Post 2014
DSREF	2	2	2	2
REST	2	51	50	2
UPREF	2	17	2	2

Table 1.2. Pairwise 2-Sample Kolmogorov Smirnov test statistics testing for differences in pebble size distribution within the restoration site between different phases of the project. P values for each test are shown in parenthesis. Pebble distributions were estimated through Wolman-style pebble counts.

		Pre-Restoration		Post-Restoration	
		2012	2013	2013	2014
Pre-Restoration	2012	-	0.344 (<0.001)	0.492 (<0.001)	0.05 (0.99)
	2013		-	0.149 (0.18)	0.384 (<0.001)
Post-Restoration	2013			-	0.532 (<0.001)
	2014				-

Table 1.3. Mean embeddedness at each site during each phase of the project. Embeddedness was estimated along transects spaced every 3m along the site. Standard deviation is shown in parenthesis. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

	Pre		Post	
	2012	2013	2013	2014
DSREF	100.0 (0.0)	99.0 (4.7)	98.1 (5.6)	100.0 (0.0)
REST	98.4 (7.1)	84.7 (21.6)	65.3 (37.4)	95.8 (10.1)
UPREF	99.5 (3.5)	98.5 (5.4)	94.1 (17.8)	97.7 (9.5)

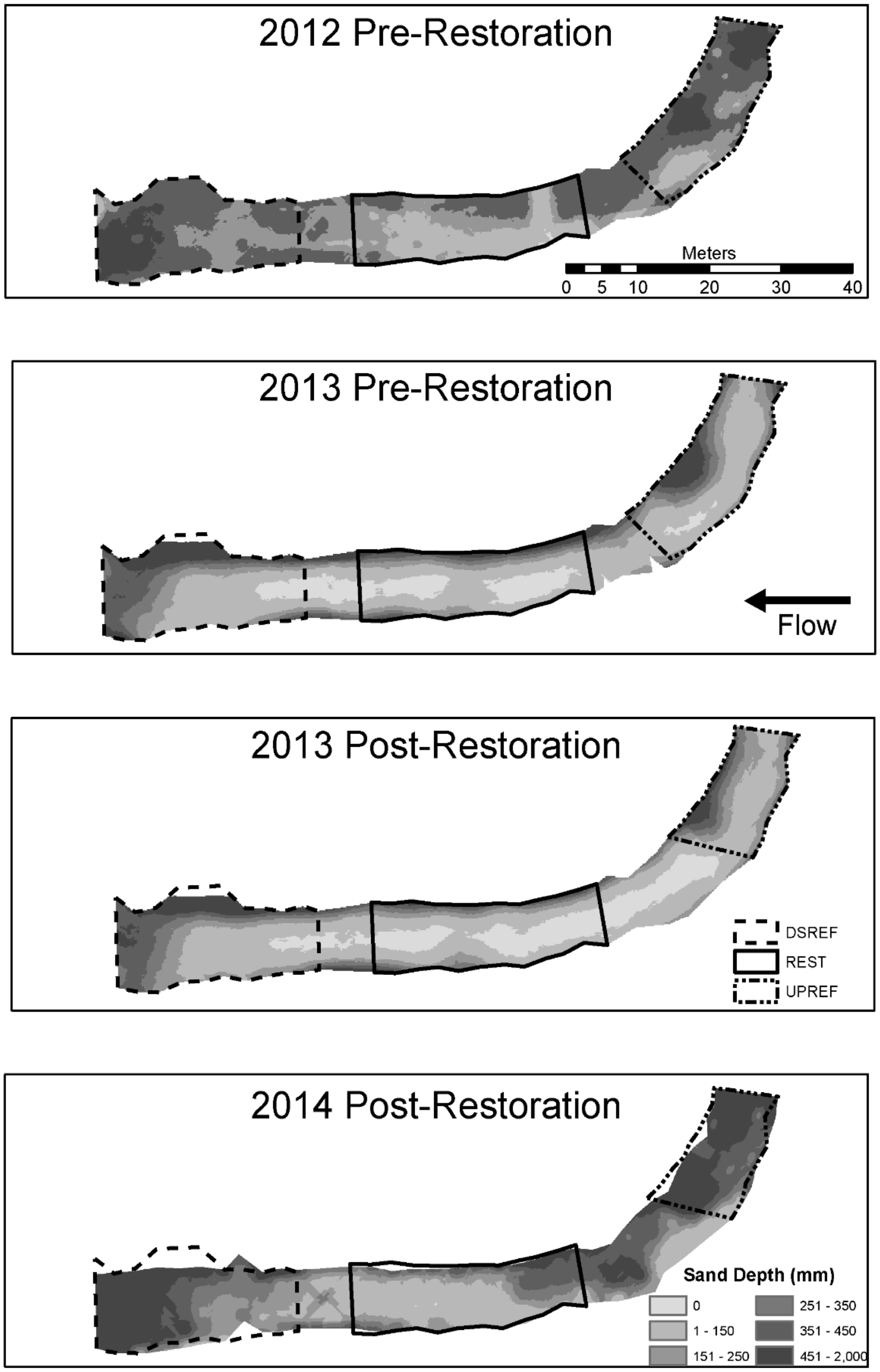

Figure 1.1. Maps of sand depths in the study sites for each phase of the study. Maps created by kriging data from transects spaced every 3 m within each site. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

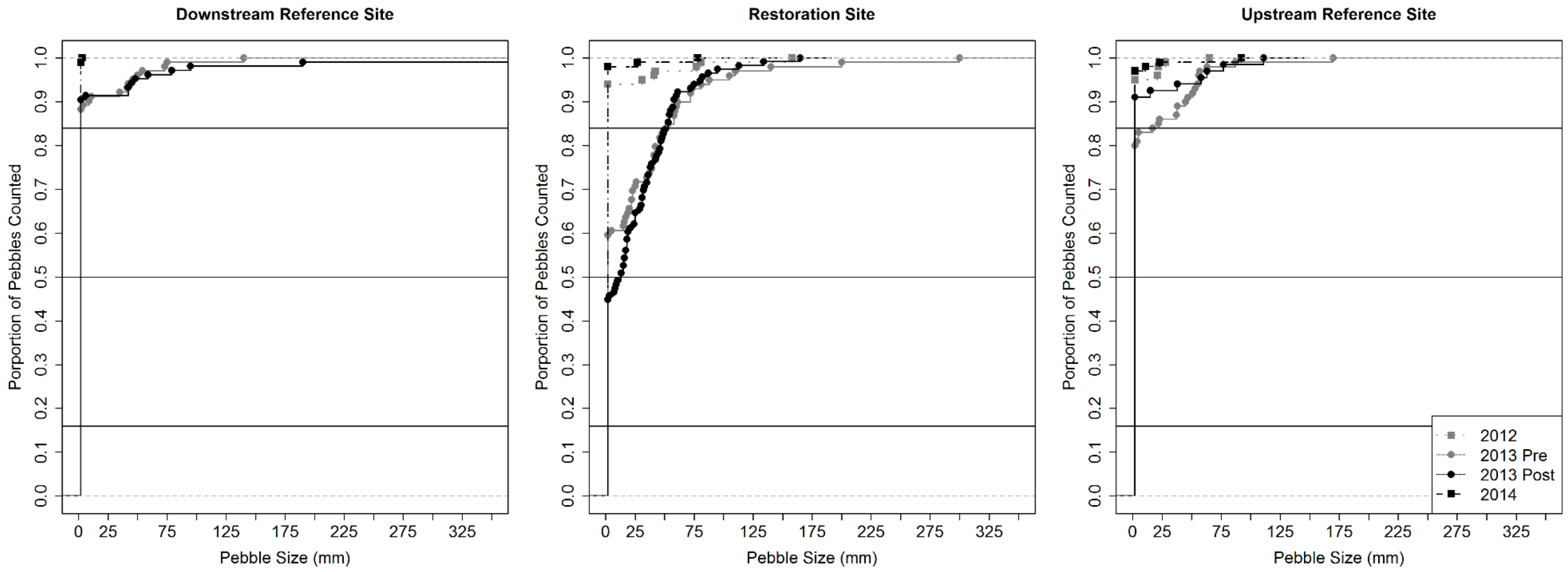

Figure 1.2. Cumulative distributions of pebbles sampled within the restoration site and two reference sites for each phase of the study. Distribution data was collected through haphazard Wolman style pebble counts. Horizontal lines represent d16, d50, and d84 respectively. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

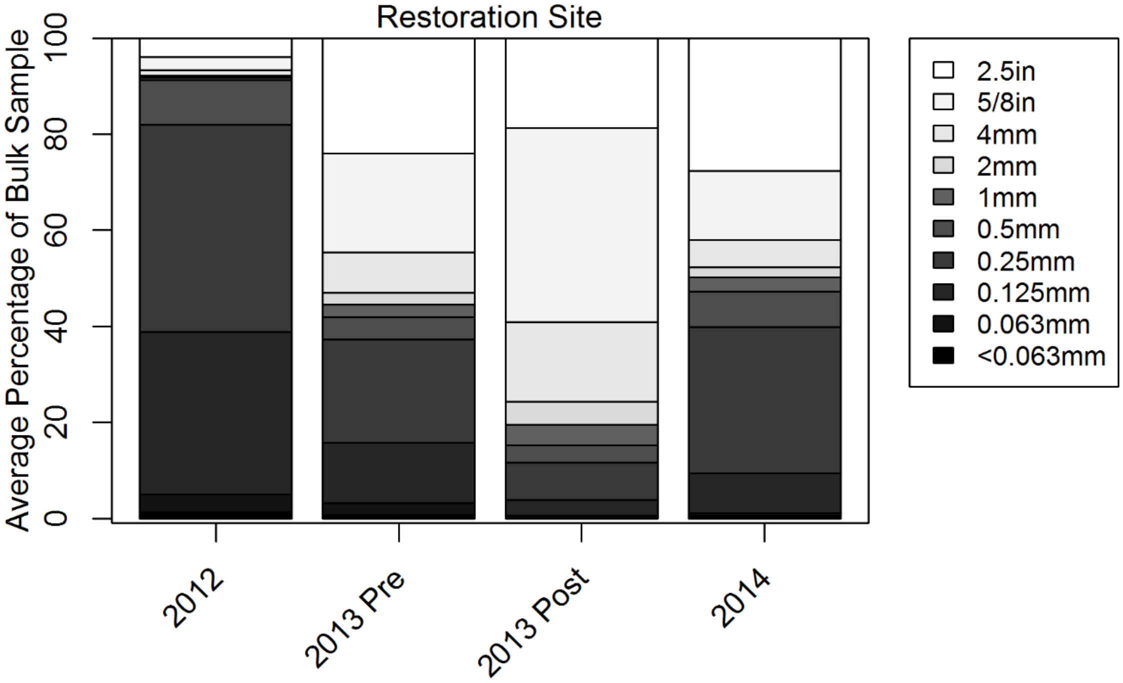

Figure 1.3. Average make–up of bulk sediment samples from the restoration reference site. The size of each box within the column represents the average percentage of sediment larger than that size sieve.

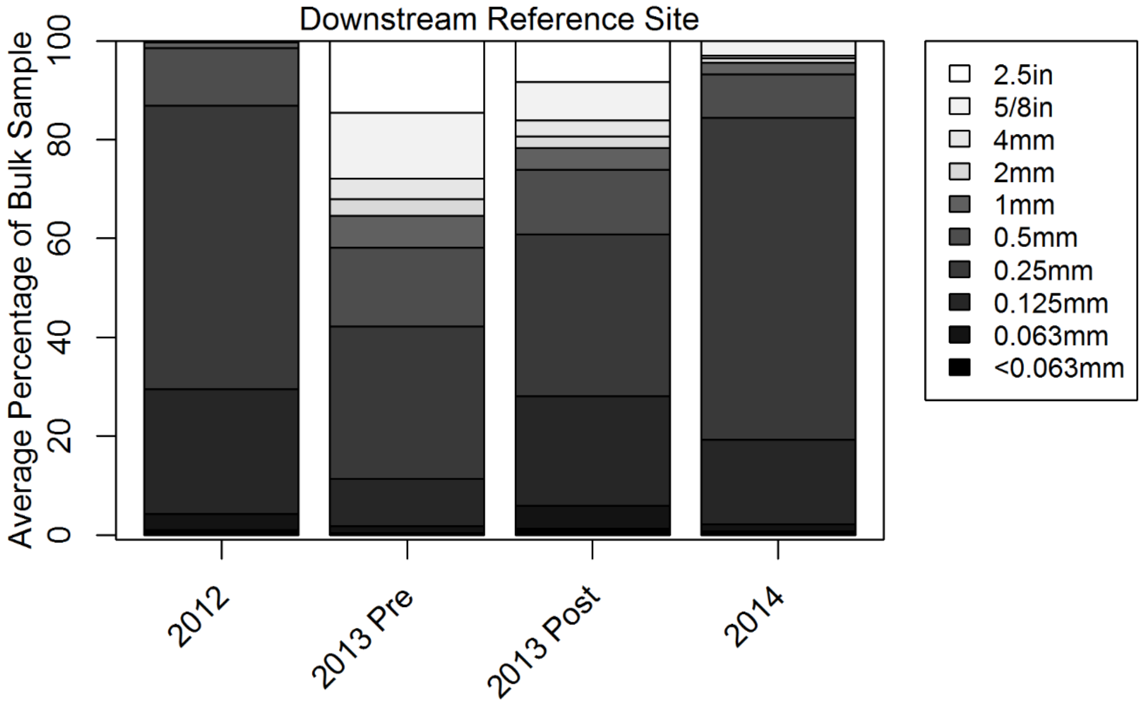

Figure 1.4. Average make–up of bulk sediment samples from the downstream reference site. The size of each box within the column represents the average percentage of sediment stopped by that size sieve.

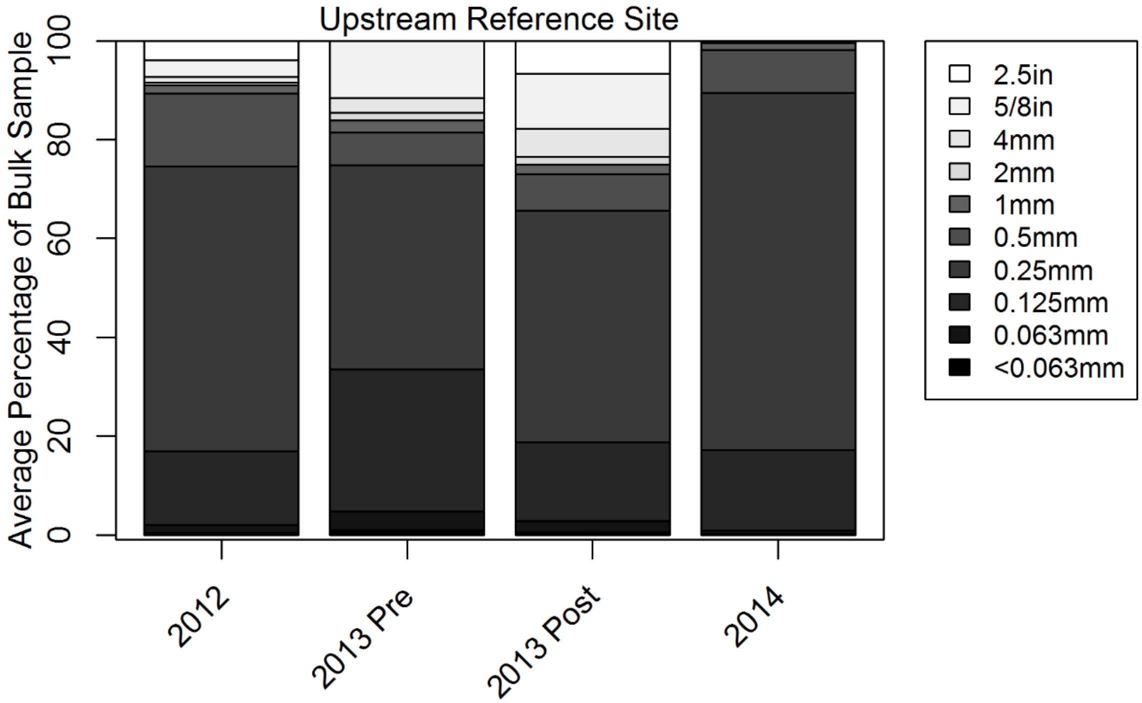

Figure 1.5. Average make–up of bulk sediment samples from the upstream reference site. The size of each box within the column represents the average percentage of sediment stopped by that size sieve.

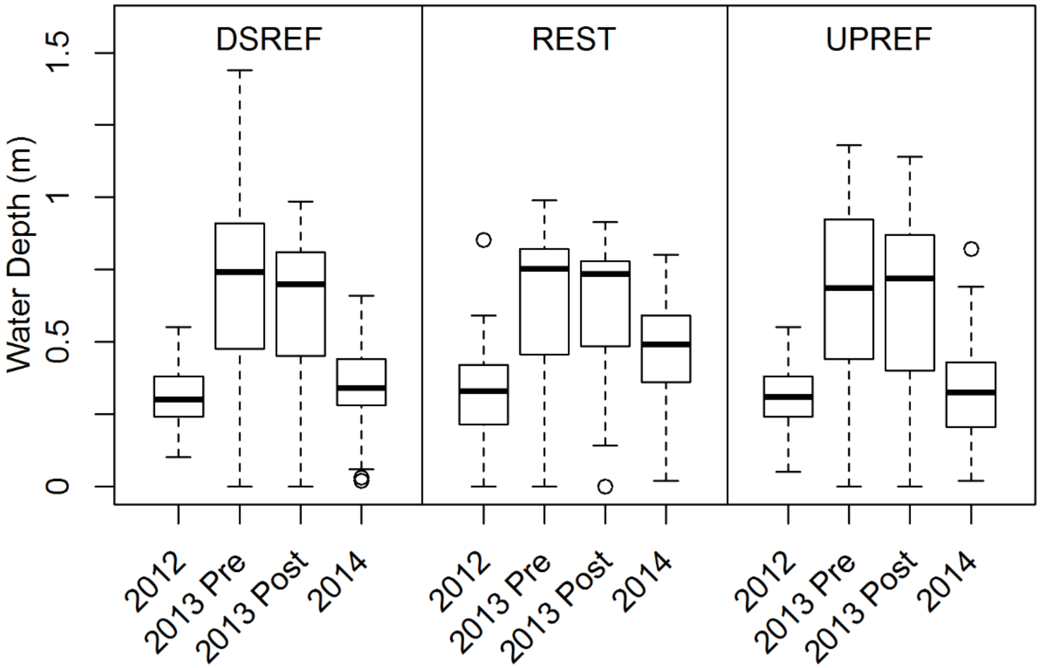

Figure 1.6. Boxplots representing water depth in each site, during each phase of the study. Boxes represent the 25th and 75th percentiles, bold line represents the median, whiskers extend to 1.5 times the interquartile distance. Any points that fell outside 1.5 the interquartile distance are represented by open circles. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

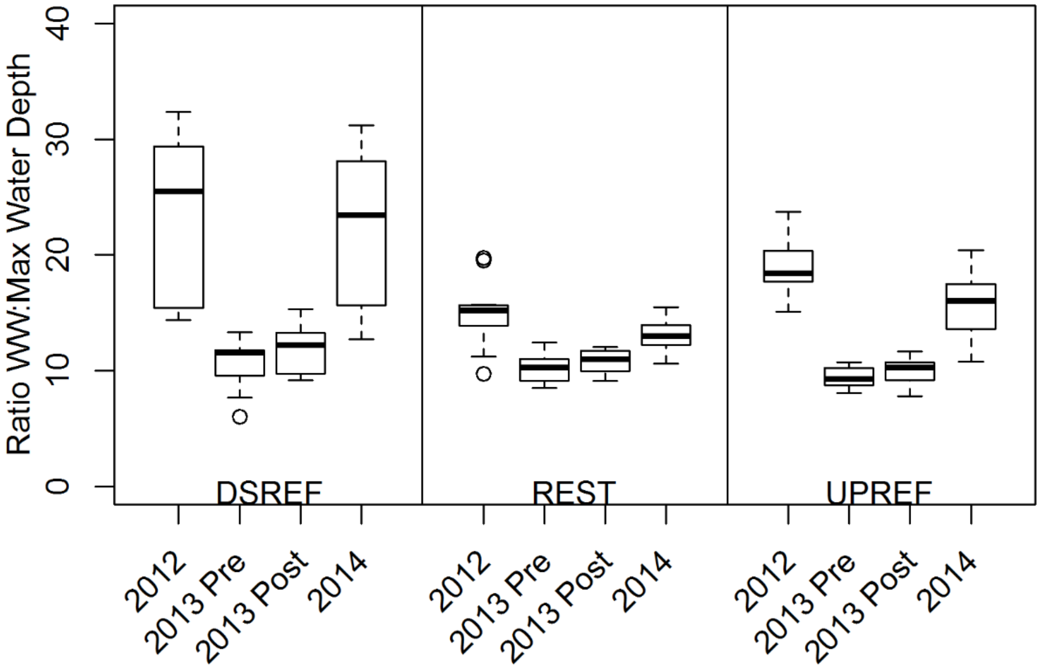

Figure 1.7. Boxplots representing the distribution of width to depth ratios in each site, during each phase of the study. Boxes represent the 25th and 75th percentiles, bold line represents the median, whiskers extend to 1.5 times the interquartile distance. Any points that fell outside 1.5 the interquartile distance are represented by open circles. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

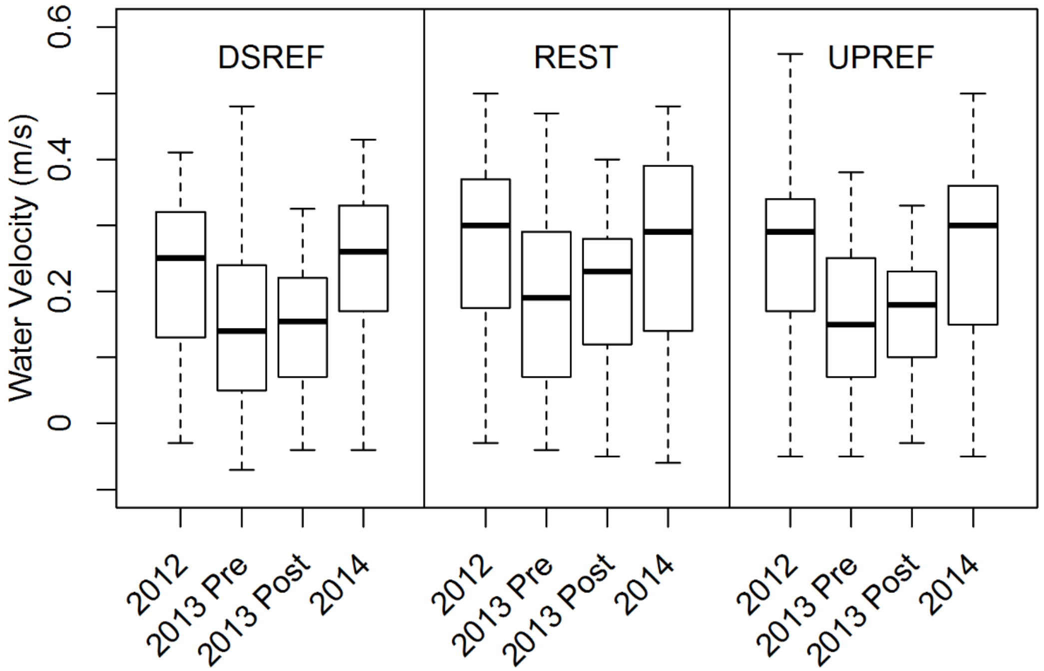

Figure 1.8. Boxplots representing water velocity in each site, during each phase of the study. Boxes represent the 25th and 75th percentiles, bold line represents the median, whiskers extend to 1.5 times the interquartile distance. Any points that fell outside 1.5 the interquartile distance are represented by open circles. Site abbreviations: Downstream Reference (DSREF), Restoration (REST) and Upstream Reference (UPREF).

Chapter 2: Metrics of Habitat Selection by Native Fish as Indicators of Relative Habitat Quality in a Cold Water Lake Superior Tributary[2]

Abstract

Improving habitat quality is the stated goal of many restorations, but actually assessing and measuring habitat quality is very difficult. We investigated how well three different metrics of habitat selection reflected assumed changes in habitat quality. We quantified brook trout (*Salvelinus fontinalis*) and sculpin (*Cottus* spp.) densities, turnover rates, and immigration rates as three potential metrics of habitat selection. We then assessed patterns of fish habitat selection through time in a manipulated site, where the streambed was manipulated through the removal of sand and its re-aggradation and in comparison with neighboring reference sites. We then determined which metric best tracked manipulated changes in small-scale fluvial habitat quality within each site.

In the manipulated site, the removal of sand transformed the site from a sand covered state with high mean embeddedness (98 ± 7% embedded, mean ± sd) to a rocky state with exposed large substrates (58 ± 37% embeddedness). The following year, the site returned to a sandy state (95% ± 10 embeddedness). Embeddedness was high and relatively unchanged in downstream and upstream reference sites over the three year period. Among the three alternative metrics of habitat selection, fish immigration rates best reflected the assumed changes in habitat quality. Patterns in fish density and turnover rates over time and across sites did not accurately reflect these assumed changes in habitat quality.

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[2] The material in this chapter is planned for submission.

Within different reaches of the same river, we then estimated immigration rates of brook trout and sculpin calculated for habitat units to identify physical characteristics of the habitats that were highly selected by fish (i.e. habitats with relatively high quality). We found that habitat selection was closely related to substrate embeddedness (r=-0.98, p=0.004 for Brook Trout and r=-0.96, p=0.008 for sculpin) in highly aggraded (i.e., sandy) reaches. However, in a rocky reach that was less impacted by aggraded sand, no single habitat characteristic we examined related closely to habitat selection.

Introduction

Accurate monitoring and manipulation of habitat quality is critical for effective wildlife management and habitat restoration, but habitat quality is difficult to measure directly (Johnson 2007). Predicting or managing human impacts on a species of concern relies on identifying how those impacts affect the biotic and/or abiotic resources that contribute to the quality and the quantity of habitat. Similarly, the stated or implicit goal for many, if not most habitat restoration projects is to improve habitat quality for some target species (Palmer et al. 2014b). Ideally, within a habitat of interest we would be able to assess habitat quality, i.e. the fitness benefit an individual derives from using a habitat (Garshelis 2000). However, accurately measuring the amount of food available, the quality of the food, the risk of predation, the amount of energy spent in aggressive interactions with rivals; and then relating these various components to the organism's fitness is often logistically impossible (Johnson 2007). For this reason, habitat quality is often estimated indirectly by quantifying behaviors like habitat selection (Garshelis 2000).

Habitat selection is a hierarchical process of behavioral responses that result in the nonrandom use of habitat that may influence survival and reproduction by individuals (Jones 2001). Because habitat selection can influence the components of fitness namely, survival and reproduction, there is the potential for populations to evolve the ability to identify and select habitats that provide fitness benefits (Fretwell 1972; see Grossman (2013) for review). For these reasons we assume that individuals are capable of recognizing and selecting high quality habitats, resulting in a strong correlation between habitat selection and habitat quality. Even though habitat selection should correlate to habitat quality, the existence of multiple measures of habitat selection demands the identification of the appropriate metric(s) for a given spatial and temporal scale and species (Gaillard et al. 2010).

We identified three alternative metrics of habitat selection used in the literature to infer habitat quality: fish density (the number of individuals in a given area), turnover rate (the per capita rate at which individuals leave a habitat at equilibrium), and immigration rate (the rate of new individuals entering a habitat at equilibrium). Density is the most commonly used or implied metric of relative habitat quality at reach and local habitat scales when monitoring or assessing restorations (for examples see Stewart et al. (2009)). When using density in this way, generally a positive relationship between density and habitat quality is assumed. This implies that populations follow an ideal free distribution, because in an ideal free distribution individuals distribute themselves so that each has an equal share of a resource, resulting in higher quality habitats having a higher density of individuals (Fretwell 1972). However territoriality and other biotic interactions may alter this relationship and result in despotic distributions which would result in inaccurate inferences under the assumption that high density equals high quality (Van Horne 1983; Railsback et al. 2003a). Turnover rate has been suggested as a movement-based predictor of habitat quality (Winker et al. 1995); suggesting high quality habitats will have lower turnover rates because of the difficulty of displacing socially dominant individuals established in high quality habitats. Finally, immigration rate into a local habitat has also been shown in an observational study to indicate relative differences in habitat selection, likely due to differences in how attractive the habitats were to new immigrants (Belanger and Rodriguez 2002).

In this study we tested how well each metric of habitat selection by fish could replicate assumed changes in habitat quality by manipulating the streambed sediments within a cold water river. Aggradation of fine sediments is widely recognized as a pollutant of cold water streams with naturally larger substrate particles in the streambed (Waters 1995; Wood and Armitage 1997a). Increased fine sediment inputs can lead to changes in streambed particle size, cross sectional channel geometry, river geometry and even thermal and disturbance regimes (Wohl et al. 2015). Increased sand has been shown to reduce the basal productivity of a sand impacted river and alter how carbon is processed within the ecosystem (Marcarelli et al. 2015). Decreased pore sizes reduces access to the hyporheic zone, an important invertebrate refugia (Sedell et al. 1990), and aggradation alters macroinvertebrate communities (Bourassa and Morin 1995; Quinn et al. 1997) to less energetically profitable taxa. Enclosure experiments in other rivers have shown that increased embeddedness led to reduced juvenile salmonid growth rates (Suttle et al. 2004). Additionally, experimental fine sediment additions have been shown to greatly reduce Brook Trout populations, suggesting decreased habitat quality (Alexander and Hansen 1986).

We manipulated habitat quality by experimentally removing aggraded fine sediments (Chapter 1), exposing large substrates from a section of a sandy reach within a cold-water river that flows through sandy surficial geology (*Soil Survey of Marquette County, Michigan* 2007) where watershed land use and resultant sediment inputs had greatly impact habitat conditions (Lindquist et al. 2007). In these rivers, removal of fine sediments (e.g., sand) exposes larger substrate particles, and will increase habitat quality for the cold-water trout that prosper in the rocky fluvial habitat. By tracking substrate composition predicted the direction of changes in habitat quality, and because the changes are so drastic we assume that these large changes in substrate compositions would change how fish perceived the quality of this habitat. Then by measuring parameters of fish habitat selection and use we can in river sections where sand was removed and in to comparison reference sections to determine which metric best matched assumed relative differences in habitat quality. Once a metric was identified that matched these changes we applied that metric of habitat selection to data from different reaches where fish habitat selection parameters and habitat features were measured to identify habitat characteristics that related to (i.e., appeared to drive) relative habitat selection.

Identifying an accurate metric of habitat and the cues organism use to assess habitat quality will provide a tool to improve assessment and monitoring of restorations. Understanding these cues fosters a more mechanistic understanding of patterns of habitat use. This is important because restoration may improve some metrics of the overall quality of habitats, but if appropriate cues are not also improved or present then fish may not use these habitats (Gowan 2006). We believe our data and the general approach could be used to address the need for better targeted and tailored habitat restoration.

Methods

Site Description

This study was conducted in the Salmon Trout River (STR), which is a tributary of Lake Superior located in Northern Marquette County in the Upper Peninsula of Michigan (Figure 2.1). The STR watershed is 94% forested and largely undeveloped, according to the 2011 National Land Cover Database; however, there are a number of road crossings mainly in the upper watershed, and land use activities, primarily logging and mining, that are recognized as sources of fine sediments (Huckins unpublished data, Salmon Trout River Watershed Management Plan). Lower gradient fluvial waters are more vulnerable to sediment aggradation (Church 2002), and we have observed increased fine sediment aggradation in the lower gradient downstream segment of the Salmon Trout River since 2004 (Huckins unpublished data). This has resulted in kilometers of riverbed being completely covered with sand, with sand depths reaching more than 1.5 meters in places. The Salmon Trout River is regionally important because it supports a remnant breeding population of coaster Brook Trout (coasters; Huckins and Baker 2008; Huckins et al. 2008; Scribner et al. 2012). Additionally, this makes the STR an effective place to study habitat selection, because the lack of resident salmonids (Scribner et al. 2012) leads to fewer age and size classes in the river (Huckins et al. 2008), as well as reduced risks of piscivory which simplifies social structures making identifying the relationship between habitat quality and habitat selection more straightforward.

Study Organisms

Coaster Brook Trout are an adfluvial life-history form of Brook Trout that were once common in the near-shore zone of Lake Superior (Becker 1983; Huckins et al. 2008), but have since been extirpated from all but a small subset of Lake Superior tributaries (Newman et al. 1997; Huckins et al. 2008; Schreiner 2008). Juvenile coasters typically spend the first 2-3 years living in their natal stream before they out-migrate to Lake Superior as 2+ individuals (Huckins and Baker 2008). Improved understanding and recognition of the factors that influence habitat quality will inform coaster Brook Trout management and protect or restore their habitat and that of other coldwater fish populations. The preservation and restoration of coaster Brook Trout populations has been a management goal across the Lake Superior Basin (Newman et al. 1997). Although it is not clear which life-history stage is the most limiting for coaster Brook Trout recovery (i.e., instream juveniles or lake-dwelling or spawning adults), understanding what channel features drive habitat quality for juveniles is important for enhancing Brook Trout recruitment.

We measured the habitat selection of juvenile Brook Trout to infer indicators of habitat quality. Additionally, we included sculpin (*Cottus* spp.) in our study of habitat quality, as they are a native nongame species in this river, and one of the few non-salmonids still abundant in the lower sandy reaches of the river (Huckins unpublished data). Further, sculpin are understudied relative to salmonids. Bellmore et al. (2013) suggest sculpin were responsible for a large portion of the flow of organic matter from macroinvertebrates to fishes. Additionally sculpin can be important predators of other fish (Bellmore et al. 2013), and specifically salmonid eggs and larvae (Swain et al. 2014). Understanding how these relatively understudied fish respond to changes in habitat quality as well as what drives their habitat selection will be an important addition to understanding their life history and the overall habitat quality of this ecosystem.

Habitat Manipulation

To verify the appropriate metric of habitat selection we chose three sites (30-33 meters in length) within the sandy lower reaches of the STR. The three sites were selected such that the manipulated site, which was determined by Brook Trout spawning activities and historic inputs of groundwater (Huckins unpublished data, Van Grinsven et al. 2012), was bordered nearly contiguously by the Upstream and downstream reference sites. The substrates in reference sites were not manipulated, but habitat characteristics and movement and density data were collected and compared to the manipulated site.

The manipulation consisted of an active fine sediment removal conducted from June 3 to June 7, 2013 using a Sand Wand^{tm} (Streamside Environmental, LLC) that hydraulically mobilizes fine sediments and pumps them away, in this case out of the floodplain where they would not return to the river. We quantified changes in habitat over the course of the study by surveying along transects spaced every 3m throughout each site following Harrelson et al. (1994). At each point on the transect, we conducted visual estimation of the percentage of substrates embedded by fine sediments within a 0.5m radius, and assigned the embeddedness to one of 5 classes: 0%, 25%, 50%, 75% and 100% of substrate (e.g., a cobble) that was embedded. Points where the substrate consisted of only sediments less than or equal to 2mm were classified as 100% embedded. This and other surveys (Chapter 1) confirmed that the Sand Wand^{tm} removed surface and interstitial fine sediment, leaving exposed, largely unembedded cobble in the manipulated site (Table 2.1, Figure 2.2). During the removal of fine sediments in 2013, onsite consultations with the restoration experts at Streamside Environmental revealed the need to remove additional sand from upstream substrates to maintain unembedded large substrates downstream in the manipulated site, which led to the removal of sand from approximately 10m of the upstream reference site. This 10m portion of the upstream reference site from which we removed fine sediments was excluded from future habitat selection sampling. Spring floods in 2014, the year after the manipulation, mobilized bedload sand and aggraded the manipulated site with fine sediment, returning it to a pre-restoration condition (Table 2.1, Figure 2.2).

Identifying a Proxy for Habitat Quality

We conducted mark-recapture surveys of fish at each site between late July and August in three consecutive years: the year before the manipulation (2012), the year of the manipulation (2013), and one year after (2014). In each site we measured fish densities and estimated turnover and immigration rates using a mark-recapture methodology described in Belanger and Rodriguez (2002). We chose this model primarily because the migratory Brook Trout in the STR are a conservation concern (Huckins et al. 2008) so minimizing tagging mortality was a priority. This method does not require individually identifying organisms, allowing us to use to use a method of tagging that has lower risk of mortality than PIT (Passive Integrated Transponder) tagging which is commonly used when individuals must be individually identified (Roussel et al. 2000; Josephson et al. 2008). We did not want to use PIT tags because the risk of mortality with PIT tags especially increases for the juvenile salmonids <84 mm fork length (Roussel et al. 2000), which can be the majority of fish salmonids in this river (Huckins unpublished data). This mark-recapture methodology we used relies on high capture rates to produce estimates of turnover and immigration, so to achieve high capture rates, study sites were meticulously blocked at the upstream and downstream ends with ¼ inch mesh netting strung perpendicular to water flow and weighted down along the bottom with chain and sandbags. We then captured as many fish as possible using backpack electrofishing units (Badger 1, ETS Electrofishing Systems, LLC), conducting multiple short electrofishing passes (5-10 passes, median 7 passes, mean time 11 minutes) within the site. During these surveys most fish (69%) were captured in the first 3 passes, the remaining passes mainly focused on capturing groups of young of year fishes not associated with habitat structures (personal observation). Electrofishing continued until no further salmonids were observed. Captured fish were kept in aerated coolers until sampling of the site was completed and handling of the fish was kept to a minimum to reduce stress. Each study site was surveyed 3 times over 7 days. During the first sampling all fish >55 mm total length were marked with Visual Implant Elastomer (VIE; Northwest Marine Technologies, Washington USA). For each individual, a mark was injected into the base of either the caudal or anal fin such that all fish had a combination of color and injection location unique for each site and year. In order to measure immigration and turnover for each site we performed two recapture surveys. The first recapture was conducted between 1 to 3 days after the initial marking, and the second recapture occurred 7 days later following the temporal schedule utilized by Belanger and Rodriguez (2002). During these two recapture surveys, the numbers of marked and unmarked fish collected from each site were recorded revealing the number of marked fish remaining in the site and the number of new unmarked immigrants.

Density of target fish of each species was calculated as the mean abundance from the marking and two recapture surveys divided by the area of each site. To obtain estimates of turnover and immigration for each species in each site we fit our data to the movement model suggested by Belanger and Rodriguez (2002):

$$\mathrm{y} = \sum \{\mathrm{n}_{\mathrm{marked}}(\mathrm{t}) - \mathrm{n}_{\mathrm{marked}}(0)\mathrm{e}^{-\lambda t}\}^2 + \{\mathrm{n}_{\mathrm{unmarked}}(\mathrm{t}) - \frac{\mathrm{I}}{\lambda}(1 - \mathrm{e}^{-\lambda t})\}^2$$

Where:

- y equals the residual sum of squares
- $\mathrm{n}_{\mathrm{marked}}$(t) equals the number of fish captured at time (t) with mark indicating it was originally caught in that site
- $\mathrm{n}_{\mathrm{marked}}$(0) equals the number of marked individuals released into the site at time(0)
- $\mathrm{n}_{\mathrm{unmarked}}$(t) equals the number of unmarked fish (or fish with marks from other sites) captured at time (t)
- I equals the immigration rate
- λ equals turnover (assuming equilibrium)

- At equilibrium:
    - I/λ=equilibrium density
    - λ=turnover
    - λ^{-1} = residence time

Minimizing the residual sum of squares (y) in this model for each site and species provided estimates of immigration and turnover rates.. This procedure was conducted in R (www.r-project.org) using the "optim" function, and the "bfgs" method. The "bfgs" method is a quasi-Newton method of minimization and provided the best convergence for a range of attempted seed values. We also calculated a standard error for each parameter by taking the square root of the diagonal members of the Hessian matrix, and used this standard error as a measure of model fit. The turnover rates calculated by this method are the loss rate, which is equivalent to turnover at equilibrium. While these rates are analogous, turnover rates reported in other publications that report the proportion of new immigrants in a site, or the inverse proportion of marked fish remaining in a section (e.g., Cunjak and Randall 1993, Gowan and Fausch 1996b, Schrank and Rahel 2006) may not be directly comparable.

To identify which metric(s) of habitat selection (i.e., density, turnover, or immigration) best indicate habitat quality at this spatial scale, we determined which one showed a response that best reflected the assumed changes in habitat condition (i.e., habitat quality). For the reasons previously discussed, we assume that the exposure of large streambed substrates in a cold-water trout stream increases the habitat quality of the site. If fish density, as it is commonly used in restoration, was an effective metric of habitat quality in the manipulated site, fish density should have increased in 2013 (i.e., year of improved habitat) and then decreased in 2014 when the sand re-aggraded the site (Figure 2.3C). Furthermore, density would be predicted to be greater in the manipulated site than the Upstream and downstream reference sites in 2013 (Figure 2.3C). This prediction assumes that these fish follow an ideal free distribution resulting in higher densities within higher quality habitat, assuming less sandy habitats could support more individuals (Fretwell 1972). If turnover rate is an appropriate proxy for habitat quality at this spatial scale we would expect a decrease in turnover in 2013, after manipulative improvement of the habitat (i.e. better habitat retains fish longer), followed by an increase in 2014. Similarly, turnover would be predicted to be lower in the manipulated site than the Reference Sites in 2013 (Figure 2.3B). This would be due to dominant fishes establishing and defending territories in the higher quality manipulated reach, reducing turnover (Winker et al. 1995). Finally, if immigration rate correlates positively with habitat quality as observed by Belanger and Rodriguez (2002), we would expect immigration rate to have increased in the manipulated site in 2013 and then decrease in 2014, with the highest immigration rates being observed in the manipulated site in 2013 (Figure 2.3A). This increase in immigration rate in 2013 would likely be due to the manipulated site being more attractive to fish searching for new local habitats

Identifying Habitat Cues Used for Habitat Selection

The survey of habitat characteristics that habitat selection that report the proportion of new immigrants in a site, or the inverse proportion of marked fish remaining in a section occurred in two distinct reaches of the STR. We selected a nearly uniformly Sandy Site in lower sandy reaches of the STR, and a Rocky Site approximately 6.1 km further upstream (Figure 2.1) with a heterogeneous mix of sand, pebble and cobble substrate. These two sites were divided into local habitats based on channel geomorphic conditions (Hawkins et al. 1993). In these local habitats we measured a suite of habitat conditions (e.g., substrate embeddedness, depth) and estimated habitat selection by Brook Trout and sculpin to identify physical habitat characteristics that may drive the fish's perception of habitat quality.

To characterize physical habitat within each habitat and relate this physical characteristic to habitat selection, we measured the depth, water velocity at bottom and at 60% depth using a Marsh-McBirney 2000 Flo-mate with an integrated wading rod, and we measured sand depth using a metered probe at 5 sampling points spaced equally along each of 3 transects. Transects were located perpendicular to flow at 10%, 50%, and 90% of the length of each habitat unit to characterize habitat features and to avoid measuring conditions at the borders between local habitats and obscuring their differences.

We used embeddedness as the metric of substrate composition because we determined through literature review that embeddedness best represented the variation in surface substrate within and between local habitats that we observed. Although embeddedness estimates vary by technique and practitioner (Pontyondy and Sylte 2008), in this study all estimates were conducted using the same technique and by the same person, who had previous experience using this technique. Alternative estimates such as the Wolman style pebble counts have a well described bias against small grains (Marcus et al. 1995), which would have been problematic within the Rocky Site, which has little sand cover but observable variation in embeddedness (Table 2.1). To classify substrate particle size distributions, bulk methods (Kondolf 2000) work well for quantifying substrate conditions within a matrix of cobble and interstitial sand, e.g. spawning substrates. However, relative to visual estimation of embeddedness, bulk methodology would overestimate the proportion of large substrates within the surface layer by including particles not visible or detectable to fish (e.g., with a nearly complete cover of sand as in local habitats 4 and 5 in the sandy downstream reach, Table 2.1).

Measuring Habitat Selection

We estimated habitat selection for Brook Trout and sculpin in each local habitat using immigration rates estimated from the model developed in Belanger and Rodriguez (2002). We used mark-recapture data collected from within local habitats with mean length of 14.9 ± 3.9m (± 1 standard deviation) to fit the model for each site. Surveys occurred from August 1 to August 8, 2011 for the Sandy Site, and August 10 to August 16, 2011 for the Rocky Site. Fish sampling methods were similar to those used in the manipulation and reference sites, however due to the number of local habitats, sampling was less intense (3-5 passes, mode of 4 passes). We again used two recapture surveys to estimate movement, the first recapture survey occurred 1 day after the initial marking survey at both sites, and the second recapture occurred after 5 days later in the rocky site and 6 days later at the sandy site, and 5 days later in the Rocky Site. During sampling each individual fish greater than 55 mm total length was injected with Visual Implant Elastomer in two of four body locations of each fish (near the caudal fin, either the left or the right side near the eye or anal fin) such that all fish had a combination of color and injection location unique for each local habitat. This double tagging also allowed us to estimate tag loss. Captured fish from each local habitat were held in floating in-stream mesh containers until electrofishing of that local habitat and at least the adjacent local habitat had been completed, at which time the fish were released into the center of the local habitat where they had been collected.

We compared drivers of habitat selection by calculating Pearson's product moment correlation coefficients between sculpin and Brook Trout immigration rate and the various habitat variables we measured. We looked for habitat characteristics that drove both Brook Trout and sculpin habitat selection.

Results

Performance of Habitat Metric following Manipulation

Immigration rate outperformed the alternative metrics of habitat selection (i.e., fish density or turnover) by best matching the predicted responses to changes in habitat quality of the manipulated site for both sculpin and Brook Trout. In 2013, the year of the fine sediment removal, immigration into the manipulated site increased from 4.4 fish/day in 2012 to 31.0 fish/day for Brook Trout (Figure 2.3D), and from 3.7 fish/day in 2012 to 24.7 fish/day for sculpin (Figure 2.3G). When the manipulated site became re-aggraded in 2014, immigration decreased to 13.9 fish/day for Brook Trout and 6.9 fish/day for sculpin (Figures 2.3D and 2.3G, respectively). Immigration rate also tracked the change in habitat quality of the manipulated site relative to the Reference Sites in 2013, when both Brook Trout and sculpin had a considerably greater immigration rates in the manipulated site than the Downstream and upstream reference sites (Figures 2.3D and 2.3G). The changes in immigration rate between years, and the differences measured in 2013 matched expected patterns (Figures 2.3A, 2.3D, 2.3G).

Patterns of turnover rate reflected the expected differences in relative habitat quality between sites in 2013, such that turnover was the lowest in the manipulated site compared to the downstream and upstream reference sites for both Brook Trout and sculpin (Figures 2.3E and 2.3H).

However, turnover rates did not match the expected temporal pattern of habitat quality over the course of the experiment. Contrary to the expected pattern, in the manipulated site, turnover increased from 0.17 fish/(fish·day) and 0.21 fish/(fish·day) for Brook Trout and sculpin, respectively in 2012, to 0.43 fish/(fish·day) for Brook Trout and 0.93 fish/(fish·day) for sculpin in 2013 after sand removal. In 2014, after the manipulated site became aggraded with fine sediments, turnover rate decreased to 0.29 fish/(fish·day) for Brook Trout and 0.38 fish/(fish·day). This was the opposite of the expected pattern if turnover tracks habitat quality at this spatial scale (Figures 2.3E and 2.3H). Patterns in turnover rate matched relative differences in habitat quality between the sites within a year, but did not accurately reflect expected changes in habitat quality across multiple years.

Relative changes in density, like the other two considered metrics of habitat selection, also reflected the differences in relative habitat quality between sites in 2013 when densities of both Brook Trout and sculpin were greatest within the manipulated site as expected (Figures 2.3F and 2.3I). However, the performance of fish density as an effective metric to track changes in habitat quality across years was mixed. Sculpin, density within the manipulated site increased, as would have been expected, from 0.11 fish/m^2 in 2012 to 0.20 fish/m^2 in 2013 after the manipulation. Then in 2014 after aggradation, sculpin density decreased to 0.13 fish/m^2,again as expected. However, it should be noted that error bars for sculpin density overlap all three years (Figure 2.3I). Brook Trout density within the manipulated site appeared to increase from 43 fish/m2 in 2012, to 71.7 fish/m2 in 2013, and then further increase to 88.3 fish/m2 in 2014, which is contrary to the expected pattern of habitat selection if density was an accurate predictor habitat quality at this temporal and spatial scale (Figure 2.3F).

Identifying Habitat Cues Used for Habitat Selection

Because immigration rate best matched expected patterns of habitat quality before, during, and after the manipulation, we used immigration rates to identify physical characteristics driving differences in relative habitat quality. We found that immigration rates varied both within and between the Rocky and Sandy Sites, and they tended to be greater for sculpin than for Brook Trout (Table 2.2). Immigration rates of sculpin were generally greater in local habitats within the Rocky Site relative to the Sandy Site, but this pattern was not observed for Brook Trout (Table 2.2). In the Sandy Site, habitat selection by Brook Trout as indicated by their immigration rates was highest in Local Habitat 4, which was a scour pool with relatively low embeddedness (Table 2.3). In addition to also highly selecting habitat 4 (the scour pool), sculpin also highly selected Local habitat 5, an adjacent fast non-turbulent run. In the Rocky Site, estimated habitat selection for both sculpin and Brook Trout was highest in local habitat 1 (Table 2.2), which was a riffle with a variable substrate and velocity profile (Table 2.3). The model fits were generally good, resulting in low model standard errors (Table 2.2), however, in some cases model standard errors for immigration and/or loss rate indicated poor model resolution (SE >3). In these cases the model fits were examined graphically to confirm the absence of clear minima in the residuals, and were then excluded from subsequent analyses. We believe the failure for the model to converge is due to particularly low fish densities observed in this study and in previous surveys in the STR (Huckins and Baker 2008 and Casey Huckins, unpublished data). At these low densities, even small variations in fish capture rates (e.g., missed fish due to deep water and/or undercut banks) could affect the convergence of the model on a stable solution.

Relative selection of the local habitats by Brook Trout in the Sandy Site, as indicated by their estimated immigration rates, was negatively correlated with substrate embeddedness (Figure 2.4A).

A similar relationship was not detected in the Rocky Site where sand was less abundant and exposed large substrates were more abundant. (Figure 2.4B). Sculpin immigration rates were also negatively correlated with substrate embeddedness in the Sandy Site, and matching the pattern observed for Brook Trout, there was no detectable relationship between immigration rates in local habitats and the substrate conditions (i.e., embeddedness) in the Rocky Site (Figure 2.4C, 2.4D). No other measured habitat variables including: water velocity, sand depth, water depth, or wetted width were as well correlated with immigration rates across sites for either species (Table 2.4).

Discussion:

Although density is intuitive and a commonly used metric of habitat quality for the monitoring and assessment of restorations, the use of density as a metric of habitat quality has long been criticized (Wiens and Rotenberry 1981; Van Horne 1983). Theoretical and empirical investigations have illustrated that density does not track changes in habitat quality at smaller spatial scales (10s of meters) (Belanger and Rodriguez 2002; Railsback et al. 2003b). Our study supports these findings that density does not reliably reflect changes in habitat quality at the local habitat scale over time. Abundance or population size may be an appropriate metric of habitat quality at larger spatial scales (1000s of meters) at which population dynamics drive abundances. At smaller local habitat spatial scales, densities may be more strongly influenced by biotic interactions and temporal trends, for example by territoriality, which can force subdominant individuals out of the best habitats and into marginal habitats where they gather at higher densities (Van Horne 1983). The inability for density to track habitat quality was clearly illustrated by Railsback et al. (2003) through individual based simulations. Virtual “trout”, (i.e. mathematical constructs that follow movement rules observed in real trout populations) moved through a created habitat matrix of variable but precisely known habitat quality. Railsback et al. (2003) found that at small spatial scales, density of the virtual trout performed poorly at predicting the known habitat quality of a given habitat. Results of this study provide real *in situ* support for these modeled predictions of Railsback et al. (2003). Density is also a poor tool for tracking habitat quality through time because the density of a given habitat can be affected by temporal changes in recruitment (Wiens and Rotenberry 1981). These lagged responses in densities could cause a temporal disconnect between habitat quality and density. We suspect that the increase in density within manipulated site in 2014 was the result increased recruitment due to the restoration. Alternatively, large scale stochastic fluctuations on longer time scales in population size or non-random local movements at smaller time (Chapter 3) could be easily misattributed to changes in local habitat quality if density is being used as a proxy of habitat quality.

We found immigration rate to best reflect the changes in the assumed habitat quality caused by the manipulation. This supports Belanger and Rodriguez (2002) who found immigration rate better matched expected patterns of habitat selection than did turnover rate at a local habitat unit scale. The mechanism that explains why immigration rate outperforms density and turnover at predicting habitat quality at this spatial scale warrants further study. We speculate it is due to how fish perceive habitat cues and the social hierarchy within the habitat, which determines whether an individual can actually use the habitat. For example, a pool in a sandy reach may have an abundance of exposed large substrates that serve as a habitat cue, signaling high quality habitat. This attractive habitat trait occurs over a relatively large scales ($>1m^2$), and is easily assessed by prospective migrants resulting in the pool attracting many immigrants. However, once in the pool, the immigrant must occupy an energetically profitable, acceptably risky, and available (unoccupied or occupied by a displaceable fish) location (<1 m^2) within the pool. It seems plausible that fish can quickly assess larger scale habitat suitability using habitat cues (Gowan 2006), however the availability of a location is likely more difficult to assess *a priori*. Essentially, even if every suitable location in the pool is occupied by fish that the immigrant cannot displace, this will not deter immigration because fish can only assess the availability of the locations through direct experience or observation by the fish (White and Gowan 2012). This would likely lead to higher quality habitat attracting many potential immigrants but with high turnover as the immigrants compete for limited number of suitable patches within the habitat. This mechanism would also explain the increase in turnover rates we observed when we reduced fine sediments (ostensibly increasing habitat quality) within the manipulated site.

In the Sandy Site lower relative embeddedness appeared to be a powerful habitat cue, signaling higher quality habitat, and resulting in increased habitat selection. However, this pattern did not hold in the Rocky Site. The Rocky Site was upstream of a major source of anthropogenic sand, and generally had a lower embeddedness. The relative pressure for a given habitat cue to elicit habitat selection may depend on its relative availability and quality. The strength of exposed large substrates as a cue or indicator of high quality habitat may be nonlinearly related to its availability. This could result if the relative benefit realized by an individual using habitat with more exposed large substrates is reduced in reaches with relatively low embeddedness overall. For instance, the benefit derived from moving from a site with 100% embeddedness to a site with only 80% embeddedness (the approximate range of embeddedness in the lower sandy site) may be relatively greater than the benefit from moving from a local habitat that is ~80% embedded to one that is ~50% embedded (the approximate range of embeddedness in the upper less sandy site). Somewhat low power does limit the inferences and statistical tests that can be made using this data set. In 2011, we initially planned to sample a greater number of local habitats but long set up times limited the number of sites that could be sampled in a day, and for continuity of the relative dynamics across sites we did not want sets of sampling events to span beyond one day. Additionally, some local habitats were not sampled intensively enough (i.e., a few fish were visible in some sites even after 7 passes) resulting in poor model fits and exclusion from analysis further limiting power. These issues were rectified during sampling at the Manipulated and Reference sites, and do not necessarily limit the utility of this methodology.

Our data supports the work of Belanger and Rodriguez (2002) in showing that at local habitat scales immigration rate best reflects habitat quality suggesting that researchers and managers may be misled if they use an inaccurate measure of habitat selection such as assuming fish density directly reflects the quality of the habitat across all scales. Measuring relative differences in habitat selection inferred from immigration rates could help improve management and restoration of stream habitat and inform managers to better target and tailor management and restoration within a watershed by identifying habitat more highly selected by a target species. For example, increasing the prevalence of exposed cobbles in sandy reaches would be predicted to increase habitat selection and likely add some benefit for fish, but other restorations may be more appropriate within the rocky reaches upstream. Restored habitats that may create high quality habitat but do not contain the appropriate habitat cue may not be selected at the expected rates (Gowan 2006). Therefore, it seems possible that perceived and/or actual success or failure of small scale stream habitat restorations could in part be driven by presence or absence of appropriate physical habitat cues perceived by the species targeted for restoration.

Table 2.1. Habitat characteristics within the Manipulated and Reference Sites located within the lower sandy reaches of the Salmon Trout River. For each mean value presented, standard deviations are presented within parenthesis.

Site	Date Sampled	Wetted Width (m)	Mean Depth (m)	Mean Water Velocity (m/s)	Mean Sand Depth (m)	Mean Embeddedness (%)
			2012			
DSREF	Jul 19	9.48 (1.40)	0.28 (0.09)	0.23 (0.1)	0.41 (0.19)	100 (0)
MANIP	Jul 18	7.85 (0.58)	0.31 (0.14)	0.27 (0.14)	0.24 (0.14)	98 (7)
UPREF	Jul 18	9.10 (0.69)	0.32 (0.11)	0.25 (0.12)	0.34 (0.17)	99 (3)
			2013			
DSREF	Jun 10	10.38 (1.47)	0.67 (0.21)	0.15 (0.09)	0.22 (0.16)	97 (6)
MANIP	Jun 11	8.94 (0.41)	0.70 (0.17)	0.21 (0.1)	0.08 (0.12)	58 (37)
UPREF	Jun 11	9.56 (0.93)	0.71 (0.25)	0.17 (0.09)	0.24 (0.19)	93 (19)
			2014			
DSREF	Jul 15	9.93 (1.32)	0.38 (0.12)	0.25 (0.1)	0.39 (0.19)	100 (0)
MANIP	Jul 16	8.35 (0.40)	0.47 (0.14)	0.26 (0.14)	0.17 (0.16)	95 (10)
UPREF	Jul 16	9.26 (0.83)	0.35 (0.15)	0.27 (0.13)	0.38 (0.22)	97 (10)

Table 2.2. Estimated rates of immigration (fish/day), loss (day^{-1}), and model standard error (in parentheses) obtained by fitting mark-recapture abundances to a dynamic turnover model from Belanger and Rodriguez (2002). Estimates in grey had exceptionally large standard errors indicating poor model fit, these estimates were graphically confirmed to not have clear minima and were excluded in subsequent analyses due to poor model fit.

			Recap. #1		Recap #2				
Species	Local Habitat	Initial Marks	Marked	No Mark	Marked	No Mark	Catch By Pass 2 (%)	Immigration Rate (I)	Loss Rate (λ)
					Rocky Site				
Brook Trout	1	13	5	10	1	6	79	6.16 (0.90)	0.7 (0.11)
	2	3	2	2	1	7	59	1.62 (0.29)	0.14 (0.06)
	3	8	6	7	2	4	72	2.01 (0.33)	0.27 (0.06)
	4	5	1	21	1	11	57	79.45 (93.64)	4.97 (5.85)
	5	4	0	6	1	3	63	23.69 (118.28)	5.26 (26.28)
sculpin	1	108	27	80	8	63	79	70.31 (1.35)	0.92 (0.02)
	2	51	3	30	5	19	81	61.75 (23.02)	2.51 (0.95)
	3	27	6	26	0	24	68	27.6 (2.05)	1.04 (0.08)
	4	30	4	15	2	15	76	16.91 (1.43)	1.06 (0.09)
	5	104	20	80	0	53	79	84.51 (2.32)	1.23 (0.04)

Table 2.2 Continued. Estimated rates of immigration (fish/day), loss (day^{-1}), and model standard error (in parentheses) obtained by fitting mark-recapture abundances to a dynamic turnover model from Belanger and Rodriguez (2002). Estimates in grey had exceptionally large standard errors indicating poor model fit, these estimates were graphically confirmed to not have clear minima and were excluded in subsequent analyses due to poor model fit.

			Recap. #1		Recap #2				
Species	Local Habitat	Initial Marks	Marked	No Mark	Marked	No Mark	Catch By Pass 2 (%)	Immigration Rate (I)	Loss Rate (λ)
					Sandy Site				
	2	7	0	1	1	5	73	3.4 (1.17)	1.02 (0.40)
	3	7	0	0	0	5	62	2.81 (0.93)	0.98 (0.37)
	4	11	2	8	3	14	82	7.41 (0.89)	0.54 (0.08)
	5	19	0	11	3	7	73	35.10 (36.71)	3.90 (4.08)
	6	1	0	1	0	2	40	0.99 (0.88)	0.52 (0.59)
sculpin	1	10	0	6	2	2	75	19.76 (4.94)	69.94 (17.48)
	2	17	3	12	4	15	75	12.29 (0.82)	1.28 (0.10)
	3	8	2	3	1	9	68	3.43 (0.40)	0.52 (0.08)
	4	23	7	24	6	13	81	24.53 (1.29)	3.07 (0.17)
	5	26	4	22	5	22	84	25.55 (1.10)	2.21 (0.10)
	6	8	0	5	1	9	65	6.8 (0.87)	1.45 (0.22)

Table 2.3. Habitat characteristics at the upstream Rocky Site and the downstream Sandy Site. For each mean value presented, standard deviations are presented within parenthesis. Channel geomorphic unit abbreviations: FNTR: Fast Non-Turbulent Run, MCP: Mid-Channel Pool, SCP: Side Channel Pool. Channel geomorphic unit designation based on (Arend 1999). Data were collected July 25-26, 2011.

CGU	Local Habitat	Mean Wetted Width (m)	Length (m)	Mean Depth (m)	Mean Water Velocity		Mean Sand Depth (m)	Mean Embeddedness (%)
					60% Depth (m/s)	100% Depth (m/s)		
				Rocky Site				
Riffle	1	9.3 (0.87)	17.5	0.23 (0.12)	0.39 (0.25)	0.15 (0.13)	0.01 (0.06)	48 (18)
FNTR	2	9.1 (0)	8.0	0.32 (0.13)	0.30 (0.14)	0.12 (0.10)	0.02 (0.02)	65 (14)
SP	3	9.1 (2.20)	17.1	0.30 (0.16)	0.28 (0.25)	0.17 (0.20)	0.02 (0.05)	47 (32)
MCP	4	10.5 (0.26)	17.7	0.42 (0.22)	0.14 (0.12)	0.08 (0.09)	0.07 (0.10)	81 (24)
SCP	5	10.8 (0.22)	18.4	0.40 (0.18)	0.12 (0.12)	0.06 (0.06)	0.08 (0.08)	82 (23)
				Sandy Site				
SP1	1	9.8 (0.30)	10.3	0.55 (0.17)	0.13 (0.05)	0.05 (0.04)	0.38 (0.17)	100 (0)
SP2	2	11.7 (0.70)	15.1	0.64 (0.26)	0.10 (0.05)	0.03 (0.01)	0.28 (0.20)	93 (15)
MCP	3	8.1 (0.08)	11.2	0.80 (0.27)	0.11 (0.07)	0.02 (0.03)	0.24 (0.21)	98 (7)
SP3	4	11.9 (2.07)	16.7	0.55 (0.24)	0.09 (0.08)	0.01 (0.01)	0.16 (0.17)	78 (28)
FNTR	5	9.1 (1.28)	20.1	0.49 (0.16)	0.15 (0.09)	0.09 (0.07)	0.12 (0.15)	69 (25)
SCP	6	9.1 (0.99)	11.9	0.59 (0.20)	0.15 (0.08)	0.01 (0.01)	0.41 (0.24)	100 (0)

Table 2.4. Pearson's product moment correlation coefficients and their associated P-values between immigration rate and assorted habitat variables for juvenile Brook Trout and sculpin at the Rocky and Sandy Sites.

Species	Mean Wetted Width (m)	Mean Depth (m)	Water Velocity (m/s)		Mean Sand Depth (m)
			60% Depth	100% Depth	
Rocky Site					
Brook Trout	0.98 (0.11)	-0.99 (0.11)	0.97 (0.16)	0.19 (0.88)	-.99 (0.05)
sculpin	0.24 (0.76)	-0.21 (0.79)	0.11 (0.89)	-0.24 (0.76)	0.10 (0.90)
Sandy Site					
Brook Trout	0.69 (0.20)	-0.22 (0.73)	-0.85 (0.07)	-0.31 (0.61)	-0.89 (0.04)
sculpin	0.47 (0.42)	-0.82 (0.09)	-0.04 (0.95)	0.54 (0.35)	-0.76 (0.13)

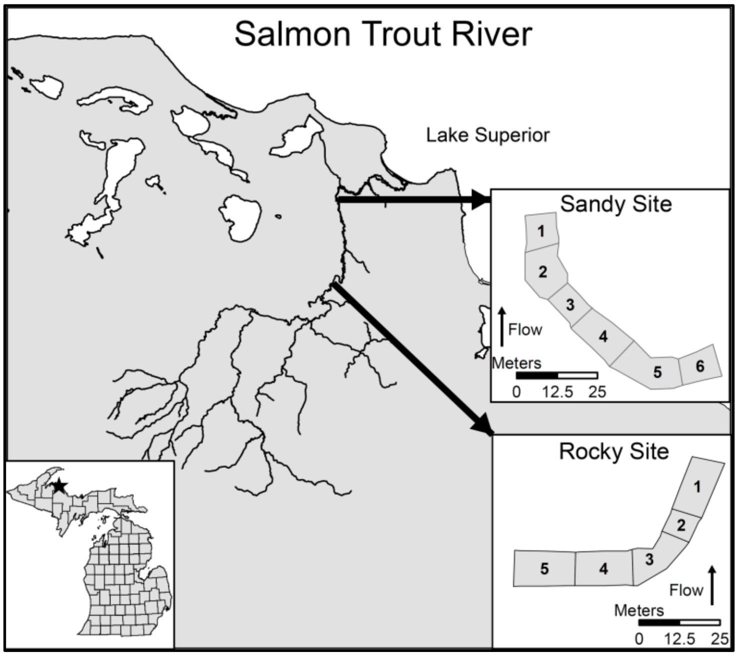

Figure 2.1. Map of the Salmon Trout River Watershed, Marquette County Michigan, showing the location of the Rocky and Sandy Sites used to identify drivers of habitat quality. Insets show the relation and general shape of local habitat within the sites where drivers' relative differences in habitat quality were identified. The Manipulated and Reference Sites from the sediment manipulation study are located between the sandy and rocky reaches.

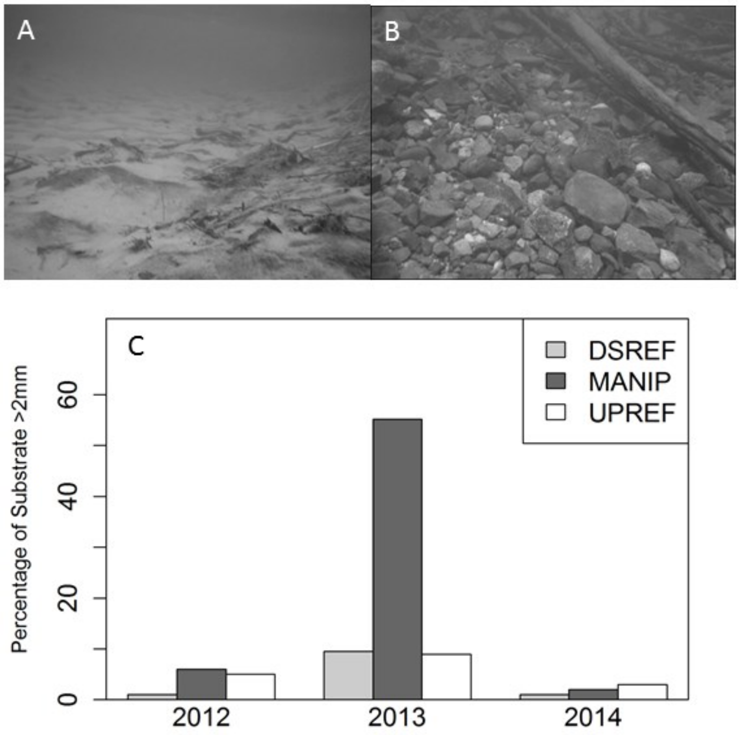

Figure 2.2. A & B are representative photos of the Manipulated Site in an embedded state (2012) and a restored state (2013), respectively. Figure C shows the percentage of substrates (>2mm, i.e., larger than sand) based on Wolman style pebble counts during each year of the experiment. The three sites, Downstream Reference Site (DSREF), Manipulated Sites (MANIP), and Upstream Reference Site (UPREF) were nearly contiguous.

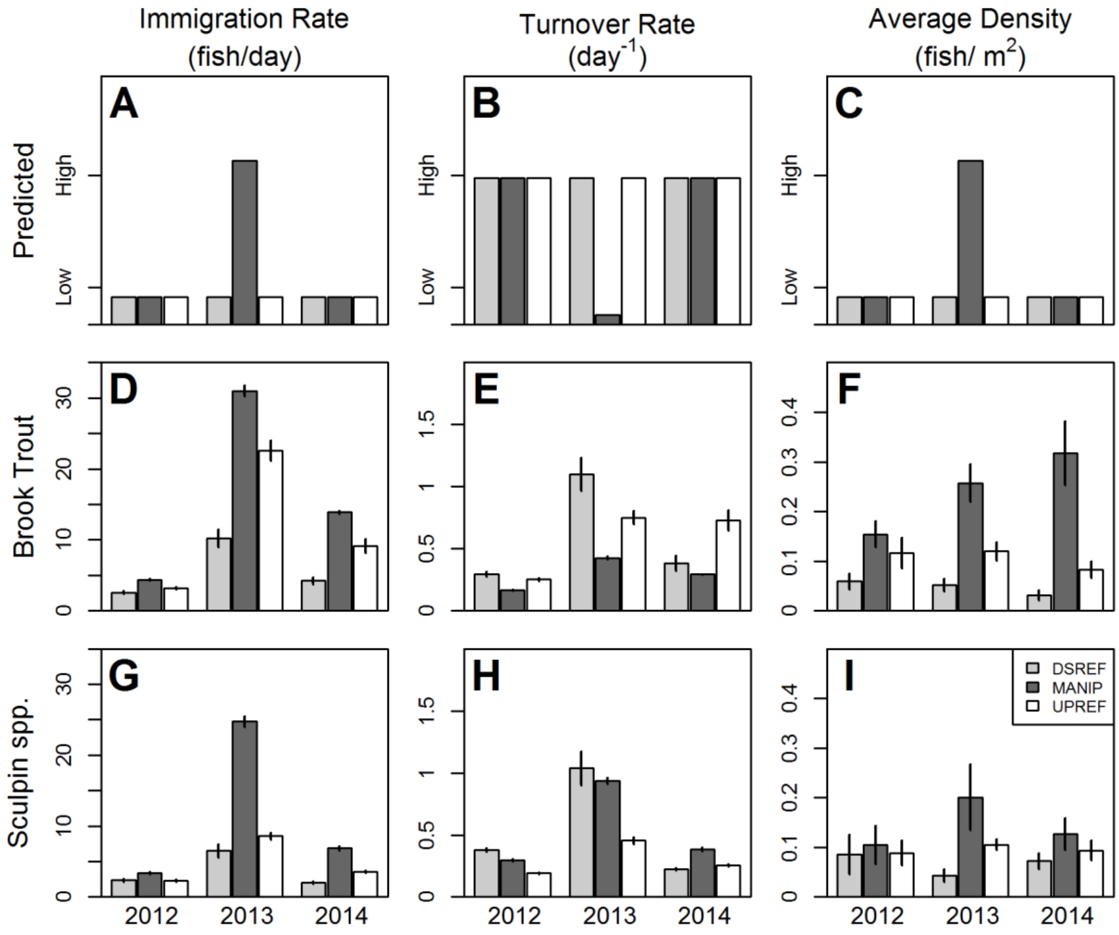

Figure 2.3. The predicted and observed (Brook Trout and Sculpin) response patterns of three metrics of habitat selection: First Column: immigration rate (fish/day), Second Column: turnover rate (fish/fish·day), and Third Column: Density (fish/m^2). Response patterns predicted if the metric accurately reflects changes in habitat quality are shown in panels A-C, Brook Trout response to manipulation shown in panels D-F, and sculpin spp. response shown in panels G-I. Measurements were taken before a habitat quality manipulation (2012), immediately after manipulation (2013) and after the site was allowed to return to its original condition (2014) in three nearly contiguous sites: the Downstream Reference Site (DSREF), the Manipulated Site (MANIP) and the Upstream Reference Site (UPREF). Error bars for density show the standard error, from the 3 surveys in each site. Error bars for immigration and turnover rates, are a measure of model fit, the square root of the diagonal members of the Hessian matrix, which is the standard error of the model fit.

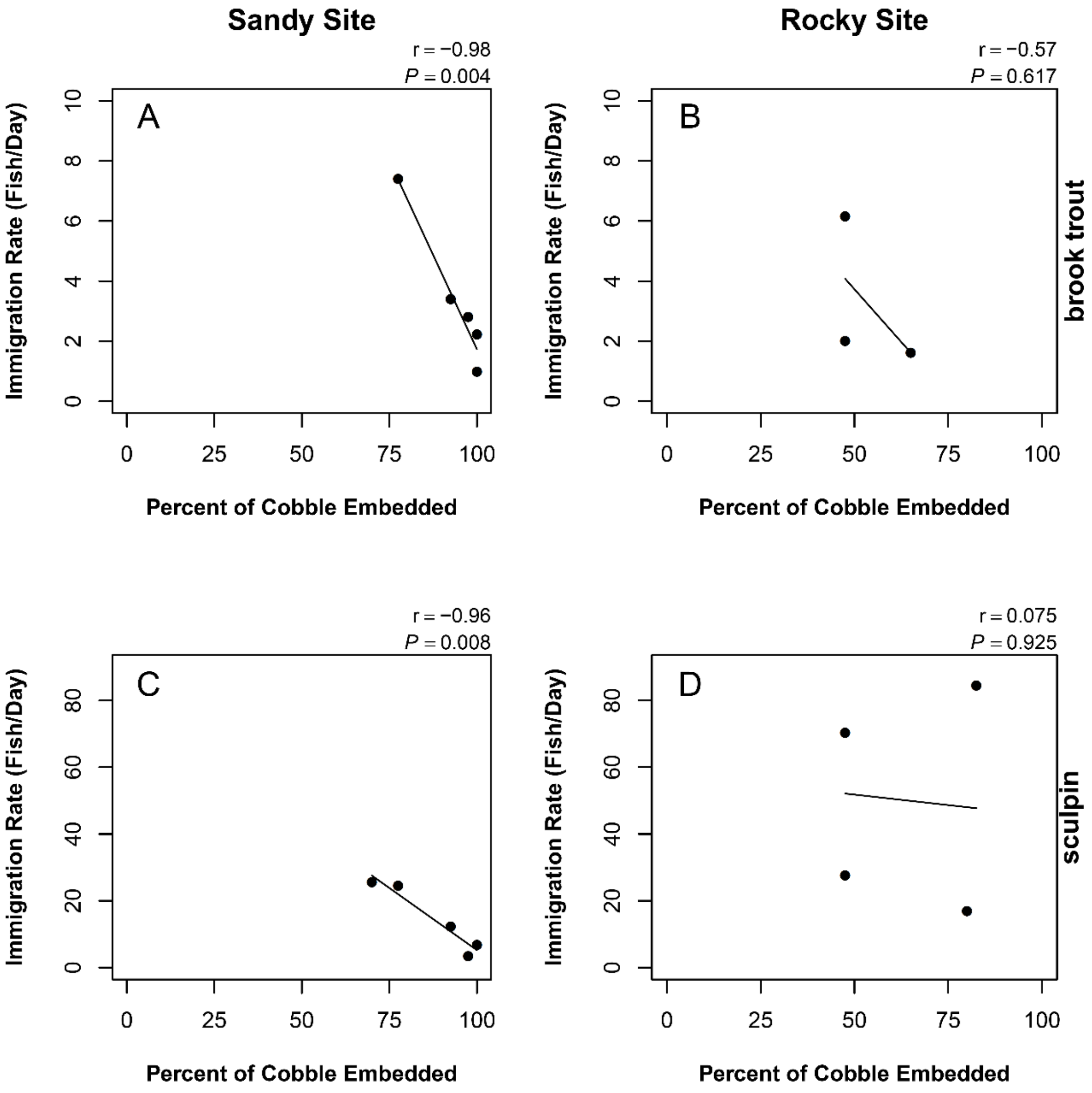

Figure 2.4. Immigration rates of Brook Trout (A, B) and sculpin (C, D) relative to the percent embedded cobble in the local habitat in the Sandy Site downstream (A, C) and the Rocky Site upstream (B, D). Pearson's product moment correlation coefficients are presented for each species*site combination.

Chapter 3: Multiple Surveys Reveal Need to Account for Short Term Fluctuations in Local-Habitat and Reach Scale Abundance[3]

Abstract

Many fishery sampling designs estimate abundance based on a set of sampling sites which are sampled once each year for a number of years. These sampling designs only account for spatial and annual variability. In these designs, short term variation in abundance due to local movements are assumed to be small relative to the annual and spatial variation. We present data that shows that in at least some systems, short term variation in abundance can be large, and if left unaccounted for, can limit the power of a sampling design. We repeatedly measured abundances of sculpin (*Cottus* spp), longnose dace (*Rhinichthys cataractae*), brook trout (*Salvelinus fontinalis*), coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*). Abundances were sampled within both small-scale local habitats (~10 m long) and larger sites (~90m long) up to 4 times over 14 days. We estimated abundances using two complementary techniques repeated snorkeling surveys and repeated electrofishing surveys. We also conducted a simple power analysis, where short term variability was the only source of variation, to demonstrate how short term variability can obscure changes in population abundances.

Our data suggests abundances within sites and local habitats vary on daily time scales, and that these variations are large enough to obscure even large changes in population size. Site scale abundances had coefficients of variation that ranged from 11.9% for sculpin, and 61.6% for rainbow trout. The average coefficient of variation across species, sites and sampling techniques was 31.6%. At the local habitat scale abundances were generally more variable. At the local habitat scale, abundance coefficients of variation ranged from 3.7% for sculpin to 173% for longnose dace. The average coefficient of variation across sites and sampling techniques was 60.9%.

Our power analysis tested the ability to detect a change in abundance, given varying amounts of short term variation. We found that at a 10% coefficient of variation, approximately

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[3] The material in this chapter is planned for submission.

the smallest amount of site scale variation we observed, we had 100% power detecting a 50% change in abundance with 5 samples before and after the change. Power decreased to 37% when the amount of variation increased to 30%, which was approximately the average amount of site scale variation we observed.

Introduction

Abundance varies over large spatial and temporal scales (Wiens and Rotenberry 1981; Brown et al. 1995), which can bias abundance-based studies that do not account for both sources of variation (Wiley et al. 1997). In addition to this large and long scale variation, local nonrandom movements over short time scales are common (Gowan and Fausch 1996; Lonzarich et al. 2000; Rodríguez 2002) and may be an additional source of variation in some sampling designs. For example, directly measuring abundance fish by comprehensively sampling the entire river would eliminate local movements as a source of variation, but this sampling regime is generally too logistically challenging to implement. Therefore some sort of randomized sampling regime of smaller, more manageable study sites is required to capture the large scale spatial variation in abundances (Dunham et al. 2009). However the transition from entire ecosystem to smaller sampling sites may introduce nonrandom local movements as an additional source of variation.

This small scale, short-term variation was often ignored, or assumed to be relatively small compared to the larger spatial and temporal variation, which is generally the focus of studies, and is thus not considered in the frequently cited abundance sampling methods paper like Platts et al. (1983). American Fisheries Society protocols recommend sampling during 'low-movement' periods, but they also attribute difficulty in detecting a 20% change in abundance to purely interannual variation without any mention of short-term variation (Temple and Pearsons 2007). The US Forest Service Monitoring guide recognizes short term movement as a potential source of noise, but it recommends simply designing monitoring programs to detect larger effect sizes rather than trying to account for this variation (Vesely et al. 2006). Further, papers evaluating sampling techniques seem focused on ensuring the accuracy of individual sampling efforts (Thurow and Schill 1996; Peterson et al. 2004), while not broadly considering the overall precision of the estimate. This approach may be a holdover from the restricted movement paradigm (Gerking 1958), where it was assumed fish movements were highly localized, and that at least some fish spend their lives within short reaches. Today we recognize that it is common for at least a part of the population to move relatively large distances (10's- 100's m) over short time scales (Gowan et al. 1994; Booth et al. 2013). These movements are not necessarily migratory in nature; they are often simply local movements within a home range (Rodríguez

2002). If this movement was random, it would not bias samples of abundance, because any fish leaving would randomly be replaced by new immigrants. However, fish movement is not purely random; fish use habitat non-randomly and move as conditions change (Gowan and Fausch 2002). These nonrandom movements may cause changes in abundance within a reach as conditions within the river change over short time scales. In systems with relatively mobile populations, if the sampling regimes do not account for the variability in abundances from non-random movements between local and reach scale habitat, the conclusions reached from the samples may be flawed or skewed.

Here we use data collected as part of different projects to document how short term variation in abundance can be large, and that single sample snap-shot measurements of abundance could lead to erroneous conclusions. We use data from two experiments: the first using repeated snorkel surveys originally designed to test how patterns of native Brook Trout habitat use may respond to nonnative salmonids, the second consisted of abundances collected during repeated electrofishing surveys within different sites as part of a survey of local fish movements. Finally we performed a power analysis to illustrate how short term variations in abundance can affect monitoring programs.

Methods

Site Description

The Salmon Trout River (STR) is located in Marquette County, Michigan, and is largely contained within the landholdings of a single private landowner. The watershed is 94% forested and largely undeveloped (2011 NLCD). However, land use changes, road crossings and road maintenance appear have resulted in increased aggradation of fine sediments, especially in the downstream reaches of the STR (Huckins et al. 2008). Due to this large-scale spatial heterogeneity in substrate composition, we selected two heavily aggraded sites (hereafter sandy sites, i.e. substrate was nearly homogeneously sand) and two lightly aggraded sites (hereafter rocky sites, i.e. interstitial spaces between larger substrate particles such as cobbles were not uniformly filled with sand). Two of these sites were sampled using snorkel surveys: a 105m rocky site hereafter the rocky snorkel site, and 79m sandy site, hereafter the sandy snorkel site. The other two sites, an 85m sandy reach and a 79m rocky reach, were sampled using electrofishing and are referred to as the sandy electrofishing site and rocky electrofishing site, respectively. Additionally, to track variation of abundance at smaller spatial scales, each of these sites was subdivided into local habitats based upon dominant channel geomorphic units (e.g. pools, riffles, runs) (Hawkins et al. 1993). Within each local habitat we collected descriptive habitat data along three transects consisting of five equidistant points taken at 10%, 50% and 90% of local habitat section length. At each point we measured water depth, water velocities, using a wading rod and Marsh McBirney flowmeter, sand depth, using a metered probe, and embeddedness. We also recorded the predominant channel geomorphic unit (Hawkins et al. 1993) of the local habitat and the wetted width along each transect. Habitat data were collected in the rocky and sandy shocking sites July 25, 2011 and July 26, 2011 respectively, rocky and sandy snorkel sites were sampled August 5, 2011 and September 9-10, 2011, respectively. Habitat data was collected when the Salmon Trout River was at base flow, and snorkeling and electrofishing surveys were conducted while the river was at a similar stage.

Snorkel Survey Data

Habitat use was measured using daytime snorkel surveys following American Fisheries Society protocols (O'Neal 2007) between July 31 and August 14. In brief, a single observer snorkeled in an upstream direction, recording the number and species of each fish in each local habitat. The boundaries of each local habitat within a site were demarcated by instream flagging, and local habitats ranged from 65.6 m^2 to 166.5 m^2 in area (Table 3.1). To account for the occasional difficulty of properly identifying fish, we excluded any observations where the observer was not confident of the species identification. Six percent of fish observed were excluded for this reason. Species abundances within each site were obtained by summing the fish detected within local habitats during each snorkel survey. Each site was snorkel surveyed four times between July 30 and August 14, 2011.

This dataset was collected as part of an experiment designed to explore how nonnative salmonids affect Brook Trout habitat use. After the first two snorkel surveys were completed, we conducted a 3-pass backpack electrofishing survey on August 4th in the sandy site and August 11th in the rocky site. Rainbow Trout and Coho Salmon captured during these surveys were removed from the river and euthanized with an overdose of clove oil. Captured Brook Trout were held in in-stream nets until the completion of survey and then released in the middle of the site just before the blocking nets were removed. The 3rd and 4th snorkel surveys were conducted within each site the two days immediately following electrofishing. Even though the electrofishing sampling was likely a disturbance to the system, this electrofishing and nonnative removal did not reduce abundances within the sites or local habitats. We detected no statistically significant effects on the abundance of any salmonids within the study sites (Repeated Measures ANOVA, $P>0.86$, Appendix 2).

Electrofishing Data

We complemented the snorkeling data with data from the rocky and sandy shocking sites where we conducted repeated electrofishing surveys. To sample a site, we carefully blocked the upstream and downstream ends of a given local habitat with ¼ inch mesh netting strung perpendicular to water flow and kept it on the stream bottom using rebar rods and chains in sandy sites or rocks when they were available. Local habitats ranged in size from 72.8 m^2 to 198.7 m^2 (Table 3.2). Starting in the most downstream local habitat, multi-pass electrofishing surveys (3-5 passes, mode of 4 passes) were conducted in an upstream direction using two backpack mounted electrofishing units (Badger 1, ETS Electrofishing Systems$_{\text{LLC}}$),). Captured fish were anesthetized with clove oil, measured, weighed and if greater than 55mm total length they were marked with visual implant elastomer as part of a separate movement survey. Fish were held in flow through nets until the sampling of adjacent local habitat was completed and then were released into center of the local habitat. Each reach was surveyed 3 times over 7 days between August 1 and August 16.

Power Simulation

We created an R-based simulation (R version 3.0.0) to perform a power analysis to demonstrate the effect that short-term movement has on the ability to detect changes in abundance (Appendix 3). In the simulation the abundances were randomly drawn from a normal distribution with a mean of 32.5, which was the mean Brook Trout abundance we observed in this study. To represent differing levels of short-term variation in abundance, the standard deviation in the model runs were varied to achieve coefficients of variation for short-term abundance from 0.1%, an essentially sessile population, to 10%, 20%, 30%, 40%, and 50%. This was the only source of variation included in the model.

To obtain an estimate of power at a given coefficient of variation, we simulated 5 samples before a change in abundance and 5 samples after the change. The magnitude of change in abundance varied from 0-50% in 5% increments. This could be analogous to annual monitoring surveys 5 years before and 5 years after a restoration. The ability of the restoration to increase the abundance in the analogy varied from 0-50%. To calculate power we performed a 2-sample Student's T-test with an alpha of 0.05 to test for a change in abundance before and after the change. Each model run was iterated 10,000 times, and we computed the number of iterations where the p value of the Student's T-test was less than 0.05 to obtain power of the test.

Results

Abundances at each site varied greatly (Table 3.3). For example, the largest proportional difference in abundance among snorkeling surveys was for Brook Trout at the rocky snorkel site, which differed 363% from 8 individuals to 29 individuals (Figure 3.2). These large ranges were also observed in the electrofishing data, for example at the sandy shocking site Rainbow Trout ranged from 10 to 39 individuals (Figure 3.3). To better examine this variation, we compared coefficients of variation of the number of individuals of each species observed in a sample. This metric allows us to compare variation even when means differed. Coefficients of variation ranged between 16.9% and 52.6% for snorkel surveys and 11.9% and 61.6% for the electrofishing surveys (Table 3.3). The greatest coefficient of variation observed was for Longnose Dace with mean value of 45.0% across both shocking sites, while the lowest coefficient of variation was observed for Sculpin sp. estimated to be 22.8% averaged across both shocking sites (Table 3.3). Within the salmonids, Rainbow Trout abundance generally had the greatest coefficient of variation: 32.6% averaged across snorkel sites and 40.5% averaged across shocking sites, although Brook Trout also had a high coefficient of variation 34.8% at the snorkel sites and 30% at the shocking sites (Table 3.3).

In addition to site scale variations, abundance also varied on short timescales at the local habitat scale and these fluctuations were generally larger than variation at the site scale. (Table 3.4). The average coefficient of variation across species, sites and sampling methods was 60.9% at the local habitat scale but only 31.6% at the site scale (Tables 3.3 and 3.4). At the local habitat scale, Longnose Dace generally had the largest coefficients of variation ranging from

12.4% to 173.2%. Sculpin abundances at the local habitat scale generally had the lowest coefficients of variation, ranging from 3.7% to 45.8% and averaging 31.9% across sites (Table 3.4).

Sampling multiple local habitats within a site allowed us to compare how the distribution of individuals between these sites changed on short time scales. Species generally had similar distributions within a site, although there were exceptions. Brook Trout within the rocky snorkel site were distributed differently each sample (Figure 3.2). Within the Sandy snorkel site Coho Salmon and Rainbow Trout both show differences in their distributions. The sites that were sampled through electrofishing generally had more stable distributions than sites that were snorkeled (Figures 3.1-3.4), but we still observed changes in distributions; for example Brook Trout in the rocky shocking site (Figure 3.4).

The simulation showed that the ability to detect even large changes quickly declines as the variation in site abundance increases (Figure 5). When site abundance has a coefficient of variation of 30%, roughly the coefficient of variation we observed for Brook Trout across sites and gears, we can detect a 50% change in abundance only 37% of the time. If the coefficient of variation increases to 50%, similar to variations observed for Long Nose Dace, the likelihood of detecting a 50% increase in abundance drops to 17%.

Discussion

Wildlife scientists have long recognized that habitat use can vary annually (Schooley 1994). Our study builds on these findings by suggesting that the abundance and distribution of fish within a reach vary on daily time scales, and that these variations are large enough to obscure even large changes in population size if not accounted for during sampling. We believe that local non-random movements of fish are responsible for these fluctuations (Rodríguez 2002). Understanding how even non-migratory fish move through their life-time is important for understanding habitat connectivity and gene flow within a population (Kanno et al. 2014a). On shorter, daily time scales, short-term fluctuations of abundance have also been documented in oceanic prey fishes (Suryan et al. 2002), *Catostomus* suckers (Booth et al. 2013), and in other cold-water stream systems (Belanger and Rodriguez 2002). Yet, snapshot measurements (e.g., unreplicated within years) are still used to establish fish-habitat associations (Johnson and Chalupnicki 2014) or to assess habitat restorations (Stewart et al. 2009; Louhi et al. 2016), even though these point measurements are vulnerable to bias due these short term fluctuations in habitat use or sampling effectiveness.

Abundance or the related metric density is commonly used because it is an easily measured and intuitive metric of habitat use. However in at least some systems, abundance estimates will only provide a snapshot of how fish are using restored and control habitats on the day of sampling; this may obscure, confound or lead to simply erroneous conclusions. This danger is most clearly illustrated Figure 3.2C. Depending on the days sampled before and after the nonnative removal, that in this case was part of a different experiment, we could have concluded that the removal was successful in decreasing Rainbow Trout abundance, utterly failed and increased Rainbow Trout abundance, or had no effect. By sampling to account for short term replication we can see that fluctuations in abundance and distribution were similar both before and after the restoration, suggesting that the removal had no effect. This potential for misunderstanding appears to increase as the size of the sample site decreases because local habitats were more variable than sites regardless of sampling method.

Reaching valid conclusions requires properly attributing variance within models and analyses. For example, Wiley et al. (1997) demonstrated that improper or unbalanced replication over long time scales or large spatial scales led to bias by erroneously attributing spatial variation as temporal variation and vice versa. We believe many sampling designs may suffer from an analogous problem where short term variation obscures treatment effects due to excessive noise, or short term variation is erroneously attributed to a treatment effect. For example Myrvold and Kennedy (2015) modeled steelhead density across space and time (years), but relied solely on snapshot measures of density measured within 100m sites; in their model 41.4% of variance was unexplained, which limited the inferences they were able to draw. If steelhead densities vary to a similar degree as Rainbow Trout in this study, much of the unexplained variation could be due to short-term fluctuations in density.

One strategy to more accurately measure abundance is to simply sample multiple times within a season and then statistically accounting for short term variation in abundances. Alternatively, larger sampling sites may reduce short term variation within the site. Many fishes have home ranges that most fish stay within, these home ranges for stream fishes are often, though not always, in the 10’s of stream meters (Rodríguez 2002). Since fish regularly move within these home ranges (Gowan et al. 1994) a small sampling site’s abundance will vary as residents move throughout their home range and as a result enter and/or leave the sampling site. A larger site that encompasses a majority of its residents' home range will vary less as most residents simply move within the site rather entering or leaving. However, for fishes with larger home ranges, these sites would have to be hundreds of meters long, since some populations of salmonids have home ranges that can be in the hundreds of meters (Gowan et al. 1994; Rodríguez 2002). Both of these methods would improve estimates of abundance, but would also increase the time and cost required to sample.

In conclusion, in at least some systems short term variation in abundances can be large enough to greatly reduce the power of snapshot sampling designs. Our work suggests that researchers and managers who are measuring site scale abundance should at least take steps to quantify the amount of short term variation in abundances at their site. This would reveal how large a source short term variation is relative to annual and large scale spatial variation. If short term variation is large relative to these sources, steps can be taken to better account for short term variation in sampling designs and sample sufficiently in space and time to capture that variation.

Table 3.1. Physical habitat summary for Sandy Snorkel and Rocky Snorkel Sites. Each column contains averages of three transects consisting of five equidistant points taken at 10%, 50% and 90% of local habitat section length. Water velocities were measured using a wading rod and Marsh McBirney flowmeter, mean sand depth was measured using a metered probe. Standard deviations for each measure are shown in parenthesis. Median pebble size comes from 60 count pebble counts following Kondolf (2000). Local habitats were defined based upon dominant channel geomorphic units (CGU) (Hawkins et al. 1993), CGU abbreviations: FNTR- Fast Non-Turbulent Run

Local Habitat	CGU	Mean Wetted Width (m)	Length (m)	Mean Depth (m)	60% Depth (m/s)	100% Depth (m/s)	Mean Sand Depth (m)	Mean Embeddedness (%)	Median Pebble Size
					Rocky Snorkel Site				
1	Riffle	6.2 (1.32)	13	0.3 (0.16)	0.36 (0.35)	0.12 (0.12)	0.02 (0.03)	37 (42)	27.5
2	Riffle	7.8 (0.13)	12	0.33 (0.16)	0.29 (0.15)	0.23 (0.06)	0.01 (0.03)	52 (36)	34.5
3	FNTR	9.9 (0. 43)	10	0.34 (0.2)	0.24 (0.27)	-0.02 (0.05)	0.01 (0.03)	48 (39)	28
4	Pool	7.9 (0.83)	15	0.43 (0.2)	0.15 (0.12)	0 (0.03)	0.02 (0.04)	65 (25)	22
5	FNTR	9.8 (0.89)	12	0.33 (0.16)	0.2 (0.15)	0.07 (0.11)	0.03 (0.04)	73 (29)	33
6	Pool	9.1 (1.7)	12	0.55 (0.28)	0.14 (0.08)	0.05 (0.02)	0.07 (0.22)	77 (24)	22
7	Pool	8.8 (1.24)	16	0.55 (0.29)	0.12 (0.08)	-0.01 (0.06)	0.05 (0.12)	67 (28)	30
8	Pool	11.1 (0.93)	15	0.52 (0.24)	0.09 (0.12)	-0.01 (0.03)	0.06 (0.09)	75 (21)	2
					Sandy Snorkel Site				
1	FNTR	8.23 (0.72)	8	0.36 (0.1)	0.2 (0.14)	-0.02 (0)	0.52 (0.16)	100 (0)	2
2	Pool	7.63 (0.43)	11	0.44 (0.12)	0.22 (0.11)	0.01 (0)	0.36 (0.13)	100 (0)	2
3	FNTR	7.97 (0.56)	12	0.38 (0.12)	0.19 (0.13)	0.01 (0.03)	0.24 (0.15)	98 (6)	2
4	Pool	7.9 (0.37)	18	0.37 (0.18)	0.19 (0.11)	0.06 (0.09)	0.3 (0.17)	97 (13)	2
5	Pool	7.5 (0.17)	13	0.46 (0.21)	0.18 (0.18)	-0.01 (0.05)	0.32 (0.2)	98 (7)	2
6	Pool	6.75 (0.58)	17	0.44 (0.21)	0.21 (0.11)	0.06 (0.03)	0.32 (0.24)	100 (0)	2

Table 3.2. Physical habitat summary for Sandy Shocking and Rocky Shocking Sites. Each column contains the averages and standard deviations, shown in parenthesis, of three transects consisting of five equidistant points taken at 10%, 50% and 90% of local habitat section length. Water velocities were measured using a wading rod and Marsh McBirney flowmeter, mean sand depth was measured using a metered probe. Local habitats were defined based upon dominant channel geomorphic units (CGU) (Hawkins et al. 1993), CGU abbreviations are as follows: FNTR- Fast Non-Turbulent Run, SP- Scour Pool, MCP-Mid Channel Pool, SCP-Side Channel Pool.

Local Habitat	CGU	Mean Wetted Width (m)	Length (m)	Mean Depth (m)	Mean Water Velocity 60% Depth (m/s)	Mean Water Velocity 100% Depth (m/s)	Mean Sand Depth (m)	Mean Embeddedness (%)
Rocky Shocking Site								
1	Riffle	9.3 (0.87)	17.5	0.23 (0.12)	0.39 (0.25)	0.15 (0.13)	0.01 (0.06)	48 (18)
2	FNTR	9.1 (0)	8.0	0.32 (0.13)	0.30 (0.14)	0.12 (0.10)	0.02 (0.02)	65 (14)
3	SP	9.1 (2.20)	17.1	0.30 (0.16)	0.28 (0.25)	0.17 (0.20)	0.02 (0.05)	47 (32)
4	MCP	10.5 (0.26)	17.7	0.42 (0.22)	0.14 (0.12)	0.08 (0.09)	0.07 (0.10)	81 (24)
5	SCP	10.8 (0.22)	18.4	0.40 (0.18)	0.12 (0.12)	0.06 (0.06)	0.08 (0.08)	82 (23)
Sandy Shocking Site								
1	SP1	9.8 (0.30)	10.3	0.55 (0.17)	0.13 (0.05)	0.05 (0.04)	0.38 (0.17)	100 (0)
2	SP2	11.7 (0.70)	15.1	0.64 (0.26)	0.10 (0.05)	0.03 (0.01)	0.28 (0.20)	93 (15)
3	MCP	8.1 (0.08)	11.2	0.80 (0.27)	0.11 (0.07)	0.02 (0.03)	0.24 (0.21)	98 (7)
4	SP3	11.9 (2.07)	16.7	0.55 (0.24)	0.09 (0.08)	0.01 (0.01)	0.16 (0.17)	78 (28)
5	FNTR	9.1 (1.28)	20.1	0.49 (0.16)	0.15 (0.09)	0.09 (0.07)	0.12 (0.15)	69 (25)
6	SCP	9.1 (0.99)	11.9	0.59 (0.20)	0.15 (0.08)	0.01 (0.01)	0.41 (0.24)	100 (0)

Table 3.3. Mean abundances (standard deviations) and coefficient of variation (CV) expressed as a percentage for the four sites sampled within the Salmon Trout River. Estimates of abundance were all made between August 1 and August 16, 2011. Snorkel sites were sampled 4 times, while electrofishing sites were sampled 3 times.

Survey Type	Site	Species	Mean Abundance	CV (%)
Snorkeling	Rocky Site 1	BKT	16.8 (8.8)	52.6
		CO	247.3 (43.6)	17.6
		RBT	36.3 (15.0)	41.3
	Sandy Site 1	BKT	16.0 (2.7)	16.9
		CO	32.8 (7.7)	23.4
		RBT	19.3 (4.6)	23.8
Electrofishing	Rocky Site 2	BKT	51.3 (14.6)	28.4
		CO	318.0 (74.6)	23.5
		LND	29.7 (12.2)	41.2
		RBT	96.7 (18.8)	19.4
		SSP	305.3 (102.9)	33.7
	Sandy Site 2	BKT	45.7 (14.4)	31.6
		CO	30.0 (9.2)	30.6
		LND	35.3 (17.2)	48.8
		RBT	23.7 (14.6)	61.6
		SSP	99.3 (11.8)	11.9

Table 3.4. Coefficient of variation, the ratio of the standard deviation to the mean, for abundance within local habitats within each sampling site.

Local Habitat	Brook Trout	Coho Salmon	Longnose Dace	Rainbow Trout	Sculpin sp.
		Rocky Shocking Site			
1	38.4	61.5	68.1	10.4	42.2
2	36.7	24.6	81.1	33.3	37.5
3	31.6	22.4	12.4	54.2	15.6
4	59.2	59.3	-	103.9	32.2
5	32.9	53.7	99.0	52.7	30.6
		Sandy Shocking Site			
1	92.5	65.5	173.2	124.9	45.8
2	72.1	96.4	132.3	66.1	33.6
3	87.4	91.7	86.6	100.0	43.3
4	13.3	33.5	40.1	76.3	33.2
5	37.0	50.0	45.2	47.2	3.7
6	34.6	105.4	86.6	100.0	32.8
		Rocky Snorkel Site			
1	127.7	61.3		66.9	
2	62.9	23.8		47.8	
3	100.7	23.8		56.9	
4	81.6	42.5		22.5	
5	81.6	42.5		58.2	
6	73.6	42.8		58.2	
7	71.9	24.5		76.6	
8	127.7	17.7		115.5	
		Sandy Snorkel Site			
1	141.4	42.1		91.3	
2	27.2	51.6		127.7	
3	64.5	52.9		73.4	
4	55.9	42.6		86.1	
5	40.8	75.9		73.6	
6	25.5	93.5		23.6	

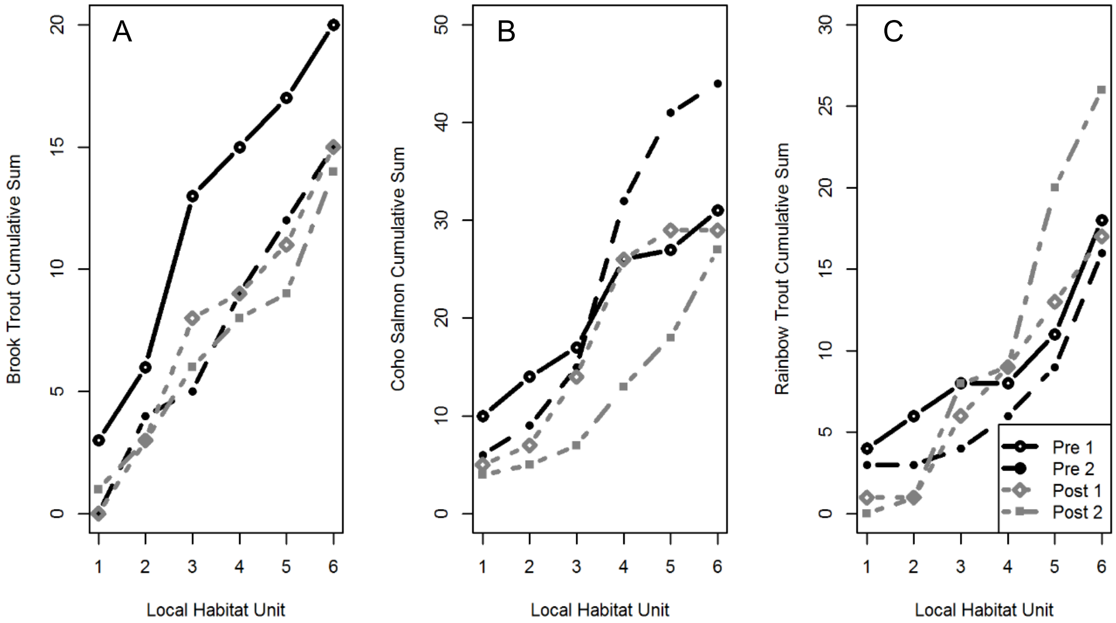


Figure 3.1. Cumulative sums of Brook Trout (A), Coho Salmon (B) and Rainbow Trout (C) abundances sampled by snorkeling in the sandy snorkel site of the Salmon Trout River show the distribution of fishes within and between the local habitat units. The difference between any two points on a line shows the abundance within the local habitat(s), and the overall shape of the curve represents the distribution of fish within the site on that sampling date. Local habitats are ordered from downstream to upstream, and information describing the physical habitat of each local habitat is found in Table 3.2. Abundance was quantified during upstream snorkeling surveys conducted twice before and twice after a nonnative removal within each local habitat section. Black lines represent the cumulative abundances before the nonnative removal; grey lines represent post removal cumulative abundances. There was no statistically significant difference in the abundance of any salmonids within the snorkel sites (P>0.86, Appendix 2), or any clear patterns between pre and post surveys.

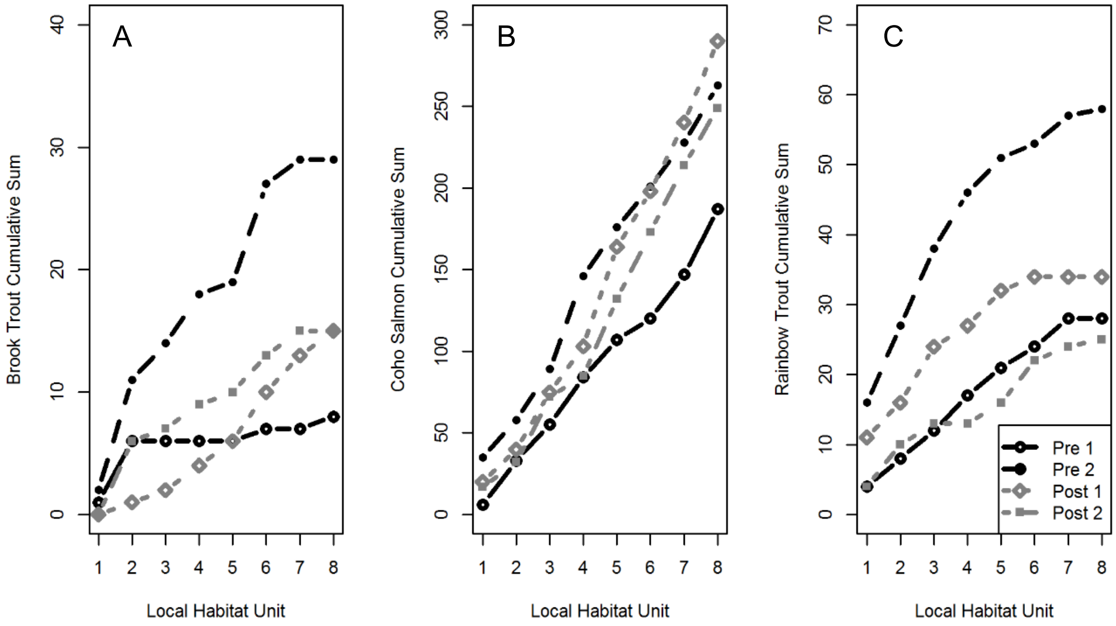


Figure 3.2. Cumulative sums of Brook Trout (A), Coho Salmon (B) and Rainbow Trout (C) abundances sampled by snorkeling in the rocky snorkel site of the Salmon Trout River show the distribution of fishes within and between the local habitat units. The difference between any two points on a line shows the abundance within the local habitat(s), and the overall shape of the curve represents the distribution of fish within the site on that sampling date. Local habitats are ordered from downstream to upstream, and information describing the physical habitat of each local habitat is found in Table 3.2. Abundance was quantified during upstream snorkeling surveys conducted twice before and twice after a nonnative removal within each local habitat section. Black lines represent the cumulative abundances before the nonnative removal; grey lines represent post removal cumulative abundances. We detected no statistically significant difference in the abundance of any salmonids within the snorkel sites (P>0.86, Appendix 2), or any clear patterns between pre and post surveys.

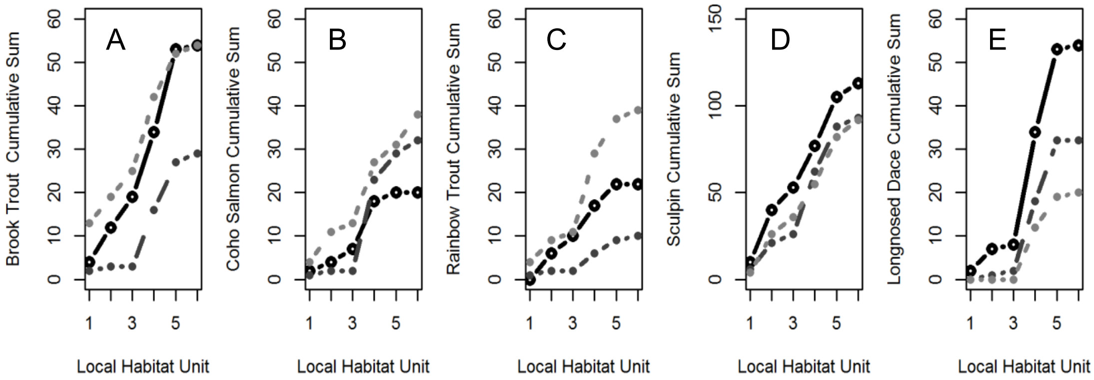


Figure 3.3. Cumulative sums of Brook Trout (A), Coho Salmon (B), Rainbow Trout (C), Sculpin (D) and Longnose Dace (E), abundances in a sandy shocking site of the Salmon Trout River show the distribution of fishes collected during electrofishing surveys within and between the local habitat units. The difference between any two points on a line shows the abundance within the local habitat(s), and the overall shape of the curve represents the distribution of fish within the site on that sampling date. Abundances were measured using upstream electrofishing surveys conducted three times over 7 days. Black lines bars represent the first survey; dark grey lines the second survey, and the grey line represents the final survey. Local habitats are ordered from downstream to upstream, and information describing the physical habitat of each local habitat is found in Table 3.1.

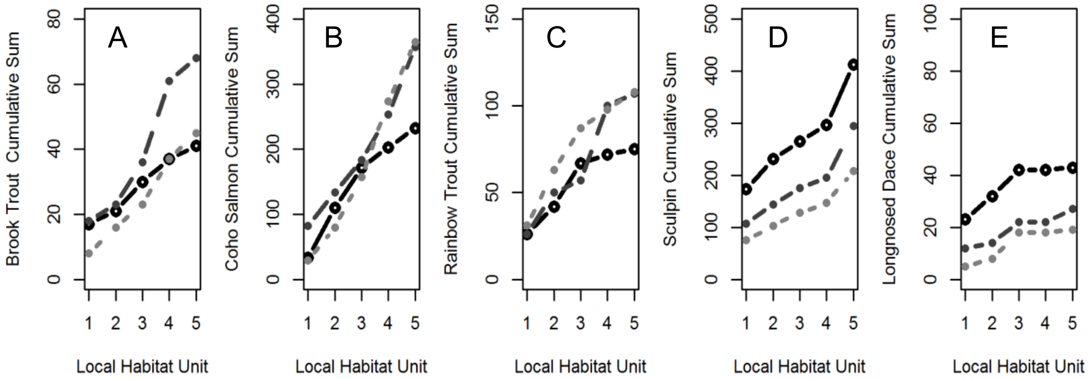


Figure 3.4. Cumulative sums of Brook Trout (A), Coho Salmon (B), Rainbow Trout (C), Sculpin (D), and Longnose Dace (E) abundances in a rocky site of the Salmon Trout River show the distribution of fishes within and between the local habitat units. Abundance was measured using upstream electrofishing surveys conducted three times over 7 days. Black lines bars represent the first survey; dark grey lines the second survey, and the grey line represents the final survey. The difference between any two points on a line shows the abundance between those points, the overall shape of the curve represents the distribution of fish within the site on that sampling date. Local habitats are ordered from downstream to upstream, and information describing the physical habitat of each local habitat is found in Table 3.1.

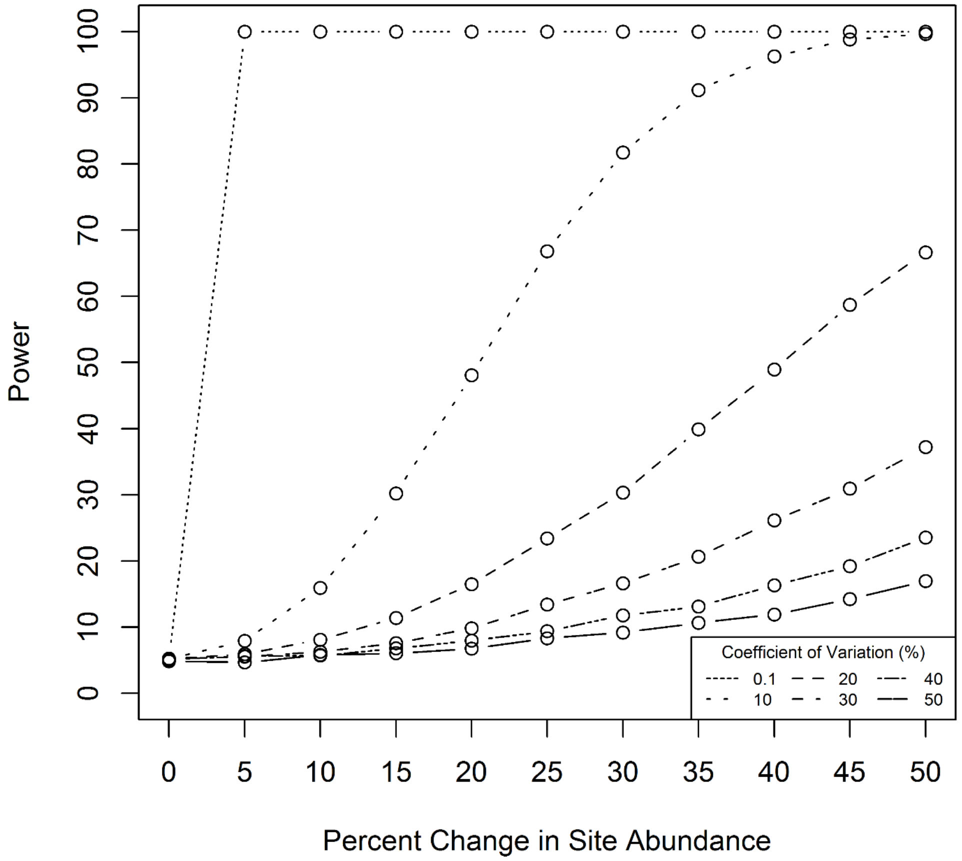


Figure 3.5. Ability to detect various simulated changes within a site at differing coefficients of variation. Each point is the power calculated from 10,000 simulations. Each simulation consisted of a Student's T-test comparing 5 samples before and 5 samples after a given change in the mean abundance. Each line represents a different level a variation within the samples.

Chapter 4 – Test of Boulder Attractiveness as Habitat in Varying Habitat Contexts

Introduction

Developing a more mechanistic understanding of why fish select and use habitat will improve the management of stream fishes. A review by Stewart et al (2008) showed little evidence that the addition of small scale stream structures increased the number of individuals using a site. However, instream structure and heterogeneity has long been considered an important part of quality trout habitat. We hypothesized that there may be two reasons for the varying responses to added structures in Stewart et al (2008): The first could be that boulders and other stream structure become relatively more attractive when they are rare. During our 2011 survey of fish movement within the Salmon Trout River we observed an interesting trend where embeddedness or the proportion of cobble buried by sand, had a strong correlation with immigration rate in the sandy site, indicating that the less embedded local habitats were more preferred (Chapter 2). However, we did not observe a similar relationship between immigration rate and embeddedness in the other rocky site that we sampled. We argued that this relationship was due to the relative value of exposed in sandy sites versus sites with a more heterogeneous substrate. This suggests that structure additions may only attract fish in sandy or other homogenous sites where stream structure is rare, and that there are diminishing returns to adding structures to otherwise heterogeneous habitats. Secondly, most of the studies reviewed relied on snapshot samples of abundance or density to measure habitat use. In Chapter 3 we found these metrics to be increasing variable at smaller spatial scales. This led us test that if by using a more robust metric of habitat use to test if boulders were more likely to be used in sandy habitats relative to rocky parts of the river.

Predicting habitat selection at this at this smaller spatial scale requires different methodologies and metrics that what was used in previous movement studies within the Salmon Trout. Previous work within the Salmon Trout River tested the ability of different metrics of habitat selection to reliably infer habitat quality (Chapter 2). We found that estimating immigration rate can be used to reliably infer habitat quality and preference at the local habitat scale (~250m^2). We applied a conceptually similar, habitat selection based methodology to test how individuals respond to boulders within different habitat contexts. However at the smaller microhabitat scale (~1m ^{2}) we expect the relationship between immigration and habitat quality to break down. We argue that at smaller spatial scales, habitat availability can be better assessed by individuals searching for habitat. We think this is the case because dominance hierarchies in microhabitats are likely shorter and simpler than hierarchies in the larger local habitats, due to fact the number of fish that could use a microhabitat is much smaller than the spatially larger local habitat. Therefore fish can more easily assess the dominance hierarchy within the microhabitat (White and Gowan 2012), and determine if that microhabitat is socially available. Since we expect dominant fish to occupy high quality microhabitats, this dominant individual may be large enough to intimidate other fishes and discourage subdominant fishes from selecting that microhabitat. This would lead to high quality microhabitats having a lower immigration, the opposite relationship of what we observed at the larger spatial scale. At these smaller scales where the spatial grain of the study corresponds to the size of territory that can be defended, turnover should correspond to habitat quality (Winker et al. 1995). Dominant individuals who are unlikely to be displaced should inhabit the best microhabitats, this leads to lower turnover in high quality habitats. Calculating turnover would require individual identification of fishes or video to measure how long individuals spent at each location. However, based on our experiences collecting underwater video data, we did not expect this approach to yield usable data. Instead, we argued that more attractive habitats would be more likely to be occupied than less attractive locations. This led us to decide on a revised camera sampling regime based on time lapse photographs to measure site occupancy.

Methods

To test the hypothesis that habitat context (i.e. a rocky vs sandy site) affects the attractiveness of boulders, we added artificial boulders to sandy and rocky sites of two rivers: the Salmon Trout River, Marquette County, and the West Branch of the Sturgeon River, Baraga County.

We followed a Before-After-Control-Impact-Paired design. We collected data at locations within sandy and rocky sites before the addition of artificial boulders, and again after the addition. To control for any temporal variation we paired locations of artificial boulders with reference locations. We predicted that salmonids would be more likely to use a boulder in a sandy site (i.e., in an aggraded reach) than in a less sandy site in a less aggraded reach (Figure 4.1).

We sampled sandy and rocky sites in the Salmon Trout River and the West Branch of the Sturgeon River. These reaches had a relatively uniform substrate (either embedded or exposed large substrates) 250m in both the upstream and downstream directions. This ensured that the sedimentation observed in the reach is due to larger scale differences in sediment regimes and not local effects (e.g. a beaver dam or road crossing).

Within each site we randomly selected 8 sampling locations within the center 2/3 of the stream to ensure sufficient depth for the cameras and minimize edge effects. Each of these locations was separated by at least 10 meters. I chose this spacing to keep reaches small enough to be relatively homogenous (i.e. exclude deep pools and/or large woody debris jams that may not be represented in both contexts) but large enough that fish at one sampling location could not monitor the occupancy of other sampling locations without moving. We then randomly assigned sampling locations to a treatment (control or boulder addition). We sampled each location before the boulder addition, then again 1-2 weeks after the boulder addition and compare changes in habitat use between treatments and reaches after the boulder additions. Figure 4.1 provides a graphical representation of the sampling regime within each river. At each location we measured the water depth and water velocity using a Marsh-McBirney flowmate with an integrated wading rod. We took measurements at 0m, .5m and 1m directly downstream of the boulder or pin at each location both before and after the boulder addition.

Data was collected within each river on 5 consecutive days both before and after the boulder addition. Each day we sampled a randomly selected set of 4 sampling locations within the river. Sampling was limited to a maximum of 4 locations by the number of cameras; to reduce the influence of temporal variation each day I sampled 2 locations from the sandy site and 2 locations from the rocky site. For each sample I deployed GoPro Hero 3 cameras equipped with Cam-Do intervalometers (CamDo Solutions Inc., Vancouver, British Columbia). The intervalometer allows a GoPro video camera to capture time lapsed still images. Cameras were set to take a photo every 3-6 minutes, this allowed cameras to operate from dawn to dusk. At each sampling site cameras were deployed 1.25m downstream of a focal point marked by a colored pin or an artificial boulder. These focal points helped define the field of view and ensured that fields of view were similar during multiple samples. Pre boulder addition samples were collected between July 20 and July 24 at the West Branch of the Sturgeon River and July 12-16 at the Salmon Trout River. Boulders were added July 24, 2015 at the West Branch of the Sturgeon and July 18, 2015 in the Salmon Trout River. Data collection after the boulder addition occurred August 26-September 1, 2015 in the West Branch of the Sturgeon and August 9-13, 2015 in the Salmon Trout River.

Data Analysis

I used ImageJ to score each usable image by enumerating the number of fish in each frame and each fish's location within the image. I considered any image with the focal point visible useable, and I scored the entire field of view for each usable image. I estimated occupancy by calculating catch per unit effort: dividing the total number salmonids observed by the total number of usable frames. I also calculated the average number of salmonids in frames containing salmonids. This metric is similar to density and is a metric of how often multiple fish were using this sampling location. I also plotted the location in the frame of each fish observed to test if there were any changes in how fish used each location after the boulder addition.

Results

The addition of boulders created areas of lower velocity within the river (Figure 6 and 7). However, the boulders did not appear to create any significant scouring, because there was not an increase in depth at the boulder addition sites, relative to the reference sites (Figures 4 and 5). Conversely, in the rocky sites the slower water appeared to encourage sediment aggradation as water depths actually declined relative to the reference sampling locations (Figures 4 and 5).

The time lapse cameras captured approximately 10,000 images, and of these 5,699 had sufficient lighting to count fish. The large number of discarded photos was because sampling continued through the night on most deployments. In the Salmon Trout River, catch per unit effort ranged from 4.6 fish/frame to 0 fish/frame, and was especially low in the sandy site (Table 4.1). Very few fish were observed in the West Branch of the Sturgeon River, which overall had a catch per unit effort of only 0.05 fish/frame (Table 4.2). Across both rivers, catch per unit effort in the sandy sites were very low and did not change after the boulder addition (Figure 4.3). In the rocky sites there was actually a relative decline in the catch per unit effort at sampling locations with boulders (Figure 4.3).

We observed some changes in where fish were located within the habitat at individual sampling locations, but there was no clear pattern within or between sites (Figures 4.4-4.35).

Discussion

Stewart et al (2008) conducted a review of instream structure restorations and found that in similar small scale interventions, the addition of instream stuctures did not reliable attract more fish to these sites. We were not deterred by this finding because the studies cited by Stewart et al (2008) mainly used snapshot estimates of density, which we found to be highly variable in this river (Chapter 3). Estimating occupancy using time lapse cameras addresses some of this variation by incorporating observations from hundreds of samples throughout the day, not just a single snorkel or electrofishing survey. Further, observations made during previous sampling also suggested that this design would likely increase fish occupancy in the sandy sites. Fish appeared to use any available structure in the sandy parts of the Salmon Trout River, like ripples in the sand, and YSI sonde cases etc. (personal observation).

However, we did not observe the hypothesized response to the boulder addition. The boulders may have failed to increase occupancy in sandy sites because in the sandy sites much of the boulder got buried (personal observation). One goal of the boulder addition was to locally increase scour, creating pockets of deeper water, but this did not occur. The habitats behind the boulders were relatively shallow (Tables 4.3 and 4.4) and had very little cover (personal observation). Since the boulder habitats were very exposed and fish may not have used the boulders the risk of avian predation (Lonzarich and Quinn 1995). Future additions of boulders in sandy sites should consider adding multiple boulders forming a vane structure that increases scour (Radspinner et al. 2010) which may result in deeper habitats that will be more likely to be occupied.

In the rocky site, boulders appeared to actually decrease occupancy, but this relationship is driven by a single observation. Catch per unit effort within sampling location Reference 2 increased by an order of magnitude after the boulder addition (Table 4.1). This increase appears to be mainly driven by multiple individuals using the habitat simultaneously (Table 4.1). This increased the catch per unit effort in the reference sampling location causing boulder sampling locations to decrease in occupancy relative to the references. This evidence suggests to us that how fish use microhabitats is highly variable and overall it appears the boulder addition did not affect occupancy within either site

The use time lapse cameras allowed us to capture multiple samples simultaneously over the course of a day. This helps to account for minute to minute and hour to hour variation in habitat use. Sampling the same sampling location over multiple days could have also provided an estimate of the variability in habitat use over daily time steps. We accounted for this variation by randomly sampling over time. However while this reduces the risk of bias it converts that daily variation into noise. In future time lapse work, we recommend using more cameras so that all sites can be sampled simultaneously eliminating this source of variation.

Our analyses lead us to conclude that while further study of these questions may be warranted in the future, further data collection utilizing time lapse cameras and single boulders in these systems is unlikely to yield useful results.

Table 4.1. Total number of salmonids observed, catch per unit effort (CPUE) and the mean number of salmonids in photos where salmonids are present before and after the addition of boulders in the Salmon Trout River Locations are numbered in a downstream to upstream direction.

			Before Boulder Addition			After Boulder Addition		
Reach	Sampling Location	Treatment	Total Salmonids Observed	CPUE	Mean number of salmonids in photos where salmonids are present	Total Salmonids Observed	CPUE	Mean number of salmonids in photos where salmonids are present
Rocky	1	Boulder	47	0.8	1.3	177	1.4	1.5
	2	Reference	4	0.1	1.0	22	0.2	1.2
	3	Reference	10	0.4	1.4	636	4.6	4.9
	4	Boulder	335	2.6	2.7	31	0.2	1.0
	5	Boulder	12	0.2	1.1	13	0.1	1.1
	6	Boulder	34	0.5	1.3	47	0.4	1.1
	7	Reference	16	0.4	1.3	179	1.3	1.7
	8	Reference	38	0.6	1.4	271	1.9	2.2
Sandy	1	Boulder	0	0.0	-	0	0.0	-
	2	Reference	33	0.8	1.1	2	0.0	1.0
	3	Reference	0	0.0	-	0	0.0	-
	4	Boulder	0	0.0	-	0	0.0	-
	5	Boulder	0	0.0	-	0	0.0	-
	6	Reference	4	0.1	1.0	0	0.0	-
	7	Boulder	0	0.0	-	0	0.0	-
	8	Reference	1	0.0	1.0	73	0.6	1.0

Table 4.2. Total number of salmonids observed, catch per unit effort (CPUE) and the mean number of salmonids in photos where salmonids are present before and after the addition of boulders in the West Branch of the Sturgeon River Locations are numbered in a downstream to upstream direction

			Before Boulder Addition			After Boulder Addition		
Context	Sampling Location	Treatment	Total Salmonids Observed	CPUE	Mean number of salmonids in photos where salmonids are present	Total Salmonids Observed	CPUE	Mean number of salmonids in photos where salmonids are present
Rocky	1	Boulder	23	0.4	1.0	15	0.1	1.0
	2	Reference	0	0.0	-	22	0.2	1.0
	3	Boulder	12	0.2	1.0	5	0.0	1.0
	4	Reference	0	0.0	-	8	0.1	1.0
	5	Reference	2	0.0	1.0	1	0.0	1.0
	6	Boulder	0	0.0	-	0	0.0	-
	7	Boulder	2	0.0	1.0	12	0.1	1.0
	8	Reference	2	0.0	1.0	9	0.1	1.1
Sandy	1	Boulder	4	0.1	1.3	3	0.0	1.0
	2	Reference	0	0.0	-	0	0.0	-
	3	Boulder	0	0.0	-	0	0.0	-
	4	Reference	0	0.0	-	0	0.0	-
	5	Boulder	0	0.0	-	58	0.4	1.1
	6	Reference	0	0.0	-	2	0.0	1.0
	7	Reference	1	0.0	1.0	0	0.0	-
	8	Boulder	1	0.0	1.0	1	0.0	1.0

Table 4.3. Average Water depth and velocity in the rocky and sandy sites of the Salmon Trout River. Before the boulder addition data was collected between July 17-18, 2015 and after the boulder addition data was collected between August 14-17, 2015. Depth and Velocity were measured at 0m, 0.5m and 1m downstream of the focal point at each sampling location, the mean of these three measurements is shown below. Standard deviations are shown in parenthesis.

			Before Boulder Addition		After Boulder Addition	
	Sampling Location	Treatment	Depth (m)	Velocity (m/s)	Depth (m)	Velocity (m/s)
Rocky	1	Boulder	0.31 (0.01)	0.41 (0.05)	0.31 (0.08)	0.12 (0.16)
	2	Reference	0.34 (0.03)	0.83 (0)	0.6 (0.08)	0.6 (0.08)
	3	Reference	0.49 (0.01)	0.26 (0.04)	0.46 (0.01)	0.19 (0.02)
	4	Boulder	0.59 (0.03)	0.33 (0.01)	0.59 (0.03)	0.14 (0.1)
	5	Boulder	50.67 (1.15)	0.43 (0.06)	0.45 (0.02)	0.1 (0.18)
	6	Boulder	43.33 (3.06)	0.45 (0.02)	0.42 (0.04)	0.04 (0.07)
	7	Reference	79 (2.65)	0.17 (0.04)	0.75 (0.03)	0.17 (0.02)
	8	Reference	58 (5.57)	0.09 (0.05)	0.59 (0.05)	0.13 (0.03)
Sandy	1	Boulder	0.58 (0.06)	0.27 (0.02)	0.51 (0.08)	0.13 (0.12)
	2	Reference	0.73 (0.12)	0.15 (0.02)	0.26 (0.01)	0.34 (0.04)
	3	Reference	15.91 (26.92)	0.38 (0.07)	0.27 (0.03)	0.4 (0.04)
	4	Boulder	0.36 (0.01)	0.36 (0.06)	0.3 (0.04)	0.37 (0.1)
	5	Boulder	0.38 (0.02)	0.39 (0.03)	0.35 (0.01)	0.17 (0.19)
	6	Reference	0.37 (0.01)	0.28 (0.02)	0.34 (0.02)	0.32 (0.01)
	7	Boulder	0.35 (0.01)	0.4 (0.03)	0.29 (0.02)	0.19 (0.05)
	8	Control	0.54 (0.11)	0.34 (0.01)	0.5 (0.12)	0.27 (0.05)

Table 4.4. Average Water depth and velocity in the rocky and sandy sites of West Branch of the Sturgeon River. Before the boulder addition data was collected on July 24, 2015 and after the boulder addition data was collected on August 26, 2015. Depth and Velocity were measured at 0m, 0.5m and 1m downstream of the focal point at each sampling location, the mean of these three measurements is shown below. Standard deviations are shown in parenthesis.

			Before Boulder Addition		After Boulder Addition	
	Sampling Location	Treatment	Depth (m)	Velocity (m/s)	Depth (m)	Velocity (m/s)
Rocky	1	Boulder	0.44 (0.03)	0.26 (0.02)	0.42 (0.02)	0.15 (0.15)
	2	Reference	0.46 (0.03)	0.32 (0.1)	0.44 (0.03)	0.27 (0.05)
	3	Boulder	0.39 (0.03)	0.22 (0.03)	0.37 (0.05)	0.1 (0.09)
	4	Reference	0.57 (0.03)	0.2 (0.02)	0.52 (0.02)	0.19 (0.03)
	5	Reference	0.48 (0.01)	0.19 (0.03)	0.54 (0.01)	0.14 (0.03)
	6	Boulder	0.43 (0.01)	-0.06 (0.01)	0.42 (0.02)	-0.01 (0.02)
	7	Boulder	0.22 (0.03)	0.36 (0.06)	0.19 (0.01)	0.04 (0.06)
	8	Reference	0.92 (0.07)	0.08 (0.04)	0.64 (0.43)	0.09 (0.03)
Sandy	1	Boulder	0.35 (0.02)	0.44 (0.03)	0.37 (0.01)	0.15 (0.14)
	2	Reference	0.33 (0.05)	0.31 (0.04)	0.32 (0.01)	0.32 (0.02)
	3	Boulder	0.32 (0.01)	0.42 (0.02)	0.35 (0.03)	0.17 (0.14)
	4	Reference	0.35 (0.04)	0.32 (0.03)	0.37 (0.02)	0.29 (0.03)
	5	Boulder	0.45 (0.11)	0.31 (0.09)	0.51 (0.09)	0.29 (0.06)
	6	Reference	0.44 (0.01)	0.41 (0.05)	0.44 (0.02)	0.31 (0.02)
	7	Reference	0.32 (0.04)	0.33 (0.03)	0.29 (0.02)	0.28 (0.03)
	8	Boulder	0.29 (0.01)	0.34 (0.02)	0.3 (0.03)	0.12 (0.13)

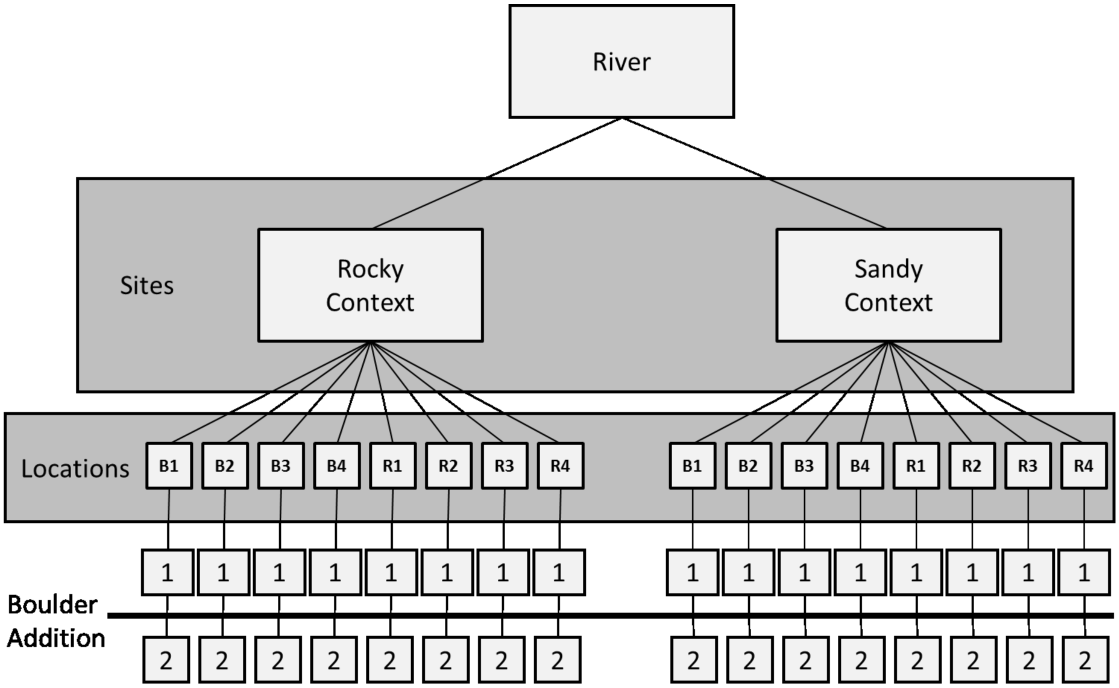


Figure 4.1. Graphical representation of the sampling regime within the Salmon Trout River and the West Branch of the Sturgeon River. Within each river I selected two 100m sites one site was within a rocky part of the river, the other was sandy. Within each site 8 randomly chosen locations will be assigned to a treatment either a boulder addition or reference location. Each location was be sampled before the boulder addition (1) and then 1-2 weeks after the boulder addition (2).

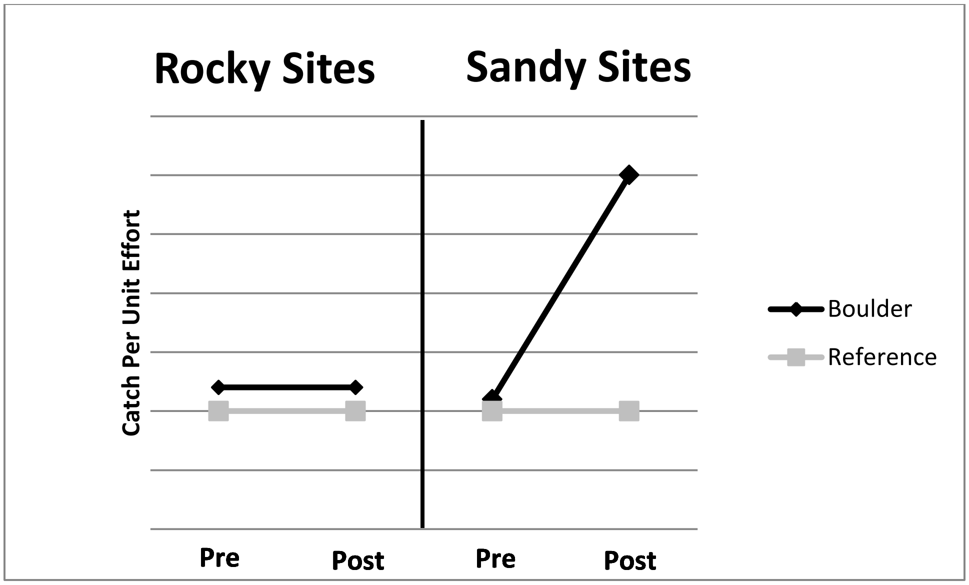


Figure 4.2. Hypothetical effects plot showing they hypothesized response to the boulder addition.

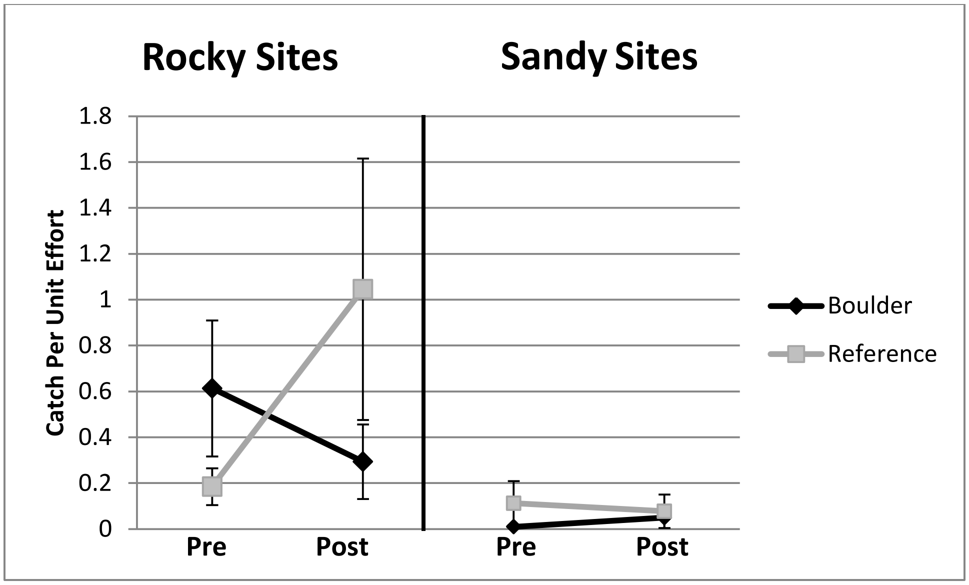


Figure 4.3. Effects plot showing the impact of the boulder addition on salmonid occupancy measured as catch per unit effort, within sandy and rocky reaches in both the Salmon Trout River and the West Branch of the Sturgeon River.

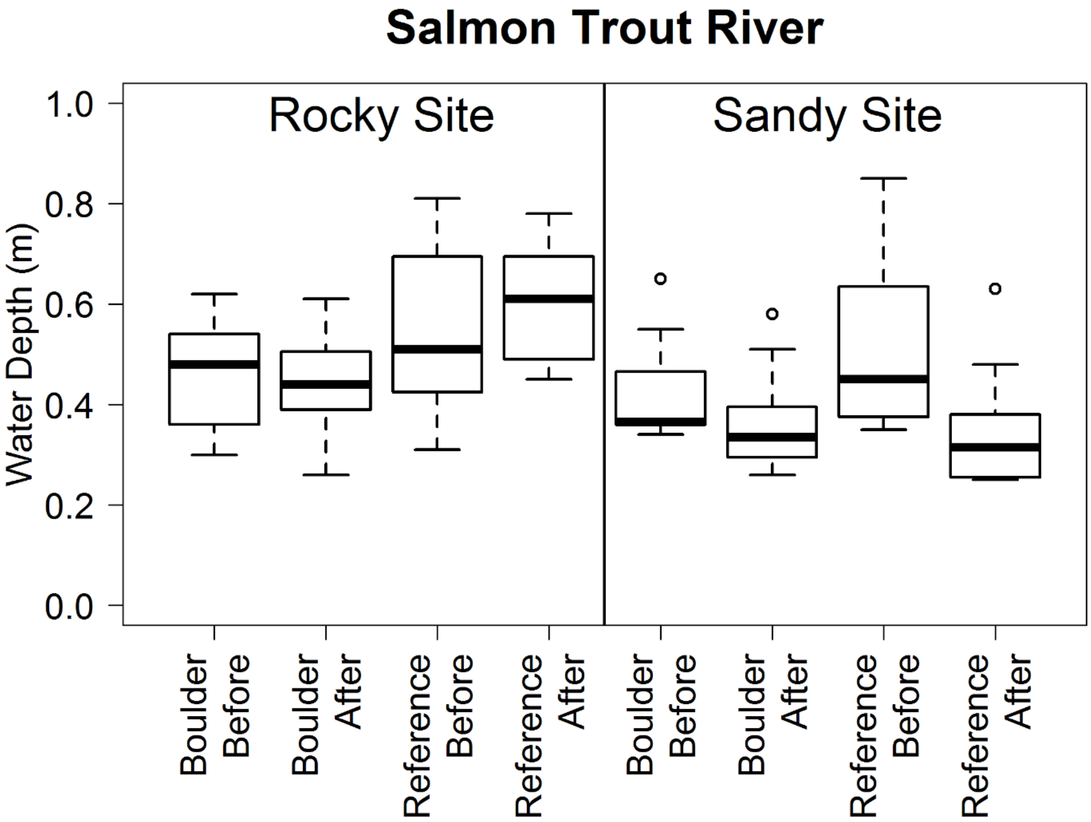


Figure 4.4. Boxplots representing water depth at sampling locations before and after the boulder addition within the Salmon Trout River. Any observation less than or greater than 1.5 times the interquartile distance from the mean is represented as an open circle.

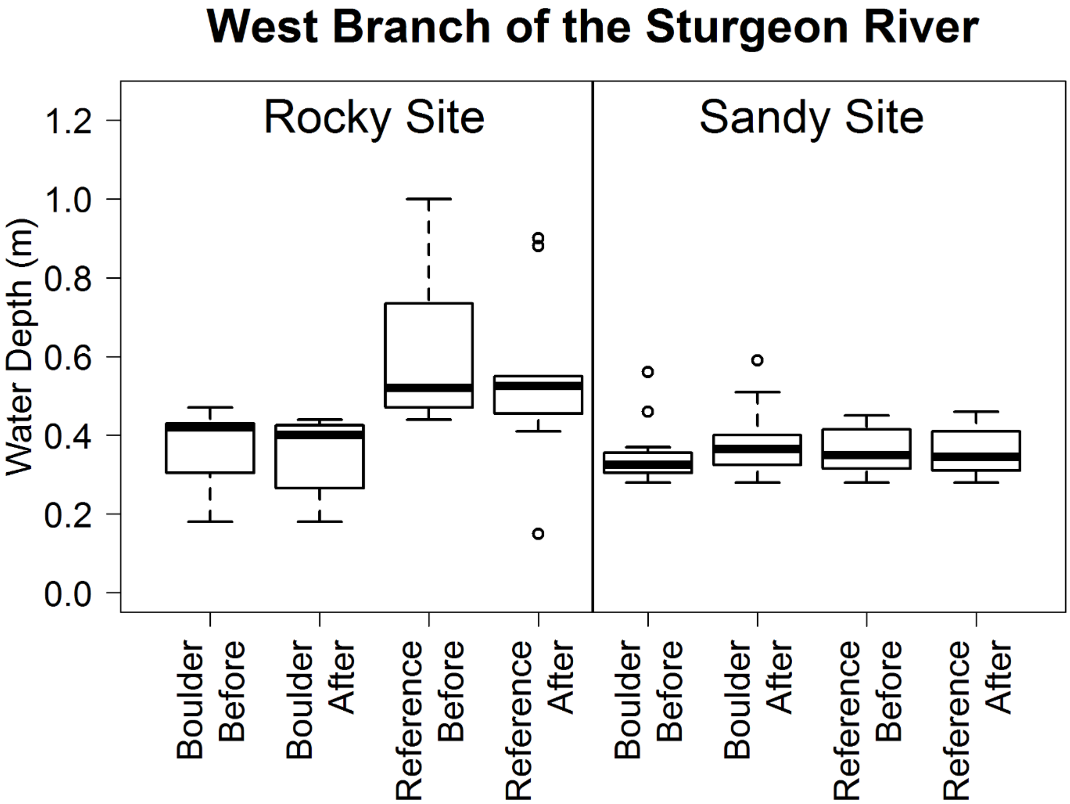


Figure 4.5. Boxplots representing water depth at sampling locations before and after the boulder addition within the West Branch of the Sturgeon River. Any observation less than or greater than 1.5 times the interquartile distance from the mean is represented as an open circle.

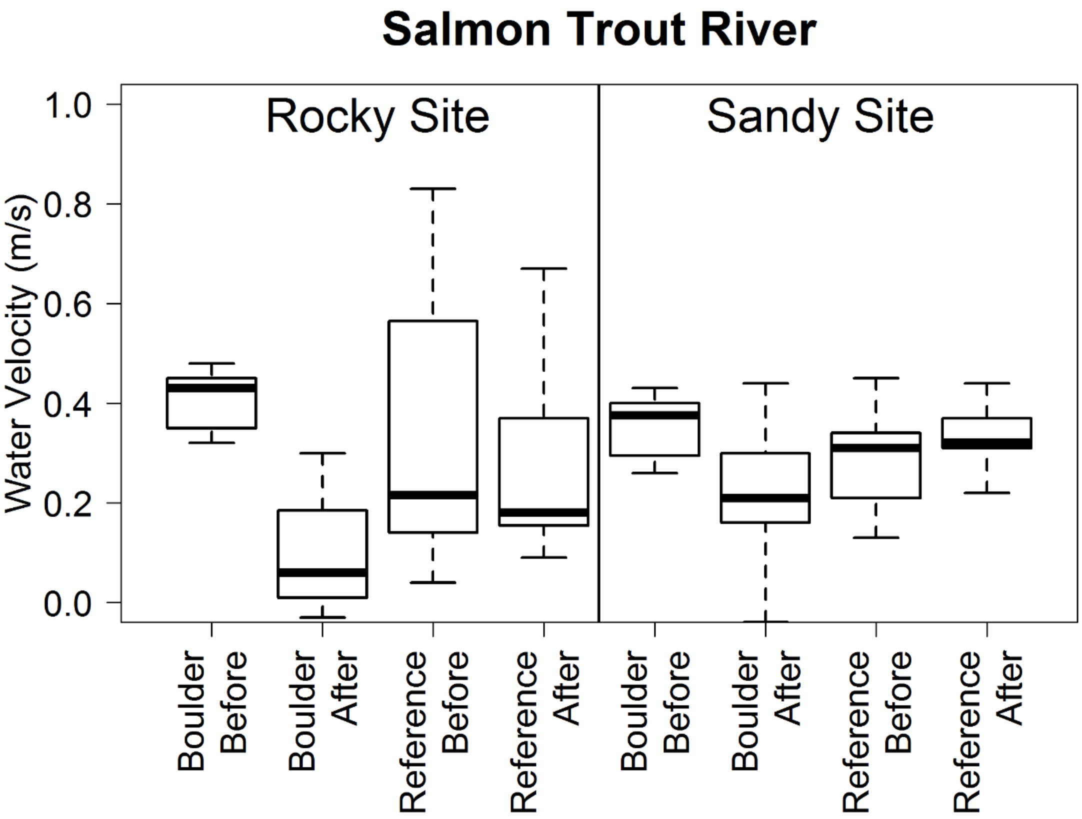


Figure 4.6. Boxplots representing water velocity at Boulder and Reference sampling before and after the boulder addition within the Salmon Trout River.

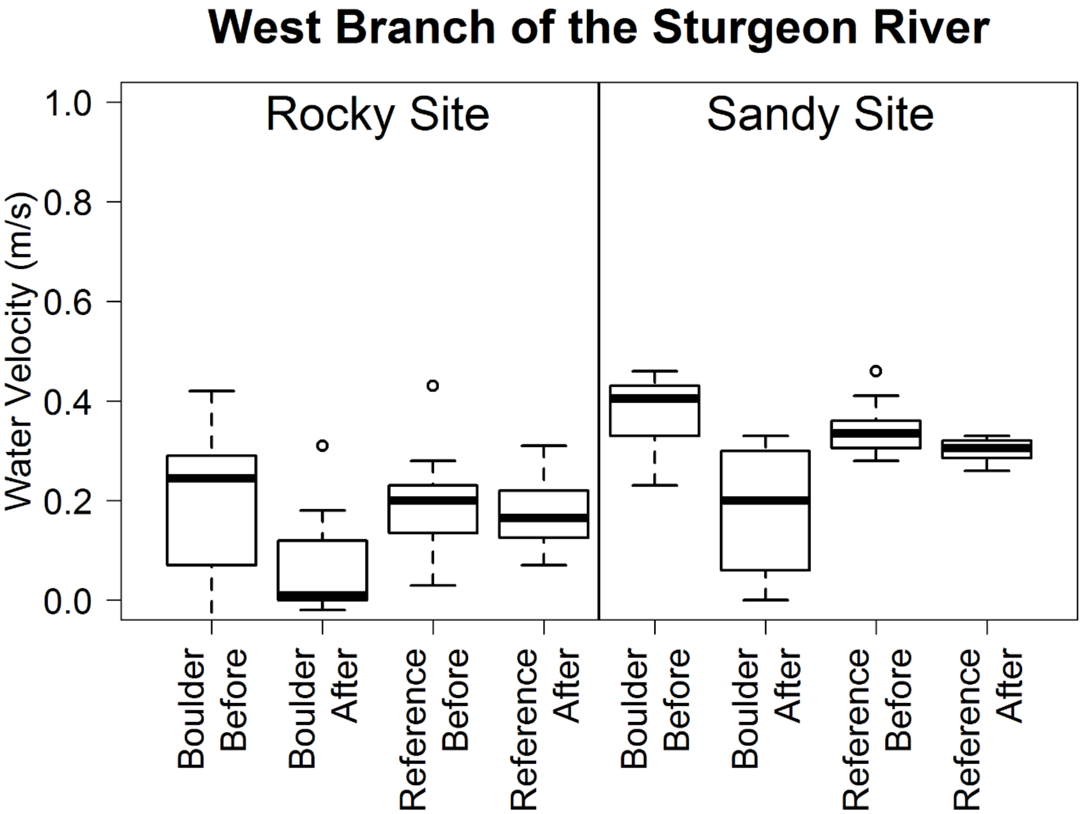
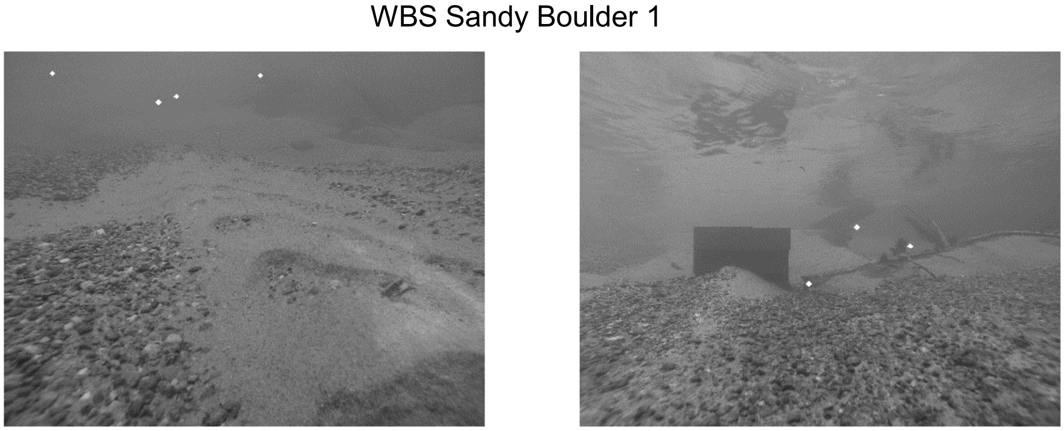


Figure 4.7. Boxplots representing water velocity at sampling locations before and after the boulder addition within the West Branch of the Sturgeon River. Any observation less than or greater than 1.5 times the interquartile distance from the mean is represented as an open circle.



WBS Sandy Boulder 1

Figure 4.8. Composite image showing locations of every observed salmonid within Boulder 1, the first sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

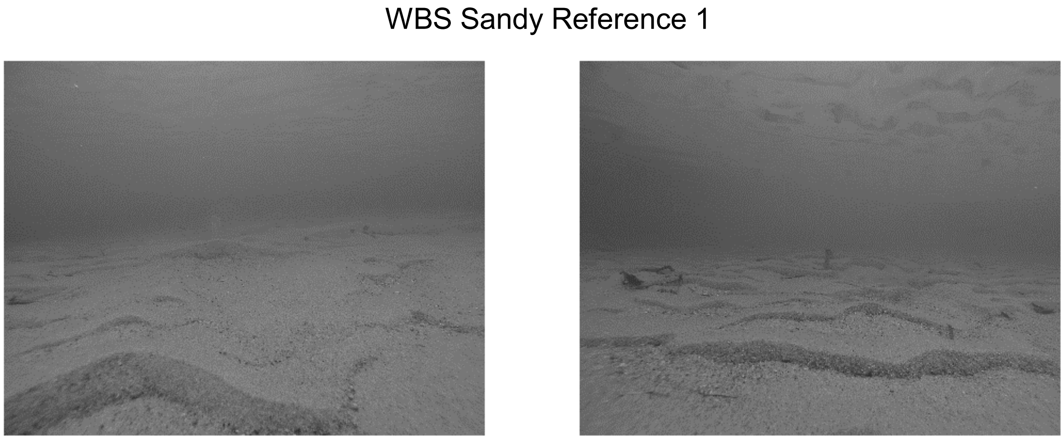
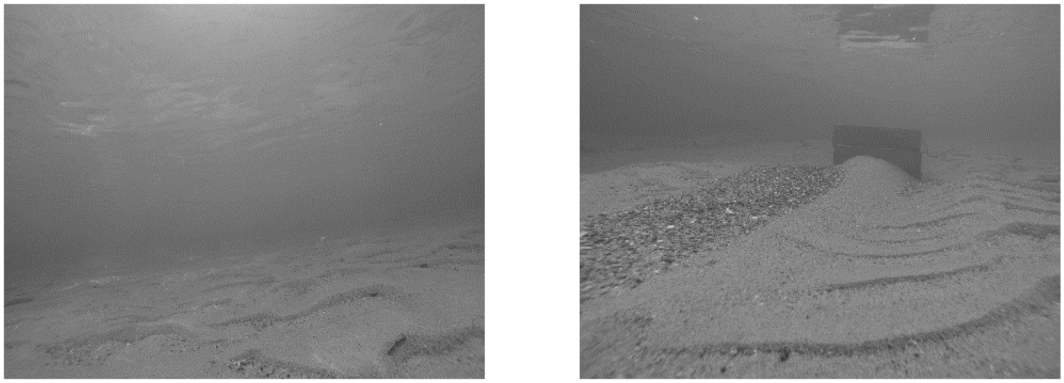


Figure 4.9. Composite image showing locations of every observed salmonid within Reference 1, the second sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Sandy Boulder 2

Figure 4.10. Composite image showing locations of every observed salmonid within Boulder 2, the third sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

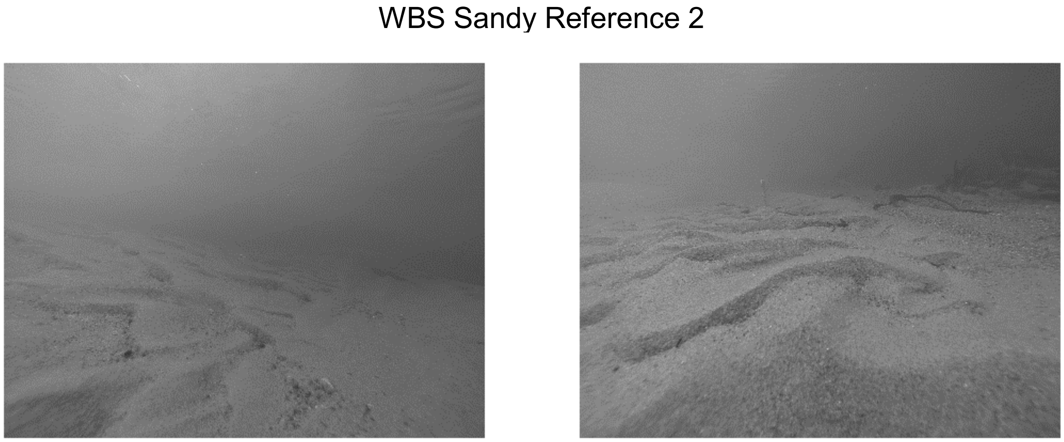
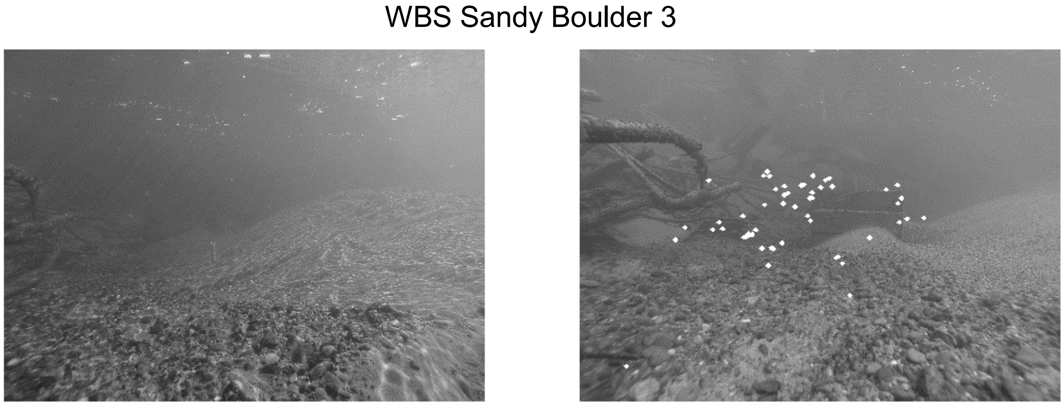
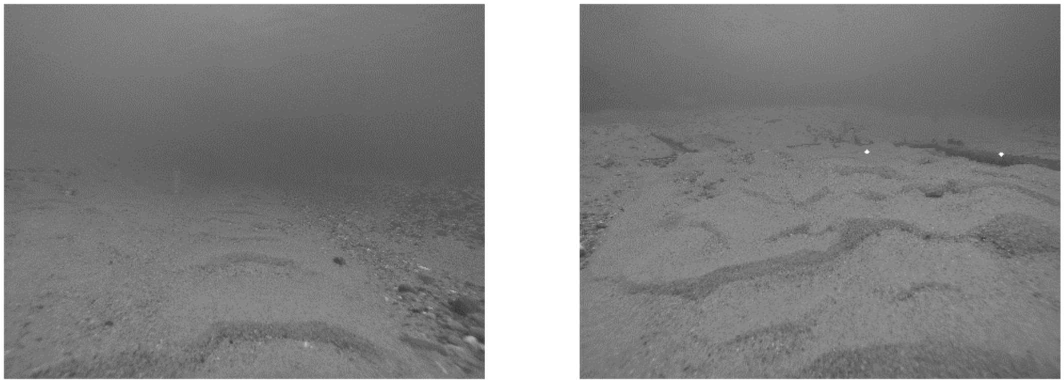


Figure 4.11. Composite image showing locations of every observed salmonid within Reference 2, the fourth sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



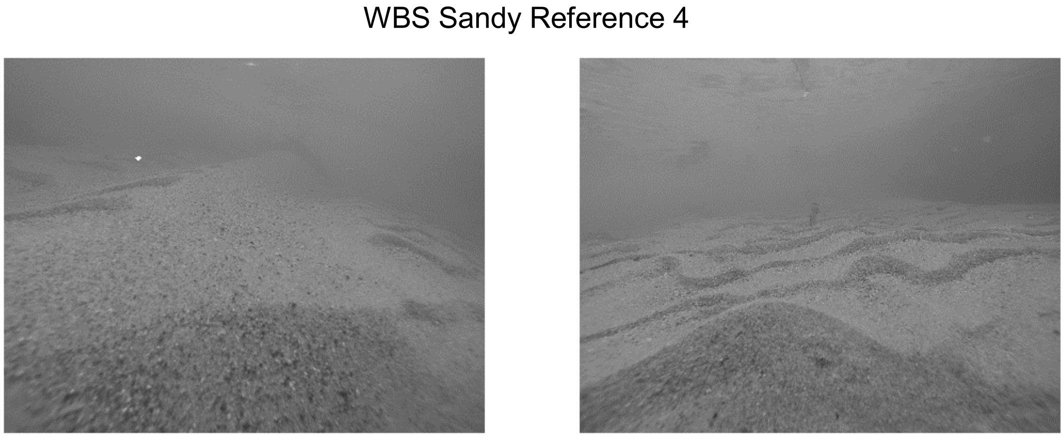
WBS Sandy Boulder 3

Figure 4.12. Composite image showing locations of every observed salmonid within Boulder 3, the fifth sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Sandy Reference 3

Figure 4.13. Composite image showing locations of every observed salmonid within Reference 3, the sixth sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Sandy Reference 4

Figure 4.14. Composite image showing locations of every observed salmonid within Reference 4, the seventh sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

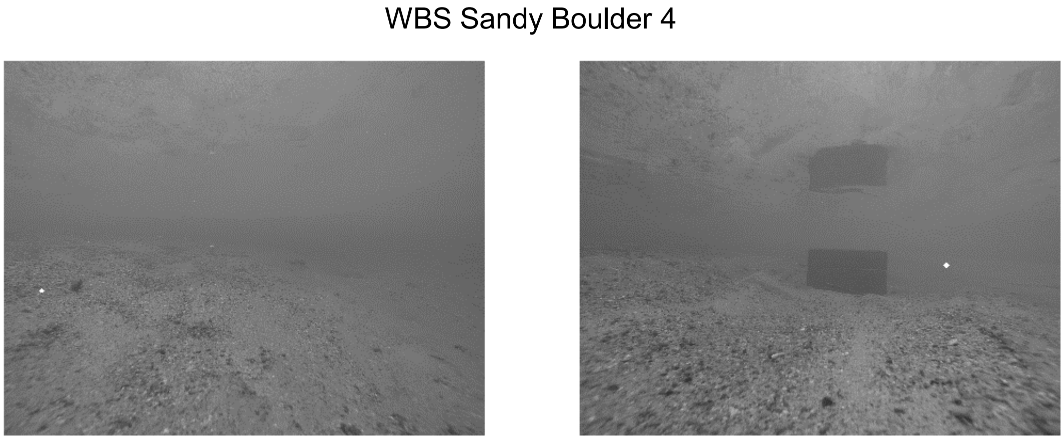


Figure 4.15. Composite image showing locations of every observed salmonid within Boulder 4, the eighth sampling location within the Sandy Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

WBS Rocky Boulder 1

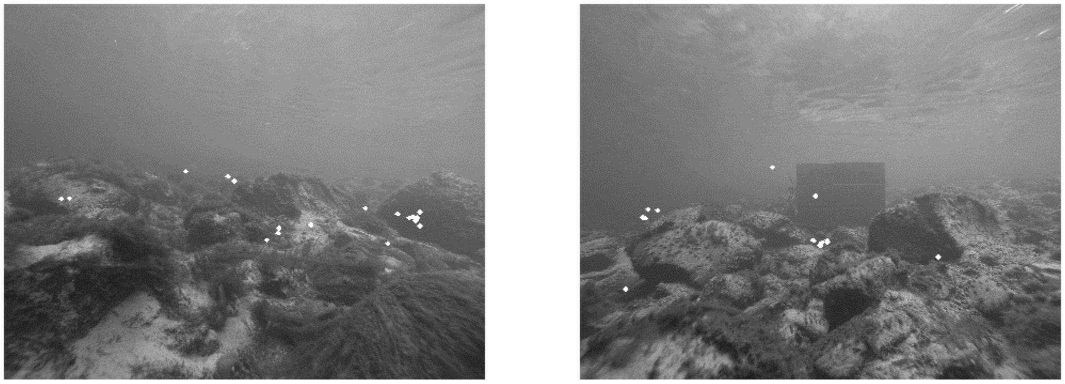


Figure 4.16. Composite image showing locations of every observed salmonid within Boulder 1, the first sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

WBS Rocky Reference 1

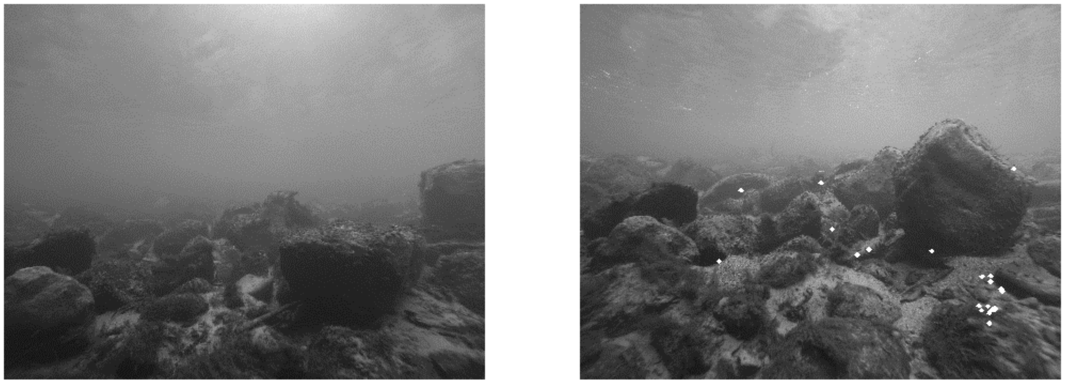
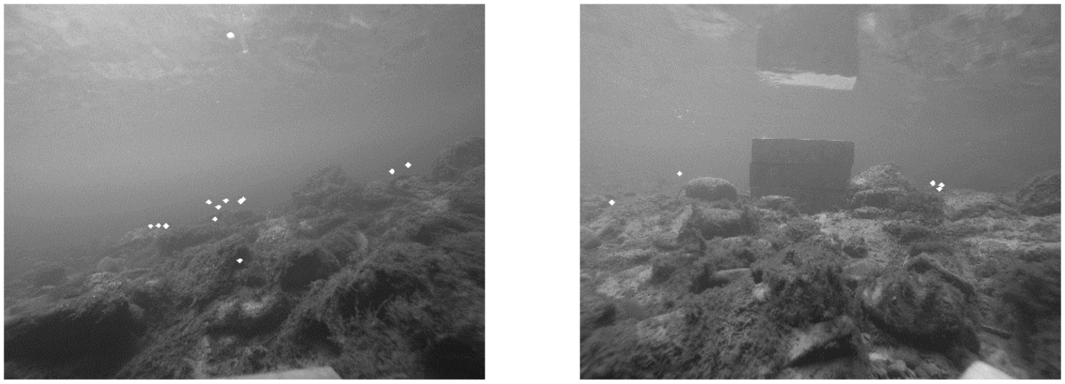


Figure 4.17. Composite image showing locations of every observed salmonid within Reference 1, the second sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Rocky Boulder 2

Figure 4.18. Composite image showing locations of every observed salmonid within Boulder 2, the third sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

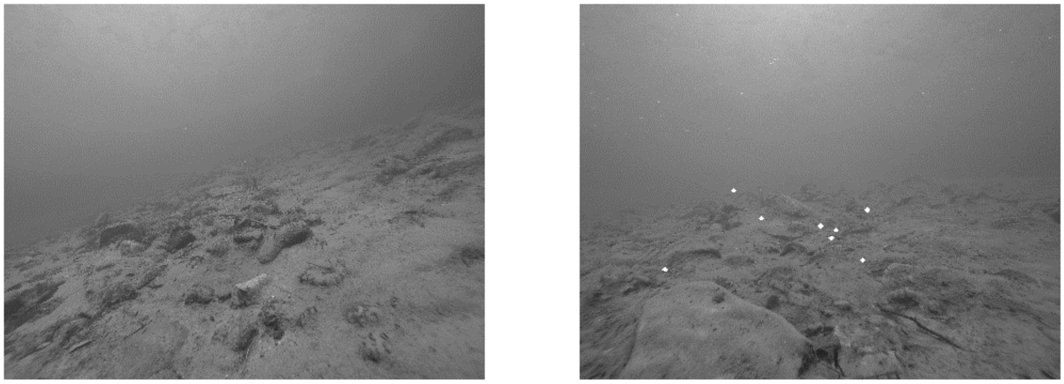
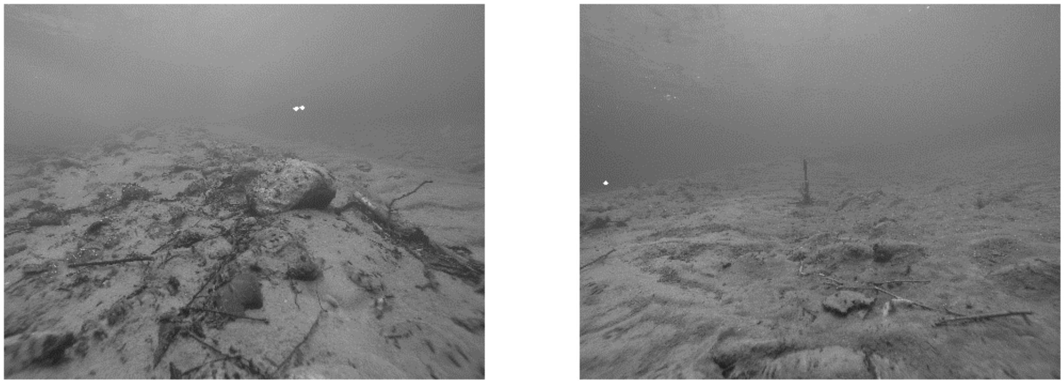
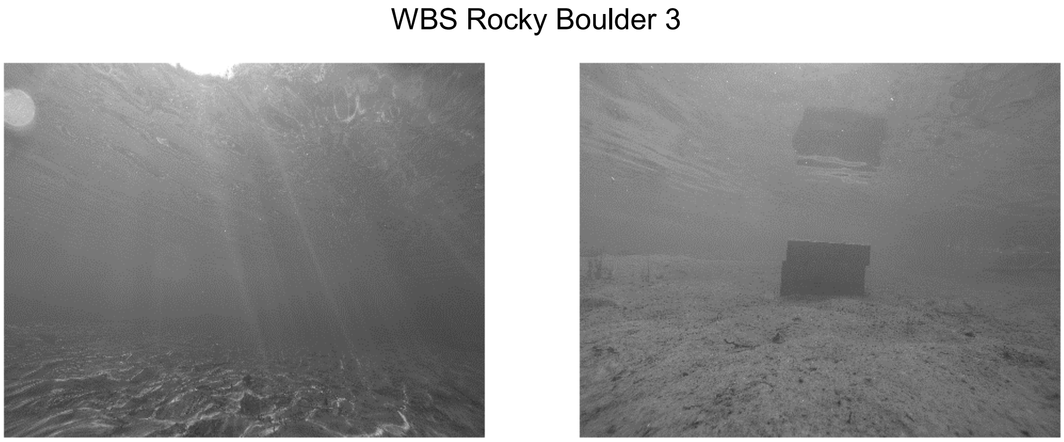

WBS Rocky Reference 2

Figure 4.19. Composite image showing locations of every observed salmonid within Reference 2, the fourth sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Rocky Reference 3

Figure 4.20. Composite image showing locations of every observed salmonid within Reference 3, the fifth sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



WBS Rocky Boulder 3

Figure 4.21. Composite image showing locations of every observed salmonid within Boulder 3, the sixth sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

WBS Rocky Boulder 4

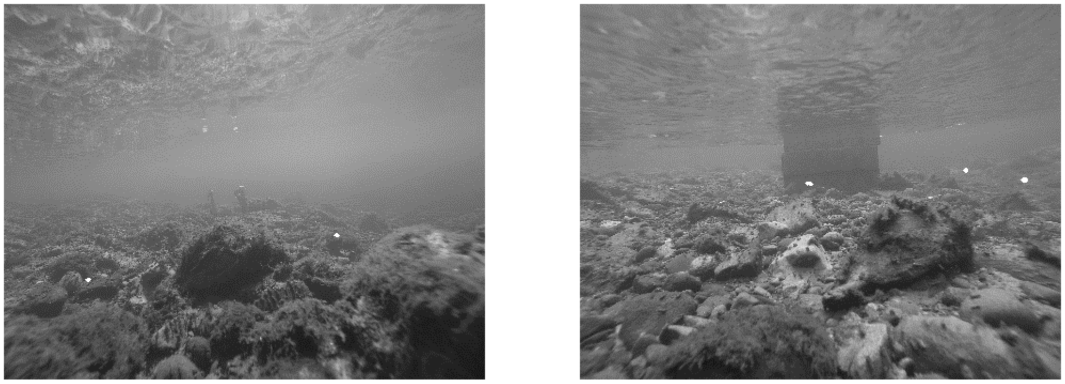


Figure 4.22. Composite image showing locations of every observed salmonid within Boulder 4, the seventh sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

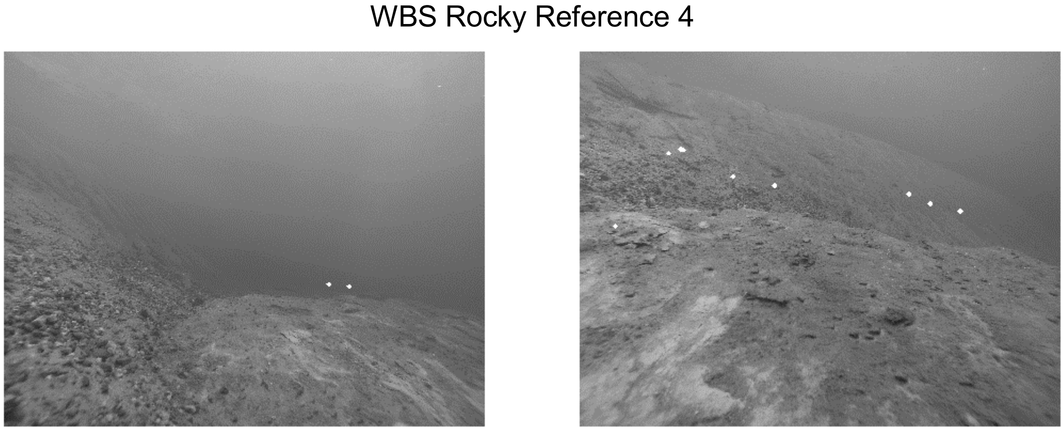
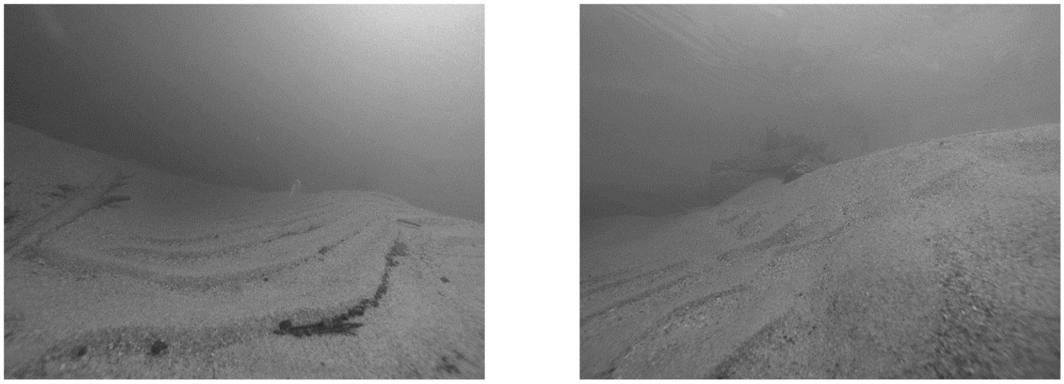


Figure 4.23. Composite image showing locations of every observed salmonid within Reference 4, the eighth sampling location within the Rocky Site of the West Branch of the Sturgeon River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Sandy Boulder 1

Figure 4.24. Composite image showing locations of every observed salmonid within Boulder 1, the first sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

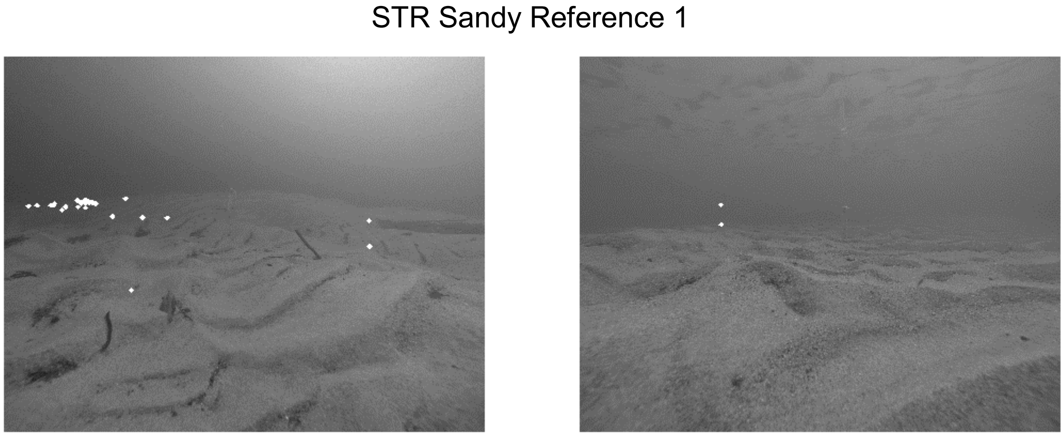
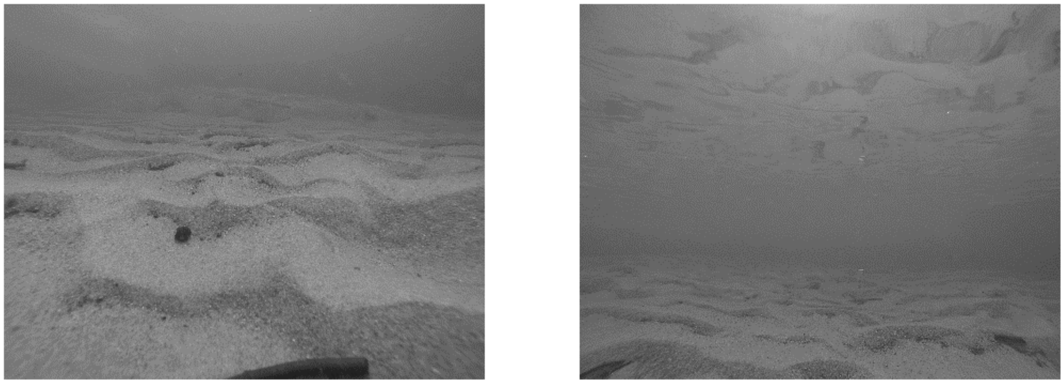


Figure 4.25. Composite image showing locations of every observed salmonid within Reference 1, the second sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Sandy Reference 2

Figure 4.26. Composite image showing locations of every observed salmonid within Reference 2, the third sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

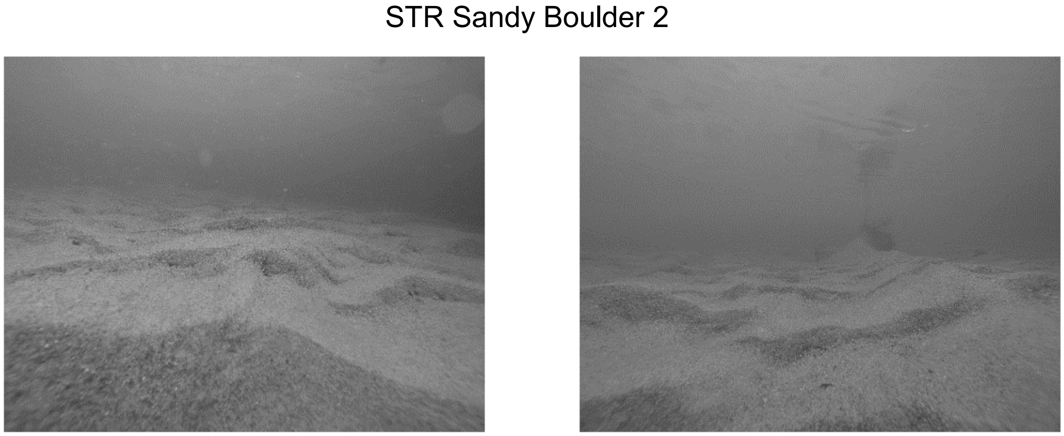


Figure 4.27. Composite image showing locations of every observed salmonid within Boulder 2, the fourth sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Sandy Boulder 3

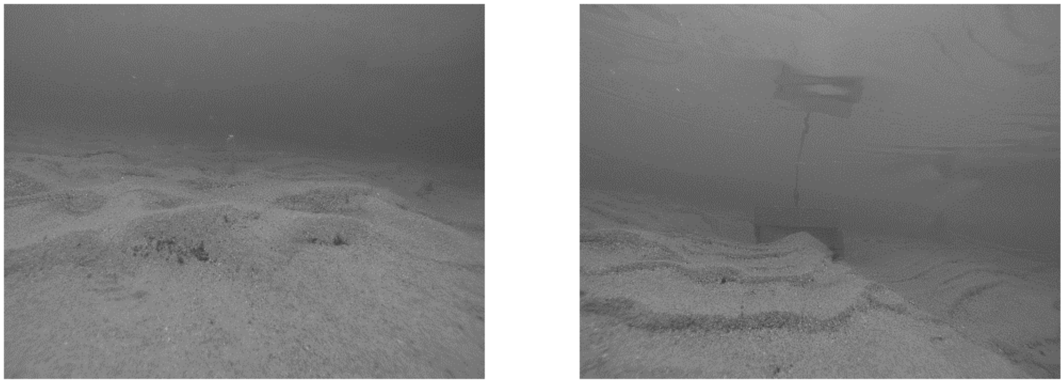


Figure 4.28. Composite image showing locations of every observed salmonid within Boulder 3, the fifth sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Sandy Reference 3

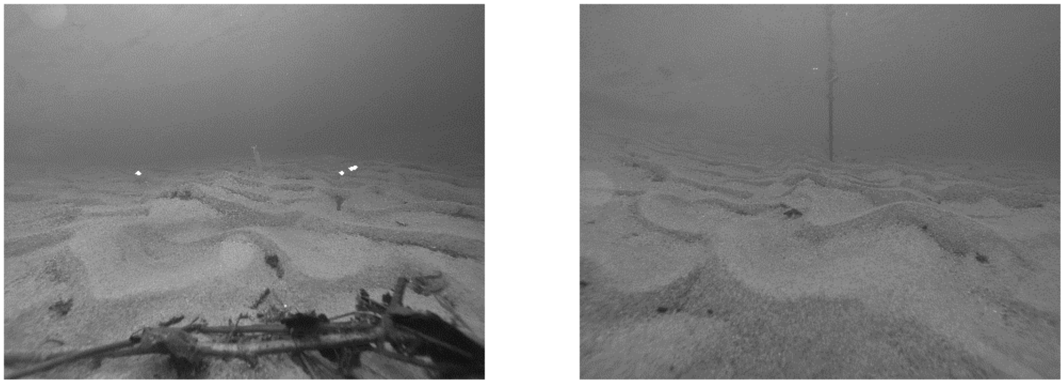
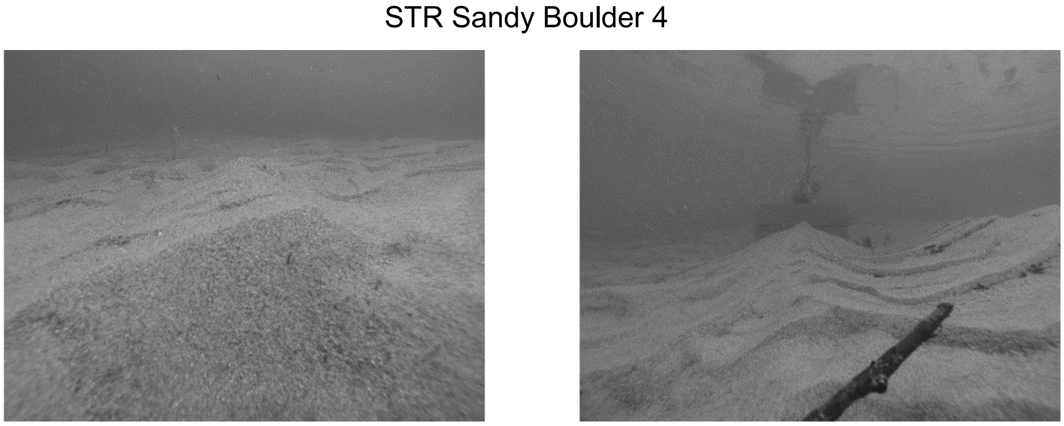


Figure 4.29. Composite image showing locations of every observed i salmonid Reference 3, the sixth sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Sandy Boulder 4

Figure 4.30. Composite image showing locations of every observed salmonid within Boulder 4, the seventh sampling location within the Sandy Site of the Salmon Trout River Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Sandy Reference 4

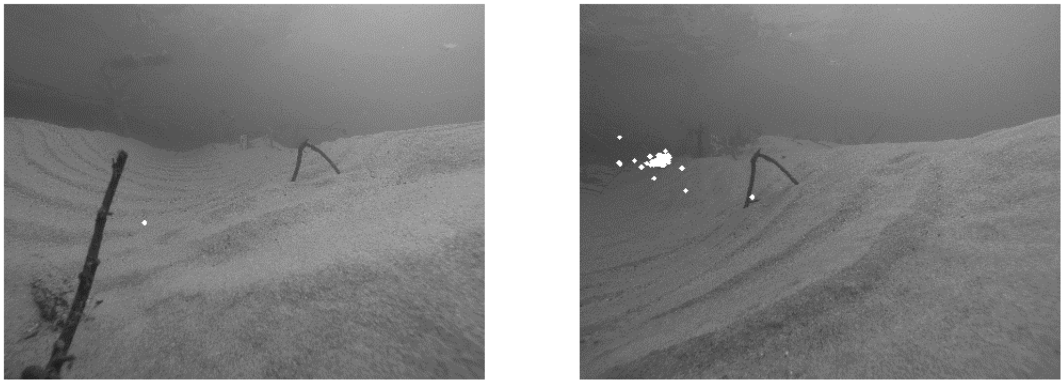


Figure 4.31. Composite image showing locations of every observed salmonid within Reference 4, the eighth sampling location within the Sandy Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Rocky Boulder 1

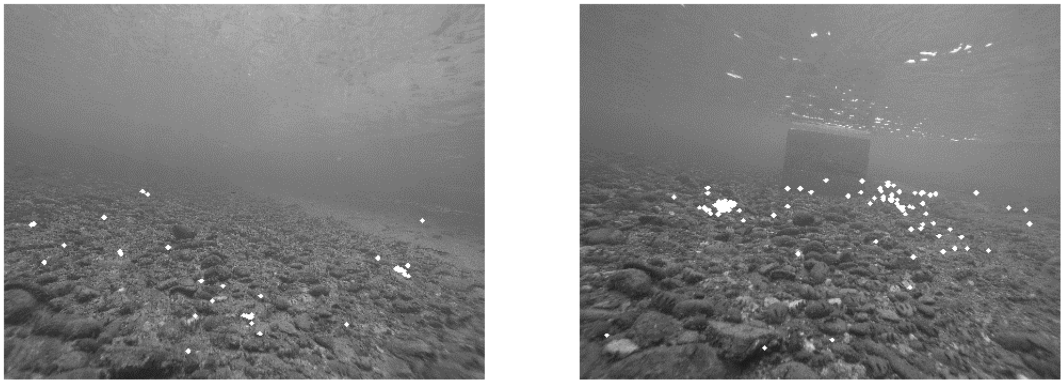
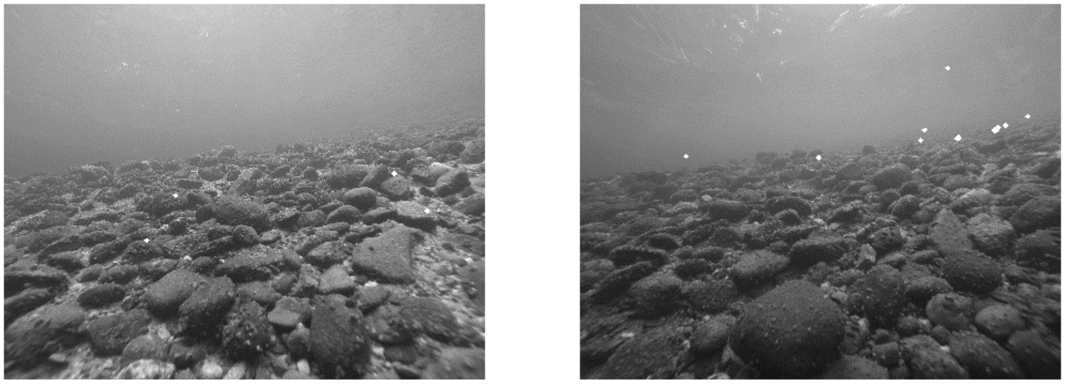


Figure 4.32. Composite image showing locations of every observed salmonid within Boulder 1, the first sampling location within the Rocky Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Rocky Reference 1

Figure 4.33. Composite image showing locations of every observed salmonid within Reference 1, the second sampling location within the Rocky Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Rocky Reference 2

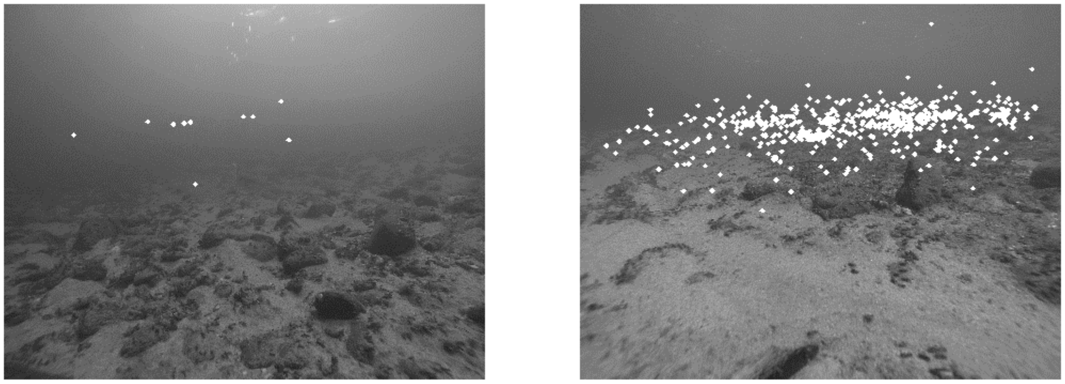
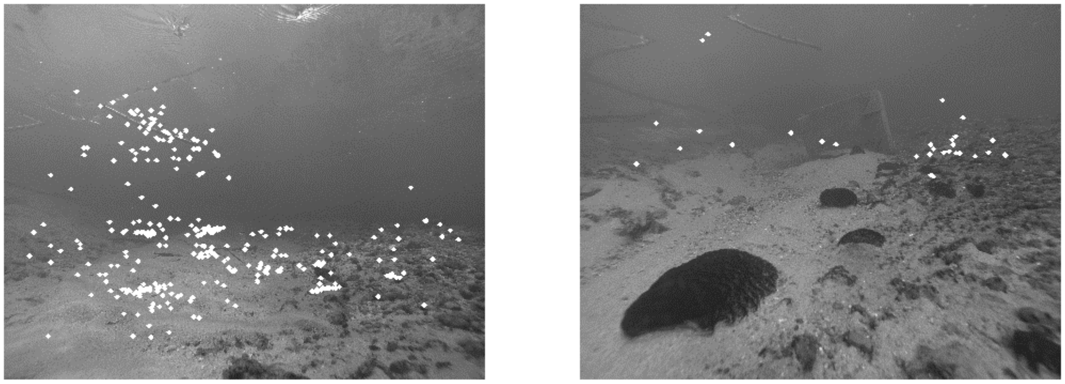
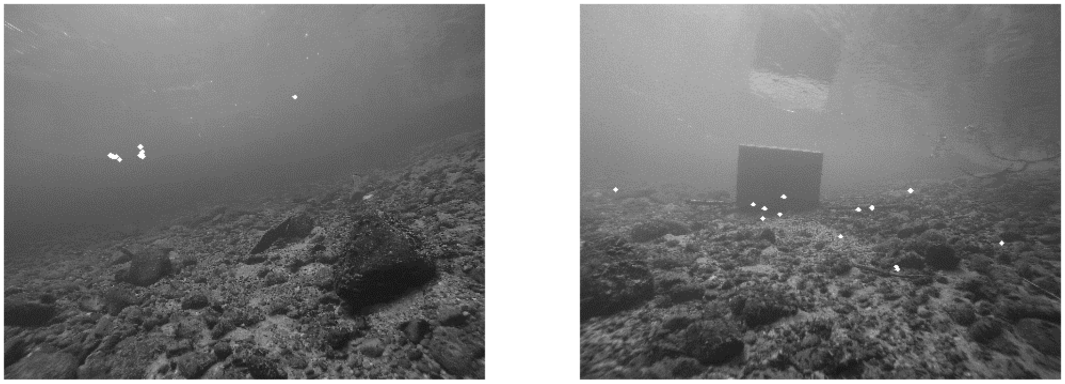


Figure 4.34. Composite image showing locations of every observed salmonid within Reference 2, the third sampling location within the Rocky Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Rocky Boulder 2

Figure 4.35. Composite image showing locations of every observed salmonid within Boulder 2, the fourth sampling location within the Rocky Site of the Salmon Trout River Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Rocky Boulder 3

Figure 4.36. Composite image showing locations of every observed salmonid within Boulder 3, the fifth sampling location within the Rocky Site of the Salmon Trout River Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

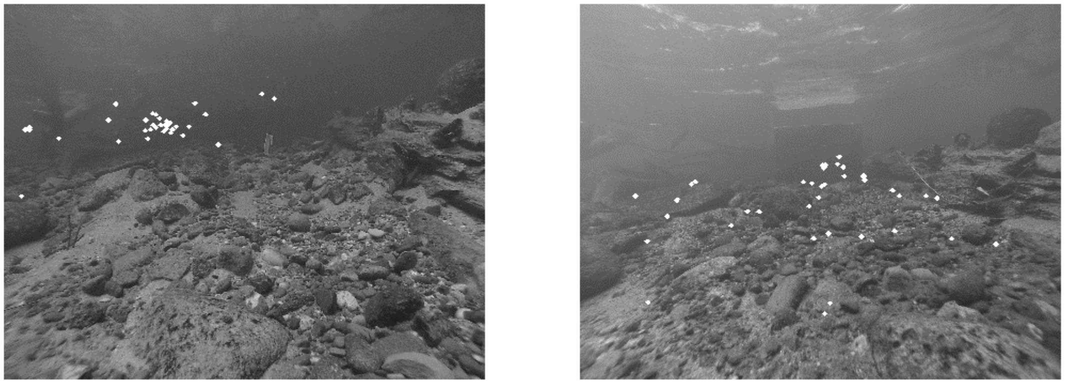
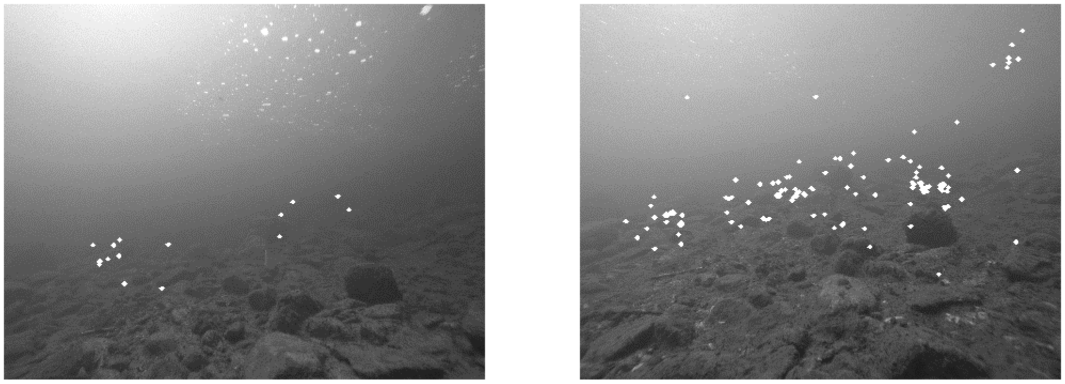


Figure 4.37. Composite image showing locations of every observed salmonid within Boulder 4, the sixth sampling location within the Rocky Site of the Salmon Trout River Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.



STR Rocky Reference 3

Figure 4.38. Composite image showing locations of every observed salmonid within Reference 3, the seventh sampling location within the Rocky Site of the Salmon Trout River Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

STR Rocky Reference 4

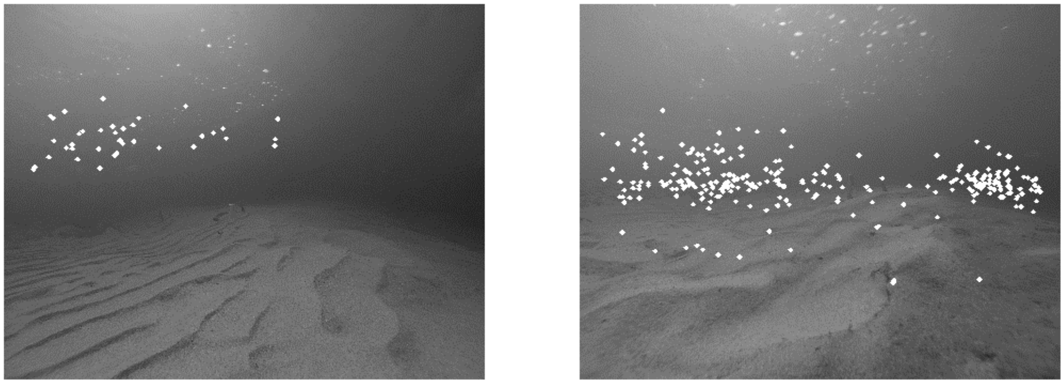


Figure 4.39. Composite image showing locations of every observed salmonid within Reference 4, the eighth sampling location within the Rocky Site of the Salmon Trout River. Locations of fish were measured by identifying the pixel coordinates of the anterior tip of the mouth using ImageJ and plotting the location as a white dot on a representative image.

Appendix 1. Results of snorkeling surveys at the Sandy Snorkel and Rocky Snorkel sites. Two surveys were conducted within 7 days of one another both before and after the nonnative removal during the summer of 2011. LH stands for Local Habitat, which is based mainly on channel geomorphic unit see Tables 1 and 2 for habitat information. Num. represents number or the abundance of a specific species in that sample. Den. stands for density, which corrects for size differences between local habitat sections.

			LH 1		LH 2		LH 4		LH 4		LH 5		LH 6		LH 7		LH 8	
Site	Spp	Sample	Num.	Den.	Num.	Den.	Num.	Den.	Num.	Den.	Num.	Den.	Num.	Den.	Num.	Den.	Num.	Den.
Sandy Snorkel Site	BKT	Pre 1	1	0.01	5	0.049	0	0	0	0	0	0	1	0.008	0	0	1	0.008
		Pre 2	2	0.021	9	0.088	3	0.030	4	0.035	1	0.008	8	0.068	2	0.017	0	0
		Post 1	0	0	1	0.010	1	0.010	2	0.017	2	0.015	4	0.034	3	0.026	2	0.016
		Post 2	0	0	6	0.059	1	0.010	2	0.017	1	0.008	3	0.025	2	0.017	0	0
	CO	Pre 1	6	0.062	27	0.265	22	0.219	29	0.252	23	0.173	13	0.110	27	0.236	40	0.327
		Pre 2	35	0.362	23	0.226	31	0.309	57	0.496	30	0.225	25	0.212	27	0.236	35	0.286
		Post 1	20	0.207	20	0.196	35	0.349	28	0.243	61	0.458	34	0.288	42	0.367	50	0.408
		Post 2	17	0.176	15	0.147	40	0.399	13	0.113	47	0.353	41	0.348	41	0.358	35	0.286
	RBT	Pre 1	4	0.041	4	0.039	4	0.04	5	0.043	4	0.030	3	0.025	4	0.035	0	0
		Pre 2	16	0.166	11	0.108	11	0.11	8	0.070	5	0.038	2	0.017	4	0.035	1	0.008
		Post 1	11	0.114	5	0.049	8	0.08	3	0.026	5	0.038	2	0.017	0	0	0	0
		Post 2	4	0.041	6	0.059	3	0.030	0	0	3	0.023	6	0.051	2	0.017	1	0.008
Rocky Snorkel Site	BKT	Pre 1	3	0.038	3	0.042	7	0.061	2	0.015	2	0.015	3	0.036				
		Pre 2	0	0	4	0.056	1	0.009	4	0.030	3	0.022	3	0.036				
		Post 1	0	0	3	0.042	5	0.043	1	0.007	2	0.015	4	0.047				
		Post 2	1	0.013	2	0.028	3	0.026	9	0.015	1	0.007	5	0.059				
	CO	Pre 1	10	0.125	4	0.056	3	0.026	17	0.067	1	0.007	4	0.047				
		Pre 2	6	0.075	3	0.042	6	0.052	12	0.127	9	0.067	3	0.036				
		Post 1	5	0.063	2	0.028	7	0.061	0	0.089	3	0.022	0	0				
		Post 2	4	0.05	1	0.014	2	0.017	2	0.045	5	0.037	9	0.107				
	RBT	Pre 1	4	0.038	2	0.028	2	0.017	3	0	3	0.022	7	0.083				
		Pre 2	3	0.013	0	0	1	0.009	0	0.015	3	0.022	7	0.083				
		Post 1	1	0.014	0	0	5	0.043	4	0.022	4	0.030	4	0.047				
		Post 2	0	0.01	1	0.014	7	0.061	2	0.007	11	0.081	6	0.071				

Appendix 2. ANOVA table for a repeated measure ANOVA testing for difference of abundances within sites and species before and after a nonnative species removal.

	DF	SS	MS	F	p
Error: Site					
Residuals	1	38721	38721		
Error: Species					
Residual	2	82205	41103		
Within					
Before or After	1	113	113	0.032	0.86
Residuals	19	67163	3535		

Appendix 3. R code used to simulate power.

```
avg<-32.5  #average abundance in a site-32.5 average BKT abundance Observed in 2011
stDev<-10.25  #average standard deviation of site abundance -10.25 average BKT sd Observed in 2011
coef<-avg*c(.1,.2,.3,.4,.5)
years<-5 #years sample before and after change
sites<-1 #number of sites you want to sample Currently designed for only 1 site-code will be wonky/not
work for multiple sites
samples<-1 # number of intra-year samples
dif<-c(seq(from=1.0,to=2,by=.05)) # Percent differences
p<-c()
iterations<-10000
powArray<-array(dim=c(length(coef),length(dif)))
total<- (length(coef)*length(dif)*years*sites*samples +1)*iterations/10
q<-1 #progress bar counter
h<-1 #counter for coef
 pb <- winProgressBar(label= "Simulation 2 progress bar", min = 0, max =total , width = 300)
while(h<=length(coef))
{
  samps<-c()
  pow<-c()
  k<-1   #counter for dif
  while(k<=length(dif)){
    i<-1 #counter for iterations
    while(i<=iterations)
    {
      trend<-array(dim=c(years*2,sites,samples))
      samp<-c()
      n<-1  #counter for samples
      while(n<=samples)
      {
      l<-1 #counter for sites
      while(l<=sites)
      {j<-1 #counter for years
      while(j<=years*2)
      {
       if(j<=years)
         {year<-c(1:years)
        trend[j,l,n]<-mean(rnorm(1,mean=avg,sd=coef[h]))
        j<-j+1}
        if(j>years)
        {year<-c(1:years)
        #samp[j]<-dif[k]*avg  can probably delete
        trend[j,l,n]<-mean(rnorm(1,mean=dif[k]*avg,sd=coef[h]))
        j<-j+1}
            }l<-l+1
      }
      n<-n+1
```

```
      }
     if(samples==1)
     {
      if(ncol(trend)>1) #danger this script is not set up for multiple sites this line is a relic if it is true there are likely problems
      {meanTrend<-rowMeans(trend)}
      if(ncol(trend)==1)
      {meanTrend<-trend}
      p[i]<-t.test(meanTrend[1:years],meanTrend[years+1:years*2],var.equal=T)$p.value
      setWinProgressBar(pb, q, title=paste( round(q/total*1000, 0),"% done"))
      q<-q+1
      i<-i+1
      pow[k]<-length(p[p<.05])
      }
     if(samples>1)
   {
      if(ncol(trend)>1)  #danger this script is not set up for multiple sites this line is a relic if it is true there are likely problems
      {meanTrend<-rowMeans(trend)}
      if(ncol(trend)==1)
     {
     vecTrend<-c(trend)
     PrePost<-rep(c("PRE","POST"),samples,each=years)
     vecSamp<-rep(1:years,2*samples)
     cbind(vecTrend,PrePost,vecSamp)
    # anova(lme(vecTrend~PrePost,random=~1|vecSamp/PrePost))$'p-value'[2]
     p[i]<-anova(lme(vecTrend~PrePost,random=~1|vecSamp/PrePost))$'p-value'[2]
    setWinProgressBar(pb, q, title=paste( round(q/total*1000, 0),"% done") )
    q<-q+1
     i<-i+1
     pow[k]<-length(p[p<.05])
      }
    }
    }
    k<-k+1
  }
  powArray[h,]<-pow
  h<-1+h
}
close(pb)
powArray<-powArray/100
colnames(powArray)<-dif
rownames(powArray)<-coef/avg
```

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