MOVEMENT BEHAVIOR OF UNIONID MUSSELS IN CENTRAL TEXAS

by

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ABSTRACT

Freshwater mussels are one of the most imperiled groups of aquatic organisms. Burrowing and horizontal movement of freshwater mussels are behaviors integral to their ecology, yet mussel behavior is still relatively understudied. Thus, more insight into mussel behavior is needed to establish effective survey protocols and to inform the development of long-term conservation strategies. My objectives were to 1) examine and compare burrowing depth in the field among species and sites in the Guadalupe and San Antonio Rivers; 2) examine the effect of (a) differences in species, (b) decreases in temperature and (c) different substrates on burrowing behavior in experimental studies; and 3) examine the effect of dewatering on movement behavior. Seasonal differences were found at two sites in the San Marcos and Guadalupe River, with more mussels burrowing deeper in winter. In contrast, this was not observed at a predominately sandy site in the San Antonio River, where mussels burrowed significantly deeper compared to the other gravel/cobble dominated sites, independent of season. Lab experiments showed that differences in substrate affected burrowing behavior, and mussels responded to temperature changes. Burrowing depth was significantly deeper in sand compared to gravel. Further, when temperature was decreased from above 20°C to 15°C, 9% of the mussels stopped burrowing in sand but 58% stopped in gravel. Significant differences between species were only found in lab experiments with sand, in which *Amblema plicata* burrowed significantly deeper than *Quadrula aurea*. Horizontal movement rates differed significantly when comparing dewatering manipulations. At the fastest dewatering manipulation (15 cm/6 hours), 100% of the mussels became stranded, whereas 20 to 30% became stranded during slow (5 cm/10 days) and moderate (10 cm/4 days) dewatering manipulations. Thus, mussels in Central Texas may not have the ability to respond fast enough when water levels change rapidly, i.e., due to operations of dams. Our results also suggest that surveys may need to follow different guidelines depending on local conditions.

I. INTRODUCTION

Freshwater mussels are integral components of aquatic ecosystems and can reach high densities in patches known as mussel beds, where densities are 10 to 100 times higher than outside of these beds (Vaughn 1997, Haag 2012). Mussels remove particles from the water column (i.e., algae, detritus) via their filtering activity thereby increasing water clarity (Byllaardt and Ackerman 2014) and re-direct nutrients from the water column to the benthos (Strayer 2008). The shells of mussels offer physical habitats for other aquatic organisms such as macroinvertebrates and algae (Strayer 2008). Burrowing bivalves bioturbate sediments as they move, which can increase oxygen and nutrients in the sediments (Vaughn and Hakenkamp 2001). They also excrete feces and pseudofeces near the bottom enhancing growth of benthic algae (Strayer 2008).

North America exhibits the greatest diversity of unionid mussels with approximately 300 recognized taxa (Haag 2012). Freshwater mussels comprise one of the most jeopardized group of organisms in North America due to flow regulation, channelization, overharvesting, widespread habitat destruction, pollution, land use/land cover change, climate change, and non-native species introductions (Lydeard et al 2004, Strayer et al 2004, Haag and Warren 2008). In North America, 70% of these species have species status’ as vulnerable, imperiled, threatened, endangered, or extinct (Strayer et al 2004). Of the approximately 50 known species in Texas, there is one federally endangered species and 15 state threatened species; five are currently candidates for federal protection under the US Endangered Species Act (ESA); six are petitioned for listing under the ESA; and one was recently proposed as endangered. (USFWS, 2016).

Threats to mussels include extreme water fluctuations caused by short term water release regimes below dams (Galbraith et al 2015) and longer term changes due to climatic changes. Climatic changes, such as increased frequency and duration of drought, are implicated in increased mussel mortality due to desiccation and declines of 60-83% in mussel abundance relative to predrought to post drought flow regimes have been observed. This has been attributed to increased predation and desiccation of established mussel beds (Haag & Warren 2008, Walters and Ford 2013). Whether and how mussel species can react to water level fluctuations or changes in seasonal flow regimes under drought conditions will depend on their movement behavior (Schwalb & Pusch 2007, Peck et al 2014, Galbraith et al 2015)

Burrowing and horizontal movement behavior of freshwater mussels is an integral factor of freshwater mussel ecology. Juvenile mussels remain buried in the sediment (Amyot and Downing 1991, Balfour and Smock 1995) and feed by sweeping the sediment with their foot (Yeager et al 1994). As adults, however, they must come to surface to filter-feed and for reproduction. Horizontal movement may play a role during reproduction in that female and male mussels may move closer together during breading (Amyot & Downing 1997, Amyot and Downing 1998, Perles et al 2003), but movement can also help to avoid adverse conditions by moving with receding water to avoid drying out.

Different species may have different strategies in how they react to adverse conditions, such as drought or water fluctuations. A study in a drying stream reach in Alabama found that different mussel species showed different behavioral responses: tracking of receding water: tracking receding water then burrowing, and burrowing alone.

Tolerant burrowers were the most resistant to drought conditions (i.e., *Uniomerus tetralasmus*, Gough et al. 2012). The distances mussels move horizontally and burrow vertically can vary between species, (Schwalb and Pusch 2007, Allen and Vaughn 2009, Negishi et al 2011, Gough et al 2012, Galbraith et al 2015). Despite an increasing interest in mussel ecology in the past 10-20 years, movement behavior is little understood and behavioral studies in the laboratory are necessary to gain more insight, i.e., in order to identify substrate that is suitable for borrowing (Strayer 2008); furthermore, how mussels respond to dewatering is important to understand in order to develop conservation strategies (i.e., Galbraith et al 2015).

Seasonal vertical migration has suggested mussels burrow deeper in winter compared to summer, and associated with day length, water temperature, reproduction, and flow velocity (Amyot and Downing 1991, 1997, Balfour and Smock 1995, Watters et al 2001, Schwalb and Pusch 2007, Watters and Ford 2011, Gough 2012). However, seasonal vertical migration of unionid mussels has never been studied in warmer subtropical rivers represented by Central Texas systems and a better understanding of this relationship would inform applied survey designs in support of conservation measures. For example, when a large proportion of mussels are burrowed deeply, surveys, if they do not include excavations, may underestimate species presence/absence or actual population size (Strayer and Smith 2003). Excavations, however, are time consuming and disturb habitat (Miller and Payne 1993 and Smith et al 2001).

Hence, in order to gain a better understanding of movement behavior of mussels in Texas, the objectives of this study were 1) to examine and compare burrowing depth in the field among species and sites in the Guadalupe, and San Antonio River drainages in

Central Texas; 2) examine the effect of (a) differences in species, (b) decrease in temperature and (c) different substrates on burrowing behavior under controlled conditions; and (3) to examine the effect of dewatering on burrowing behavior and horizontal movement.

II. METHODS

Study Area

Field studies were conducted at three sites in the San Marcos, Guadalupe, and San Antonio River Systems in central Texas from October 2014-September 2016 (Table 1, Fig. 1). The San Marcos River originates at artesian springs in San Marcos, TX. The drainage area is 840 km^2 and composed of urban, industrial, agricultural, oil production, and recreational land uses (GBRA 2008). The San Marcos River merges with the Guadalupe River at 120km downstream near Gonzales, Texas (GBRA 2008). The Guadalupe River originates in Kerr County, Texas and flows southeasterly to the San Antonio Bay System (TCEQ 2016). Its drainage area is 9,769 square kilometers with urban, farming, and agricultural land uses (TCEQ 2016). Study sites in the Guadalupe watershed were near: (1) Luling, (2) Gonzales (collection of mussels used in the lab) (3) and Cuero (Fig. 1). Substrates at all sites on the Guadalupe River consisted of gravel, cobble and silt and were located in riffle habitats.

The San Antonio River originates in Bexar County, San Antonio, TX and flows southeastward from the San Antonio Springs to its confluence with the Guadalupe River (SARA 2012). Its drainage area consists of 6727 square km with urban, farming and agricultural land uses (SARA 2012). The study site was located near Kennedy (see Figure 1). Sites were located off the main channel near the bank and substrates consisted of sand and dead *Corbicula* shells.

Additionally, mussels utilized for laboratory experiments were obtained from the Llano River near Mason, TX (Colorado River basin), and Village Creek near Lumberton, TX, a major tributary of the Neches River (see Figure 1).

Mussel species

Quadrula aurea (I. Lea 1859); *Quadrula petrina* (Gould 1855); *Lampsilis bracteata* (Gould 1855); and *Fusconia askewi* (Marsh, 1896) are considered Texas endemics (Howells 2002), and are currently candidates for placement on the federal Endangered Species, but they can be abundant within their drainages. The largest, most stable populations of *Q. aurea* have been found in the lower reaches of the Guadalupe River (Howells 2006, Burlakova et al 2011).

The focus of the field study was on two threatened species in Central Texas *Quadrula aurea*, and *Quadrula petrina,* in conjunction with the variation in vertical movements of the co-occurring common species (i.e., *Amblema plicata,*). Laboratory experiments were conducted utilizing the state threatened species: *Lampsilis bracteata* from the Llano River and *Fusconia askewi* from Village Creek.

Monitoring movement at field sites

Visual and tactile searches were carried out along 10 m transects at each site. Transects were perpendicular to the flow at the sites near Luling and Gonzales. The transects near Cuero and Kenedy were parallel to the flow, because the velocity was too strong, and/or water depths too great to orient the transects across the stream channel. Tactile searches included digging for mussels up to 5cm into the substrate. All mussels found were placed in a mesh bag and retained in the water. Each individual was measured for width, length, and height and photographed. All mussels found during a thorough initial survey were tagged (Fig. 2). A uniquely numbered 12mm Passive Integrated transponder (PIT) Tag (Biomark, Inc., Bowase, ID, USA) was glued on the left, posterior margin of each mussel using waterproof epoxy (LOCTITE Henkel Corporation, Rocky

Hill, CT, USA). A distinctively numbered shellfish tag (Floy Tag Mfg. Inc., Seattle, WA, USA) was glued using Super Glue along the right, posterior margin of each mussel.

During regular surveys the location of mussels at the surface were detected with a PIT-tag antenna. The use of an antenna to locate tagged mussels restricted the study area to wadeable segments of the streams. Their location on the surface or burrowed were visually examined with an underwater viewer or via snorkeling or scuba. Burrowing depth was recorded on a scale of 0%, 25%, 50%, 75%, 90%, and 100% (only detected; not visible on surface) burrowed (Fig. 3). For the pilot study in the San Marcos River, we only differentiated between completely burrowed and not completely burrowed mussels, and tagged newly collected mussels not only at the first sampling date in, but also at regular surveys (Table 1) . The pilot study was conducted from October 2014-August 2015 at the San Marcos River site. However, the site was not accessible due to extensive flooding between May and July. In August 2016, 12 tags were detected with the antenna, but mussels appeared buried under shifted sand. One mussel that was excavated was found dead. Hence data for the analysis was only available for October to January, when temperatures ranged from 15°C-21°C. Surveys were conducted August 2015-February 2016 in the Guadalupe and San Antonio River sites. Temperatures decreased from 32°C to 15°C (Table 1) from August 2015 to February 2016. Sites were sampled in different months because both sites were not always accessible. In addition, initial sampling dates varied between the Guadalupe and San Antonio River, (Table 1), but both sites were surveyed in October and February.

River discharge data were obtained from USGS gage stations (Table 2). On each survey date parameters such as pH, dissolved oxygen (DO) and specific conductivity were measured with a handheld multisonde (YSI 556 MPS, YSI Inc., Yellow Springs, OH, USA). Current velocity was measured with an electromagnetic flow meter (FH950 Portable Flow Meter, Hach Co., Loveland, CO, USA) at each site at several points along the transect when surveyed.

Lab Experiments-Effect of decrease in temperature on burrowing behavior

Trials to examine the effect of decrease in temperature on burrowing behavior were conducted in mesocosms with gravel (D50 = 14 mm) and coarse sand (D50 = 0.4 mm) from September 2015 to May 2016. Mussels were held within enclosures (90 cm L, 30 cm W, 46 cm) with approximately 56 L of substrate (30 cm deep) contained within living streams (213 cm x 61 cm x 56 cm).

All mussels used in the experiments (*A. plicata*, *Q. aurea*, *L. bracteata,* and *F. askewi*) were measured for length, width, and height; and tagged with a shellfish tag. To acclimate to laboratory conditions, they were held in living streams for three weeks. A total of three experiments were conducted: 1) *A. plicata* and *Q. aurea* in gravel, with equal ratios of the two species (four *Q. aurea* and four *A. plicata*), 2) *A. plicata* and *Q. aurea* in sand, and 3) *L. bracteata* and *F. askewi* in sand. For these treatments temperature was dropped one degree per day until reaching 12°C. Vertical movements were recorded daily using a premeasured length of monofilament line glued to the mussel. The length of line remaining above the surface was measured and subtracted from the total line length to estimate the burrow depth of individual mussels daily. Temperature was measured daily.

Lab experiments – Effect of differences in substrate on movement behavior

Lab experiments were conducted to compare the effect of substrate type and temperature on burrowing in a controlled environment. Three trials were conducted in eight 38 L aquariums held in water baths at room temperature (18°C-20°C) in four living streams (213 cm x 61 cm x 56 cm). All substrate was standardized to 10 cm deep.

Four aquariums consisted of collected gravel (D50 = 14 mm) and four consisted of washed, purchased sand (D 50 = 0.4 mm). Each of the four living streams held two aquaria, one with sand and one with gravel substrates (Fig. 4 A and B). All tanks maintained 35 L of water during trials. A total of 3 trials were carried out with the following number of mussels in each of the eight tanks 1) two individuals of *Q. aurea*, 2) two individuals of *A. plicata*, 3) one individual *Q. aurea*, and one individual of *A. plicata*. Vertical movements were recorded daily for one week using a premeasured length of monofilament line glued to the mussel as noted above.

Lab experiments-Effect of dewatering on movement behavior

Quadrula petrina (30 individuals) were collected from the Llano River and used to examine vertical and horizontal movement in response to dewatering conditions. Three 3 meter insulated fiberglass tanks were used to manipulate dewatering events (slow, moderate, and fast) in a laboratory setting. A sloping depth was created using purchased sand where water depth ranged from 10 cm near the upstream end of the tank to 50 cm near the downstream end of the tank. Slow dewatering manipulation was set for 5cm/day for 10 days, moderate was 10 cm/day for 4 days, and fast was 15 cm/hr for 6 hrs.

Vertical movements were measured as described above. Horizontal movements were tracked using a flag with the mussel's identification number in the sand adjacent to each mussel. The flags were moved to the mussels' new position during dewatering events. The total length of tracks left in the sand were measured to quantify total horizontal movement.

Statistical analysis

A mixed effects model was used for the following analyses: (1) to examine differences in burrowing depth of individually tagged mussels at different field sites and between species, also testing the effect of temperature and month. Burrowing depth (% of shell burrowed) was the response variable and field sites (River), species, length, and temperature were considered fixed effects, and mussel identity was considered random effect. The fixed factor 'River' was used for all analyses and 'Species,' 'Length,' and 'Month' were added to this model; (2) to examine the effect of temperate on burrowing depth of individually tagged mussels in the lab (with species and, temperature as fixed effects: and individual mussel identity and holding tanks as random effects); and (3) to test the impact of substrate on burrowing depth and how it may vary between species, (with substrate, species, and date, as fixed effects: and mussel identity and tanks as random effects); and (4) to examine the response of mussels to dewatering with burrowing depth or horizontal movements as the response variable and mussel and tank as the random factors.

The function *lmer* was used in the R package *lme4* (Bates, Maechler, Bolker, and Walker 2015) for fitting linear mixed-effects models (LMM) and the R package *lmerTest* (Kuznetsova, Brockhoff, and Christensen 2016) was used to obtain p-values from linear mixed effect models. In addition, the function *r.squared.GLMM* in the R package *MuMIn* (Bartón 2016) was used to obtain marginal and conditional R^2 values from the linear mixed-effects models to quantify the goodness-of-fit of fixed and random effects.

Marginal R^2 describes the variance of fixed factors alone while conditional R^2 values describes the variance of both fixed and random factors (Nakagawa and Schielzeth 2013).

III. RESULTS

Monitoring movement at field sites

San Marcos River

For the pilot study in San Marcos River 35 *Q. aurea* were tagged and 13 to 25 were detected during subsequent surveys (Table 1). Their lengths ranged from 39 mm to 68 mm. As temperatures decreased from fall to winter (Table 1), the percentage of burrowed individuals increased from around 50% in late fall to 80% in winter (Fig. 5). The seasonal difference and the effect of temperature were statistically significant, despite the small sample size of tagged individuals in the fall (t=2.5, p=0.02; and t=-4.759, p=0.02; respectively). The effect of size on burrowing depth was not statistically significant (t=-0.01 p=0.99).

Guadalupe River and San Antonio River

In the Guadalupe River, 98 mussels were tagged in August 2015 consisting of 52 *Amblema plicata*, 27 *Quadrula aurea*, 11 *Cyrtonaias tampicoensis*, 7 *Quadrula petrina* and 1 *Megalonaias nervosa*. In the October 2015 survey 67 mussels were detected with the pit-tagging antenna whereas only 16 individuals were detected in the February 2015 survey (Table 1). Mussel lengths ranged from 6 mm-94 mm. The focus of the analyses presented here were on the 2 most abundant species: *A. plicata* and *Q. aurea*; with average lengths of 70 mm (range: 47 to 94 mm) and 41 mm (range: 6 to 58 mm) respectively. In the Guadalupe River both species, *Q. aurea* and *A. plicata*, showed a significant increase in burrowing depth, almost doubling (1.8 times) from summer (August) to fall (October) and a slight increase (1.1 times) from fall (October) to winter (February, Fig. 6 A and B, Table 3).

In the San Antonio River 145 mussels were tagged in October 2015, consisting of 58 *Amblema plicata*, 53 *Quadrula aurea*, 30 *Tritogonia verrucosa*, 2 *Megalonaias nervosa*, and 2 *Lampsilis teres*. In December 2015, 89 individuals were detected and 79 were detected in February 2015. Mussel lengths ranged from 30 mm – 121 mm in the San Antonio River. The average length of *A. plicata* was 63 mm (range: 30-83 mm) while average length for *Q. aurea* was 45 mm (range: 30-60 mm).

Mussels at the site in the San Antonio River (a predominantly sandy site) tended to burrow deeper than in the Guadalupe River (Fig. 6, 7). For example, up to 71% of total mussels detected were burrowed at the 90% or greater depth interval in the San Antonio River in October, whereas only 21% of total mussels detected were burrowed at the 90% or greater depth interval in the Guadalupe River during October (Fig. 7). Both the Guadalupe and San Antonio Rivers were surveyed in October and February and a direct comparison was possible. In this case, there was a significant difference in burrowing depth between the sites (Table 4). Marginal R^2 accounting for differences in the fixed factor "River" alone explained 37% of the variation, whereas the conditional R^2, accounting for the random factor "individually tagged mussel" and fixed factor "River", described only slightly more, i.e., 40% of the variation. Furthermore, differences in physiochemical properties between the rivers are shown in Table (Table 5).

In contrast to the Guadalupe River, average mussels burrowing depth did not differ much between fall and winter (Fig. 6 A and B) in the San Antonio River. There was no significant difference between October and December, and average burrowing depth was only slightly (2%) less in February. In December, the largest proportion (62 %) of mussels were completely and almost completely burrowed ($\geq$ 90%), whereas in February about 42% were burrowed that deep (Fig. 6B). The mixed effects model indicated that burrowing depth in February was significantly different than October and December (Table 4, Fig. 7).

There was no significant difference in burrowing depth between species (Table 4). In addition, 84% of the mussels in the Guadalupe River site were not detected from the first sampling date to the last, while only 33% of mussels were not detected in the San Antonio River site in spite of both sites experiencing two floods (May and October 2015) within the year (Table 1).

Lab Experiments-Effect of temperature on movement behavior

<u>Gravel and Sand Substrate</u>

Although a negligible amount of variation (<0.1%) in burrowing depth was explained by temperature in gravel substrate (effect was marginally significant, t=-2.0, p=0.05), there were some indications that changes in temperature had an effect on burrowing. After, 94% of mussels were partially burrowed between days 1-5; 78% of mussels re-emerged between days 11-15 when temperatures remained at 19°C-20°C due to water chiller failure. When chillers had been repaired and water temperature continued to decrease, mussels burrowed again (Fig 8A). As temperatures dropped from 24°C to 14°C-15°C, 57% of mussels stopped moving (Fig. 8A). Variation between individual mussels in upward and downward movements was high in both *A. plicata* and *Q. aurea* (Fig. 9A and B), and a large proportion of the variation in burrowing depth (60%) was explained by the random factor mussel identity (Table 6). There was no significant difference between species, (t=0.3, p=0.80; Fig 10 A).

An increase in burrowing depth with decreasing temperature was more obvious in sand. There, 59 % of mussels were partially burrowed between days 1-5; as temperature continued to decrease 38 % of mussels continued to burrow; and at 14°C-15°C only 9% of mussels stopped moving (Fig. 8B). The linear mixed-effects model showed a significant effect of temperature on burrowing, ($t=-12.5$, $p<0.05$; Table 6), and variation between individual mussels was less than in gravel. Thirty percent of the variation in burrowing depth was explained by the fixed factors temperature and species, but considerably more, i.e., 70% by both random (individual mussels) and fixed factors (Table 6). *A. plicata* burrowed significantly deeper (median=1.8 cm, range=0-4 cm) compared to *Q. aurea* (median=0.75 cm, range=0-2.3 cm) ($t=-4.0$, $p<0.05$, Fig. 10 B; Table 6).

Lab experiments – Effect of differences in substrate on movement behavior

Mussels burrowed deeper in sand (median=1.2 cm, range=0-4 cm, Fig. 10) compared to gravel (median=0.6 cm, range=0-9.9cm, Fig. 11) and was statistically significant ($t=4.0$, $p<0.05$; Table 7). There was no significant difference in burrowing depth between species *A. plicata* and *Q. aurea*, ($t=-0.3$, $p=0.8$; Table 7; Fig. 10). The mixed model showed a significant difference between trials 1 (*Q. aurea* only) and 2 (*A. plicata* only), but not between trials 1 and 3 (*Q. aurea* and *A. plicata* (Trial 2: $t=-2.4$, $p<0.05$; Trial 3: $t=0.5$, $p=0.60$; Table 7).

Effect of dewatering on movement behavior

Mussels did not burrow deep during dewatering rates with an average burrowing depth for the slow, moderate and fast dewatering rates of 0.4±0.03, 0.2 ±0.04 and 0.2±0.04 cm respectively (mean±SE). If mussels did not move horizontally with the receding water, they were considered stranded. Twenty percent of the mussels became stranded during the slow dewatering rate, 30% of mussels became stranded in the moderate dewatering rate, and 100% percent of the mussels were stranded during the fast dewatering rate. The linear mixed-effects model detected significant variation among slow and fast dewatering rates ($t=4.7$, $p<0.05$; $t=4.7$, $p=0.02$; Table 8), a post hoc Tukey test showed that vertical movements at the slow rate significantly differed from both the moderate and fast rates, and variation among individuals can be seen by the outliers in Fig. 11.

Horizontal movements differed significantly among all dewatering rates (Fig. 12). Mussels moved most at the moderate dewatering rate 54% of the mussels moved distances greater than 20 cm, 13% of mussels moved between 1-20 cm, and 33% did not move, but 12 mussels moved much larger distances (up to 267cm, Fig. 12). At the slow dewatering rate, 44% of the mussels moved distances greater than 20 cm, 23% moved distances between 1-20 cm, and 33% did not move, but several mussels moved much larger distances (up to 329 cm). Only one individual moved with receding water during the fast dewatering rate, resulting in an average distance of 0.02 cm (range: 0-4 cm). There was no response in horizontal movements during the fast dewatering rate ($t=0.003$, $p=0.99$; Table 8) and there was a significant response in horizontal movements in both moderate and slow dewatering rates ($t=8.0$, $p< 0.001$and $t=6.2$, $p< 0.001$; Table 7). A post hoc Tukey test showed that all dewatering rates differed significantly ($p<0.05$).

IV. DISCUSSION

Our results show that movements of freshwater mussel can differ, sometimes considerably with environmental stream conditions including substrate, temperature, water level fluctuations, and there were some indication for differences between species. Floods and droughts have the capabilities of stranding mussels. Whether the movement behavior of mussels enables them to respond adequately to receding waters after flooding or during drought conditions seems to depend on the dewatering rate. In our study every individual of *Q. petrina* became stranded during fast dewatering rates (4 cm hr^{-1}) and did not move with the receding water. This is consistent with Galbraith et al 2015, who found that *Alasmidonta heterodon*, *Alasmidonta marginata*, *Alasmidonta varicosa*, *Elliptio complanata*, *Pyganodon cataracta*, and *Strophitus undulata* became stranded during a fast experimental dewatering rate (5 cm hr^{-1}). During all of our dewatering rates mussels did not clearly follow the receding waterline, but rather tended to move in random directions. Thus, with fast receding water, which occurs downstream of hydropower dams (Graf 1999), a large proportion of mussel populations can become stranded. This is one explanation for the absence of mussels downstream of hydropower dams, as was found by Vaughn and Taylor (1999). Dewatering rates during droughts are usually lower compared to hydropower dams, however, even at low dewatering rates 37% of mussels became stranded in our study.

The southwestern United States experiences frequent and prolonged droughts with lower water levels and make mussels more susceptible to predation and desiccation in shallow waters. The detrimental effect of drought on mussels has been documented by several studies (Haag and Warren 2008, Galbraith et al 2010, Spooner et al 2011, Walters and Ford 2013). The impact may vary depending on local conditions. For instance, mussels in a small stream declined drastically, but were not significantly affected in large streams (Haag and Warren 2008). East Texas experienced a severe drought in 2011, which resulted in the drying of perennial streams and reduced flows in major rivers. A Texas state threatened species *Potamilus amphichaenus* was affected by predation during these low flows which may have contributed to the decline of this species (Walters and Ford 2013). Climate models predict an increase frequency of droughts, especially in the west and central regions of Texas (Shafer et al 2014; Strzepek et al 2010), and habitat alterations including changes in flow regimes are anticipated due to planned reservoir construction. Thus threats from dewatering for mussels in Texas will likely become more severe.

Burrowing may protect mussels from becoming dislodged during higher flow conditions (Schwalb and Pusch 2007). However, floods have the potential to mobilize the stream bed (Hastie et al 2001) where mussels reside, so in order to persist they rely on habitat areas that remain stable during floods (Strayer 1999, Howard and Cuffey 2003). The considerably lower recapture rate (~5 times lower) of mussels in the Guadalupe River compared to the San Antonio River could be attributed to losses of mussels during the two major flood events in May and October 2015 and presumably associated with differential bed mobility between these study sites. There is a complex relationship between discharge, slope, depth, velocity and sediment transport processes. Sediment transport processes are affected by types, sizes, and shapes that result in longitudinal and vertical sorting of stream bed material. The impact of flooding on mussel mortality is largely unknown (Haag 2012), but may be considerable if mussels become dislodged and either crushed while being transported downstream or fail to reestablish themselves in suitable habitat (i.e., on a sandbank that dries out after water recede, BAH observation in the Guadalupe River).

In both our field and lab experiments mussels burrowed more and deeper when substrate was finer (i.e., sandy versus gravel/cobble). This is consistent with a study in Lake Panguipulli, where *Diplodon chilensis* (Hyriidae) burrowed more quickly and on average moved more in sand versus sand-gravel substrates (Lara and Parada 2009). In our study, we also found that the response to temperature differed with substrate. The sandy substrate apparently allowed them to continue to burrow even as temperature decreased. In addition, relatively few mussels stopped moving at around 15°C in sand (9%), while a larger proportion stopped movement in gravel (57%). Movement facilitated by finer substrate may be advantageous after high flow and during dewatering events, because mussels may be better able to avoid adverse conditions.

In addition to substrate type, we found indications that changes in temperature affected burrowing behavior. For example, a large proportion (78%) of individuals of *A. plicata* and *Q. aurea* that had partially burrowed, re-emerged when temperatures did not decrease further, but remained constant (because the chillers accidentally failed). A larger proportion of *A. plicata* and *Q. aurea* stopped burrowing at temperatures between 12- 15°C in gravel (but not in sand, see above). The impact of colder temperatures on movement behavior has been investigated previously, where *Potamilus alatus* from Kentucky Lake stopped moving at 10°C when temperatures were decreased from 30°C (Block et al 2013).

Several previous studies have shown seasonal vertical migration, where mussels burrow deep during colder months starting in October and re-emerging around May. This was found for a small, first order stream in southeastern Virginia (Balfour and Smock 1995), Lac de l'Achigan, near Montréal (Amyot and Downing 1997), a lowland river in Germany (Schwalb and Pusch 2007), in experimental, recirculating mesocosms (Allen and Vaughn 2009), and in outdoor pools in Columbus, Ohio (Watters and Ford 2011). However, most of these studies were conducted in colder climates in the Northern hemisphere with seasonal water temperatures ranging from 2°C-26°C whereas long-term average water temperatures in rivers of central Texas is 20°C, ranging between 9°C and 32°C (TCEQ, 2016) for the lower Guadalupe River and ranging between 10°C and 29°C (TCEQ, 2016) in the San Antonio River. Interestingly, despite climatic differences and warmer temperatures in Texas we found the same seasonal trend in the San Marcos and Guadalupe Rivers that had been previously observed elsewhere, in that burrowing depth was deeper in October compared to August in the Guadalupe River. This suggests that either seasonal cues such as day length rather than temperature may trigger increased burrowing behavior in the fall; or, if temperature is a cue, mussels in Texas have a different thermal tolerance and start increased burrowing at warmer temperatures. The initial sampling in the San Antonio River occurred only at the end of October, and sampling during summer would be necessary in order to determine whether burrowing depth would also increase between summer and fall in this river. Interestingly, there were some indications that mussels started to emerge in February with a larger proportion of mussels being burrowed less deeply in the San Antonio River. This was not evident from the Guadalupe River, where temperature was slightly colder and sample size considerably lower (as many mussels were not detectable in February, likely due to losses caused by flooding). Unfortunately, we were not able to conduct spring sampling beginning in March, but future studies should examine whether mussels reemerge earlier in Central Texas than in other studies conducted in colder climates.

Differences in size between species can also play a role for burrowing behavior, and we found that *A. plicata* burrowed deeper compared to *Q. aurea* in sand. However, previous studies found that smaller *Potamilus alatus* individuals initiated burrowing behaviors quicker and burrowed more than larger individuals when recorded in laboratory experiments (Levine et al 2014). In addition, a higher percentage of smaller individuals of *Unio tumidis* were found at greater sediment depths (10-20 cm) when burrowing was monitored in the River Spree (Schwalb and Pusch 2007). We found a large variation in burrowing behavior in both *Q. aurea* and *A. plicata*, which could be due to unaccounted factors. For example, males and females have been found to show different burrowing behavior in different seasons (Rogers et al 2001). Mussel densities may also be a factor in burrowing behaviors. When burrowing was examined in low, moderate and high mussel densities including *Actinonaias ligamentina, Amblema plicata, Obliquaria reflexa* and *Fusconaia flava* species, mussels burrowed more in moderate to high density trials than in low density trials (Allen and Vaughn 2009).

The southwest United States experiences drought; however, it is exacerbated by climate change and anthropogenic factors such as excessive groundwater pumping that can lead to decreases of water levels in streams and rivers. More severe droughts are predicted with climate change (a citation would be nice there). A better understanding on how mussels respond to receding water levels will help guide conservation and management of species. Additional studies would also be necessary to fill these information gaps. In addition to horizontal movement, seasonal vertical movements also need to be assessed for additional species in order to guide resource managers in conducting surveys.

Furthermore, our results suggest that surveys may need to follow different guidelines depending on local conditions such as water depth, substrate, substrate stability, temperature, and flow. For example, in a sandy site, mussels may burrow deeper and a large part of the population or specific species may be overlooked.

TABLES

Table 1 Dates of start and regular surveys for field studies and temperature at sampling dates in parenthesis, and numbers of mussel marked and detection of marked mussels.

Sites	Survey start	Regular surveys	Marked	Detected
San Marcos River	10/24/2014 (21°C)		14	
		10/31/2014 (21°C)	13	13
		11/28/2014 (17°C)	8	20
		1/20/2015 (15°C)		25
Guadalupe River	8/28/2015 (32°C)		100	
		10/17/2015 (25°C)		67
		2/12/2016 (15°C)		16
San Antonio River	10/21/2015 (24°C)		145	
		12/22/2015 (16°C)		89
		2/13/2016 (18°C)		79

Table 2 Discharge data from USGS gage stations near the field sites. Stations: 12100203 San Marcos River near Luling, 08175800 Guadalupe River near Gonzales, 08188060 San Antonio River near Kenedy.

Hydrologic unit code	Long-term avg discharge m/s	Min discharge m/s	Max discharge m/s	Avg discharge during study m/s
San Marcos River	140	31	3505	147
Guadalupe River	615	41	13,868	721
San Antonio River	18	2	569	19

Table 3

Results of the Linear Mixed Effects model testing differences of burrowing depth between A) months for Guadalupe River (compared to August) and San Antonio River (compared to October), and B) the two rivers.

	t	*P*
A) Guadalupe River		
(October)	4.8	<0.05
(February)	2.6	0.01
San Antonio River		
(December)	0.6	0.5
(February)	-2.6	0.01
B) Guadalupe and San Antonio River		
(San Antonio River)	5.7	<0.05

Table 4

Results of Linear Mixed Effect models testing effect of the fixed factors ‘River,’ +‘Species,’ ‘Length,’ or ‘Month’ on Burrowing Depth (% of shell burrowed). R^2 marginal describes the amount of variation explained by the fixed factors, whereas R^2 conditional describes the amount of variation explained by both fixed and random factors. AIC and dAIC values are used in model selection. Highest numbers indicating the model that best fits the data.

		t	*P*	$R^2_{Marginal}$	$R^2_{Conditional}$	AIC	dAIC
River		13.9	<0.05	0.37	0.40	3269	45.7
River + Species		-1.6	0.12	0.37	0.41	3268	45.2
River + Length		-0.1	0.9	0.37	0.40	3271	47.7
River + Month				0.45	0.49	3223	0.00
	(October)	7.4	<0.05				
	(December)	5.4	<0.05				
	(February)	4.9	<0.05				

Table 5 Physiochemical Properties

River	Date	Temp (°C)	Cond	Sp. Cond	DO mg/L	DO %	pH
San Marcos	10/24/2014	21	n/a	n/a	n/a	n/a	n/a
	10/31/2014	21	n/a	n/a	n/a	n/a	n/a
	11/28/2014	15	n/a	520	10.03	n/a	6.75
	1/20/2015	15	n/a	534	8.84	n/a	8.15
Guadalupe							
	8/28/2015	32	527	528	3.8	42.7	8.3
	10/17/2015	25	502	499	4.7	49	4.7
	2/12/2016	15	556	454	10.83	108.6	8.35
San Antonio							
	10/21/2015	24	1250	1214	6.65	78.8	8.52
	12/22/2015	16	n/a	n/a	n/a	n/a	n/a
	2/13/2016	18	1194	1026	16.13	167	9.21

Table 6

Linear mixed effect model test results for effects of temperature, gravel, and sand substrates on burrowed depth. R^2 marginal describes the amount of variation explained by the fixed factors, whereas R^2 conditional describes the amount of variation explained by both fixed and random factors.

	t	*P*	$R^2_{Marginal}$	$R^2_{Conditional}$
Gravel				
Temperature	-1.95	0.05	0.0020	.62
Species	0.30	0.81		
Sand				
Temperature	-12.5	<0.05	0.30	.70
Species	-3.97	<0.05		

Table 7

Linear Mixed Effects model test results for effects on depth of mussel burrowed. R^2 marginal describes the amount of variation explained by the fixed factors, whereas R^2 conditional describes the amount of variation explained by both fixed and random factors. AIC and dAIC values are used in model selection. Highest numbers indicating the model that best fits the data.

	t	*P*	$R^2_{Marginal}$	$R^2_{Conditional}$	AIC	dAIC
Substrate						
(Sand)	4.0	<0.05	0.23	0.54	239.03	1.54
Species	-0.3	0.8	0.23	0.55	240.96	3.46
Trial			0.24	0.54	237.49	0.00
(Two)	-2.4	0.02				
(Three)	0.5	0.60				

Table 8

Linear mixed effect model test results for effects on burrowed depth and horizontal movements during dewatering rates. R^2 marginal describes the amount of variation explained by the fixed factors, whereas R^2 conditional describes the amount of variation explained by both fixed and random factors.

	t	*P*	$R^2_{Marginal}$	$R^2_{Conditional}$
Vertical Movements				
Rate			0.05	0.18
Fast	4.7	0.02		
Moderate	1.1	0.3		
Slow	6.1	<0.05		
Horizontal Movements				
Rate			0.11	0.12
Fast	0.003	1.0		
Moderate	8.039	<0.05		
Slow	6.164	<0.05		

FIGURES

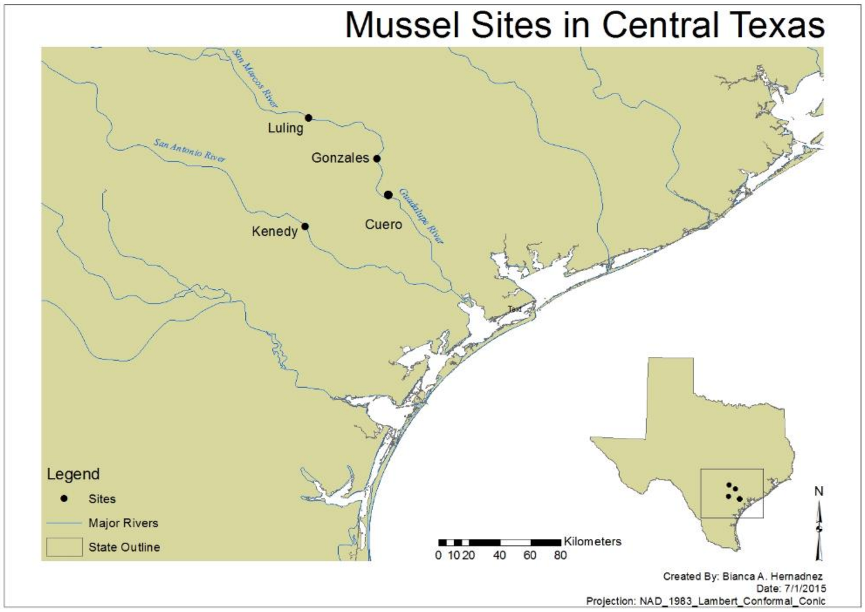


Fig. 1: Field sites in Central Texas: San Marcos, San Antonio, and Guadalupe Rivers. Mussels for lab experiments were obtained from sites near Gonzales in the Guadalupe River and from the Neches River near Lumberton

Fig. 2 Tagged *Q. aurea* San Antonio River

Fig. 3 Burrowed mussel at 50%

A)

B)

Fig 4 *Q. aurea* A) partly burrowed in gravel and B) almost completely burrowed in sand.

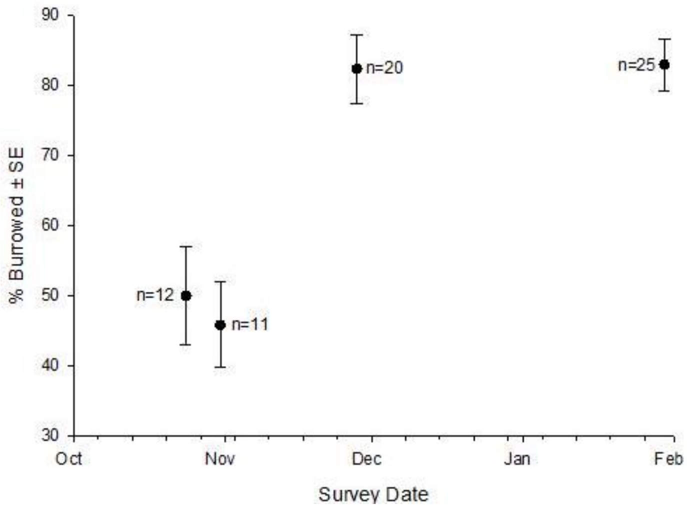
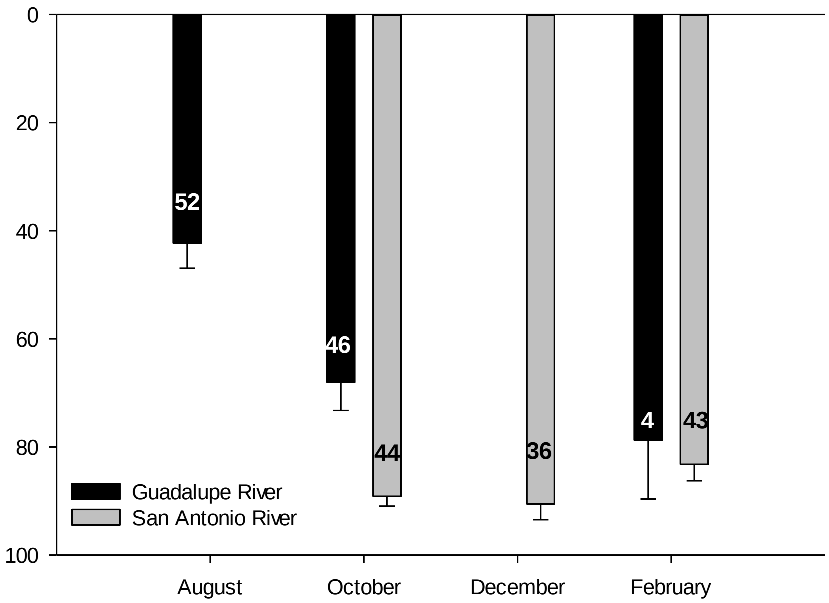


Fig. 5 Percentage (mean±SE) of mussels completely burrowed (i.e., not visible on the surface) at the site in the San Marcos River.

A)



B)

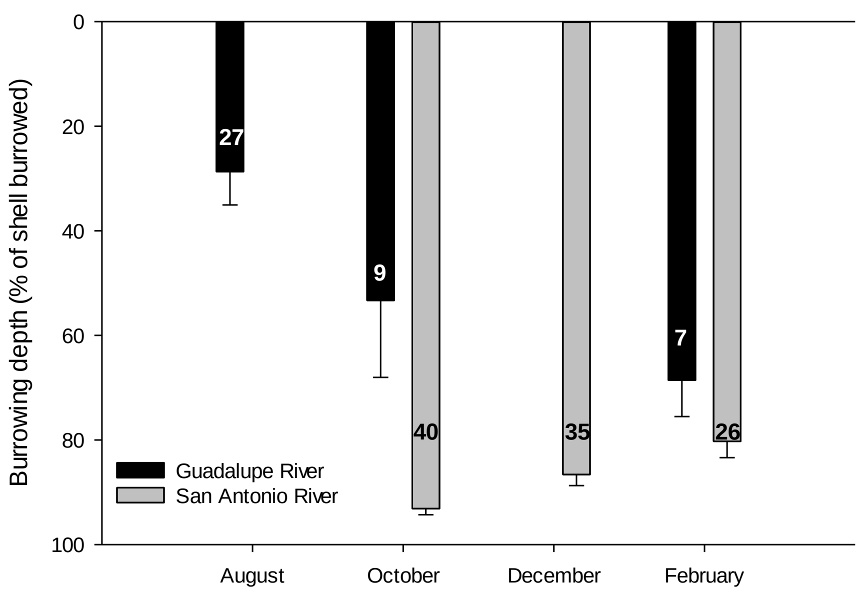


Fig. 6 Average burrowing depth±SE for A) *Amblema plicata* and B) *Quadrula aurea* at Guadalupe (black bars) and San Antonio River (grey bars). Numbers in bars represent sample size.

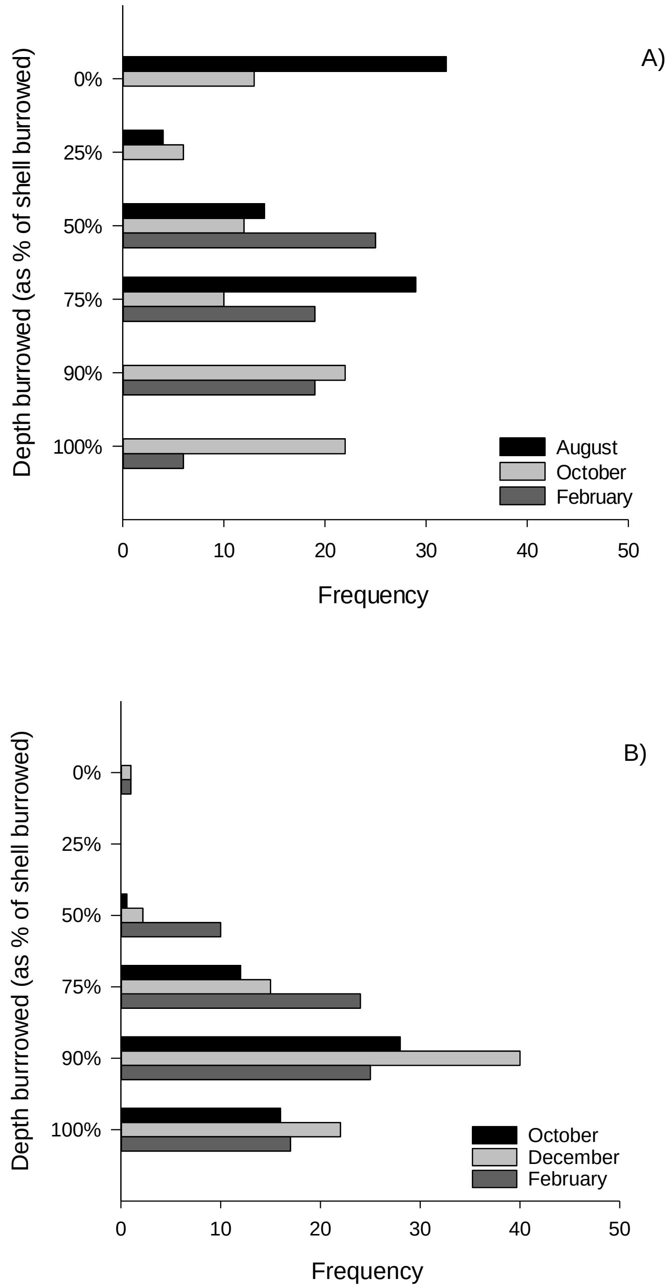
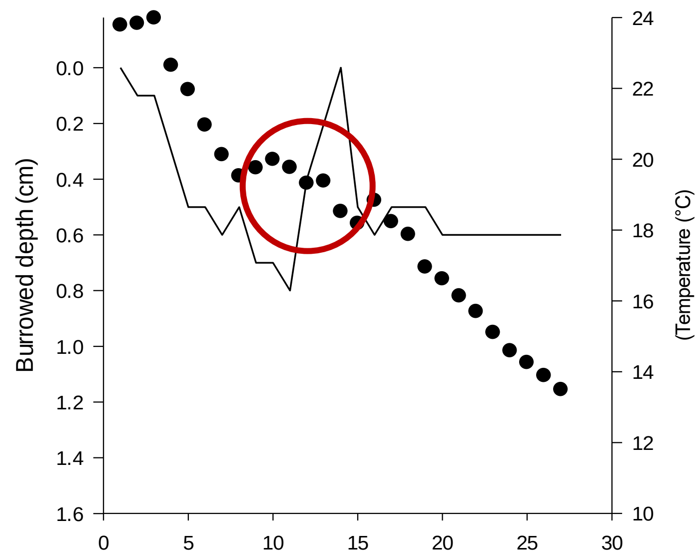


Fig. 7 Proportion of mussels burrowed (as percentage of detected mussels at particular sampling date) at different burrowing depths: completely visible (0%), ~¼ of shell burrowed (25%), about half of the shell burrowed (50%), ~3/4 of the shell burrowed (75%), almost completely burrowed (90%), and completely burrowed (100%) in A) Guadalupe and B) San Antonio Rivers in different months.

A)



B)

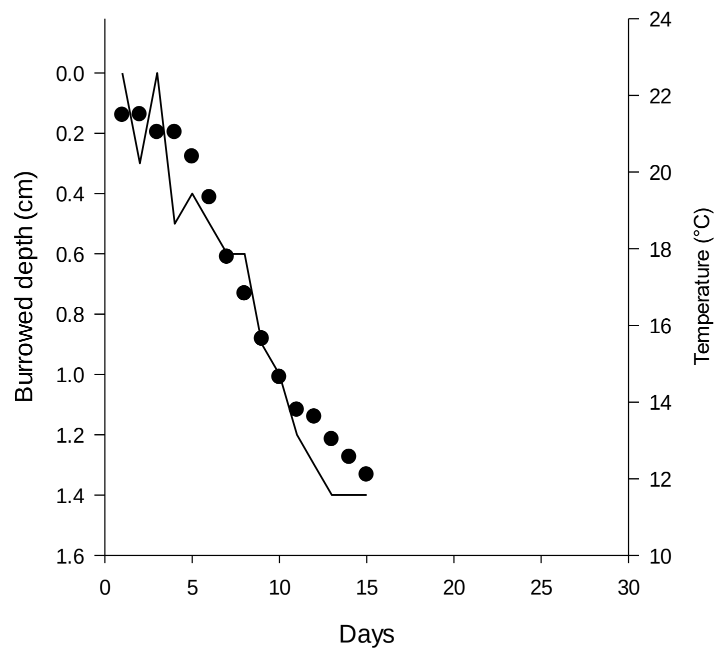


Fig. 8 Example of an individual mussel and its changes in burrowing depth (line) on different days and corresponding changes in temperature (black dots) in A) gravel and B) sand substrates. See Appendix Fig. A1 for complete set of figures for all mussels. Please note, that experiments with sand were run as planned for 15 days, whereas experiments in gravel ran longer as planned, because the chiller failed on days 8 to 12. Circle in A) indicate the time period when chiller failed and temperature remained at room temperature of 19-20C.

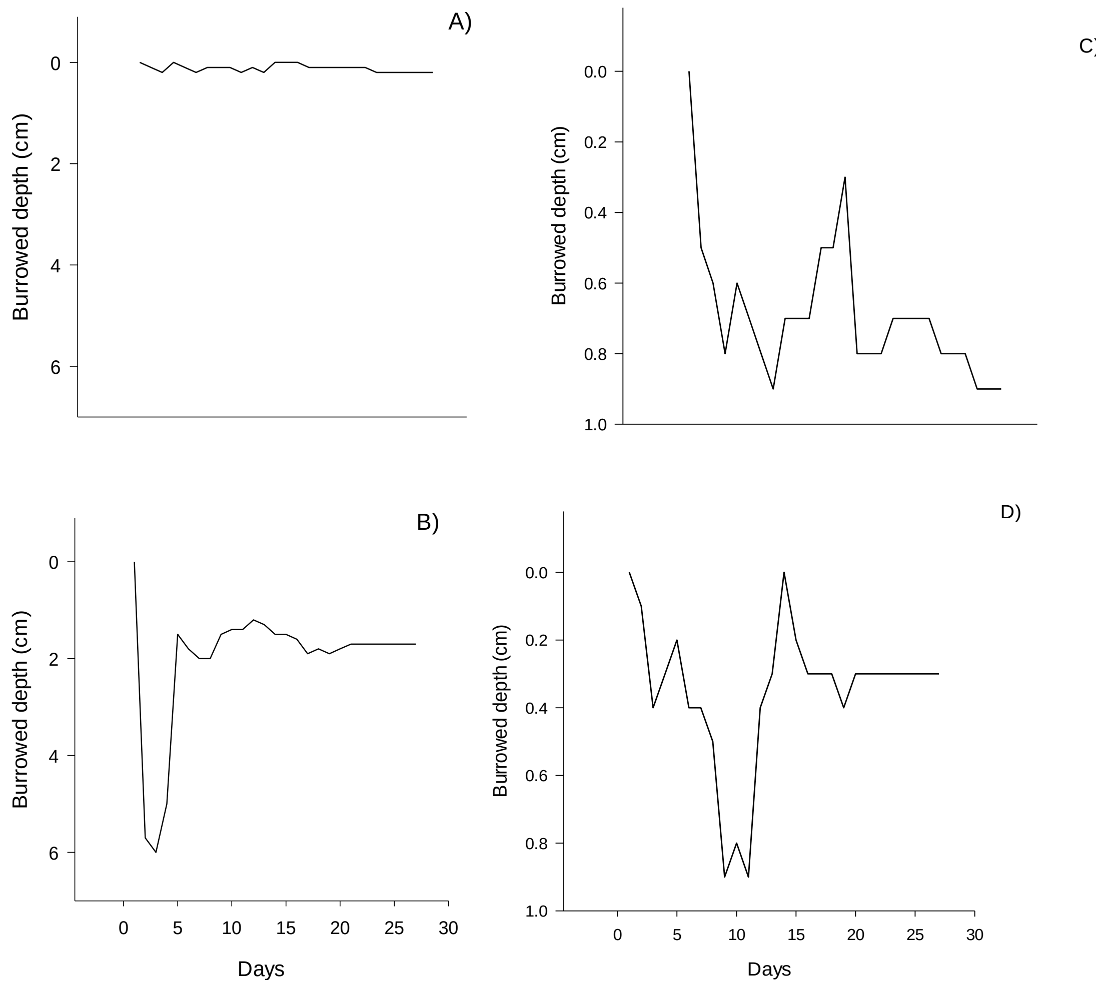


Fig. 9 Examples of individual mussels and their variation in movements in gravel substrate A) did not move much B) burrowed deep, various upward and downward movements (C, D). Complete set of figures for all mussels in appendix Fig. A2.

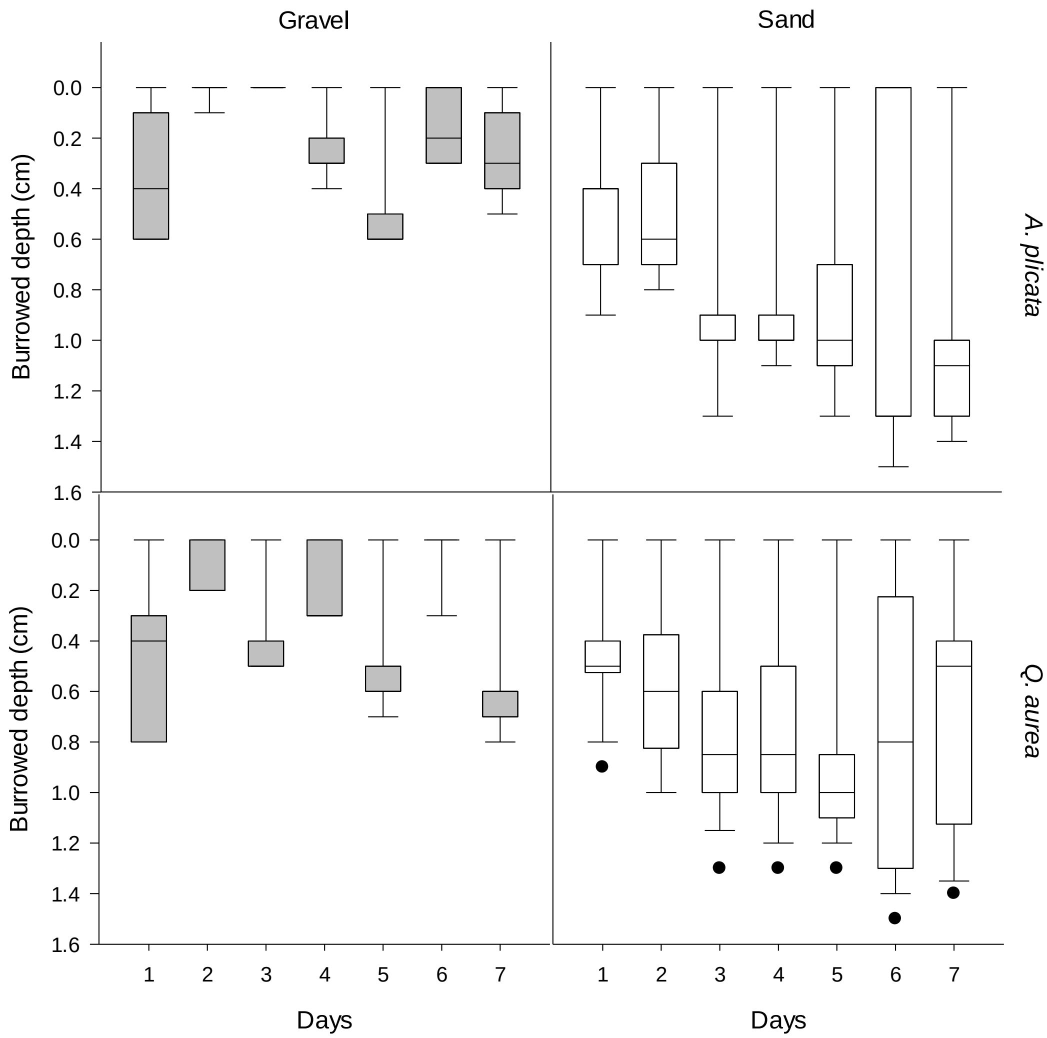


Fig. 10 Daily burrowing depth (cm) of *A. plicata* and *Q. aurea* individuals in gravel (grey) and sand (white). Boxes represents 25^{th}, median and 75^{th} percentiles Whiskers represent the 10^{th} and 90^{th} percentiles. Points represent outliers. Sample size was 1 for each boxplot.

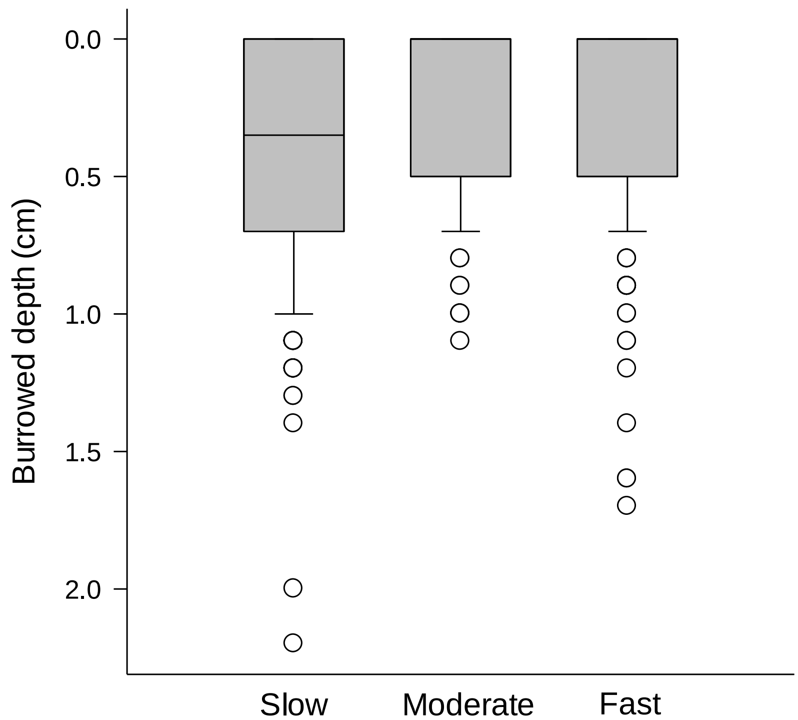


Fig. 11 Burrowed depths of *Q. petrina* at different dewatering rates. Box represents 25th, median and 75th percentiles. Whiskers represent the 10th and 90th percentiles. Points represent outliers. Sample size was 10 for each boxplot.

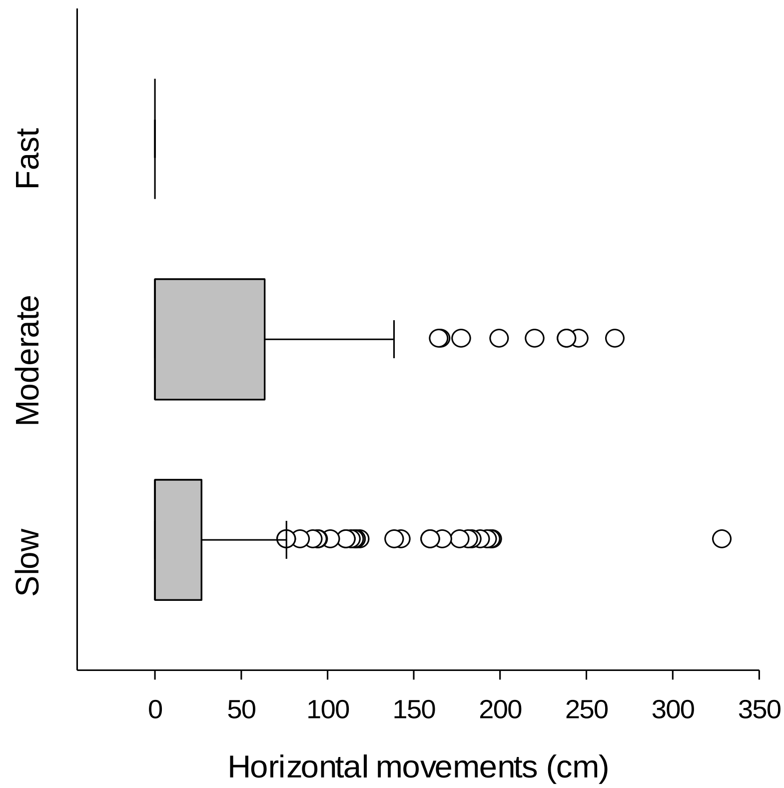
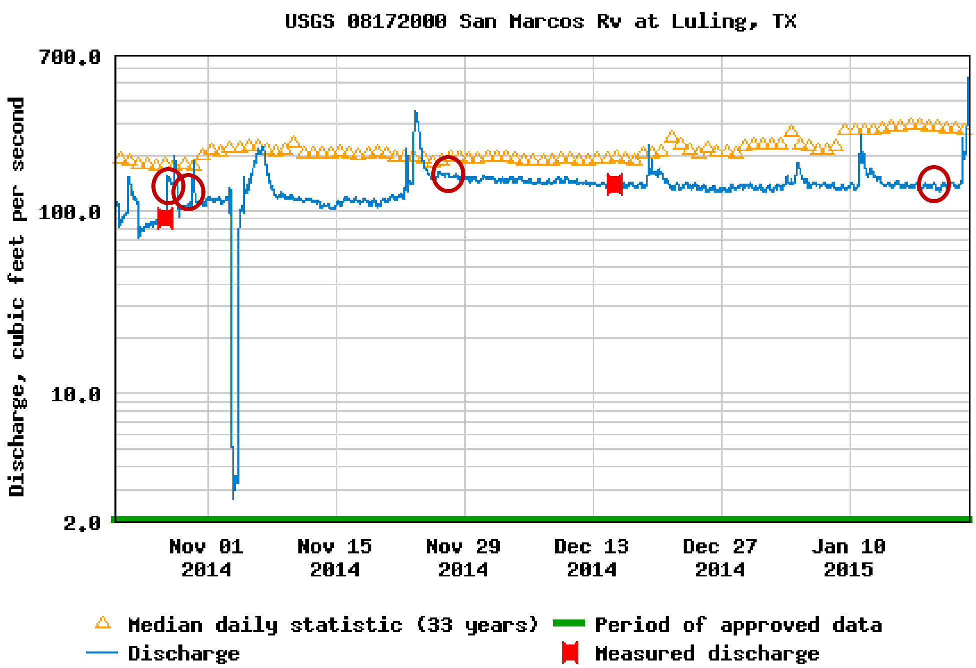


Fig. 12 Horizontal movements of *Q. petrina* among different dewatering rates. Box represents 25th, median and 75th percentiles. Whiskers represent the 10th and 90th percentiles. Points represent outliers. Sample size was 10 for each boxplot.

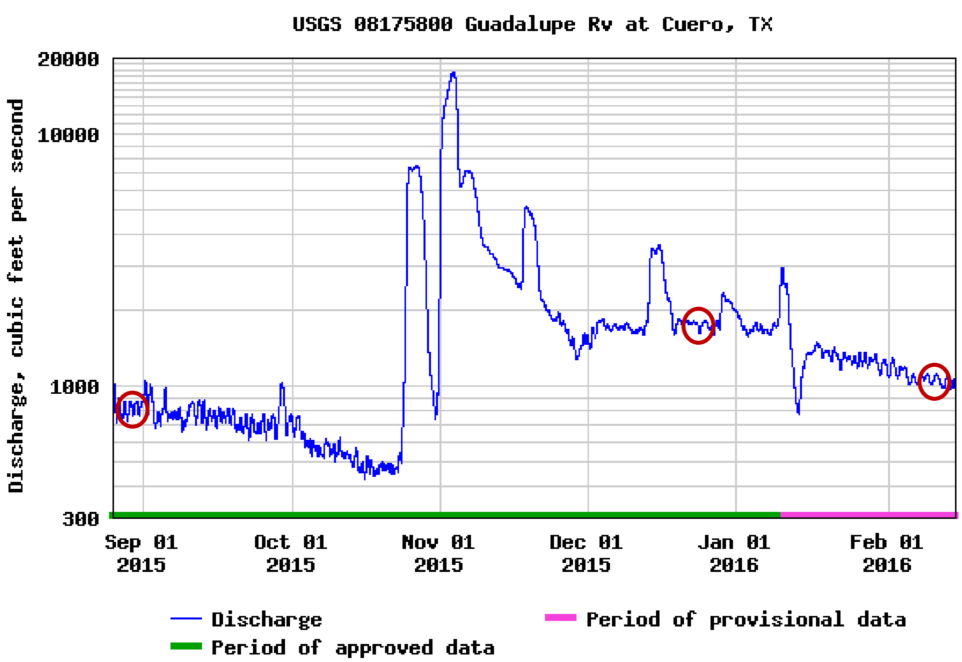
APPENDIX SECTION

A Discharge graphs and dates surveyed

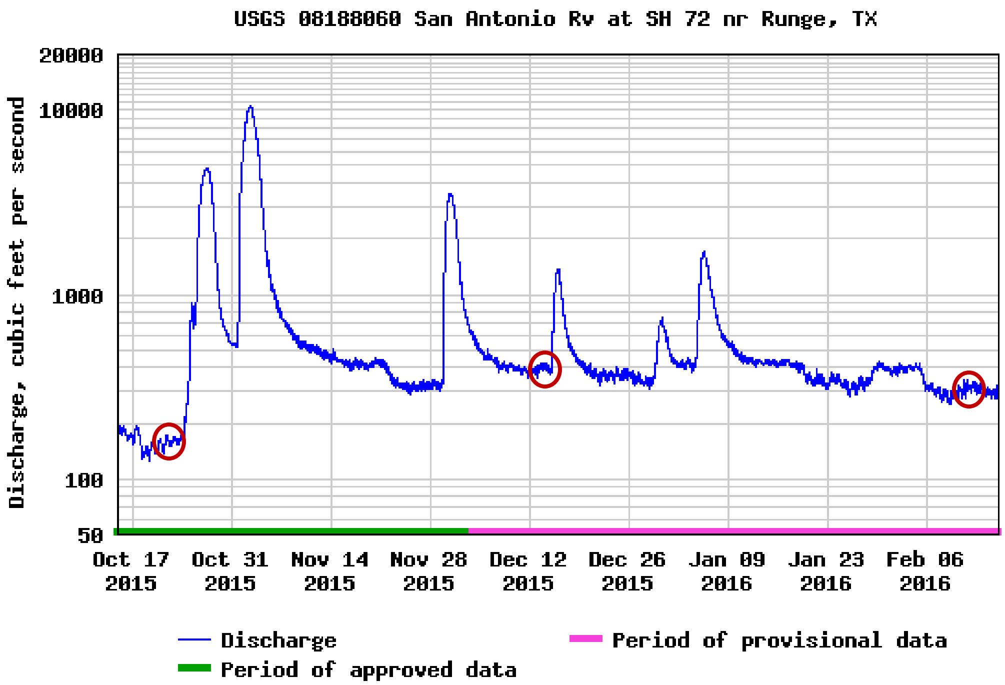
San Marcos River near Luling, TX 10/24/2014, 10/31/2014, 11/28/2014, and 1/20/2015



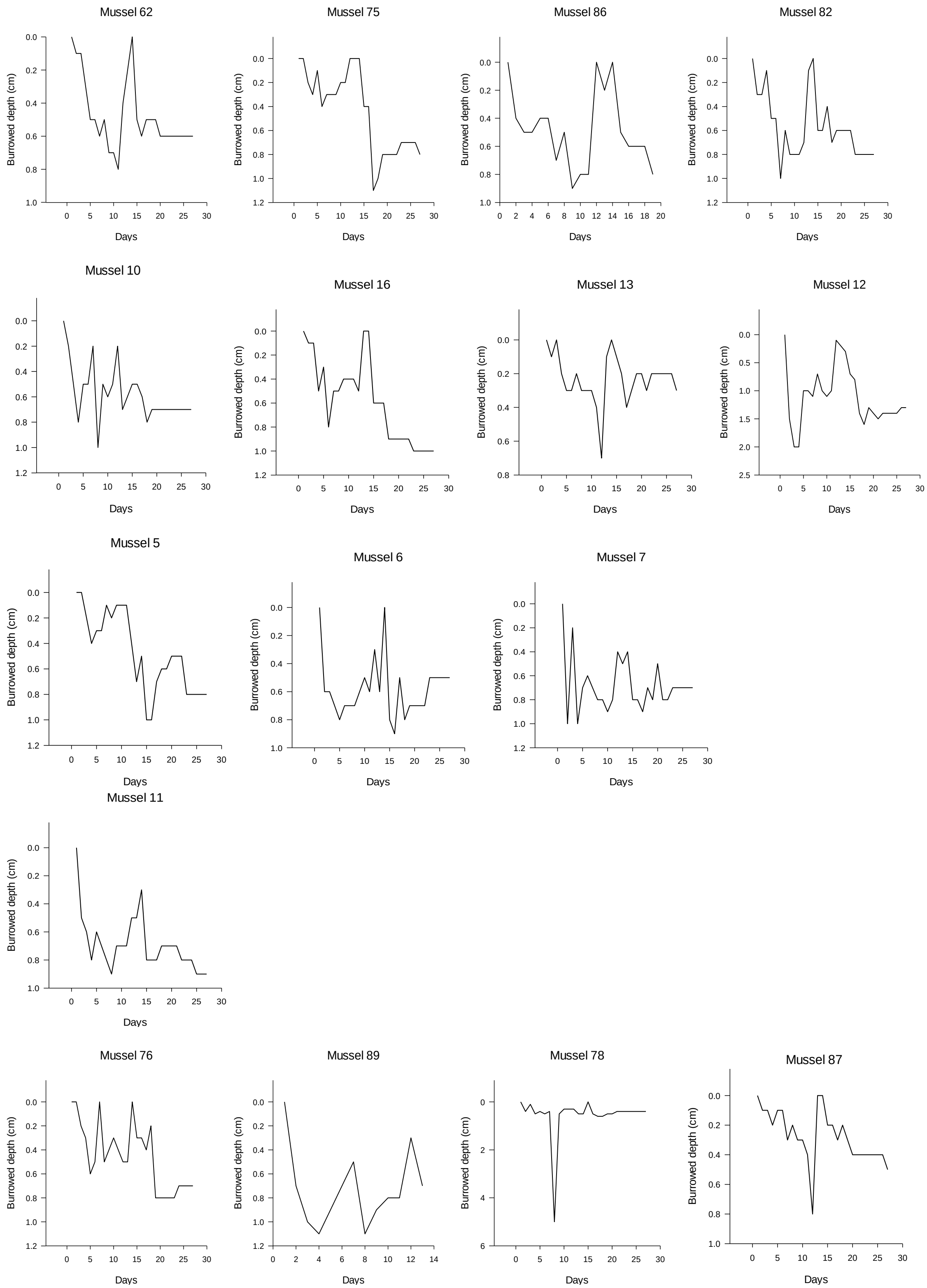
Guadalupe River near Cuero, TX 8/28/2015, 12/22/2015, 2/12/2016

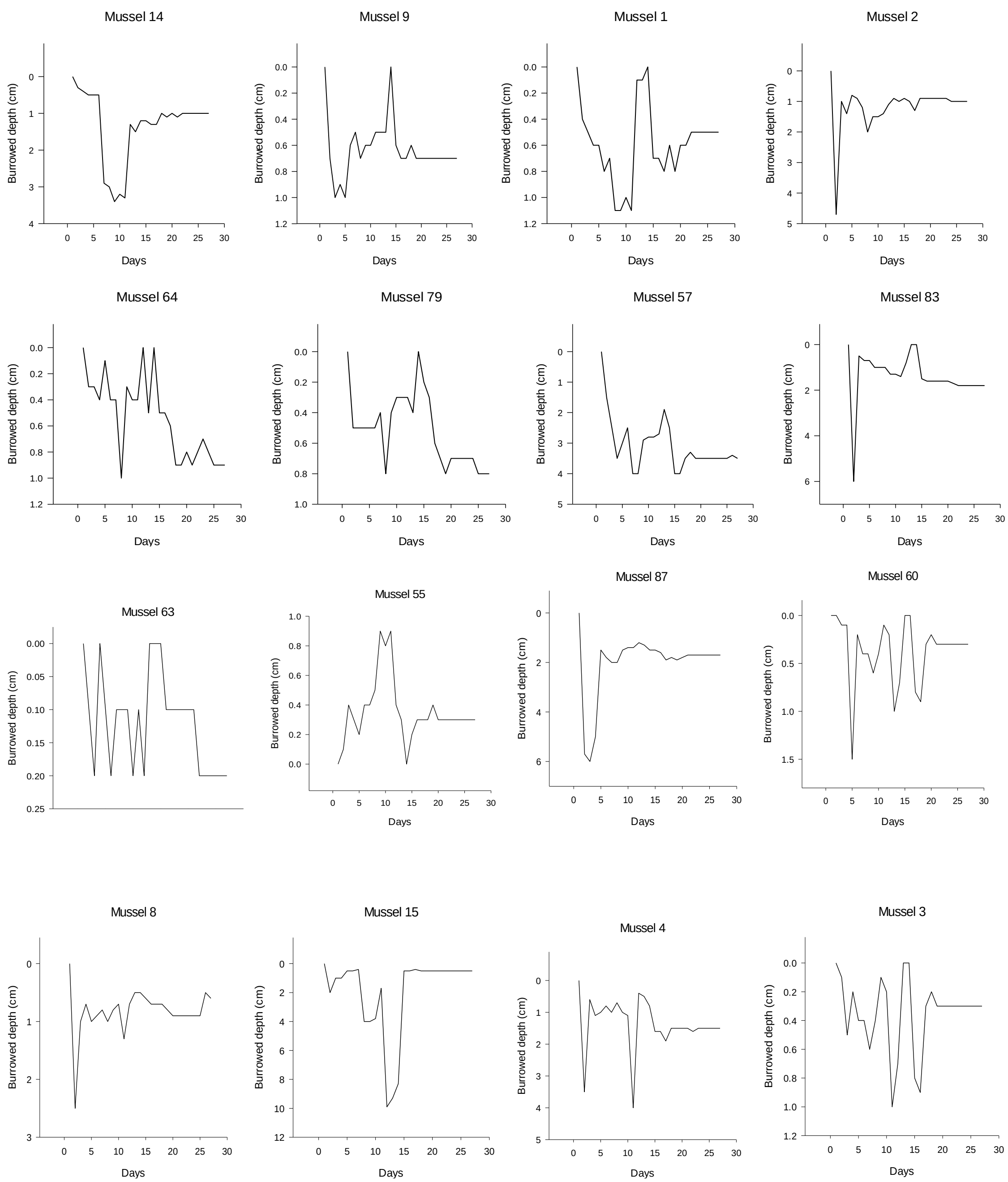


San Antonio River near Runge, TX 10/21/2015, 12/22/2015, 2/12/2016

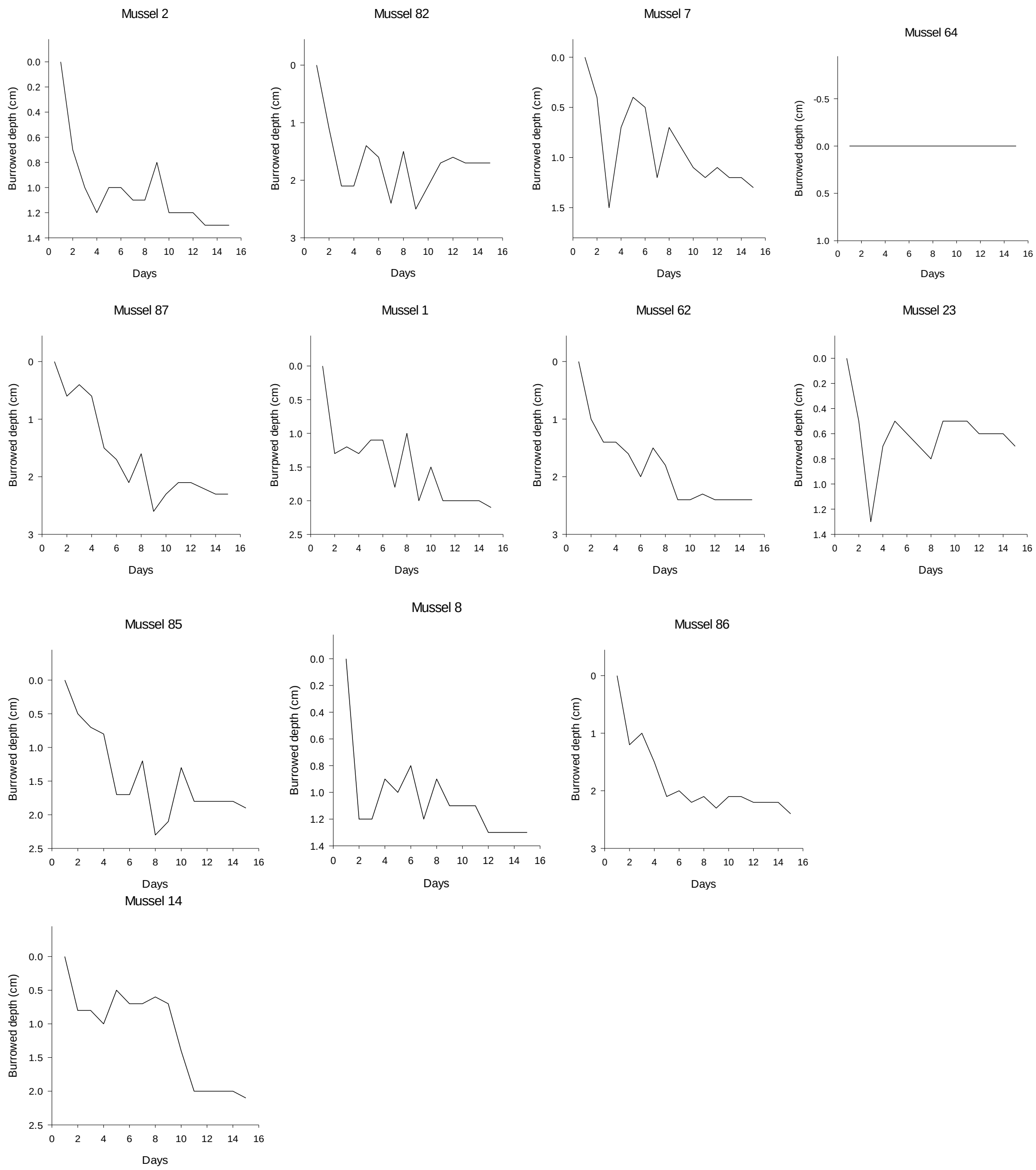


B Individual mussel movements: effect of temperature on burrowing in gravel substrate

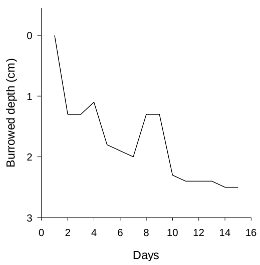



Mussel 14
Mussel 9
Mussel 1
Mussel 2
Mussel 64
Mussel 79
Mussel 57
Mussel 83
Mussel 63
Mussel 55
Mussel 87
Mussel 60
Mussel 8
Mussel 15
Mussel 4
Mussel 3
Burrowed depth (cm)
Days

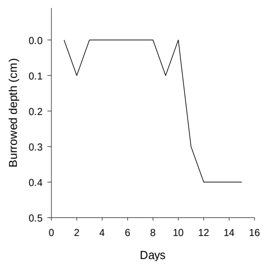
C Individual mussel movements: effect of temperature on burrowing in sand substrate



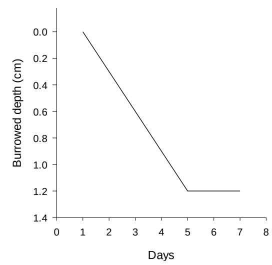
Mussel 78



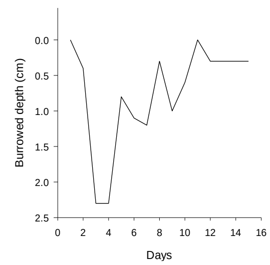
Mussel 13



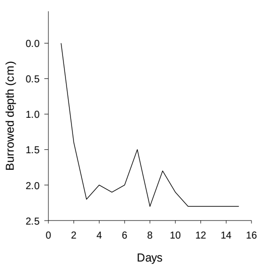
Mussel 76



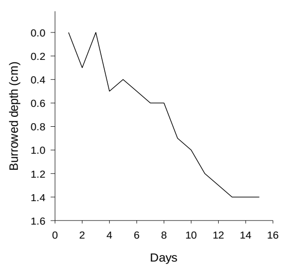
Mussel 27



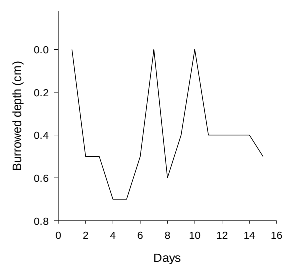
Mussel 10



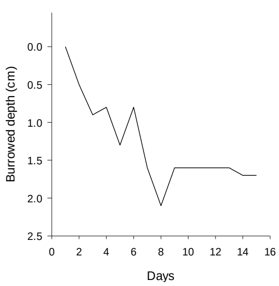
Mussel 79



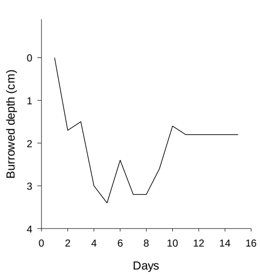
Mussel 11



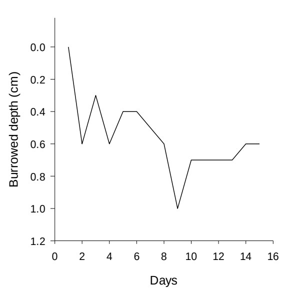
Mussel 75



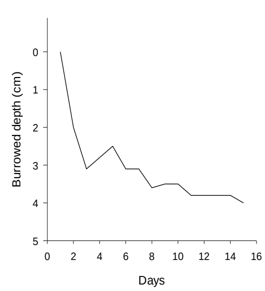
Mussel 88

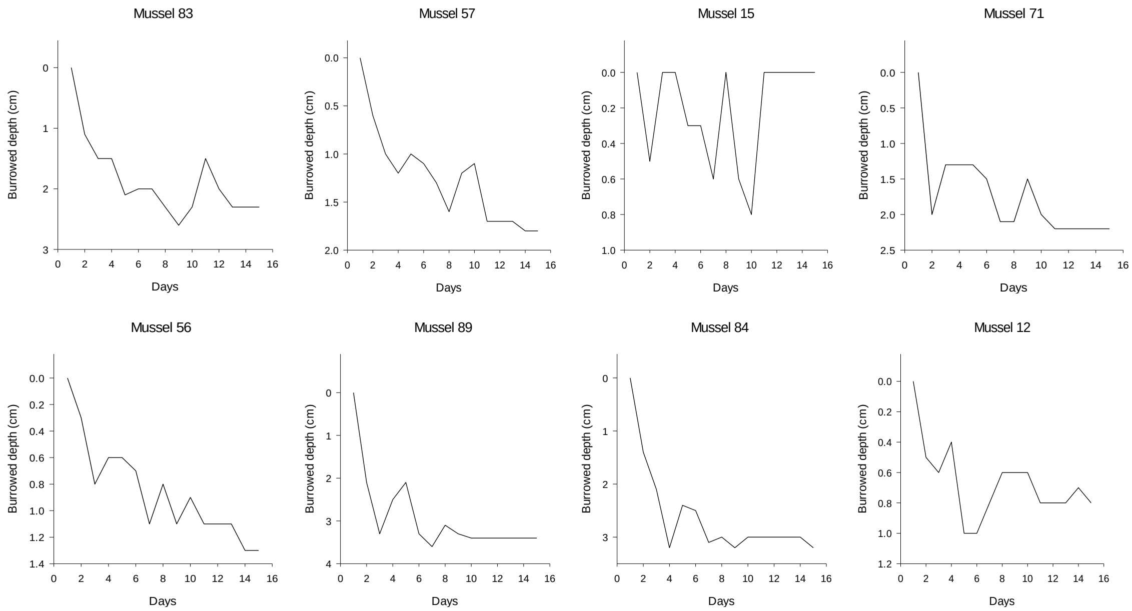


Mussel 3



Mussel 77




Mussel 83
Mussel 57
Mussel 15
Mussel 71
Mussel 56
Mussel 89
Mussel 84
Mussel 12
Burrowed depth (cm)
Days

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