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# Influence of Substrate and Hydraulic Variables on Habitat Preferences of a Sculptured and an Unsculptured Freshwater Mussel

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# INFLUENCE OF SUBSTRATE AND HYDRAULIC VARIABLES ON HABITAT PREFERENCES OF A SCULPTURED AND AN UNSCULPTURED FRESHWATER MUSSEL

by

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## INFLUENCE OF SUBSTRATE AND HYDRAULIC VARIABLES ON HABITAT PREFERENCES OF A SCULPTURED AND AN UNSCULPTURED FRESHWATER MUSSEL

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Freshwater mussels of the family Unionidae in North America have been in decline for at least the past 150 years. Major causes behind the decline are thought to be related to alteration or loss of habitat. Recent efforts by researchers have focused on understanding habitat associations of mussels so that more effective conservation efforts can be applied. Recent studies have identified variables that limit mussel community distributions. These variables are a combination of substrate and hydraulic variables that are associated with substrate stability. Furthermore, recent studies have suggested mussel studies are most informative at larger spatial scales and at high flow conditions.

In this study, I set out to identify the preferred habitats of both an unsculptured mussel and a sculptured mussel at high flow to determine if species-specific differences such as shell morphology were important in habitat preference. I also examined this question at three different spatial scales to determine what spatial scale was the best at providing the most information about the habitat selection of these two species.

Of the three spatial scales, the geomorphologically derived transect level exhibited the highest correlations between the sculptured mussel abundance and density and variables associated with substrate stability. Particularly, variables such as shear stress, Reynolds number, and mean particle size were among the strongest correlations with abundance and density. The analyses also suggested that the unsculptured mussel was more of a habitat generalist. The results of this study suggest that examining habitat associations at the species level may be more appropriate than at the community level. Studying only overall mussel communities can present issues in applied conservation as the focus is often on individual species rather than communities in general. Furthermore, the results suggest that grouping mussels by shell morphology may be an appropriate starting point for conservation applications.

# CHAPTER ONE: FRESHWATER MUSSEL ECOLOGY

## INTRODUCTION

Freshwater mussels of the family Unionidae are a diverse group of mollusks that are found worldwide. There are approximately 300 recognized extant species in this diverse faunal group in North America alone (Strayer et al., 2004; Thorp and Covich, 2001). These animals often occur in high densities in both lotic and lentic systems, with densities sometimes exceeding 100 animals/$m^2$ (Strayer et al., 1994). Unionid mussels have a complex life cycle. This group is unique in that the larvae (glochidia) have a parasitic life stage that requires a host fish to facilitate dispersal (Howells et al., 1996; Keller and Ruessler, 1997; Strayer, 2008; Zanatta and Murphy, 2006). A successful reproductive life cycle often requires specific host fish to be present during breeding events and the successful release of larvae into the fish mouth.  Once the glochidia are encysted on the fin or gill of the host fish, the host's immune system must not attack and reject the attached glochidia while it undergoes organogenesis. Finally, the glochidia must release from the host fish into a suitable physical habitat and anchor itself (Keller and Ruessler, 1997; Strayer, 2008; Vaughn and Taylor, 2000). Each step in this intricate life cycle is associated with very low survival (Bauer, 2001; Jansen et al., 2001). Once a healthy mussel survives to adulthood, it will spawn and propagate a new generation. Some mussel species are thought to live as long as 100 years (Strayer, 2008).

Mussels are benthic filter feeders which secrete a layered shell around their soft tissue in the form of two corresponding halves or valves (Howells et al., 1996). These mollusks fulfill a variety of vital ecosystem roles. As filter feeders, they remove particulate matter and phytoplankton in the water column. In high-density populations, mussels have even been suggested as being responsible for biological oligotrophication (Vaughn et al., 2004; Welker and Walz, 1998).They often serve as prey items for many organisms in associated aquatic and riparian systems. They also facilitate nutrient cycling through bioturbation of sediments (Strayer et al., 1999; Tyrrell and Hornbach, 1998; Vaughn and Hakenkamp, 2001; Vaughn et al., 2008). Also, the shells from these animals contribute to stabilization of river sediments, provide habitat for many aquatic organisms, and even serve as attachment points for some aquatic plants and algae (Vaughn and Hakenkamp, 2001; Vaughn et al., 2002). Because of all of this, these animals have been considered to be “ecological engineers” in recognition of their ability to affect entire ecosystems via movement of solutes and particles and for the physical importance of the shells of both live and dead mussels (Allen and Vaughn, 2011; Gutiérrez et al., 2003).

Mussels can be found in a variety of lentic and lotic habitats, ranging from oxygen-rich riffles in streams and rivers to backwater pools in floodplains and reservoirs (Howells et al., 1996; Strayer, 2008). This spectrum of habitats has encouraged researchers to attempt to determine habitat associations of various species and correlated variables, with an ultimate goal of accurately predicting species-specific mussel distributions. Studies have shown that water chemistry characteristics such as pH, conductivity, and dissolved oxygen may have some effect on mussel distributions, but are unreliable as predictive variables (Karatayev et al., 2008; Nicklin and Balas, 2007; Strayer and Ralley, 1993). Furthermore, because of the dynamics of lotic systems, water chemistry can vary dramatically both spatially and temporally. Simple physical variables may not adequately characterize habitat conditions of benthic invertebrates due to the three-dimensional nature of lotic systems (Statzner et al., 1988).

A more practical approach is to focus on variables that are more predictable *in situ* such as those associated with substrate stability (i.e., substrate and hydraulic parameters based on channel geomorphology). Substrate characteristics can be somewhat informative regarding mussel distributions, but substrate variables alone provide limited predictive capability (Box et al., 2002; Holland-Bartels, 1990; Huehner, 1987; Karatayev et al., 2008). Simple hydraulic variables such as current velocity and depth are also poor predictors when used exclusively (Hornbach, 2001; Karatayev et al., 2008; Layzer and Madison, 1995). Complex hydraulic variables that combine characteristics of substrate, forces on substrate, flow conditions, and channel geomorphology can be successful predictors of mussel distributions as well as of density and species richness (Gangloff and Feminella, 2007; Hardison and Layzer, 2001; Hornbach et al., 2010a; Layzer and Madison, 1995; Morales et al., 2006; Steuer et al., 2008). Regarding these substrate and hydraulic variables as “predictive” is misleading. Considering the list of other possible important factors such as host-fish presence, water quality, temperature, shell morphology, burrowing and movement behavior, and food quality and quantity, it is more practical to consider individual variables “limiting” rather than “predictive” (Allen and Vaughn, 2010). Ideally, studies should be designed to combine as many of these limiting factors as possible to provide the most accurate description of suitable mussel habitat.

## HABITAT VARIABLES

In studying mussel habitat and distributions, the focus has shifted from simple microhabitat variables to more complex variables. Recently, strong evidence suggests that mussel distributions can successfully be explained using variables that do not simply give a small snapshot of the habitat, but provide a more comprehensive view of the dynamic lotic system. Particularly, variables associated with substrate stability have been the most successful to date (Allen and Vaughn, 2010).

Variables that relate to substrate stability include shear stress ($\tau$), Reynolds number ($Re$), and Froude number ($Fr$). Shear stress is a dimensionless measure of the tangential force of friction by the water on the substrate (Gordon et al., 2004). Complimentary to shear stress is critical shear stress ($\tau_c$), which is the threshold of shear stress required to initiate substrate movement of some representative particle size. Morales et al. (2006) determined that by examining the ratio of shear stress to critical shear stress, one can determine if the habitat is generally capable of sustaining mussels. If the relative shear stress (*RSS*, ratio of shear stress to critical shear stress) rises above one, then one can assume that the substrate at that sample site would be unstable. Reynolds number represents the ratio of inertial to viscous forces, which provides insight into flow classification in general by indicating either laminar or turbulent flow (Gordon et al., 2004). A variation of this variable that is also potentially useful, known as boundary Reynolds number ($Re_*$), describes the roughness of the flow near the substrate (Gordon et al., 2004).

These hydraulic variables are thought to be limiting factors for mussel habitat because of their benthic and relatively sessile nature. Because most mussels require a secure anchoring in substrate, conditions that disturb or move substrate such as high shear stress during a high flow situation may dislodge, crush, or bury a mussel. Mussels, therefore, are more likely to aggregate in areas where shear stresses are relatively low and substrates remain stable (Strayer, 1999; Strayer, 2008).

It is important to consider the scale at which sampling and variables are examined. Holland-Bartels (1990) and Karatayev et al. (2008) found that small or micro-scaled analyses can provide some predictive power. In contrast, Hornbach et al. (2010a) found that larger scaled analysis may be more effective. Some hydraulic variables, such as shear stress, can be calculated or measured to encompass the entire channel, or only the conditions at the microhabitat scale. For example, Gangloff and Feminella (2007) found that microhabitat measures of shear stress showed no statistical relationship with mussel species richness; whereas, calculated geomorphological shear stress values were significantly associated with richness.

Variables will change depending on what flow conditions are studied. It is important to consider what flow condition is the most appropriate for a mussel study. Lotic systems exhibit hydraulic patterns of fluctuations including periods of low flows, average flows, and high flows. Low flow (i.e. baseflow) conditions can act as limiting factors to mussels. Layzer and Madison (1995) showed that water depth and current velocity at low flows were important limiting factors to mussel distributions. They also speculated that low flow conditions could limit dispersal ability because it can isolate the spawning mussels from their host fish as well as expose the mussels to terrestrial predators. Other studies have shown that hydraulic variables are more important at high flows (Allen and Vaughn, 2010; Gangloff and Feminella, 2007; Hardison and Layzer, 2001; Howard and Cuffey, 2003). The values representing high flow conditions, depending on the channel type, often characterize maximum values of hydraulic forces acting tangentially or parallel to the mussels embedded in or laying on the substrate.

Hydraulic variables are not the only factors that affect substrate stability; substrate particle size can also be an important characteristic (Allen and Vaughn, 2010; Steuer et al., 2008). Larger embedded substrate particles can increase the overall strength and compaction overall, making the substrate more stable (Gordon et al., 2004). It has even been suggested that, depending on shell morphology and burrowing behavior, mussels may actually help stabilize the substrate further (Allen and Vaughn, 2011; Strayer, 2008; Vaughn and Spooner, 2006), possibly providing a positive feedback loop of further substrate stability. For example, Zimmerman and de Szalay (2007) found that the presence of embedded mussels increased the compression and strength of the sediment overall.

## MUSSEL SHELL MORPHOLOGY

In addition to hydraulic and substrate variables, shell morphology has been suggested as having a role in the spatial distribution of mussels (Bartsch et al., 2010; Brainwood et al., 2008; Dillon Jr, 2011; Hornbach et al., 2010b; Stanley, 1970; Stanley, 1981; Watters, 1994). Mussel shell morphology can encompass overall shape and dimensions of the shell, general thickness, and external ornamentation or sculpturing. The sculpturing on the shell may function as anchoring devices for species inhabiting stronger flow systems (Watters, 1994). Watters (1994) demonstrated that species with sculpturing had significantly more anchoring drag (through sediment) than specimens with the sculpturing removed, suggesting that certain shell types may be advantageous for certain lotic habitats. Shell thickness has also been suggested as influencing a mussel’s ability to withstand substrate disturbances (Strayer, 1999). Strayer (1999) suggested that species with thick shells may be better equipped to tolerate substrate disturbances because the shell can protect against crushing and the extra weight may anchor it in place. In contrast, species found in soft substrates in weaker flow areas often tend to have thin, sculptureless, laterally compressed or inflated shells (Bartsch et al., 2010; Watters, 1994). Also, many species with sculptureless shells exhibit the ability to quickly burrow back into the substrate once displaced; whereas, those with sculptured shells take much longer (Troia and Ford, 2010). Interestingly, Allen and Vaughn (2011) demonstrated a negative correlation between abundance of smooth-shelled mussels and substrate stability. They suggested that this was attributed to the burrowing behavior of the smooth-shelled species. The bioturbation resulting from their frequent and relatively fast repositioning and burrowing likely disrupts the cohesive forces of the substrate, functionally lowering the critical shear stress, and thus allowing substrate entrainment and erosion. The difference in burrowing behaviors between sculptured and unsculptured mussels may complicate habitat variable associations. However, it can be assumed that sculptured mussels might be more tolerant of and thrive in areas with higher shear stress.

Furthermore, a majority of previous studies have examined variables and their associations with general mussel communities rather than focusing on individual species. This can be an issue for future researchers or resource management personnel who are attempting to study or seek out a specific species. There is substantial evidence to suggest that different mussels exhibit different habitat preferences, and studies focusing only on mussel communities do not account for this (Howells et al., 1996; Huehner, 1987; Strayer, 2008; Watters, 1994). While these studies provide a starting point for studying habitat preferences of mussels in general, studies focusing on specific species might be more appropriate for applied conservation efforts.

Overall, the current understanding of mussel habitats demonstrates that preferred habitats are not easily assessed. Simply recording substrate measurements or current velocity does not provide much information about mussel distributions. Combining multiple hydraulic and substrate variables has been shown to be the most successful method to elucidate the complex habitat requirements of mussels. Shell morphology has also been shown to be important, but its role in mussel distribution has not been examined extensively.

Unfortunately, freshwater mussels in the United States have been experiencing devastating declines in the last couple of centuries. It has been estimated that only 25% of the 300 species in the United States are considered to have stable populations (Strayer et al., 2004; Williams et al., 1993). Causes for this decline range from invasive species to habitat alterations (Lydeard et al., 2004; Strayer et al., 2004). Developing a better understanding of habitat requirements of mussels will help conserve this unique group of animals. I set out to contribute to that understanding by combining variables and methods that have been found to be useful in previous mussel habitat studies, and examining habitat differences at the species level. The objective of this thesis was to examine at three spatial scales the relationships between shell morphology, substrate characteristics, and hydraulic variables of two species, the pistolgrip, *Quadrula verrucosa*, and the yellow sandshell, *Lampsilis teres*, in the Sabine River in East Texas.

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# CHAPTER TWO: INFLUENCE OF SUBSTRATE AND HYDRAULIC VARIABLES ON HABITAT PREFERENCES OF A SCULPTURED AND AN UNSCULPTURED FRESHWATER MUSSEL

## INTRODUCTION

The freshwater mussel family Unionidae is a speciose group of benthic invertebrates that can be found in lentic and lotic systems on almost every continent, with approximately 300 extant species in North America alone (Strayer et al., 2004; Thorp and Covich, 2001). Of these  species, only approximately 25% are considered to have stable populations (Williams et al., 1993). The major causes for decline are related to habitat loss or alteration (Burlakova et al., 2011; Watters, 1999). Developing an understanding of appropriate habitat for mussels should aid in the conservation of this unique group of mollusks.

Mussel distributions are limited by multiple variables (Di Maio and Corkum, 1995; Hardison and Layzer, 2001; Hornbach, 2001). Particularly, mussel communities in lotic systems have been shown to have direct relationships with a variety of hydraulic and physical variables (Allen and Vaughn, 2010; Gangloff and Feminella, 2007; Hornbach, 2001). By focusing on total mussel communities, differences between mussel species are often overlooked. For example, a mussel with a textured shell may be better suited for a habitat with coarse substrate and stronger flow because of its ability to anchor itself; whereas, a similar sized mussel with a smooth shell might prefer less rough hydraulic conditions (Watters, 1994). Evaluating factors important to mussel community distributions is a good starting point, but it may complicate things for applied conservation efforts. For example, such generalized information may cause researchers and resource managers to evaluate habitat needs incorrectly for federally or state listed mussel species.

Because of the inherent relationship between mussels and substrate characteristics, most successful mussel habitat studies have focused on physical variables associated with substrate, or a combination with hydraulic variables that influence substrate. Substrate characteristics such as mean particle size have been shown to be related to some mussel species (Box et al., 2002). However, such variables may not the good predictors at all spatial scales of interest (Holland-Bartels, 1990). A combination of substrate and hydraulic variables related substrate stability have been demonstrated to be significant limiting factors of mussel distribution if measured or calculated at high flow conditions (Allen and Vaughn, 2010; Gangloff and Feminella, 2007). These variables could be examined for individual species of interest to understand specific habitat preferences.

It is important to consider the scale at which sampling and variables are examined. Small or micro-scaled analyses can provide some predictive power (Holland-Bartels, 1990; Karatayev et al., 2008). In contrast, larger scaled analysis seems to be more effective (Hornbach et al., 2010a). Some hydraulic variables, such as shear stress, can be calculated or measured to encompass the entire channel, or only the conditions at the microhabitat scale. For example, microhabitat measures of shear stress have shown no statistical relationship with mussel species richness; whereas, calculated geomorphological shear stress values have shown significant correlations with richness. (Gangloff and Feminella, 2007).

Patterns in mussel shell morphology have been correlated with spatial distribution in multiple studies (Bartsch et al., 2010; Brainwood et al., 2008; Dillon Jr, 2011; Hornbach et al., 2010b; Stanley, 1970; Stanley, 1981; Watters, 1994). Many of these studies, however, focused on associations with only substrate, simple flow characteristics, or geographic coordinates. Species with sculpturing have been shown to have significantly more anchoring drag (through sediment) than specimens with the sculpturing removed, suggesting that certain shell types may be advantageous for certain lotic habitats (Watters, 1994). Having more drag in the sediment would allow a mussel to remain lodged in place, reducing the effects of hydraulic forces on the mussel. Unfortunately, the more sculpturing a mussel has, the more difficulty it has in re-burrowing (Watters, 1994). Many mussels with unsculptured shells have compensated for their lack of sculpturing by developing the ability to burrow back into the sediment faster (Allen and Vaughn, 2009; Troia and Ford, 2010; Watters, 1994). Paleontological and biogeographical evidence suggests that unsculptured mussels in North America probably speciated in isolated headwaters where flows were generally weak, but periodic floods acted as a selective pressure for reduced sculpturing and faster burrowing ability (Watters, 1994). Examining associations of sculptured mussels and unsculptured mussels with substrate and hydraulic variables associated with substrate stability can provide empirical insight into sculpturing adaptations and their effect on mussel habitat preferences.

The two Unionid species used in my study were chosen based on shell morphology and locally high abundances (Ford et al., 2009; Ford and Nicholson, 2006). *Quadrula verrucosa* (Fig 2.1a) has been described as having sculpturing that exhibits a "generalized anchor" (Watters, 1994). The presence of this anchor suggests that this species is adapted to increased hydraulic forces and conditions. *Lampsilis teres* (Fig 2.1b) often reaches similar sizes to that of *Q. verrucosa*, and usually has a comparable weight and length-to-height ratio. However, *L. teres* possesses a smooth, unsculptured shell as well as an apparent sense of mobility in its habitat (Howells et al., 1996; Watters, 1994).

My objective was to investigate associations of abundance and density of a highly sculptured mussel, *Q. verrucosa*, and an unsculptured mussel, *L. teres*, with a suite of substrate and hydraulic variables. Specifically, my hypothesis was that sculptured mussels such as *Q. verrucosa* have likely adapted to areas of rougher flow and increased hydraulic forces, and should be correlated with such variables; whereas, unsculptured mussels such as *L. teres* would likely be habitat generalists, and not be correlated with many variables. The variables were assessed at high flow conditions to represent limiting hydraulic maximums and at three different spatial scales to assess at what scale variables are most related to mussel abundance and density.

## METHODS

### *Study area and design*

The study area was the Sabine River along the Harrison County border, Texas, USA (Fig. 2.2). The average bankfull width in the area was 58.4 ± 3.6 meters. Four sites were sampled within a 4 km length of river each with 10 equidistant transects and 45 randomly placed 1-$m^2$ quadrats, resulting in 4 reaches, 40 transects, and 180 quadrats (Fig 2.3). This nested design allowed for analyses at three different spatial scales. Using ArcGIS (version 9.3) and aerial photography, within each reach, 10 cross-section lines representing the center of each transect were spaced approximately 30 m apart along the apparent centerline of the river. Forty five quadrats were placed randomly throughout each reach using Hawth's Analysis Tools (version 3.27) for ArcMap. Parameters were set to ensure a minimum quadrat spacing distance of 3 m and a minimum of 2 quadrats per transect.

### *Mussel sampling*

A handheld Trimble GeoXM (2005 Series) GPS unit with ArcPad (version 8.0) was used to locate the preset quadrats. After habitat variables were recorded at each of the 180 1-$m^2$ quadrats, the quadrats were excavated by hand to an approximate depth of 15 cm when possible. Data were recorded for live mussels of both species of interest. Abundances and densities (#/$m^2$) were calculated in each quadrat. After mussel data were recorded, live mussels were returned to the substrate. SCUBA was utilized for sampling deeper quadrats (i.e., > 1.5 m).

All sampling was conducted during summer baseflow conditions. It should be noted that during the summer of sampling, 2011, East Texas was experiencing a severe drought and the Sabine River was at near record low flows (See Fig. 2.4 and Fig. 2.5). The low flow conditions exposed some areas of substrate, effectively demonstrating some distribution limitations. The exposed areas were avoided when randomly placing quadrats. Despite sampling at low flow conditions, all hydraulic variables were calculated to reflect bankfull conditions. Bankfull conditions are important because they have not only been shown to be correlated with mussel distributions, but bankfull represents the maximum value for most hydraulic variables (Allen and Vaughn, 2010; Gangloff and Feminella, 2007). Once the river reaches beyond bankfull, assuming appropriate floodplain connectivity exists, the water then extends out into the floodplain, effectively dissipating hydraulic forces (Ward and Trimble, 2004). To ensure sampling consistency for water-level dependent measurements (e.g., slope), sampling was planned for days with approximately similar flows by monitoring the US Geological Survey (USGS) gauging station (08020900) approximately 13 linear km upstream.

### *Habitat and hydraulic variables*

A Wolman pebble count was conducted (Wolman and Union, 1954) at each quadrat to quantify substrate. Depth was recorded at the center of the quadrat. Current velocity was measured at 0.6 × depth in the center of the quadrat using a Marsh-McBirney Flo-Mate$^{TM}$ flowmeter (Allen and Vaughn, 2010; Gordon et al., 2004).

After control-points were set using a GPS unit, geomorphology data were collected at each cross-section using a Leica TCR 1105 total station. All bankfull indicators were determined by a single observer (D.D.G). Substrate and hydraulic variables were calculated from field data using a combination of the Spreadsheet Tools for River Evaluation, Assessment, and Monitoring (STREAM Module: http://www.dnr.state.oh.us/soilandwater/water/streammorphology/default/tabid/9188/Default.aspx) spreadsheets for Microsoft Excel and the formulae in Table 2.1 (Gordon et al., 2004; Statzner et al., 1988; Ward and Trimble, 2004). Some variables were not applicable to the quadrat-level spatial scale (e.g. width-to-depth ratio).

A value of 0.065 was chosen a for Shield's parameter ($\theta_c$), because the average substrate sampled consisted of packed materials with smaller materials filling in voids between larger particles (Gordon et al., 2004). When determining critical shear stress ($\tau_c$), $D_{84}$ was used in place of a traditional $D$ or $D_{50}$ for a representative particle size because $D$ and $D_{50}$ often give a misconstrued and underestimated value of minimum force required for substrate movement. Neither $D$ nor $D_{50}$ account for larger particles which may be present that are capable of holding the substrate in place (Gordon et al., 2004).

*Data analysis*

Relationships between *Q. verrucosa* and *L. teres* abundances and densities were examined using a combination of correlation and principal components analysis (PCA). Separate analyses were conducted at each spatial scale. To reduce the number of variables used in the PCA, Spearman's rank correlation coefficients were used to identify redundancy in the variables (Allen and Vaughn, 2010). For example, at all three spatial scales, shear velocity ($U_*$) was highly correlated ($r > 0.9$) with both shear stress ($\tau$) and Reynolds number (*Re*). Previous studies have demonstrated the importance of $\tau$ and *Re*; therefore, $U_*$ was dropped from subsequent analyses (Gangloff and Feminella, 2007; Hardison and Layzer, 2001). Principal components (PC) derived from the PCA and their associations with abundance and density were evaluated using Spearman's rank correlation coefficients. If a PC showed a significant correlation ($P \leq 0.05$) with abundance or density, then the variables with the greatest influence on that PC were evaluated further using the Spearman's rank correlation coefficients associated with abundance and density. All statistical analyses were conducted using SPSS (version 20.0, SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

Total mussel abundances for the two species throughout the entire study area: *Q. verrucosa*, n = 48, *L. teres*, n = 26. The reach-level spatial scale data were unusable ($r$ = 1.0) in further analyses according to initial Spearman's rank correlations, therefore they were omitted. At the transect-level spatial scale, the first four principal components accounted for approximately 88% of the variation (eigenvalues > 1) between the 40 transects (Table 2.2). PC 1 accounted for 36.4% of the total variability, with variables showing high loadings being associated with depth and substrate-level hydraulic forces (maximum bankfull depth, mean bankfull depth, *Fr*, *Re*, $\tau$; Table 2.2). PC 2 (25.3%) consisted of variables related to substrate size, substrate movement, and flow conditions (D, $\tau_c$, *RSS*, bankfull discharge, mean current velocity; Table 2.2). PC 3 explained 16.4% of the variation with a single variable (bankfull width-to-depth ratio; Table 2.2). Finally, PC 4 was responsible for 9.8% of the total variation with a single variable (bankfull width; Table 2.2). Separate factor loading plots with sites highlighted at which *Q verrucosa* were present and *L. teres* were present are presented next to the score plot to provide a visual summary of the PCA (Fig. 2.6, Fig. 2.7).

Spearman's rank correlation coefficients indicated no significant relationships between PC scores and *L. teres* abundance or density. However, there was a significant positive relationship between PC 1 and *Q. verrucosa* abundance ($r$ = 0.494, $P$ = 0.001) and density ($r$ = 0.486, $P$ = 0.001), as well as a negative relationship between PC 2 and *Q. verrucosa* abundance ($r = -0.311$, $P$ = 0.05) and density ($r = -0.325$, $P$ = 0.04). The variables with high loadings associated with PC 1 and PC 2 were then examined for significant relationships with *Q. verrucosa* abundance and density using Spearman's rank correlation coefficients. Table 2.3 shows the significant relationships.

The PCA at the quadrat-level spatial scale indicated that the first three components were responsible for approximately 85% of the total variation (eigenvalues > 1) between the 180 quadrats. PC 1 was responsible for 43% of the total variation and consisted of variables associated with substrate roughness and movement ($D$, $\tau_c$, $Re_*$; Table 2.4). PC 2 described 26% of the overall variation with high loading variables related to substrate particle entrainment and hydraulic forces ($RSS$, $Re$, $\tau$; Table 2.4). Lastly, PC 3 (17%) contained a single variable (bankfull depth; Table 2.4). Separate factor loading plots with sites highlighted at which *Q verrucosa* were present and *L. teres* were present are presented next to the score plot to provide a visual summary of the PCA (Fig. 2.8, Fig. 2.9).

Because 1-m$^2$ quadrats were used, density and abundance are equivalent at this level of sampling; therefore, only correlations with abundance were examined. Spearman's rank correlation coefficients indicated no significant relationships between PC scores and *L. teres* abundance. PC 1 showed a significant positive relationship with *Q. verrucosa* abundance ($r$ = 0.224, $P$ = 0.002). The variables associated with PC 1 were then analyzed for significant correlations with *Q. verrucosa* abundance using Spearman's rank correlation coefficients. $D$, $\tau_c$, and $Re_*$ exhibited positive relationships ($r$ = 0.169, $P$ = 0.023; $r$ = 0.166, $P$ = 0.026;  $r$ = 0.207, $P$ = 0.005) with *Q. verrucosa* abundance.

# DISCUSSION

Significant correlations between *Q. verrucosa* abundance and density and hydraulic variables associated with substrate stability such as $\tau$, $Re_*$, $D$, $\tau_c$, $RSS$, and $Re$ support the hypothesis that *Q. verrucosa* was likely to be found in areas of rougher flow and higher hydraulic forces. Furthermore, the data demonstrated that the transect-level spatial scale was the most informative scale to study such variables, which supports conclusions of other researchers regarding mussel habitat associations. For example, positive correlations with $D$ and *Q. verrucosa* abundance and density at the transect-level corroborate conclusions by other researchers (Allen and Vaughn, 2010; Steuer et al., 2008). $D$ is a measure indicating mean particle size. Particle size has a direct effect on the overall roughness of the substrate, which describes the overall topographical variation. As a substrate increases in roughness, the hydraulic conditions at the bed surface become rougher, thus disturbing it and causing irregularities (Gordon et al., 2004). These irregularities allow for small flow refuges that mussels can then inhabit and experience the increased water movement for nutrient, gas exchange, and waste movement, while benefiting from the small refuge from direct hydraulic forces.

Some variables showed correlations that were contrary to previous studies. *Quadrula verrucosa* abundance and density were positively correlated with hydraulic variables such as $\tau$, $Re_*$, and $Re$ regardless of the scale examined. Such variables have been shown to exhibit a negative correlation with abundance or density (Allen and Vaughn, 2010; Hardison and Layzer, 2001; Morales et al., 2006). One difference between those studies and this study is that they were examining entire mussel communities rather than individual species. The difference in results suggests that averaged community correlations do not reflect species-specific habitat associations. Another fundamental difference is the size of the river examined. For example, one study involved research conducted in a river that had a mean discharge of approximately 54 $m^3/s$ at bankfull (Allen and Vaughn, 2010), whereas the Sabine River at these study sites had a greater mean discharge at bankfull of approximately 250 $m^3/s$. The size difference may be of importance because a large river with a relatively flat slope (i.e., < 1%) such as the Sabine River will have a higher prevalence of siltation areas; therefore, the lower values of shear stress will likely represent such areas (Gordon et al., 2004). Considering the hypothesis that the sculptured mussels are more adapted to rougher substrates, high abundances of mussels such as *Q. verrucosa* are unlikely in siltation areas that represent low shear stress values. A previous study that examined similar variables in another large river, the Upper Mississippi River, also found positive correlations with mussel abundance and density at high flow (Steuer et al., 2008), so this might be a general trend with larger rivers.

At the transect-level spatial scale, the strong positive correlation of $\tau$ and *Re* with *Q. verrucosa* abundance and density supports the hypothesis of this study. *Q. verrucosa* exhibits sculpturing which has been described as a "generalized anchor" (Watters, 1994). This anchor likely allows it to withstand higher $\tau$ and *Re* values. An advantage of being in such an area of hydraulically rough flow is exposure to a higher rate of nutrient and gas exchange as well as easier waste removal (Gordon et al., 2004). The disadvantage is the risk of potentially being dislodged during bankfull periods. Furthermore, the typical burrowing behavior of *Q. verrucosa* is well documented as most often being oriented with the umbo facing downstream, leaving the posterior portion exposed at a slight angle into the flow (Fig. 2.10) (Howells et al., 1996; Watters, 1994). The angle of the exposed portion on the shell makes it effectively a hydraulically streamlined body rather than a blunt body such as a rock in the substrate (Gordon et al., 2004). This parallel orientation to flow greatly reduces the effects of the flow on the mussel (Di Maio and Corkum, 1997). However, *Q. verrucosa* and other species have also been found lying on top of the substrate. It is possible these mussels had recently been dislodged and had not yet burrowed back into the substrate or it may be a response to unfavorable substrate conditions. Behavior involving mussels lying on top of the substratum should be investigated further.

The strong positive correlation of *Q. verrucosa* abundance and density with $\tau_c$ may also help explain the positive correlation $\tau$ mentioned previously. $\tau_c$ represents the maximum shear stress required to initiate substrate movement. The higher this value is, the higher the $\tau$ can be while still maintaining substrate stability. Therefore, the strong positive trend with $\tau$ likely reflects the fact that these study sites had high $\tau_c$, which allowed for greater variation in the $\tau$ values. The negative correlation between abundance and density and *RSS* may provide the most informative explanation of the relationship with $\tau$. *RSS* is the ratio of observed $\tau$ to $\tau_c$, for which values greater than 1 represent initiation of substrate movement (Morales et al., 2006). As the *RSS* increased, *Q. verrucosa* abundance and density decreased, indicating intolerance to areas that are prone to substrate instability. Only a few outliers did not adhere to this trend, but this could be because of the inclusion of sampling locations that had mostly bedrock, but provided small flow refuges in which sand and gravel gathered, thus providing small pockets of substrate for mussels to settle into. The negative correlation with $d_{max}$ follows along with the concept discussed previously regarding the large river and siltation areas. The transects which had the deepest areas were coincidentally those that had the lowest $\tau$, lowest *Re*, and finest sediments (i.e. pools).

Regarding spatial scales in this study, both the transect and quadrat-level scales were useful in determining what variables were most associated with *Q. verrucosa* abundance and density, with the transect PC scores and variables showing much stronger correlations than those at the quadrat level. The reach scale data were all highly correlated with one another ($r = 1.0$) which suggests that the variables investigated may not be appropriate to calculate at such a scale (reaches > 300 m in length). Considering a large river is not typically a homogeneous landscape along the bed, with features sometimes varying drastically within a few meters both laterally and horizontally, a single value of any variable calculated at this scale will likely overlook the substrate and hydraulic variability that can be found at smaller scales. For example, flow refuges such as the backside of boulders or shoals may be suitable habitats for mussels (Strayer, 1999). If this is correct, large-scale estimates of shear stress and other hydraulic variables likely neglect flow refuges along the channel bed that may support healthy mussel populations. At the transect and quadrat-level scales, Spearman’s rank correlation coefficients and principal components analyses revealed that both individual variables and variable combinations (principal component scores) are important for identifying suitable mussel habitat parameters for species which are not generalists.

At the quadrat level, only three variables were significantly correlated, and the correlations were not nearly as strong as those at the transect level. The variable that was correlated the strongest was $Re_*$. Boundary Reynolds ($Re_*$) combines substrate roughness with shear velocity ($U_*$) and the kinematic velocity of water and describes the overall roughness of flow near the substrate. Significance at quadrat-level sampling may indicate that microscale variation in the bed roughness could provide small pockets of suitable habitat that would be overlooked at larger scales. Furthermore, as $Re_*$ increases, so does the exchange between interstitial water and surface water (Fries, 2007). As sedentary filter feeders, mussels require such water exchange. Other studies have shown this variable to be important in mussel and other macroinvertebrate habitats as well (Quinn and Hickey, 1994; Steuer et al., 2008).

The lack of correlation and significance of *L. teres* with any particular variable or PC score suggests that *L. teres* is a habitat generalist, which supports the hypothesis of this study. *Lampsilis teres* does not appear to prefer any particular set of habitat parameters, indicating it may be able to thrive in various types of habitats. Extant mussels with unsculptured shells may be the result of speciation in headwater streams, with the subsequent infiltration of larger order streams that already were inhabited by sculptured mussels (Watters, 1994). Unsculptured mussels have developed other means of dealing with the effects of high flow events. Some smooth mussels have developed more inflated shells that act as a ballast to keep them relatively high in softer substrates (Strayer, 2008). Others have developed the ability the reestablish themselves back into the substrate quickly after being dislodged (Bartsch et al., 2010; Troia and Ford, 2010). Such adaptations have likely allowed unsculptured mussels to be habitat generalists, able to survive in a wide range of substrate and hydraulic conditions.

Overall, the reach-level spatial scale was uninformative while the quadrat-level analyses were useful and provided some insight into limiting variable associations. However, the transect-level provided the strongest correlations with *Q. verrucosa* abundance and density throughout the study sites. The PCA results suggest that combinations of substrate and hydraulic variables are important in defining habitat parameters for mussels.

The results of this study demonstrated the importance of the variability in habitat that exists at the species level. For example, the data showed that some species such as *L. teres* are habitat generalists. Habitat generalists may weaken the overall reliability of derived models in studies that focus on mussel distributions at the community rather than the species level. In addition, the discrepancy between the positive correlation of *Q. verrucosa* abundance and density with variables such as $\tau$ in this study and the negative correlations in other studies further stresses the importance of species-specific studies. If a study goal involves conservation of specific listed species, then methodology such as that outlined in this study would be appropriate. If grouping of species is necessary (e.g. to study a listed species by examining a closely associated species as a surrogate), then perhaps grouping should be by shell morphology as evidence suggests that shell morphology has an influence on behavior and habitat (Allen and Vaughn, 2009; Allen and Vaughn, 2011; Bartsch et al., 2010; Hornbach et al., 2010b; Watters, 1994). A shell morphology classification system already exists which could be applicable to such a study (Hornbach et al., 2010b). Future studies should consider utilizing more aspects of shell morphology to determine, understand, and ultimately conserve preferred mussel habitats.

## CONSERVATION IMPLICATIONS AND FUTURE RESEARCH AT THE SABINE MINE RESEARCH SITE

The placement of the reaches in this study (Figure 2.3) allows future research to focus on disturbance effects on mussels. Specifically, a permanent bridge was created after this study just downstream from Reach 2. In addition, a temporary crossing is planned to cross the center of Reach 2 for the summer of 2012. The placement of Reach 1 allows for an undisturbed comparison site and Reaches 3 and 4 provide downstream sites. Furthermore, future studies at these sites could utilize timed searches at each transect to examine if sampling methodology provides similar results. Future research could implement community or listed-species data as well because I collected data on all live species at this site. Finally, because the Sabine Mine takes high resolution aerial photographs monthly of the general area, future research may consider including riparian zone data as well as a floodplain connectivity assessment by utilizing photography from a recent high water event (winter 2011-2012).

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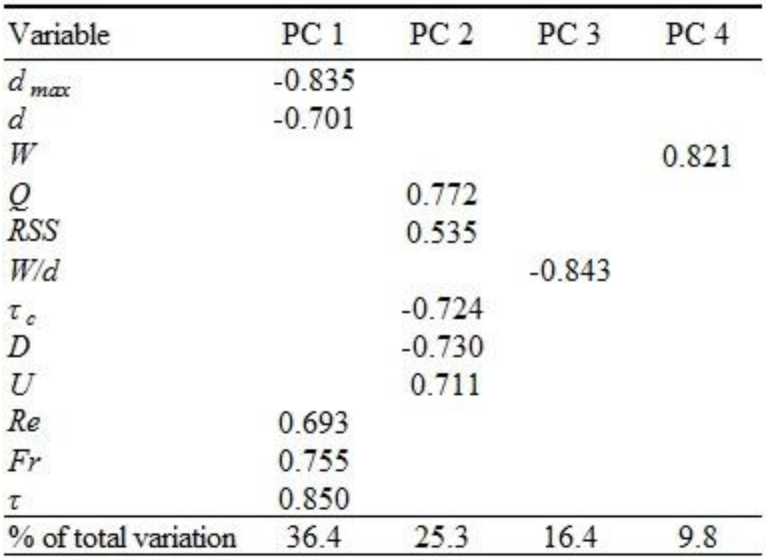
Table 2.1. Summary of substrate variables and hydraulic variables estimated at bankfull flows. $n$ = Manning's roughness coefficient, $g$ = acceleration of gravity (980 cm/s), ρ = density of water (0.998 g/cm$^3$), $\rho_s$ = density of substrate (2.65 g/cm$^3$), $\theta_c$ = Shield's parameter (0.065), $\nu$ = kinematic viscosity of water (0.01 cm$^2$/s) (Gordon et al., 2004; Statzner et al., 1988; Ward and Trimble, 2004).

| Variable | Symbol | Unit | Formula | Description |
|---|---|---|---|---|
| Substrate variables | | | | |
| Mean substrate particle | $D$ | mm | $\frac{D_{16}+D_{50}+D_{84}}{3}$ | Mean particle size of sample |
| Median substrate particle | $D_{50}$ | mm | | Median particle size of sample |
| Bed roughness | $k_s$ | mm | $3.5 \times D_{84}$ | Topographical variation of stream bed |
| Simple hydraulic variables | | | | |
| Width | $W$ | cm | | Width of stream at bankfull |
| Maximum depth | $d_{max}$ | cm | | Maximum depth at bankfull |
| Mean depth | $d$ | cm | | Mean depth at bankfull |
| Width/depth ratio | $w$ | - | $\frac{W}{d}$ | Bankfull width / bankfull mean depth |
| Hydraulic radius | $R$ | cm | $\frac{A}{P}$ | Cross sectional area ($A$) divided by the wetted perimeter ($P$); approximately equivalent to mean depth ($d$) if $w$ is ≥ 20:1 |
| Discharge rate | $Q$ | cm$^3$/s | $U \times A$ | Volume rate of water flow at bankfull |

Continued on next page

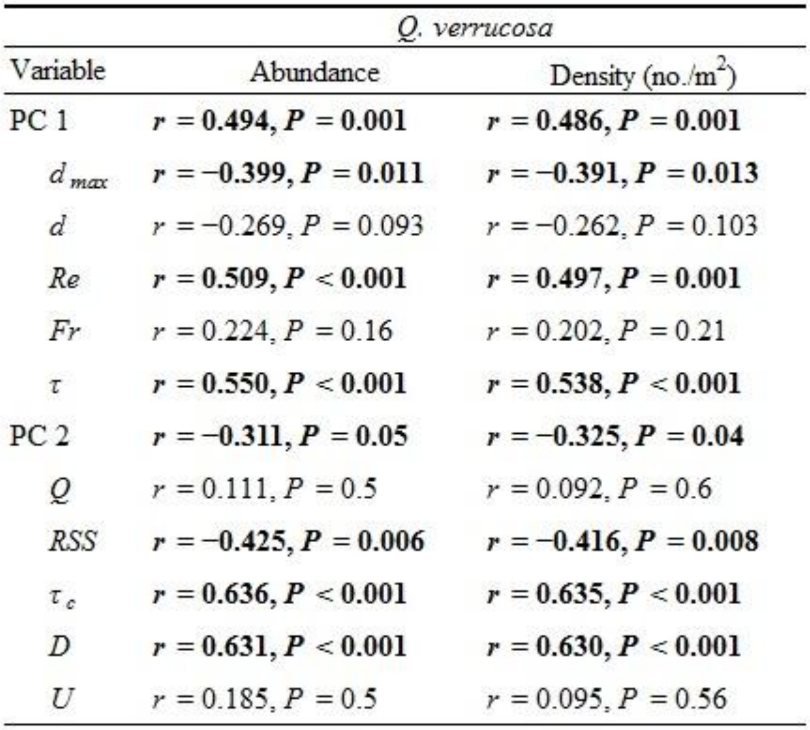
| | | | | |
|---|---|---|---|---|
| Mean current velocity | $U$ | cm/s | $1.49 \times R^{\frac{2}{3}} \frac{\left(\frac{S}{100}\right)^{\frac{1}{2}}}{n}$ | Rate of water flow |
| Slope | $S$ | - | | Rise over run of water surface over a distance |
| Complex hydraulic variables | | | | |
| Shear velocity | $U_*$ | cm/s | $(g(R\ or\ d)S)^{\frac{1}{2}}$ | Friction velocity |
| Shear stress | $\tau$ | dynes/cm$^2$ | $\rho(U_*^2)$ | Force of friction on substrate |
| Critical shear stress | $\tau_c$ | dynes/cm$^2$ | $\theta_c g(D_{84} \times 0.1)(\rho_s - \rho)$ | Shear stress required to initiate substrate motion |
| Relative shear stress | $RSS$ | - | $\frac{\tau}{\tau_c}$ | Ratio of observed to critical shear stress; values > 1 represent substrate movement |
| Reynolds number | $Re$ | - | $\frac{U_* d}{\nu}$ | Ratio of inertial to viscous forces |
| Boundary Reynolds number | $Re_*$ | - | $\frac{U_*(k_s \times 0.1)}{\nu}$ | Roughness of flow near substrate (0.1 is the conversion factor for mm to cm) |
| Froude number | $Fr$ | - | $\frac{U}{(gd)^{\frac{1}{2}}}$ | Ratio of inertial to gravitational forces |

Table 2.2. Principal components with eigenvalues >1.0 explaining approximately >10% of the instream variation among the 40 transects. Maximum factor loadings for each variable and the total percentage of habitat variability among transects explained by each component are given.



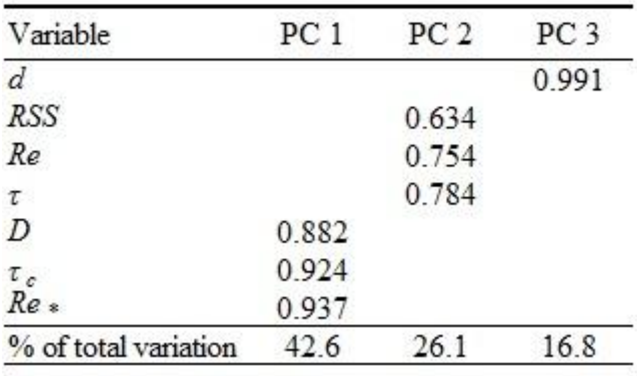
| Variable | PC 1 | PC 2 | PC 3 | PC 4 |
|---|---|---|---|---|
| $d_{max}$ | -0.835 | | | |
| $d$ | -0.701 | | | |
| $W$ | | | | 0.821 |
| $Q$ | | 0.772 | | |
| $RSS$ | | 0.535 | | |
| $W/d$ | | | -0.843 | |
| $\tau_c$ | | -0.724 | | |
| $D$ | | -0.730 | | |
| $U$ | | 0.711 | | |
| $Re$ | 0.693 | | | |
| $Fr$ | 0.755 | | | |
| $\tau$ | 0.850 | | | |
| % of total variation | 36.4 | 25.3 | 16.4 | 9.8 |

Table 2.3. Transect-level Spearman’s correlation coefficients for the two significant principal components and their associated variables. Bolded variables represent significant correlations.



| | *Q. verrucosa* | |
|---|---|---|
| Variable | Abundance | Density (no./m$^2$) |
| PC 1 | **$r = 0.494, P = 0.001$** | **$r = 0.486, P = 0.001$** |
| $d_{max}$ | **$r = -0.399, P = 0.011$** | **$r = -0.391, P = 0.013$** |
| $d$ | $r = -0.269, P = 0.093$ | $r = -0.262, P = 0.103$ |
| $Re$ | **$r = 0.509, P < 0.001$** | **$r = 0.497, P = 0.001$** |
| $Fr$ | $r = 0.224, P = 0.16$ | $r = 0.202, P = 0.21$ |
| $\tau$ | **$r = 0.550, P < 0.001$** | **$r = 0.538, P < 0.001$** |
| PC 2 | **$r = -0.311, P = 0.05$** | **$r = -0.325, P = 0.04$** |
| $Q$ | $r = 0.111, P = 0.5$ | $r = 0.092, P = 0.6$ |
| $RSS$ | **$r = -0.425, P = 0.006$** | **$r = -0.416, P = 0.008$** |
| $\tau_c$ | **$r = 0.636, P < 0.001$** | **$r = 0.635, P < 0.001$** |
| $D$ | **$r = 0.631, P < 0.001$** | **$r = 0.630, P < 0.001$** |
| $U$ | $r = 0.185, P = 0.5$ | $r = 0.095, P = 0.56$ |

Table 2.4. Principal components with eigenvalues >1.0 explaining approximately >17% of the instream variation among the 180 quadrats. Maximum factor loadings for each variable and the total percentage of habitat variability among quadrats explained by each component are given.



| Variable | PC 1 | PC 2 | PC 3 |
|---|---|---|---|
| $d$ | | | 0.991 |
| $RSS$ | | 0.634 | |
| $Re$ | | 0.754 | |
| $\tau$ | | 0.784 | |
| $D$ | 0.882 | | |
| $\tau_c$ | 0.924 | | |
| $Re_*$ | 0.937 | | |
| % of total variation | 42.6 | 26.1 | 16.8 |

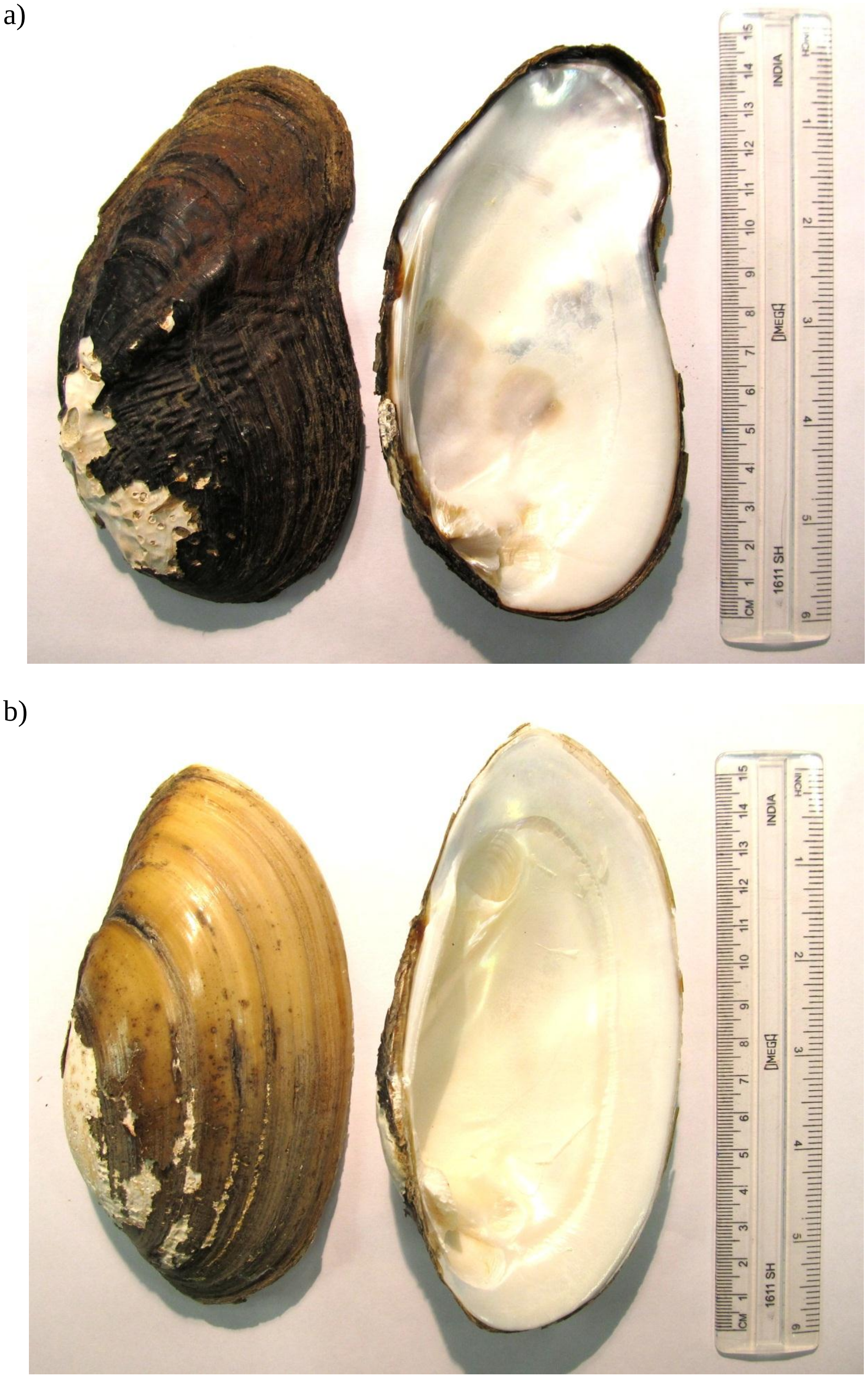


Figure 2.1. Pictures of voucher specimens of *Quadrula verrucosa* (a) and *Lampsilis teres* (b).

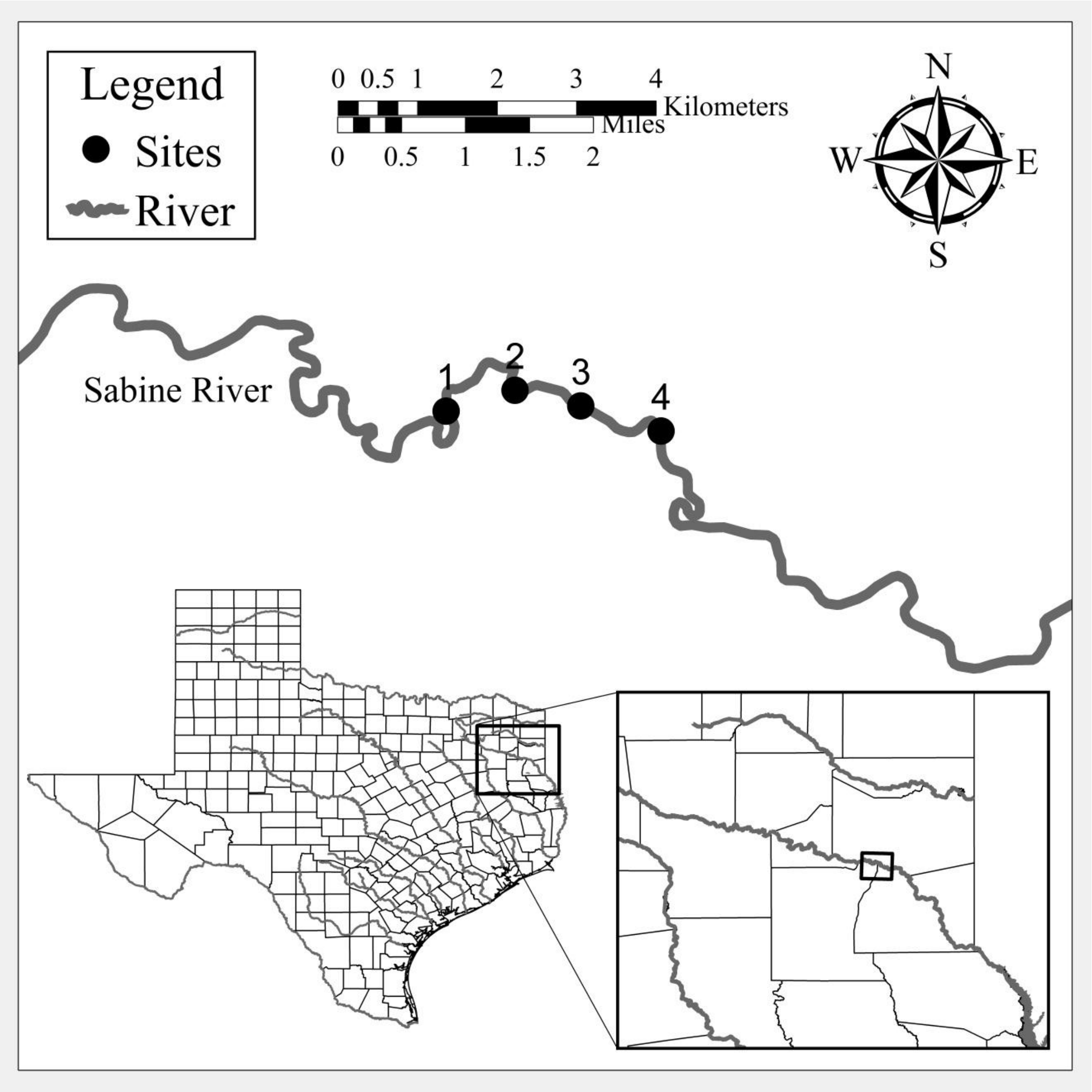


Figure 2.2. Sampling sites (reaches) on the Sabine River in eastern Texas.

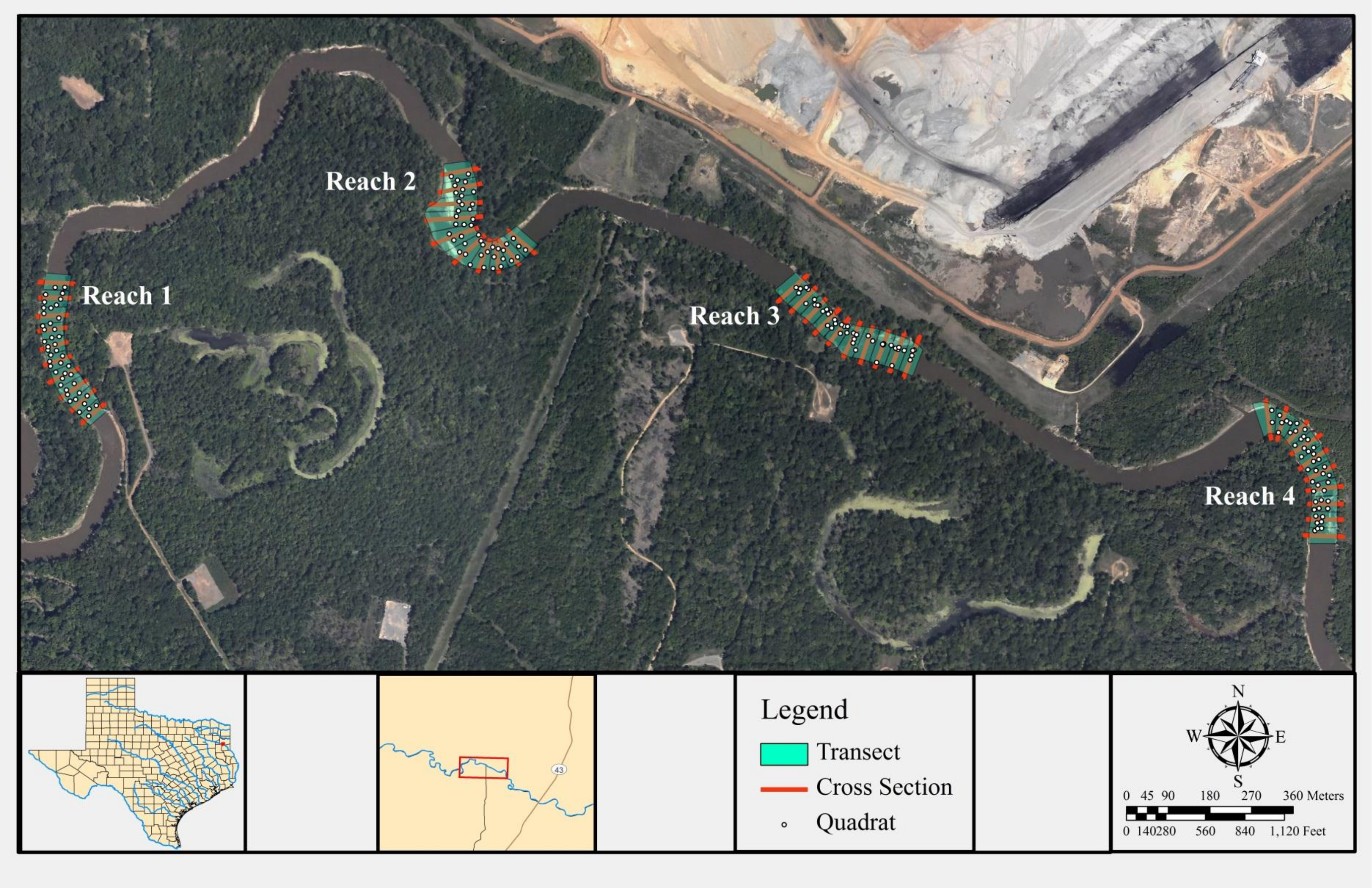


Figure 2.3. Transect and quadrat placements within the four reaches.

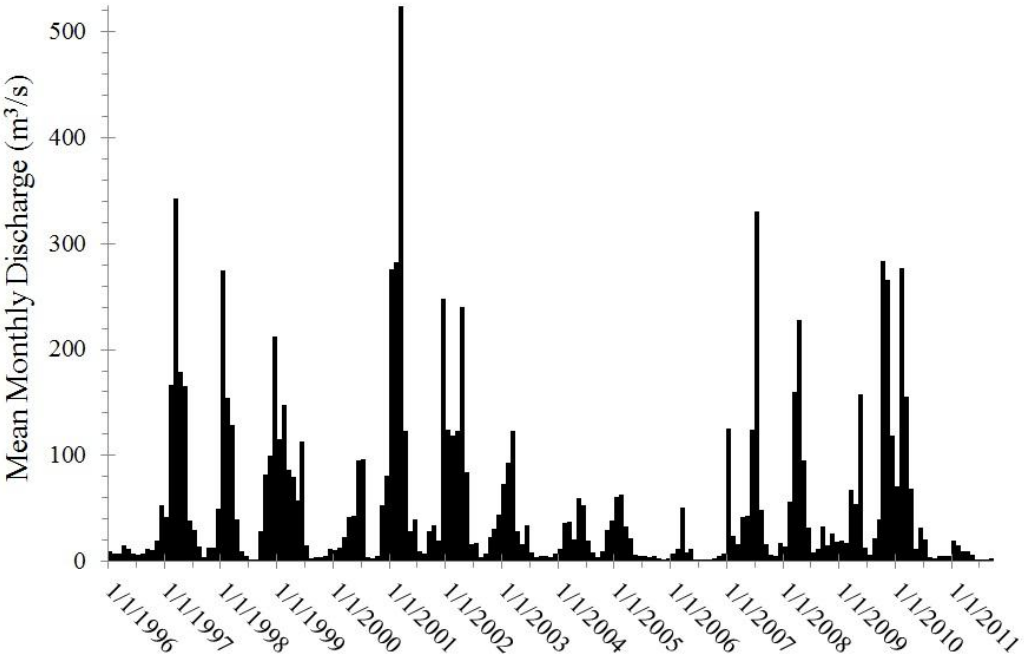


Figure 2.4. Hydrograph of upstream USGS gauge 08020900 showing yearly and seasonal variation.

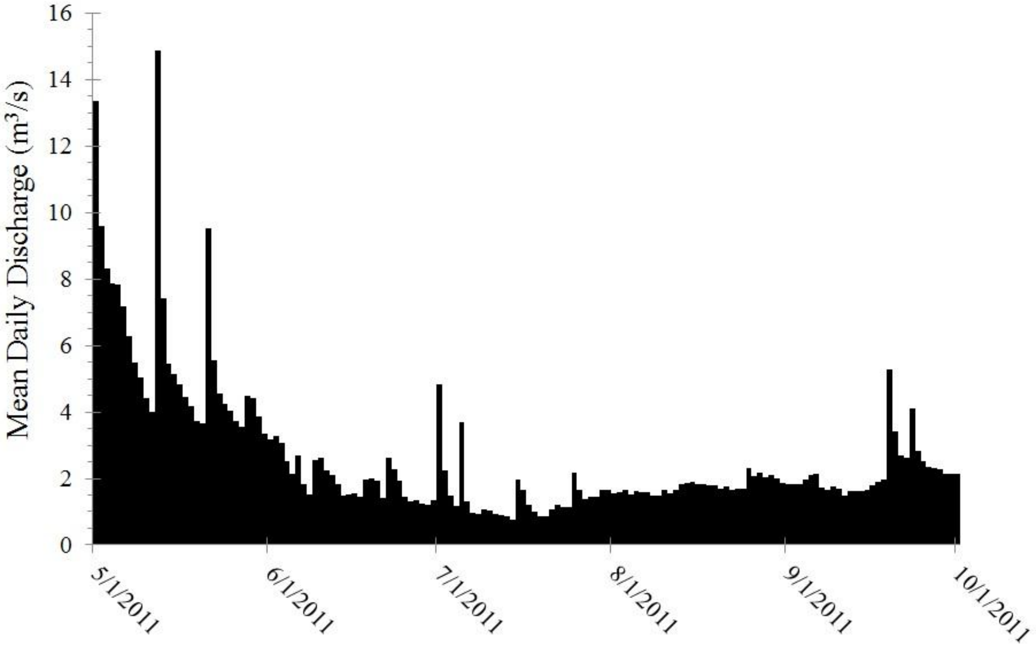


Figure 2.5. Hydrograph of upstream USGS gauge 08020900 showing low flow during time of sampling in summer 2011.

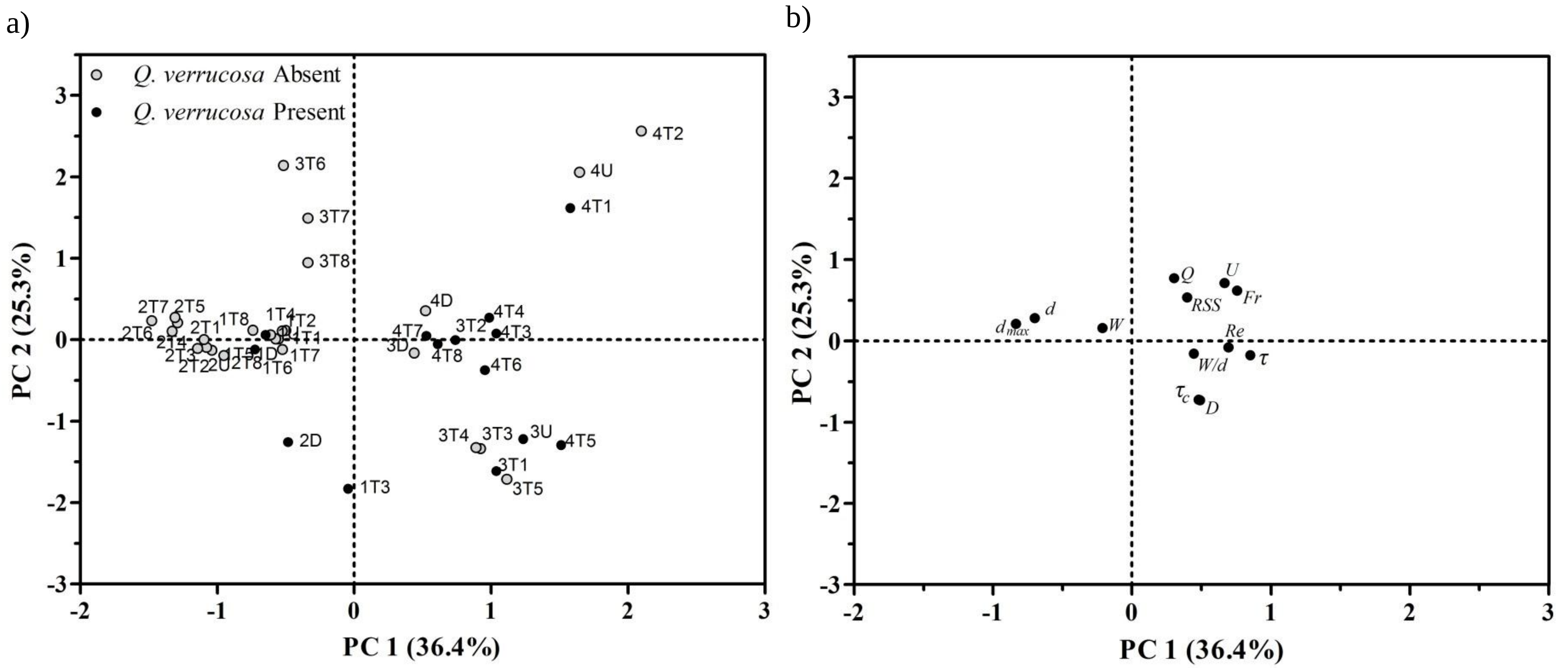


Figure 2.6. Transect PCA factor plot (a) highlighting sites at which *Q. verrucosa* were present. PCA score plot (b) provided for interpretation assistance with associated variables.

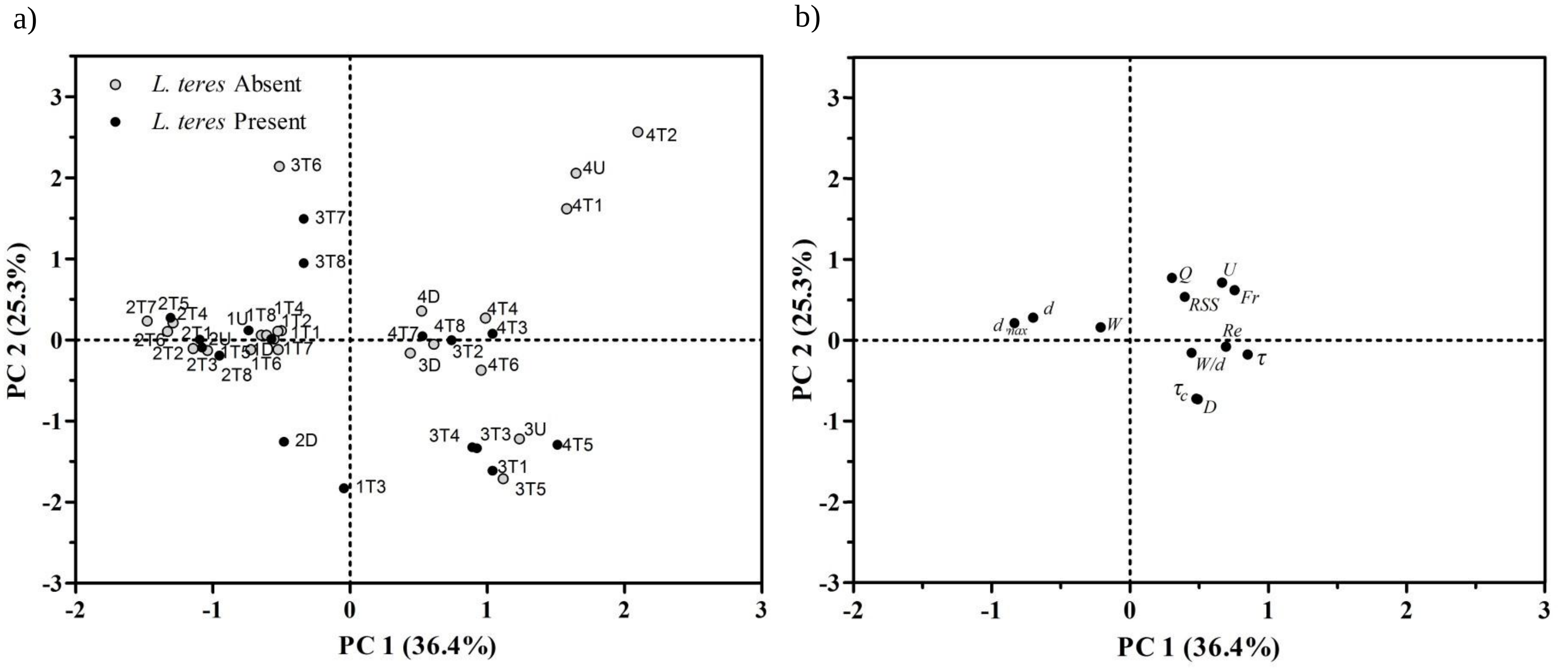


Figure 2.7. Transect PCA factor plot (a) highlighting sites at which *L. teres* were present. PCA score plot (b) provided for interpretation assistance with associated variables.

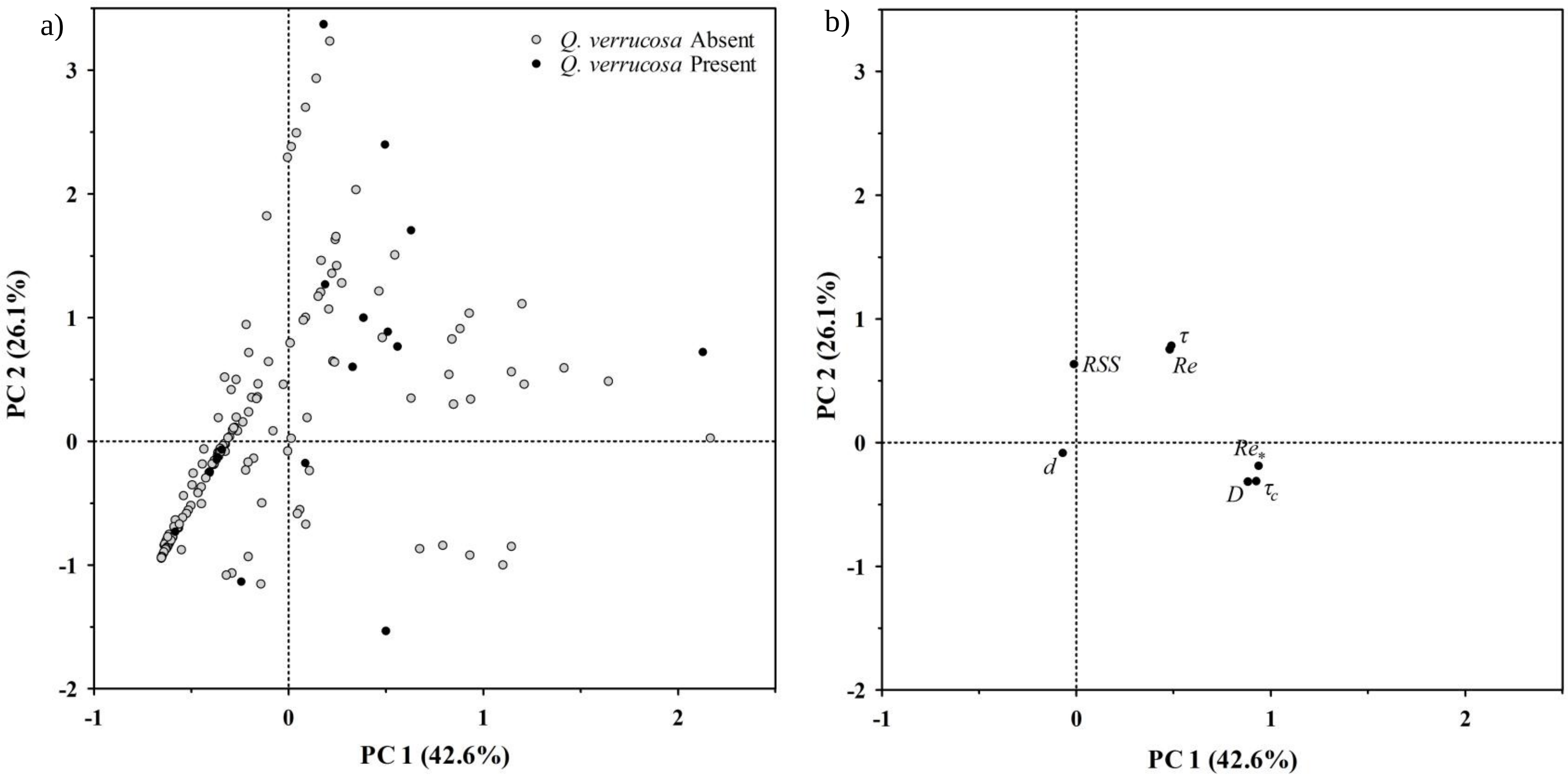


Figure 2.8. Quadrat PCA factor plot (a) highlighting sites at which *Q. verrucosa* were present. PCA score plot (b) provided for interpretation assistance with associated variables.

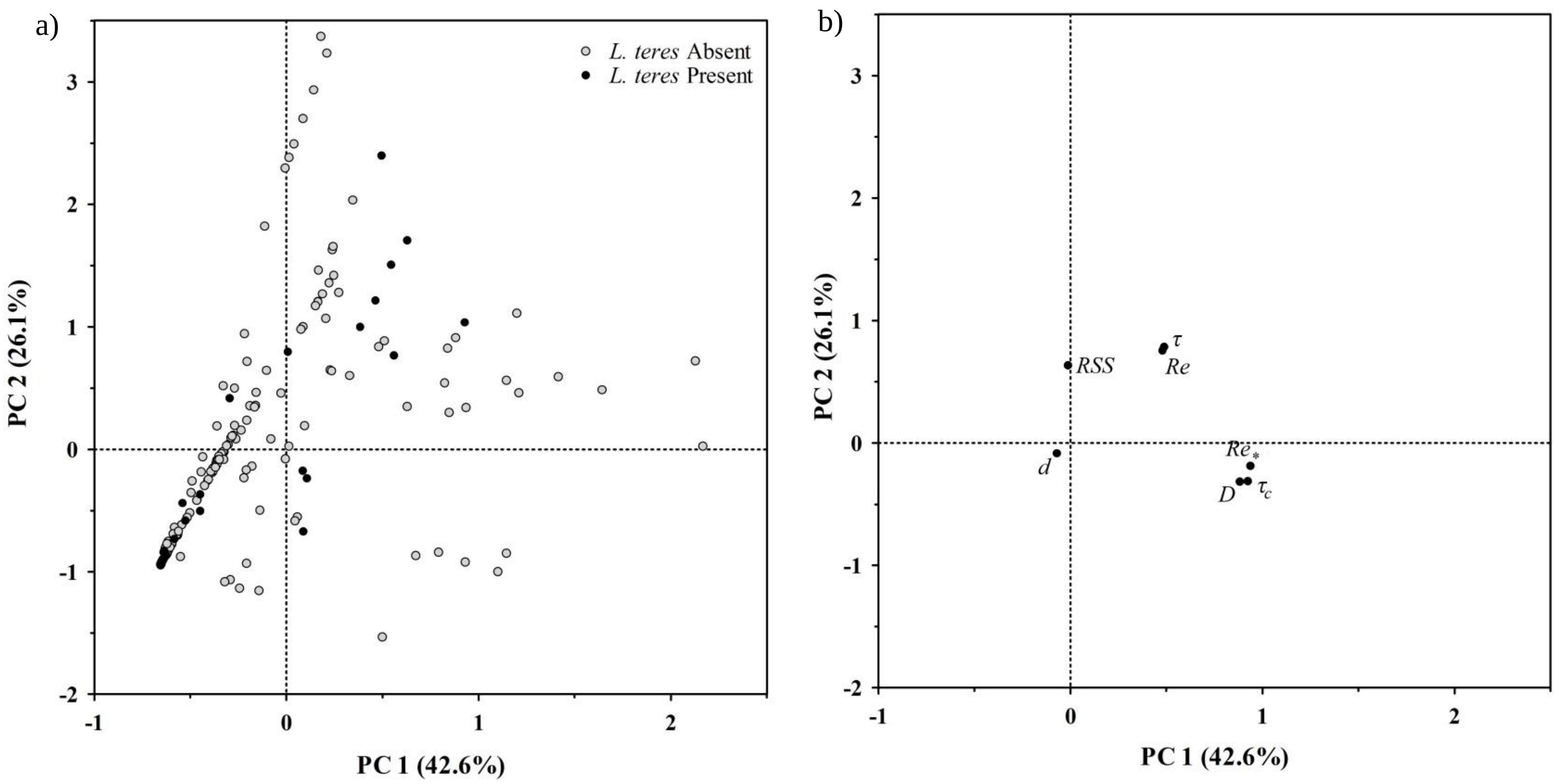


Figure 2.9. Quadrat PCA factor plot (a) highlighting sites at which *L. teres* were present. PCA score plot (b) provided for interpretation assistance with associated variables.

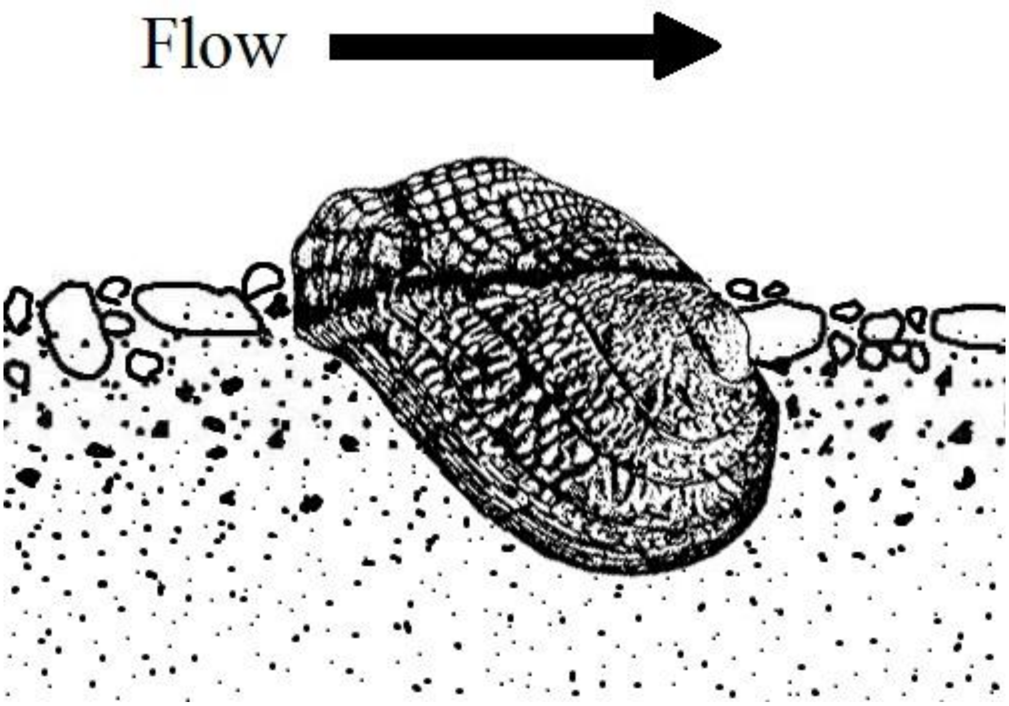
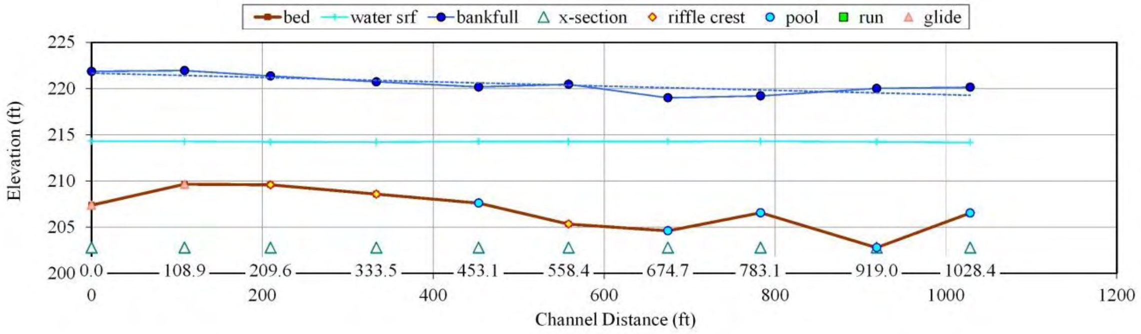
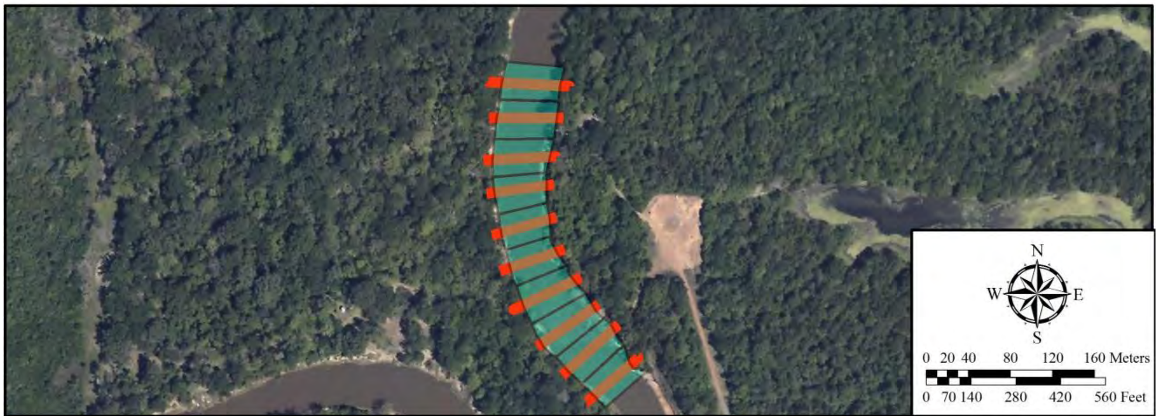


Figure 2.10. Diagram depicting a typical orientation of *Q. verrucosa* in the substrate. Original image of *Q. verrucosa* taken from Watters (1994).

# APPENDIX A: GEOMORPHOLOGY LONGITUDINAL PROFILES OF FOUR REACHES IN THE SABINE RIVER, AUGUST 2011

## REACH 1





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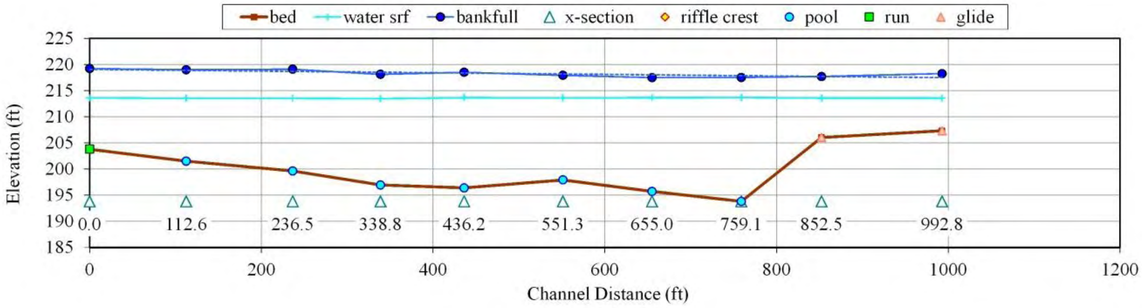
## REACH 2



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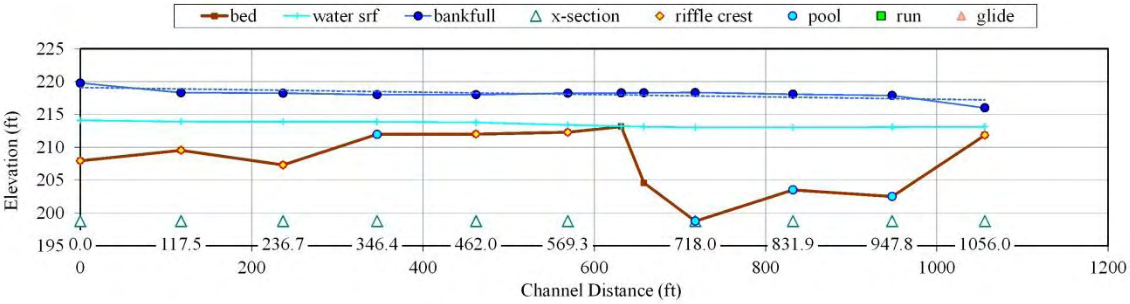
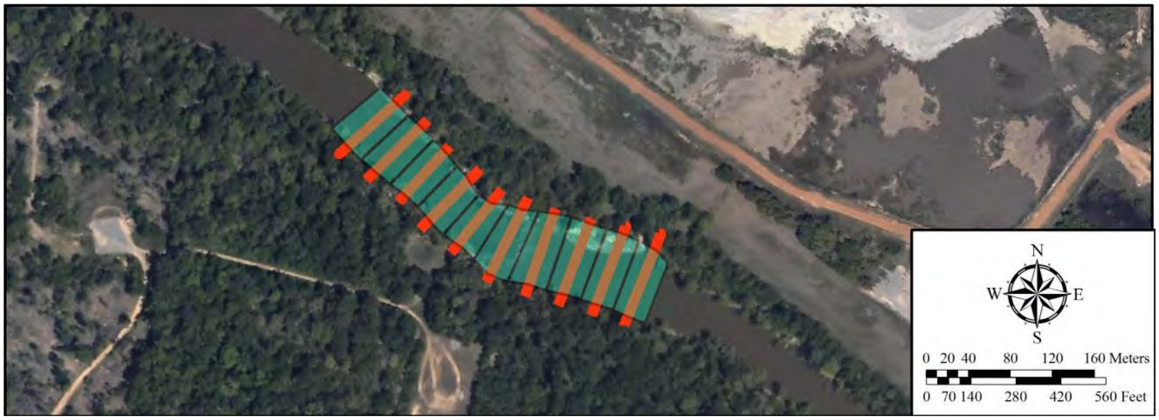
## APPENDIX A (CONTINUED)

## REACH 3





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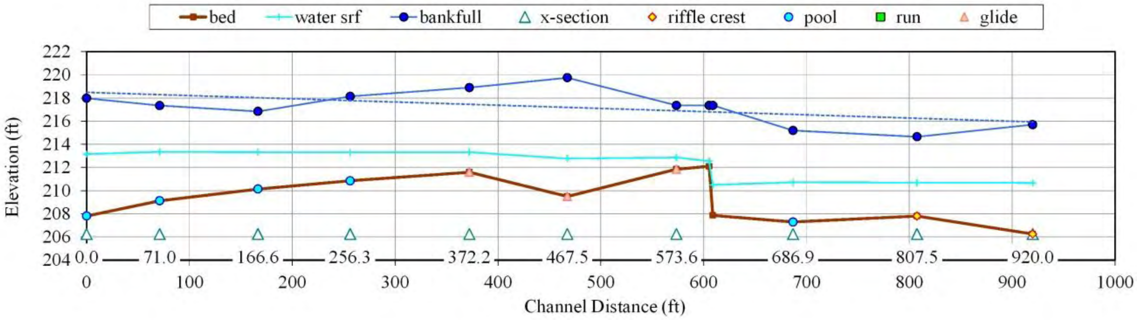
## APPENDIX A (CONTINUED)

### REACH 4



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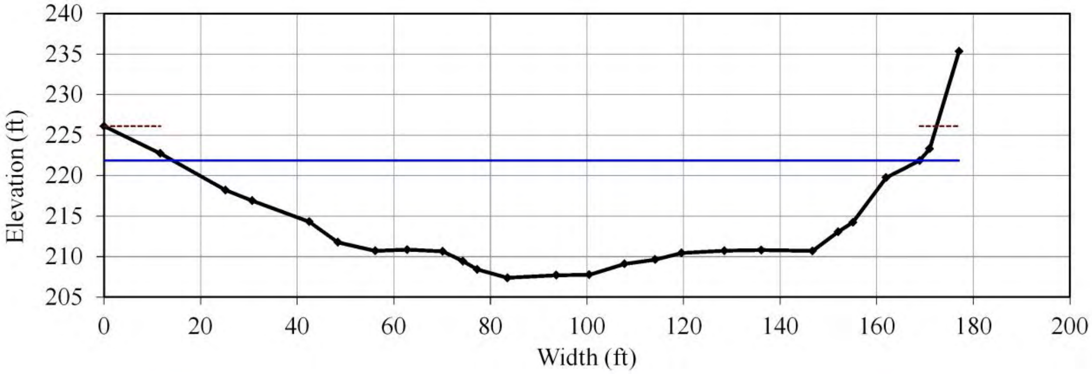
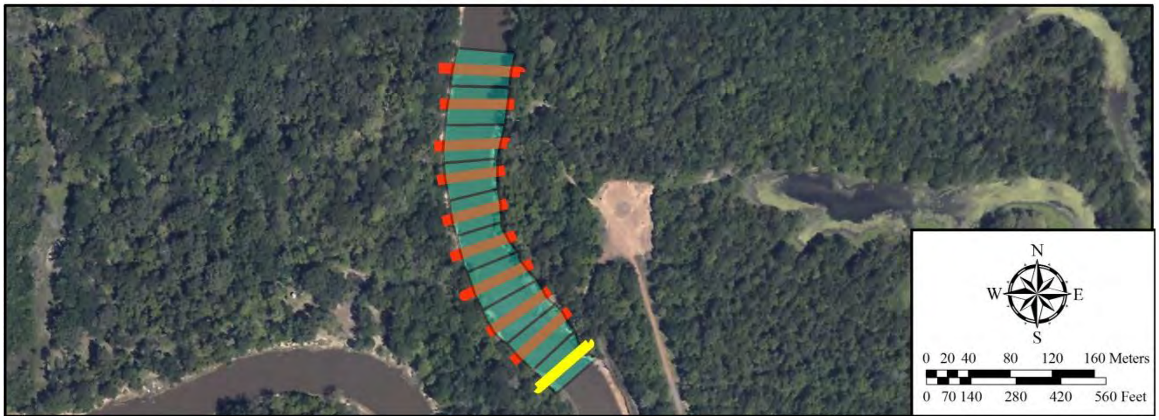
## APPENDIX B: GEOMORPHOLOGY CROSS SECTIONAL PROFILES OF FORTY TRANSECTS IN THE SABINE RIVER, AUGUST 2011

### 1TU





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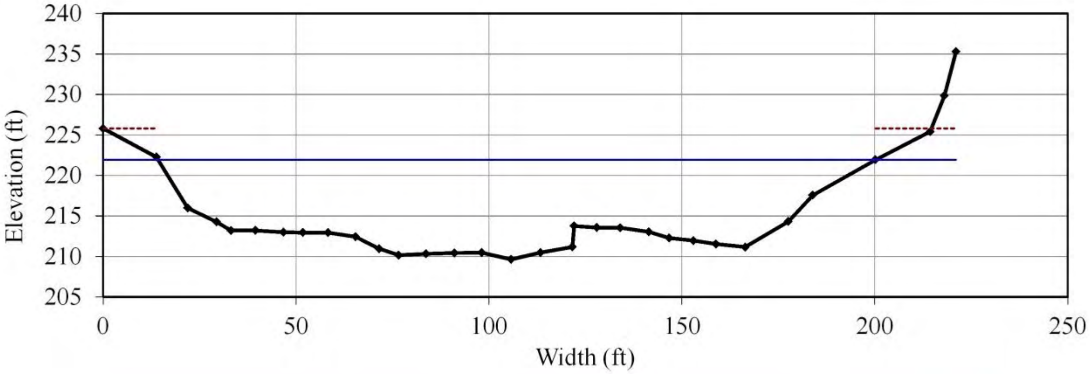
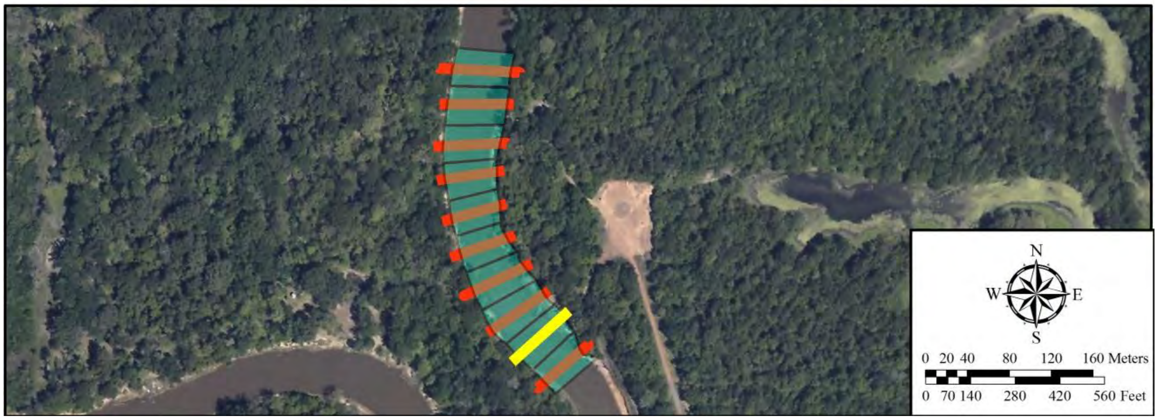
## 1T1





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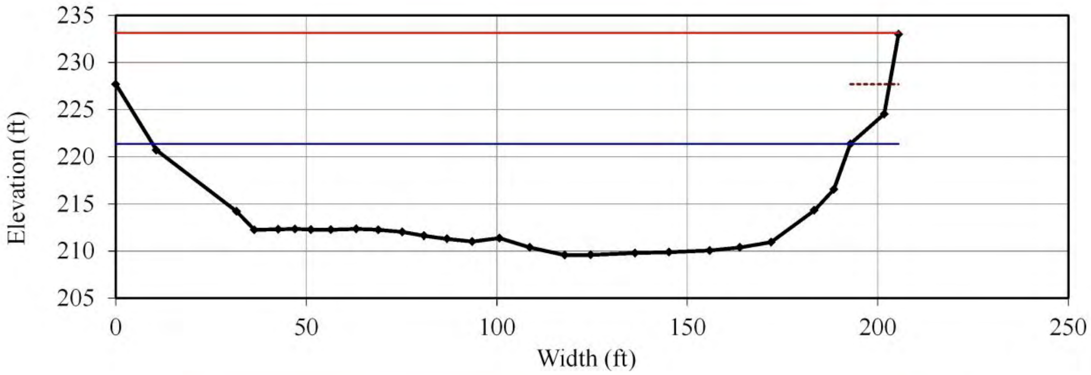
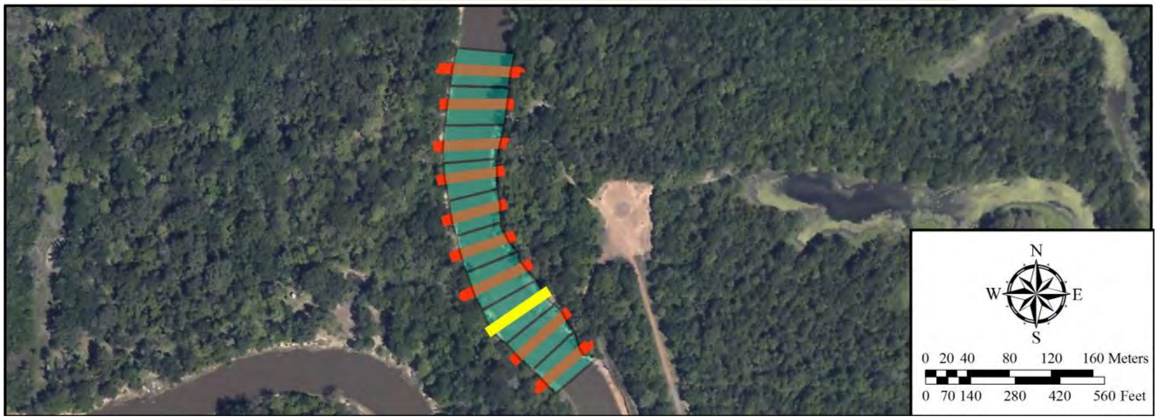
# APPENDIX B (CONTINUED)

## 1T2





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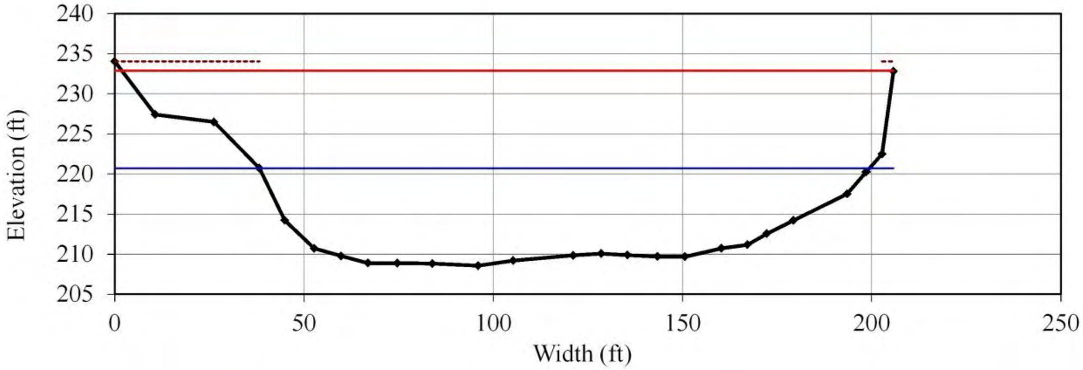
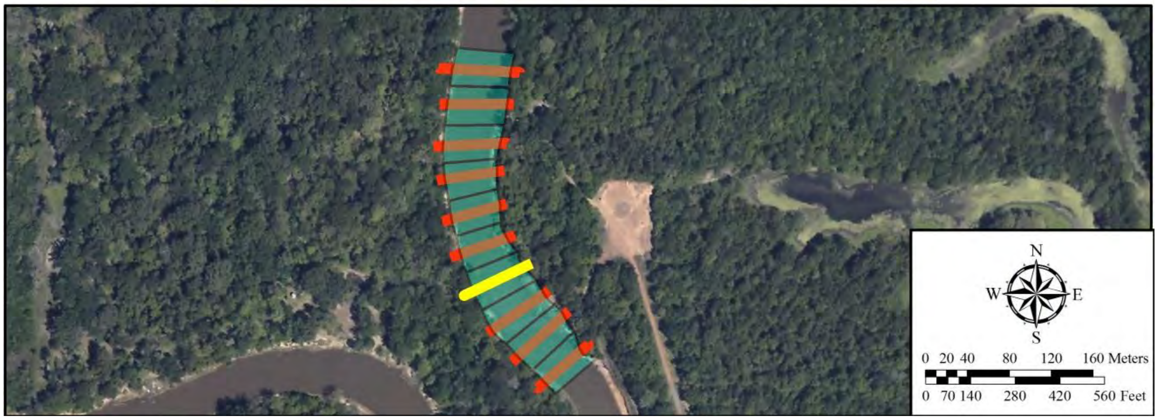
# APPENDIX B (CONTINUED)

## 1T3





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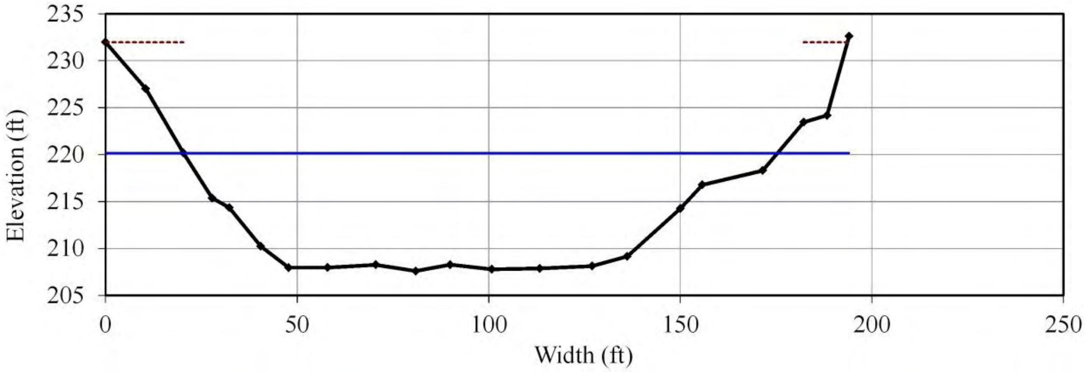
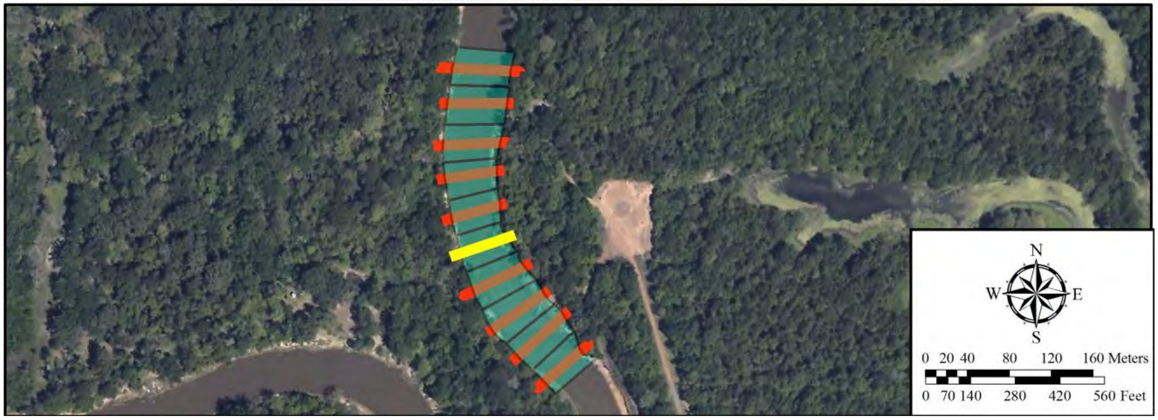
## 1T4





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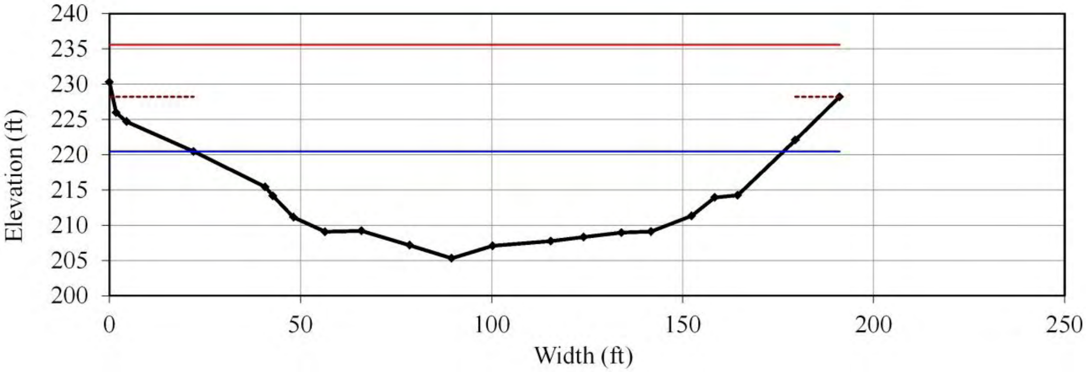
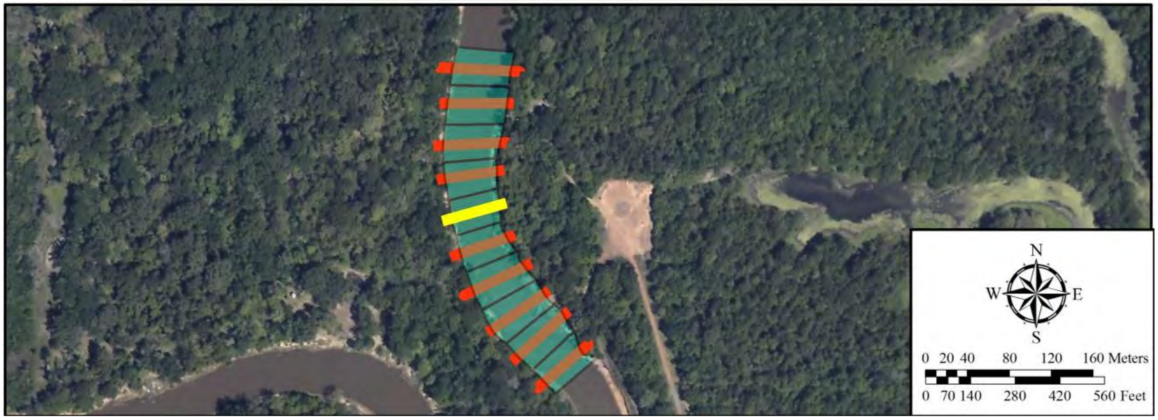
APPENDIX B (CONTINUED)

1T5





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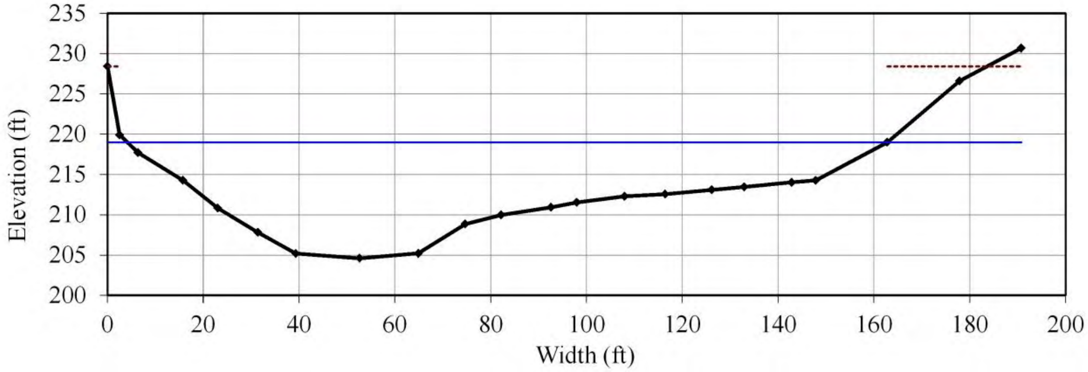
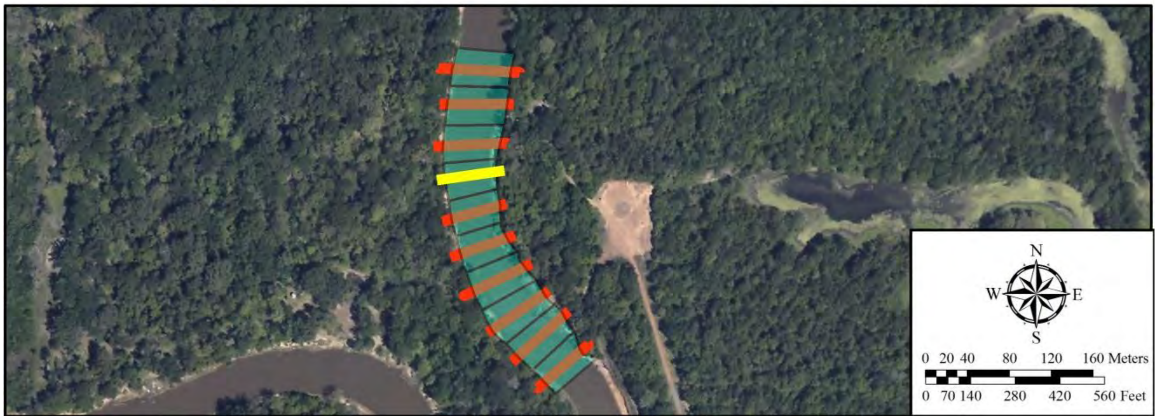
## 1T6





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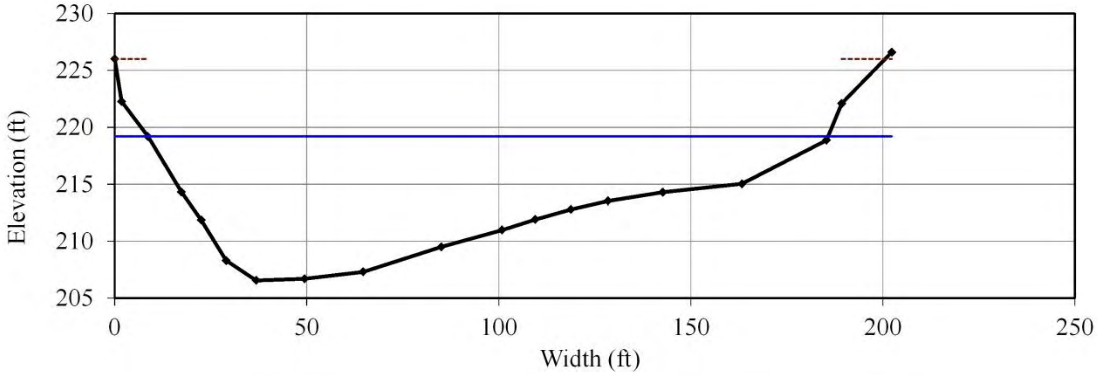
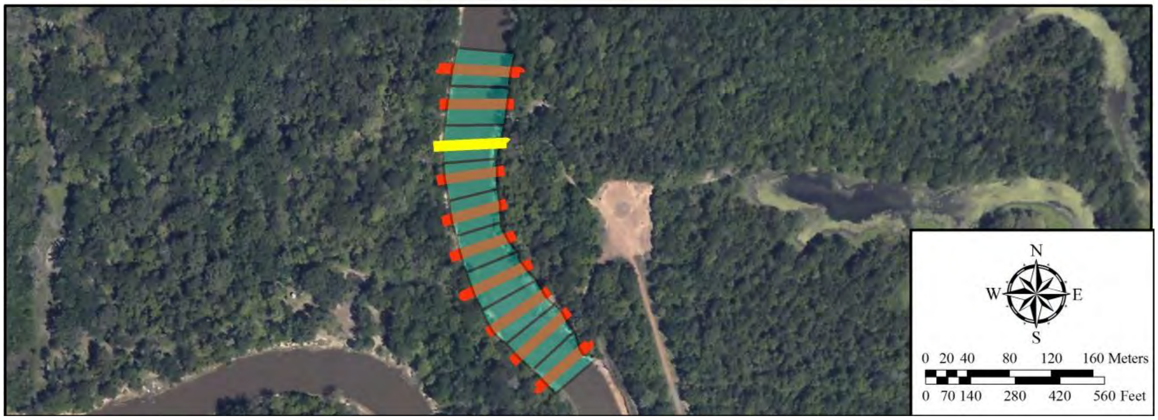
## Appendix B (Continued)

### 1T7





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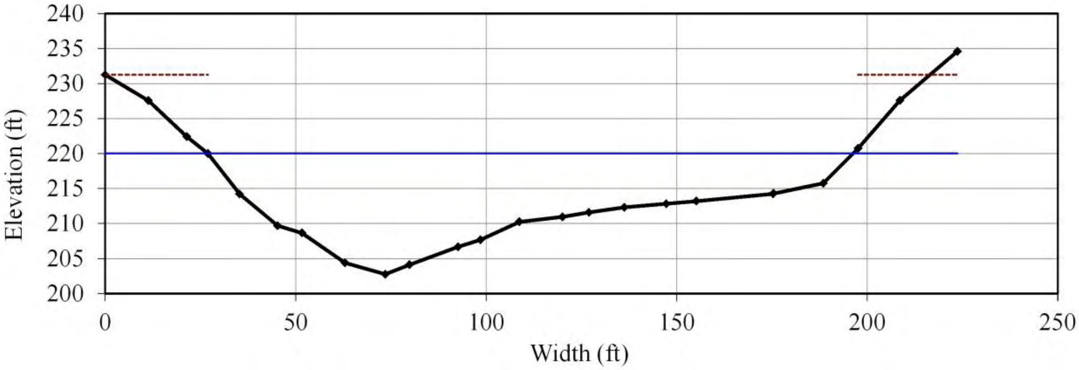
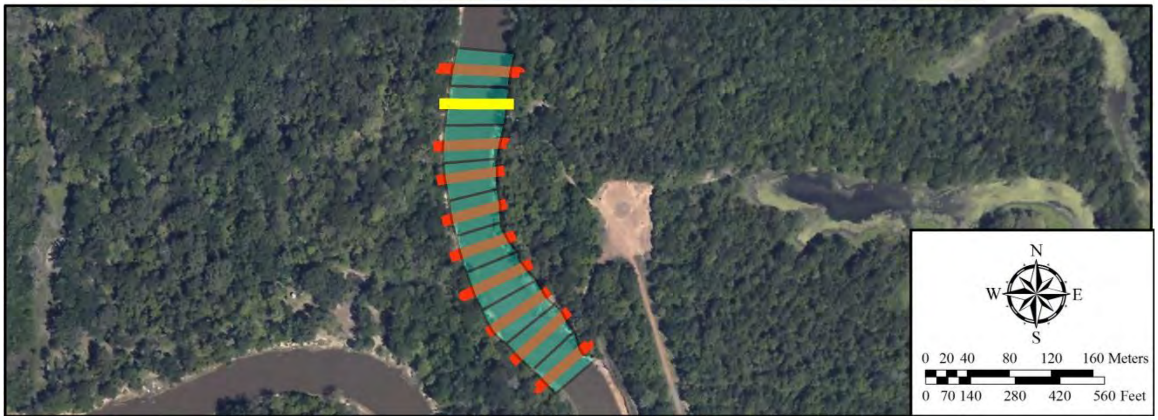
## 1T8





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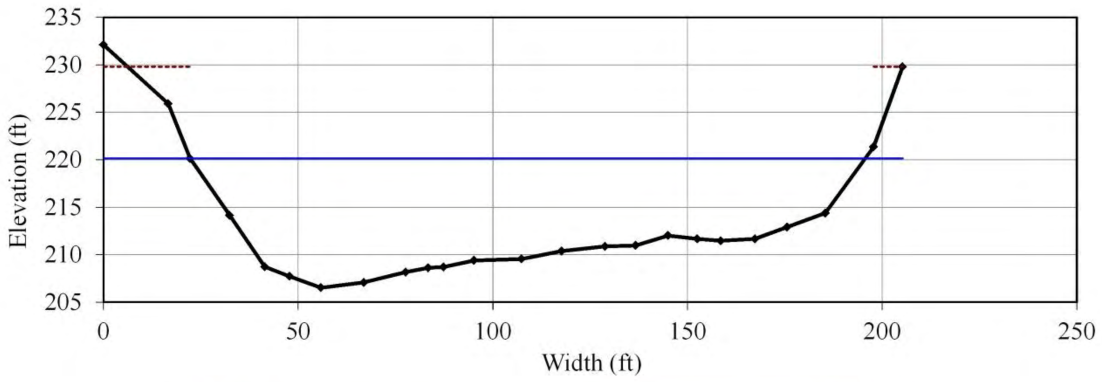
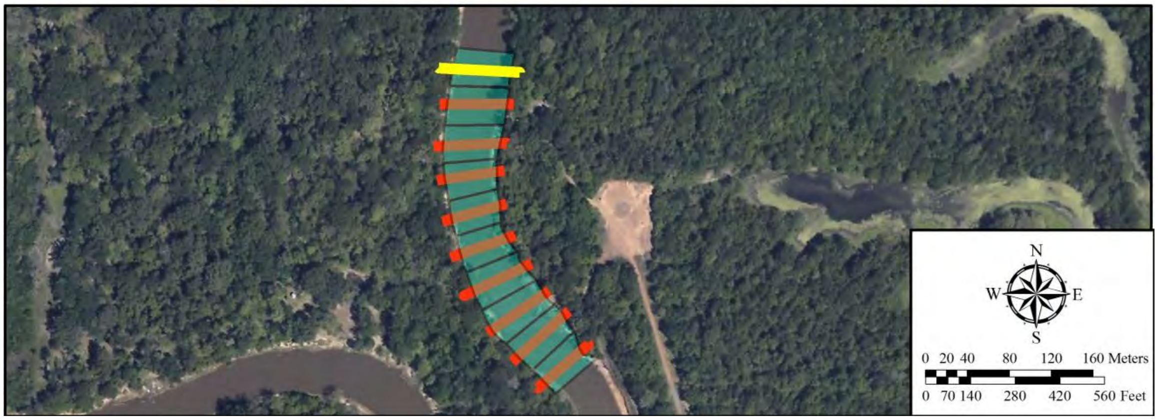
## 1TD





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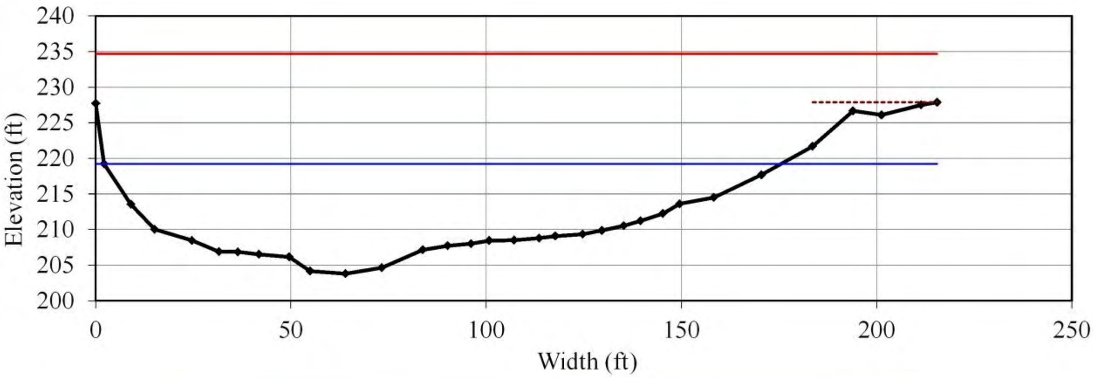
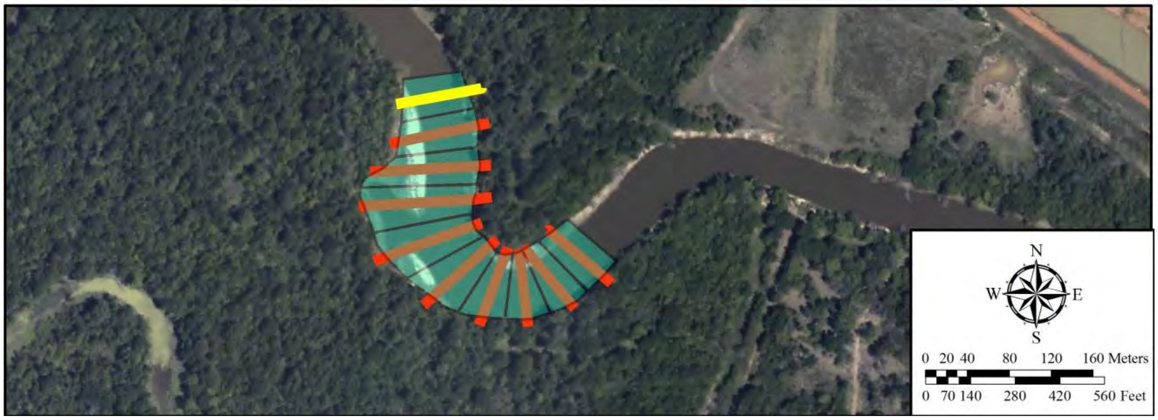
# APPENDIX B (CONTINUED)

## 2TU





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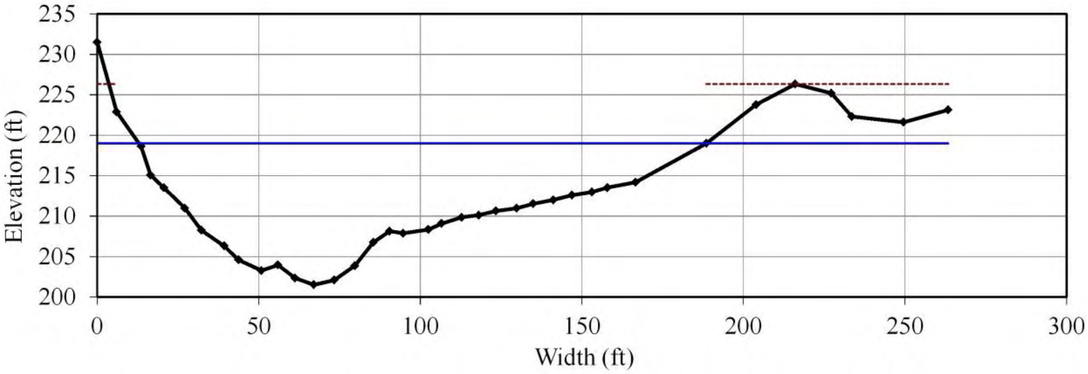
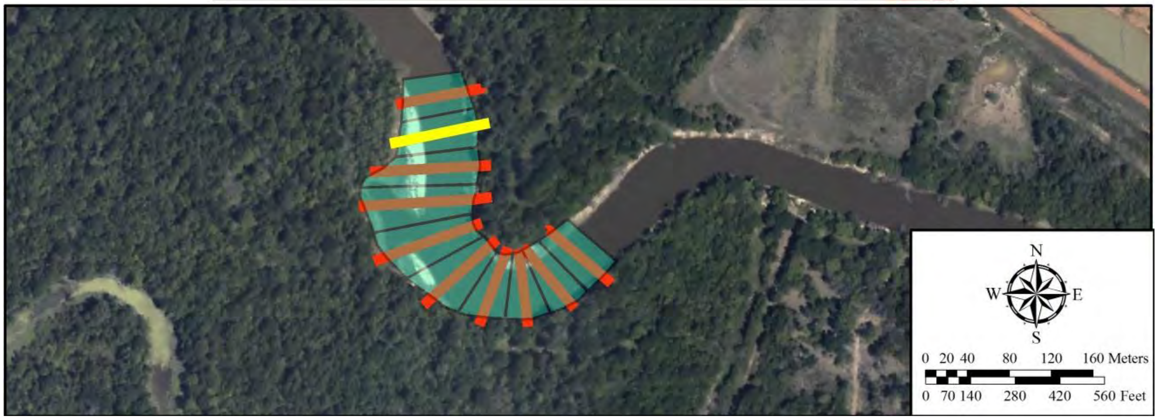
## APPENDIX B (CONTINUED)

### 2T1





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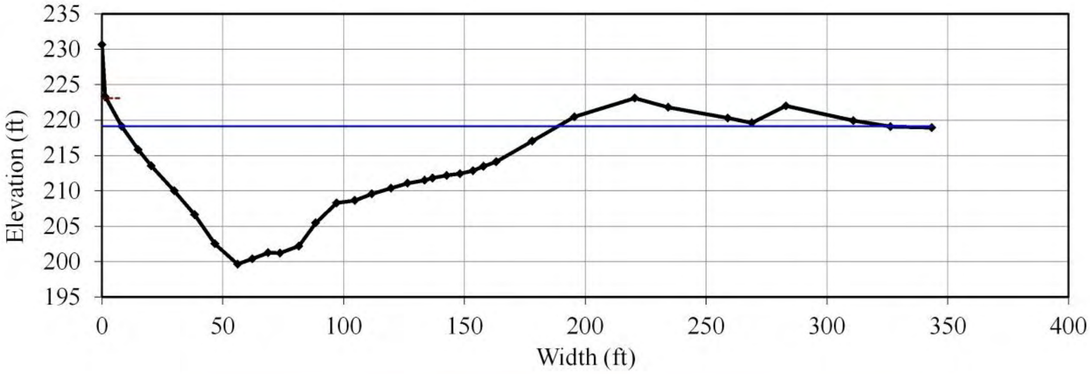
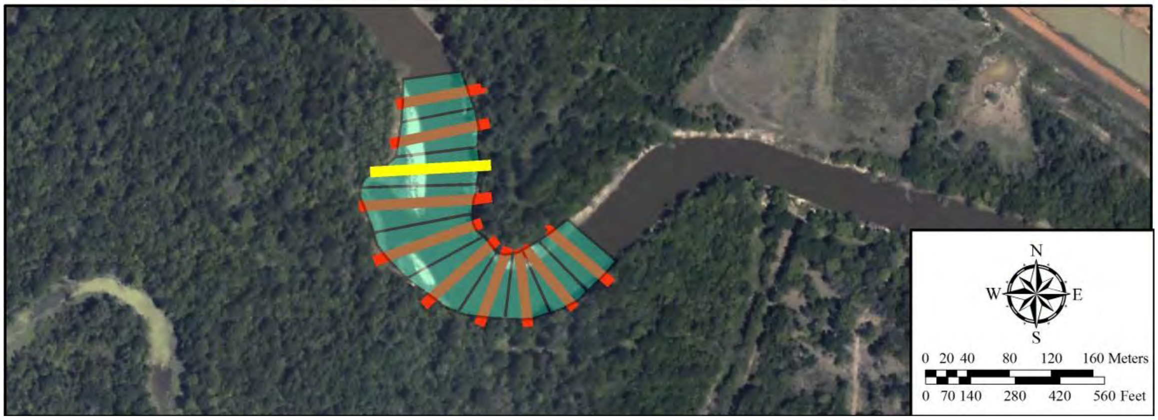
## 2T2





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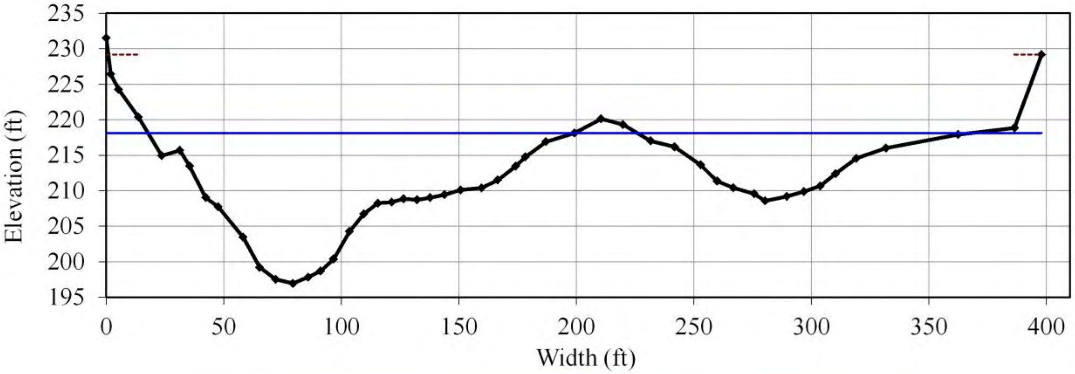
## 2T3



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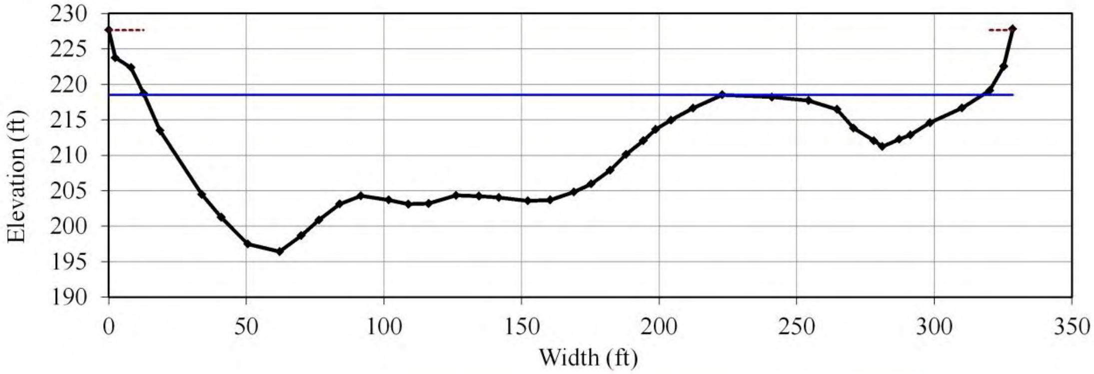
## APPENDIX B (CONTINUED)

### 2T4



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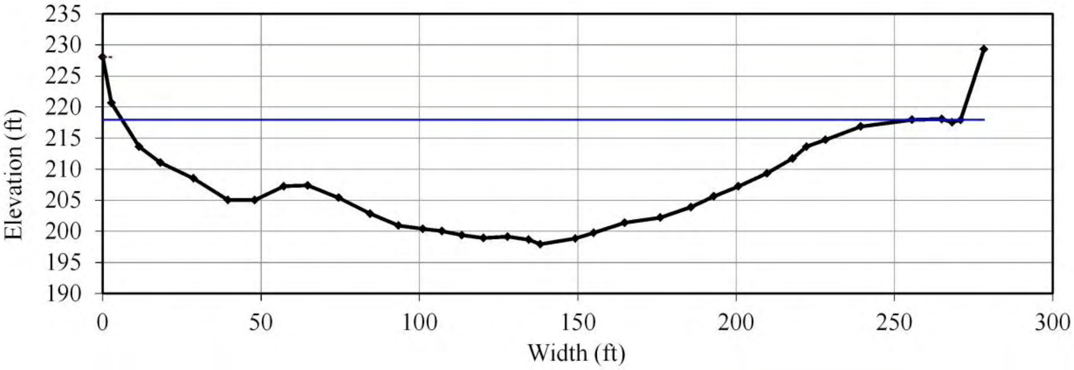
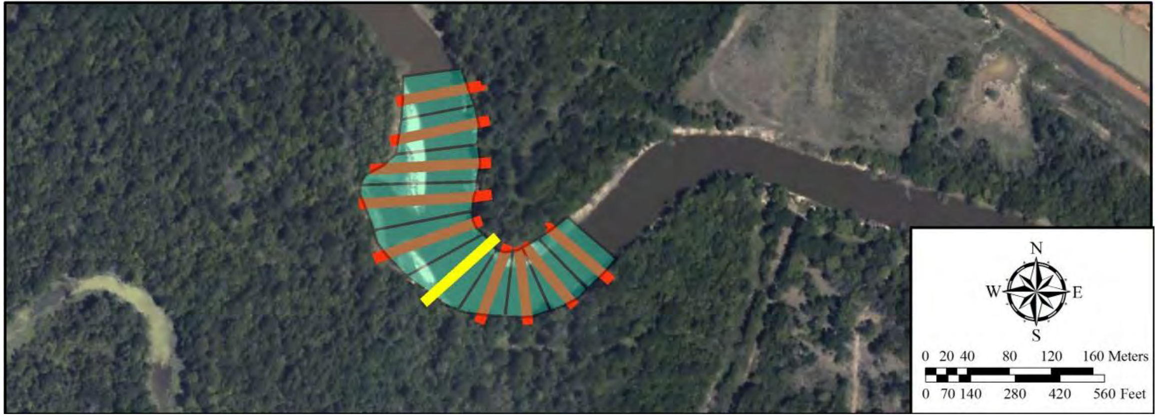
## 2T5





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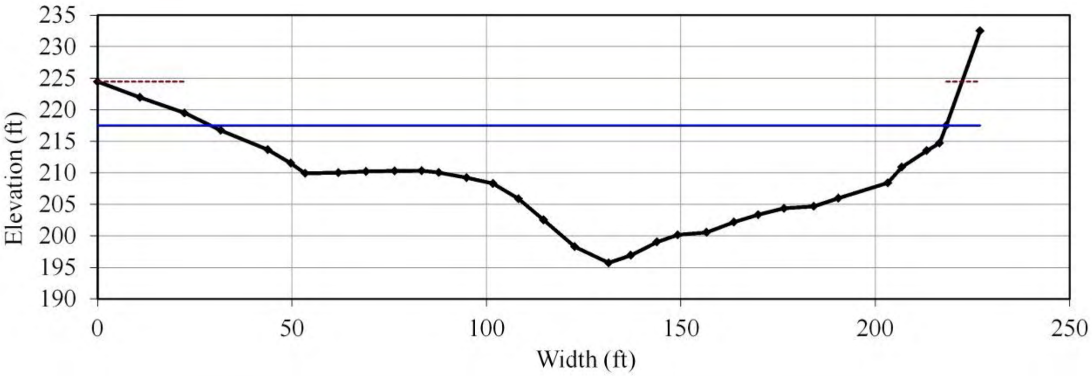
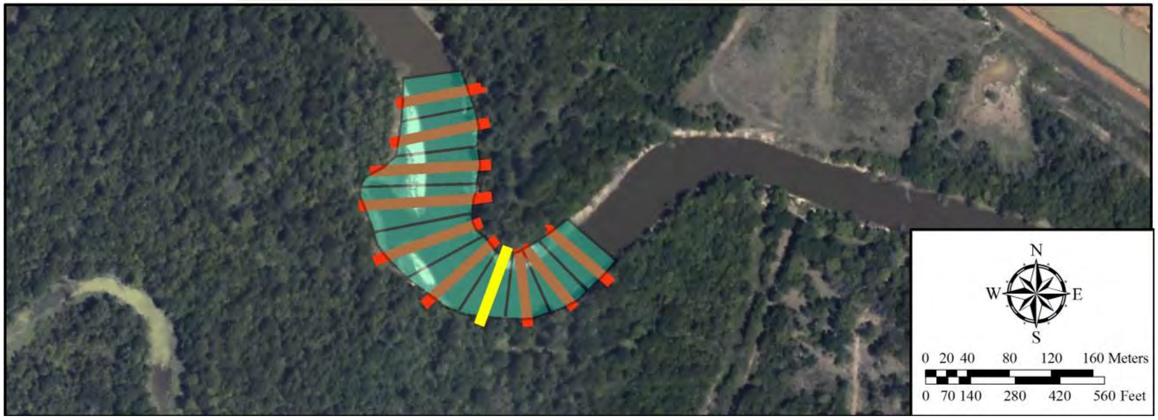
## 2T6





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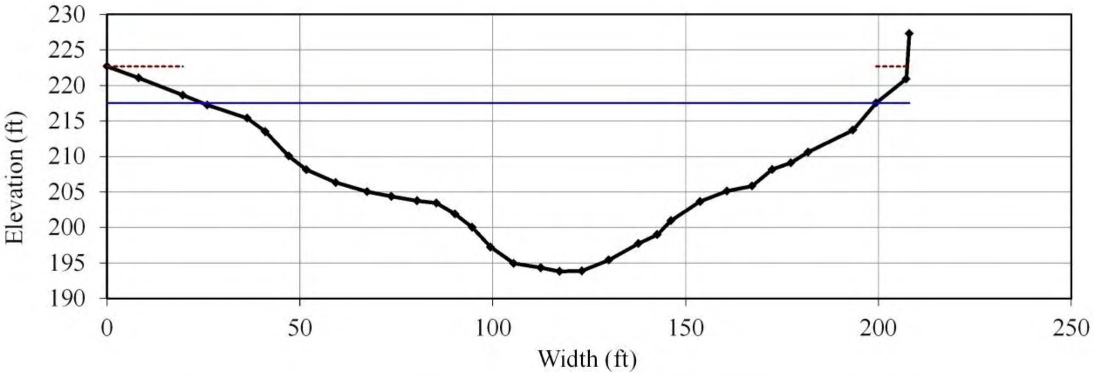

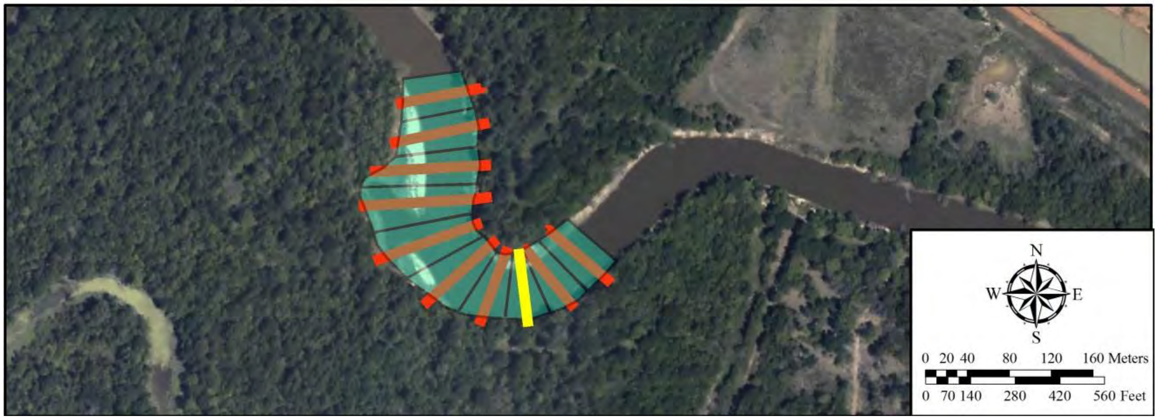

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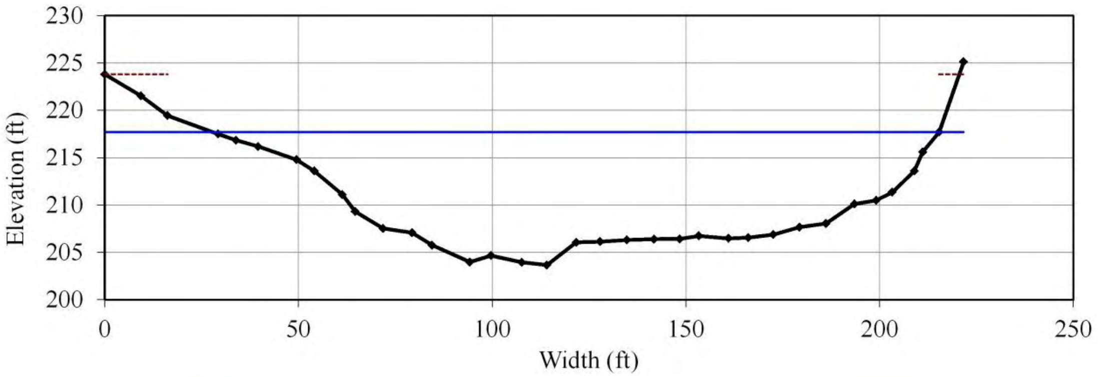
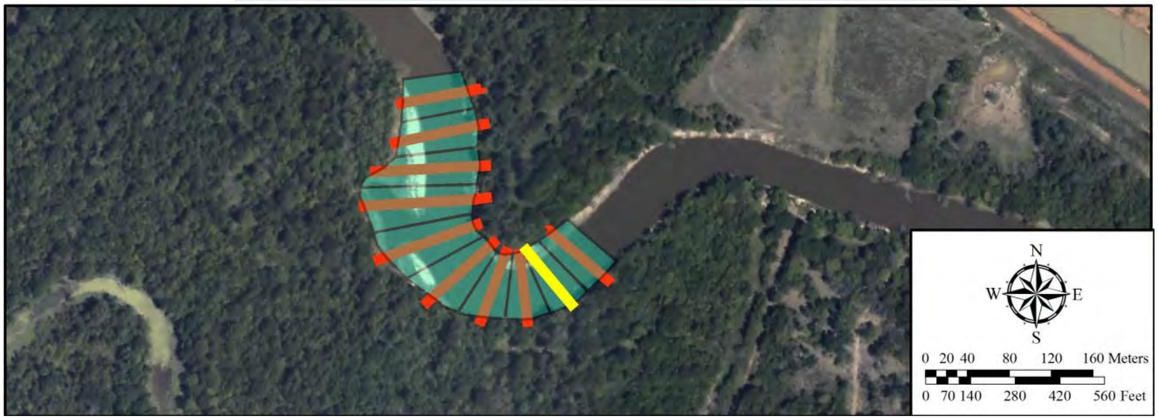
## 2T8





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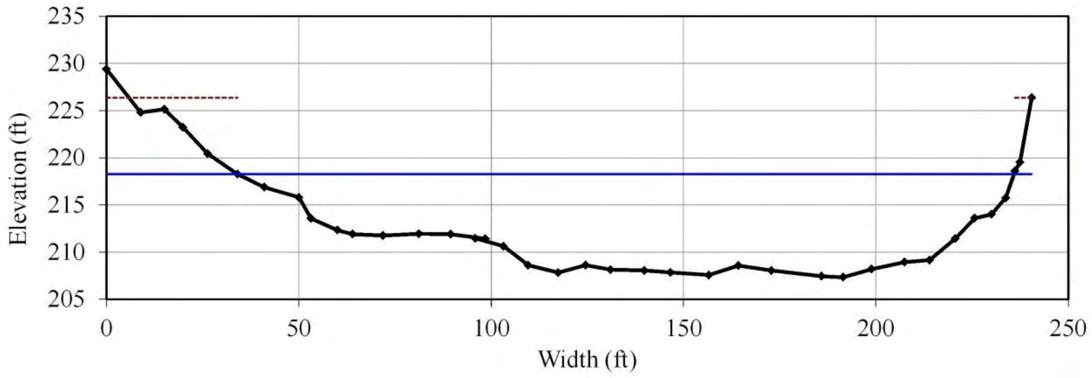
## 2TD



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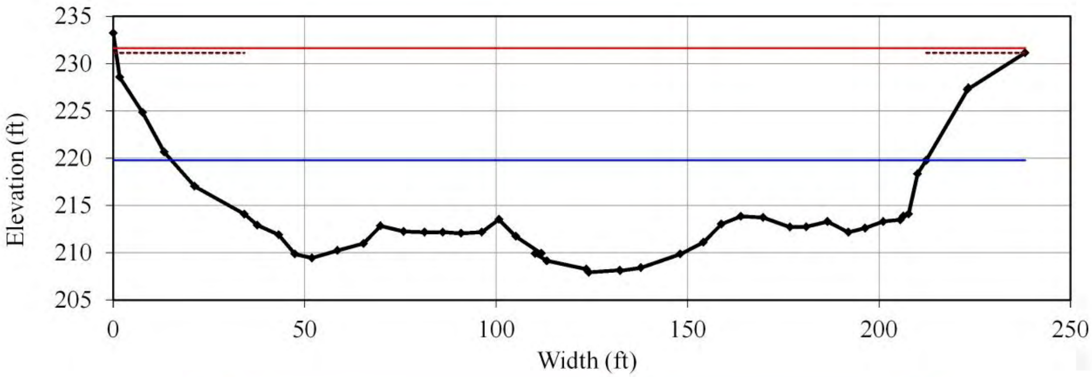
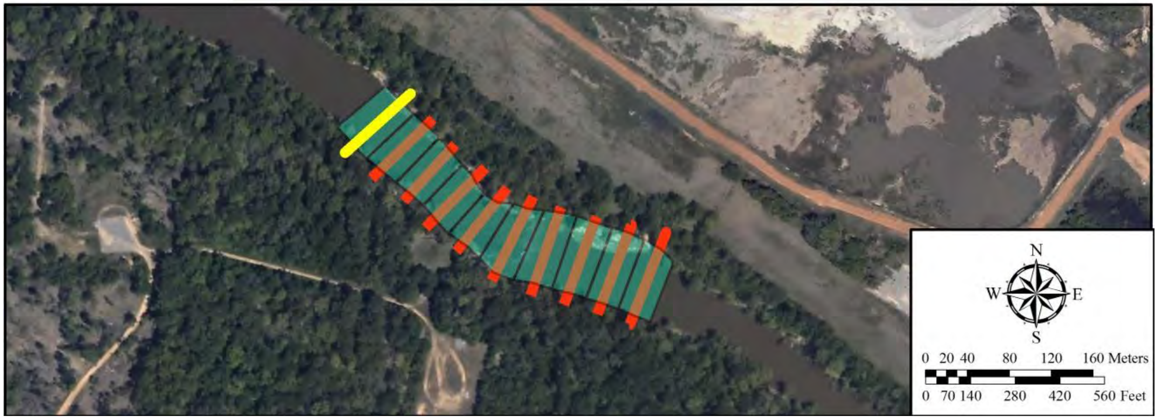
## APPENDIX B (CONTINUED)

### 3TU





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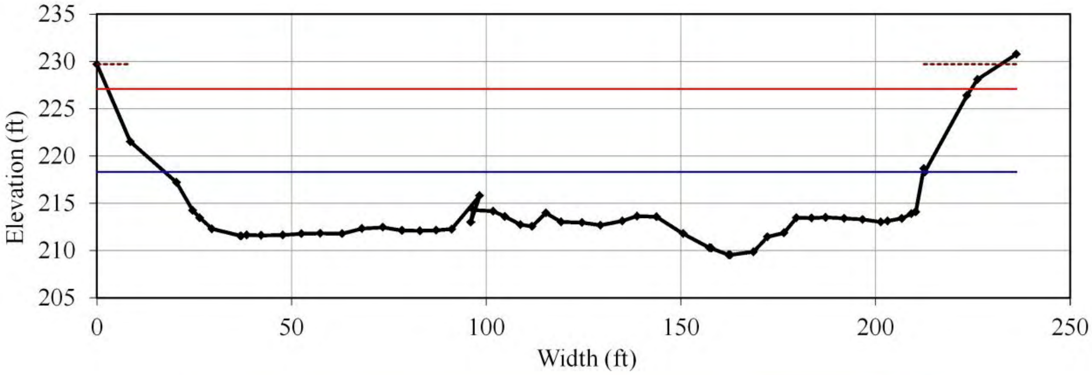
## 3T1



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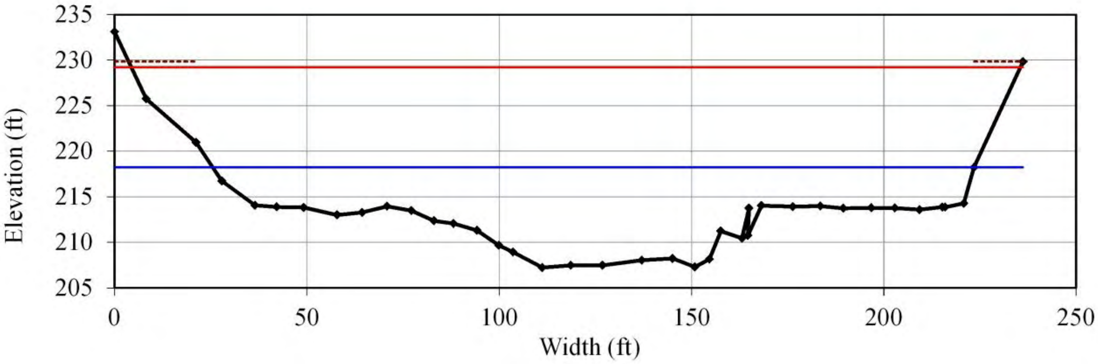
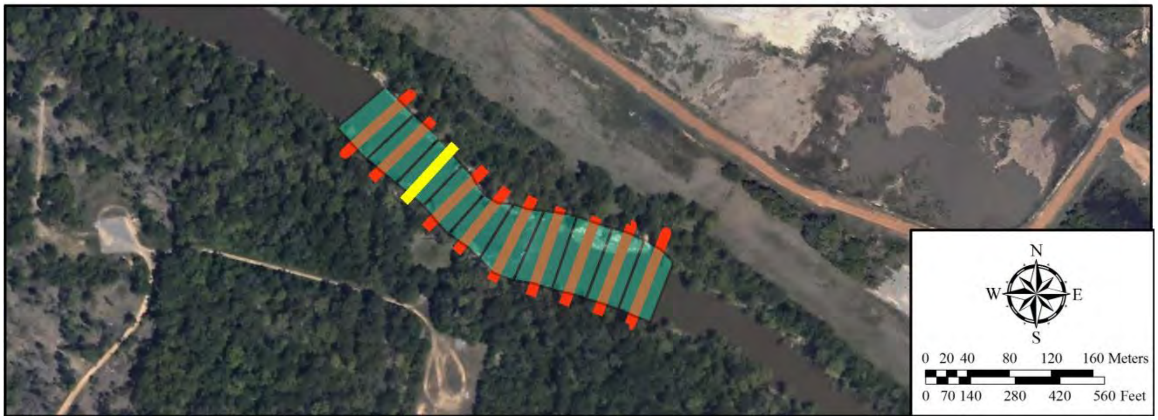
## 3T2





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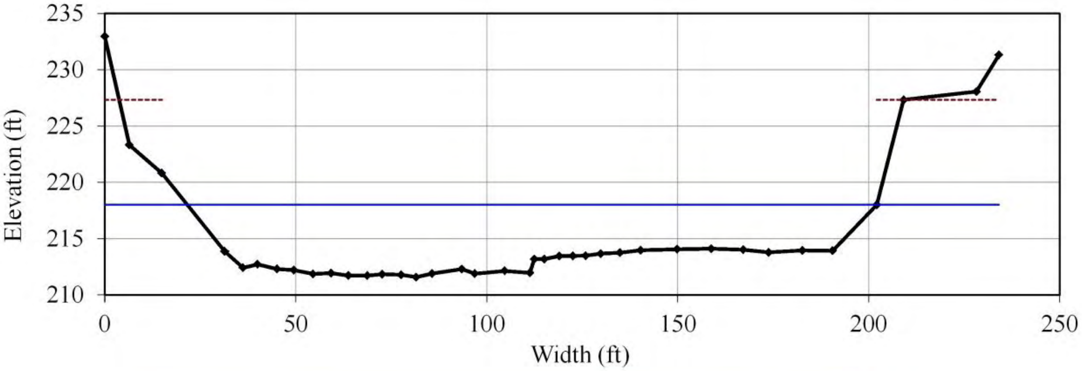
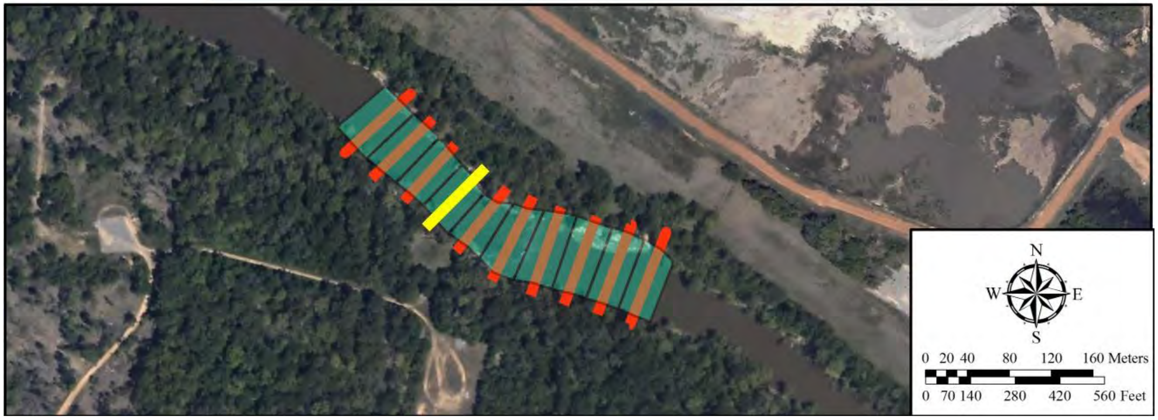
## 3T3





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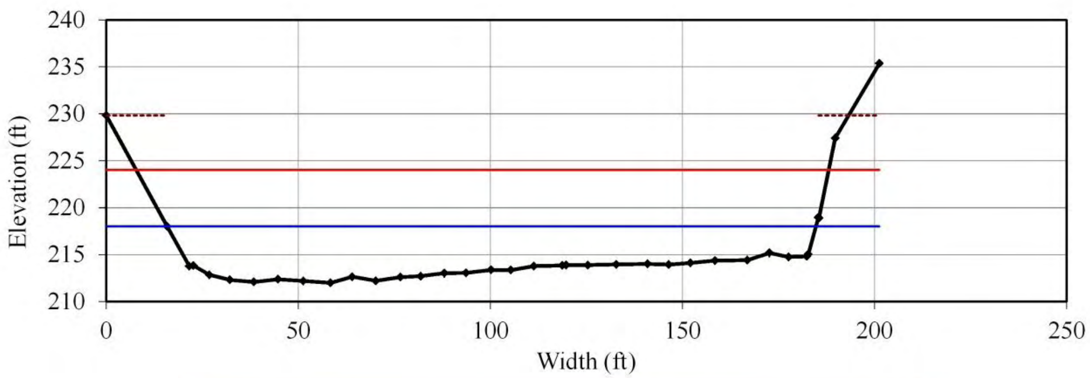
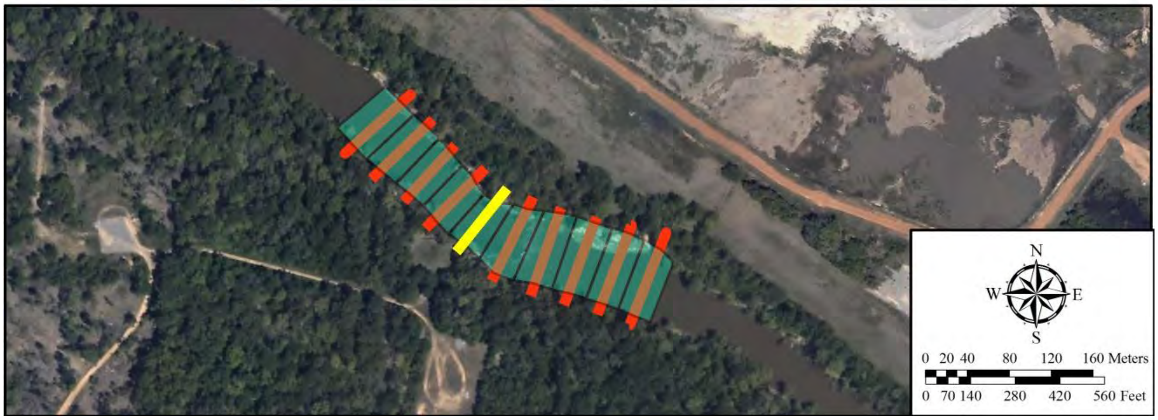
# APPENDIX B (CONTINUED)

## 3T4





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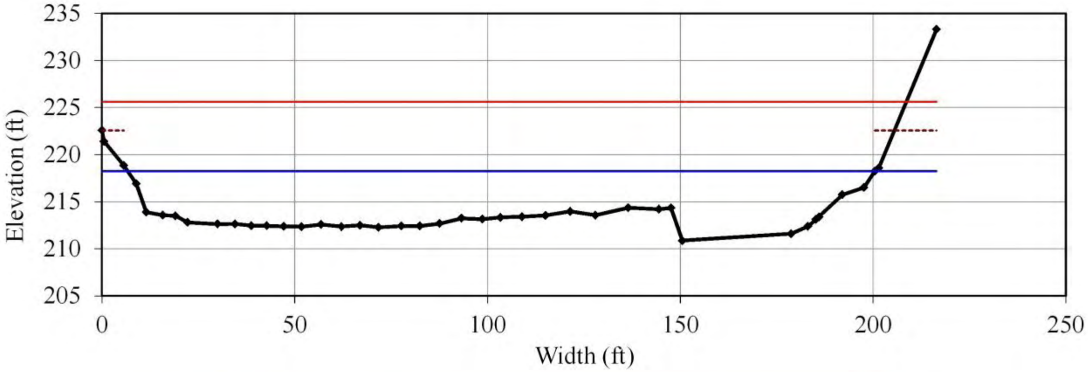
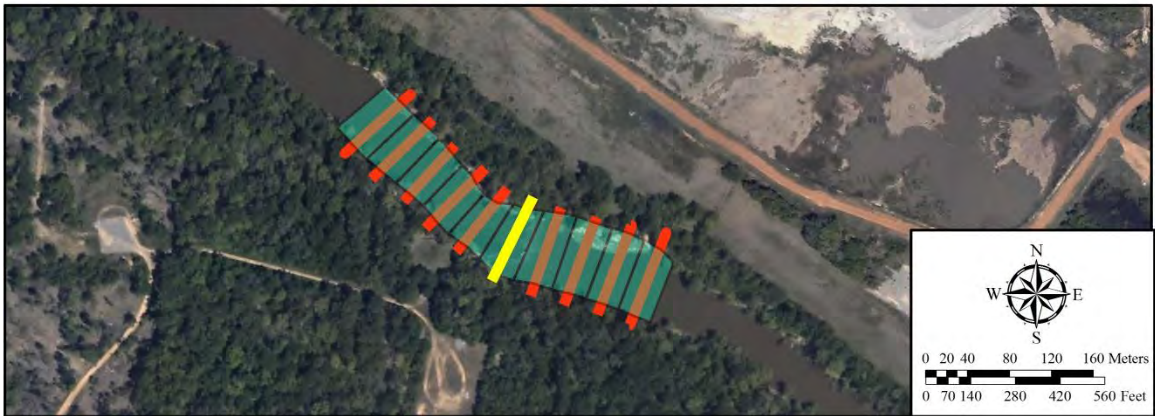
## 3T5





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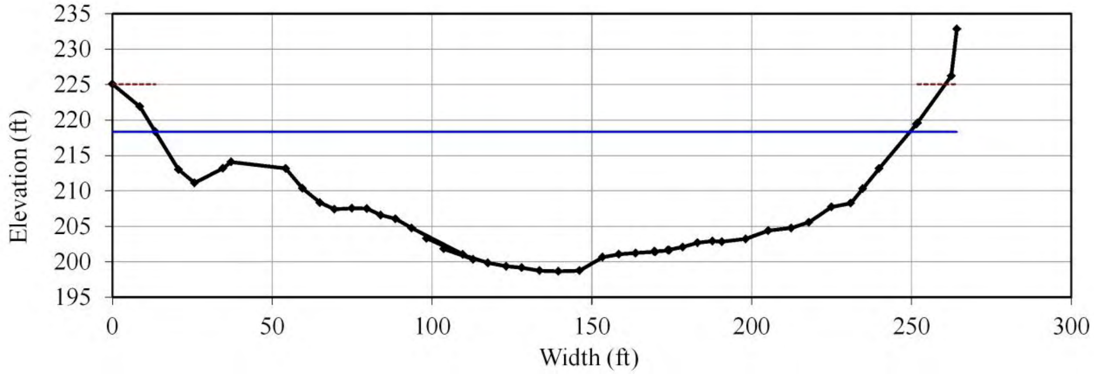
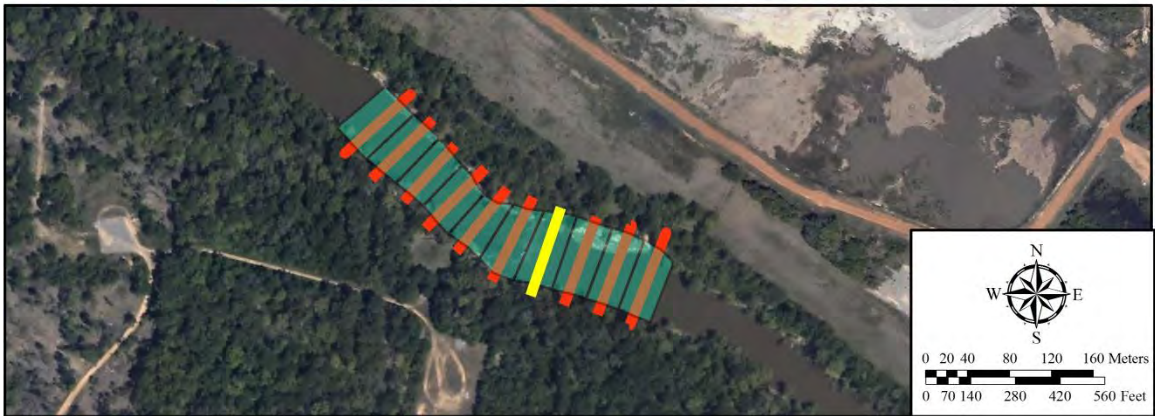
## 3T6





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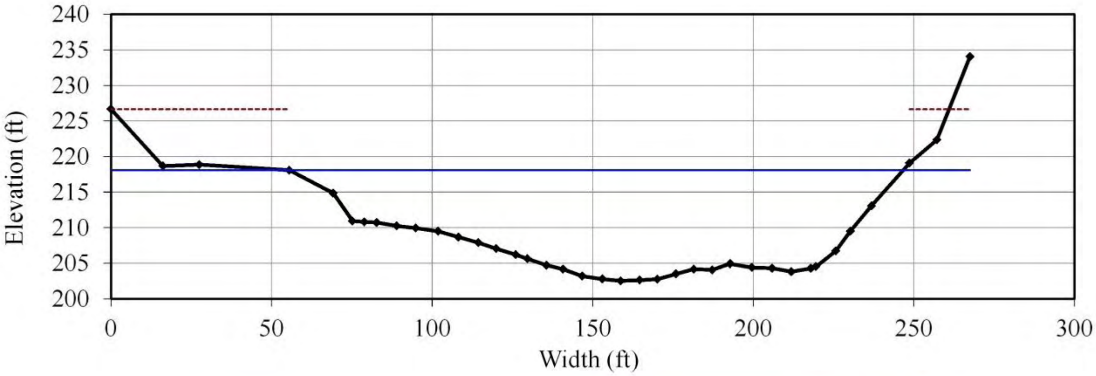
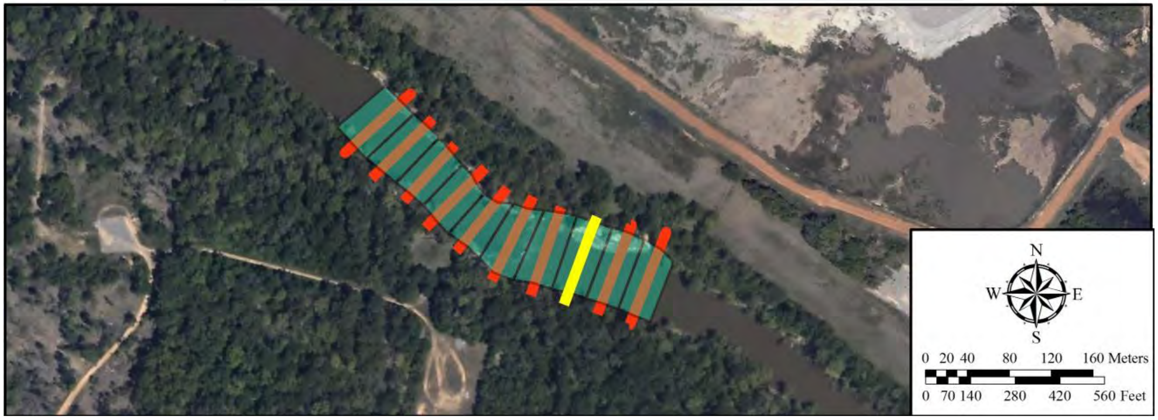
## 3T7





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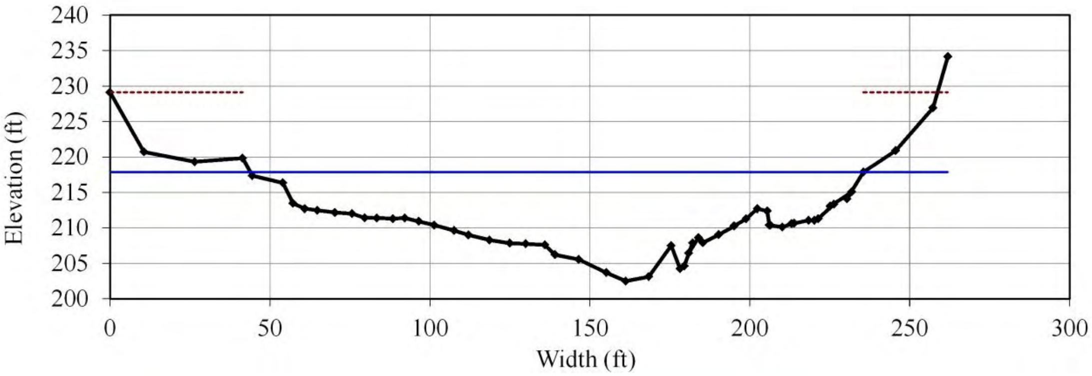
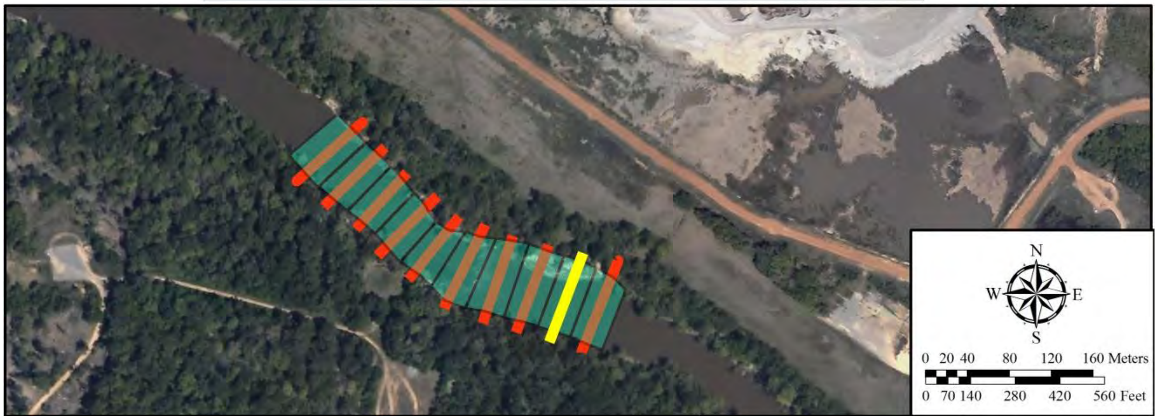
## 3T8





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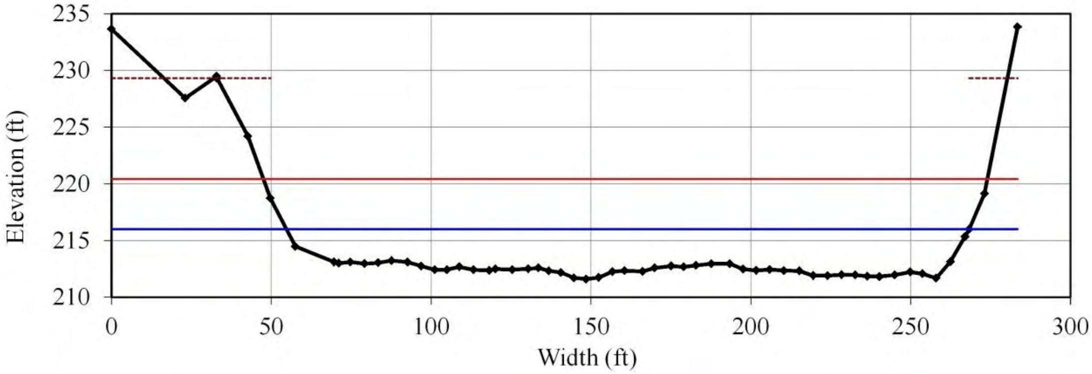

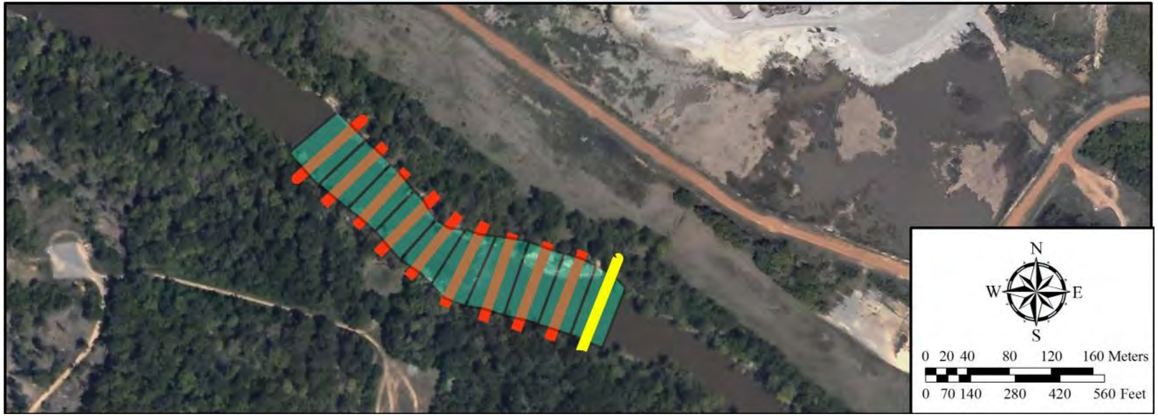

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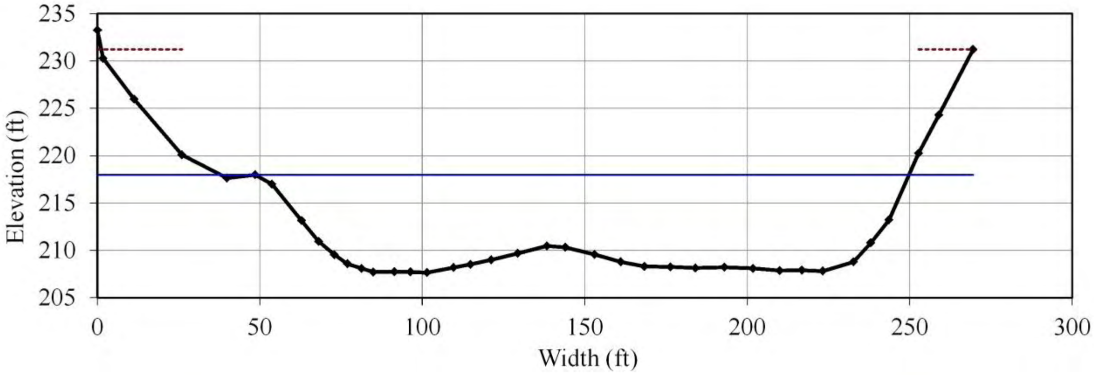
## 4TU



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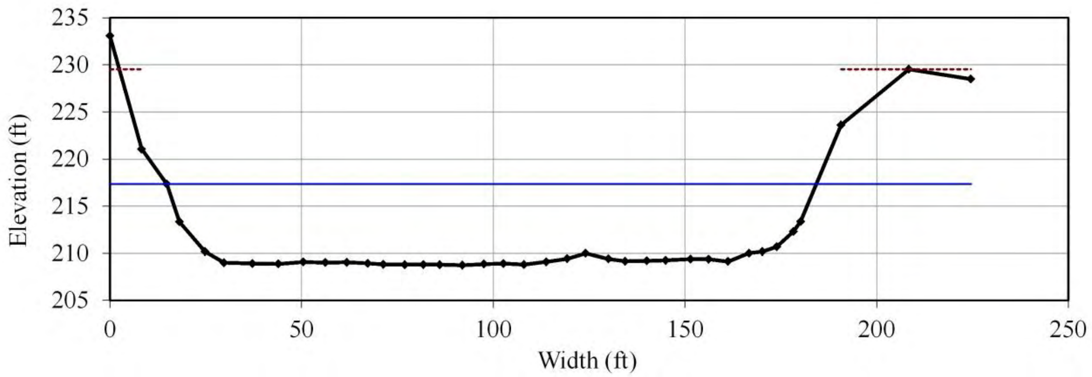
# APPENDIX B (CONTINUED)

## 4T1



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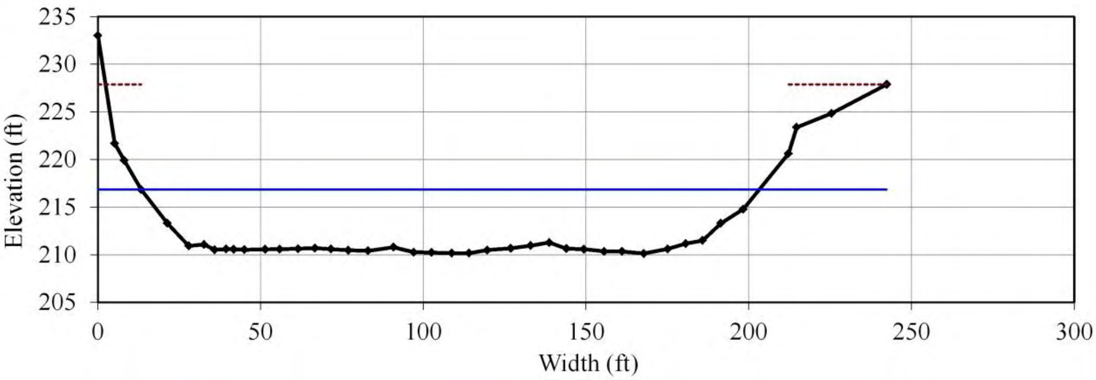
## 4T2



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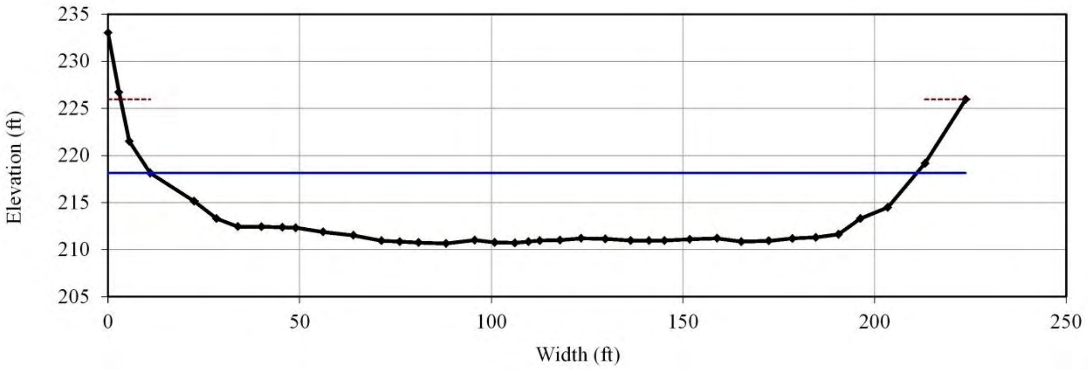
# APPENDIX B (CONTINUED)

## 4T3



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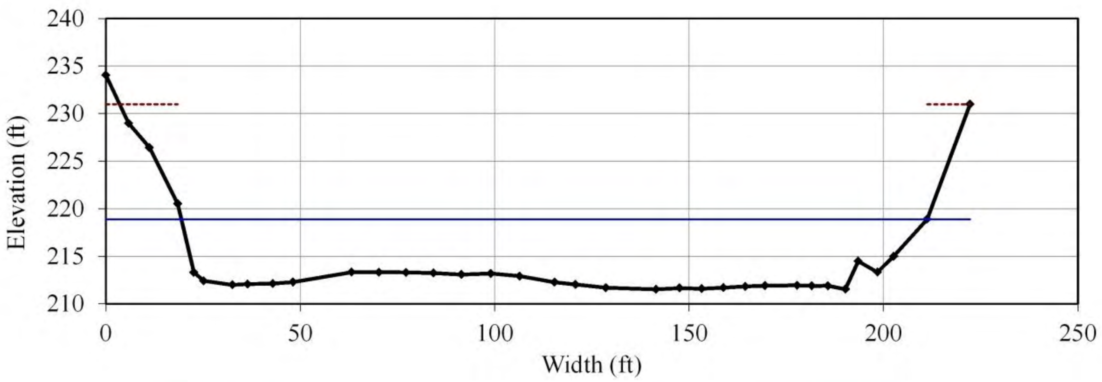
## 4T4



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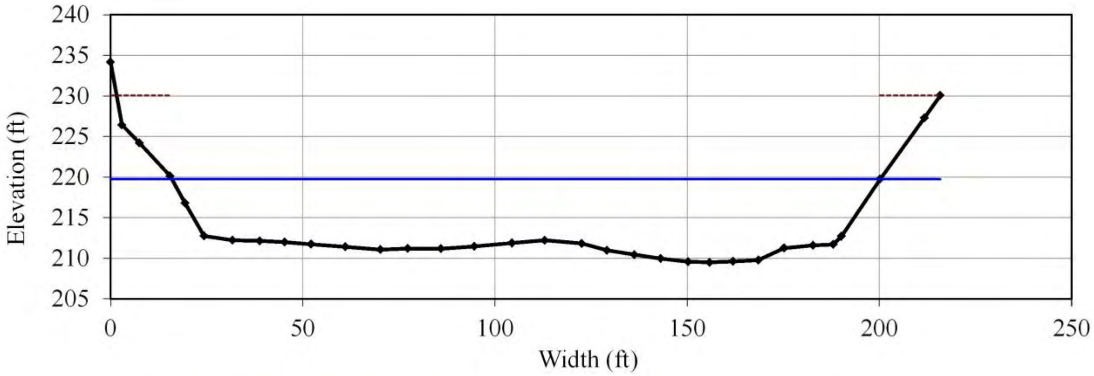
## 4T5



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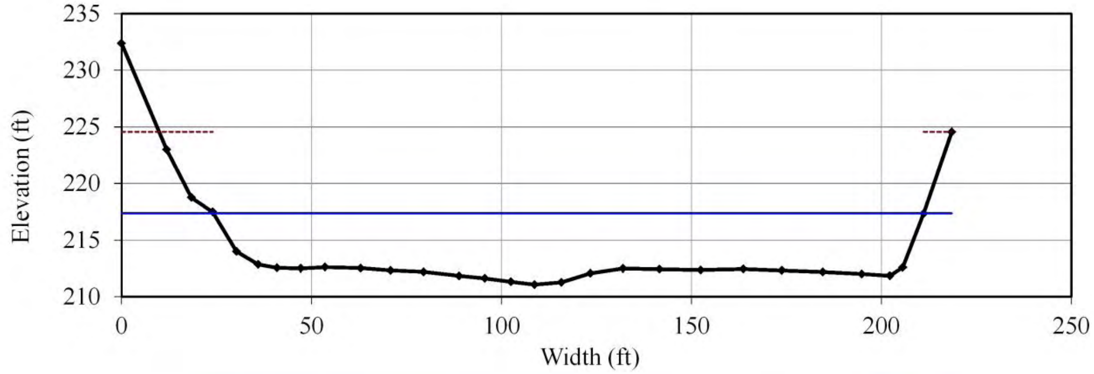
## APPENDIX B (CONTINUED)

### 4T6



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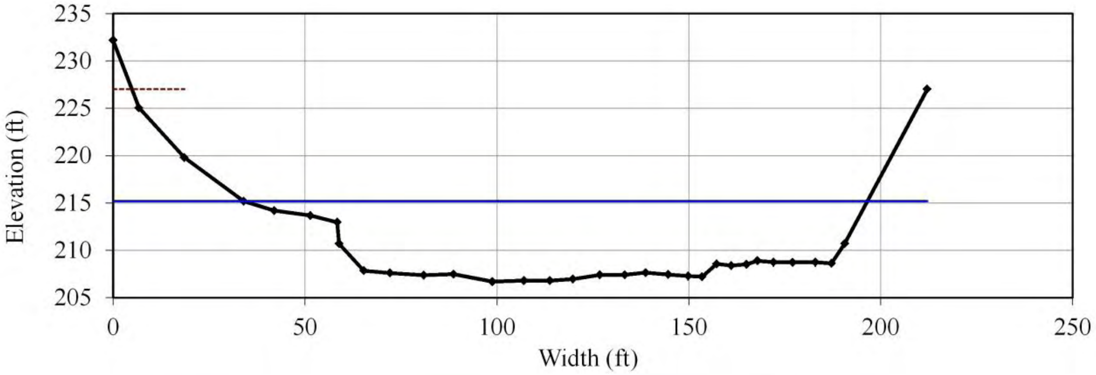
## 4T7



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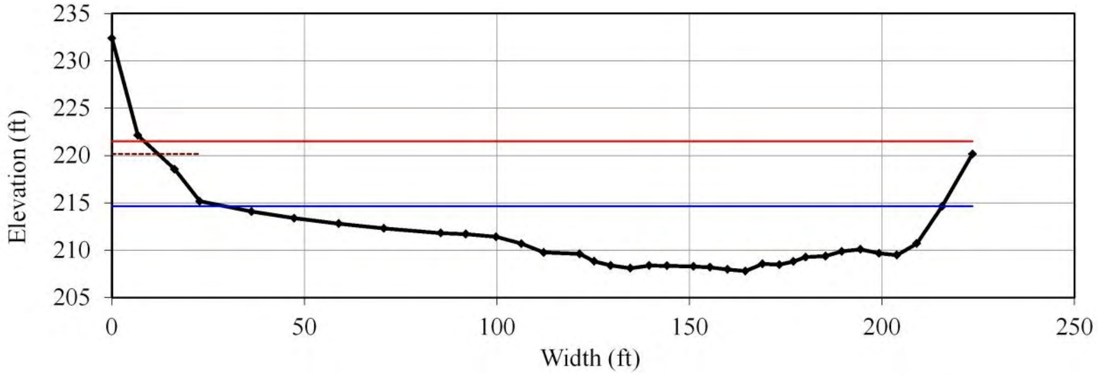
## 4T8



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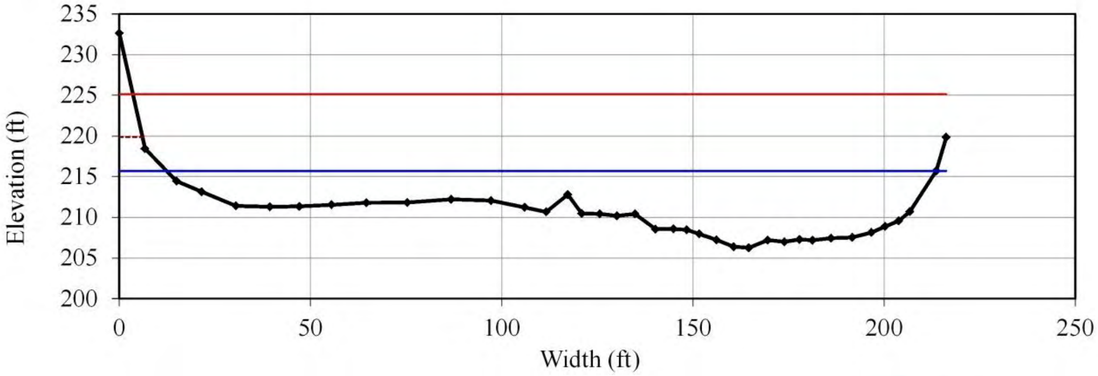
## 4TD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Elevation (ft)
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50
100
150
200
250
Width (ft)


N
W
E
S
0 20 40 80 120 160 Meters
0 70 140 280 420 560 Feet