Effects of Current Velocity on Habitat Suitability of Exotic Giant Ramshorn Snails (*Marisa cornuarietis*) in Comal Springs, Texas.

THESIS

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Acknowledgements

This document is dedicated to the memory of my aunt, Mary Louise Martin, who was killed recently in the bombing of the American Embassy in Nairobi, Kenya. Her love of science and research made such an impression on me that I felt compelled to pursue my own dreams as a scientist. She will be sorely missed.

I thank my wife Becky for the love and support she gave me through the last several years. Why she didn't just club me in my sleep will always be a mystery to me. I thank my parents for their support, guidance, and wisdom throughout this endeavor. I thank my children, Sarah and Nicole, for their love and laughter and for giving my pursuit a sense of purpose. Finally, I thank the faculty and graduate students of the Southwest Texas State University Aquatic Station that assisted me through this and many other studies. I extend a special thanks to Kat for her generous help on those incredibly long nights of sampling on Landa Lake.

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Abstract

The effect of velocity on habitat suitability of *Marisa cornuarietis* (Pilidae) was studied over a four month (28 Feb 98 - 12 June 98) period at Landa Lake, New Braunfels, Comal Co., TX, and in the laboratory. Well withdrawals and drought conditions cause decreases in springflows that lead to subsequent decreases in current velocities within the lake. Springflows during this study ranged from 9.4 to 6.7 m^3/s. Except for two instances of *M. cornuarietis* observed in *Saggitaria platyphylla*, no snails were observed in macrophyte beds other than *Vallisneria americana*. A negative relationship between velocity and snail abundance was found in field observations ($r = -0.335$). The greatest numbers of snails were found in velocities less than 0.03 meters per second (mps). The partitioning velocity in the lake was predicted to be 0.17 mps by way of a simple linear regression. No snails were found in velocities greater than 0.16 mps. In laboratory experiments, t-tests for independent samples revealed that of four size classes of snails, the three smallest were significantly impacted with respect to mobility by a velocity of 0.18 mps. The largest size class was also effected, though to a lesser degree. These findings show that there is a relationship between current velocity and habitat suitability for *M. cornuarietis* in Landa Lake.

Introduction

Exotic species have been known to significantly contribute to a decrease in biological diversity (Carpenter et al. 1996, Allan and Flecker 1993, Bowles and Arsuffi 1993, Lubchenco 1991, Ono et al. 1983). Miller et al. (1989) estimated that 68% of fish species extinctions in North America involved (to some degree) species introductions. Of 82% of recorded extinctions, generally multiple factors led to the demise of a species (Miller et al. 1989). The reasons why exotic species may successfully invade a new environment remain the subject of debate, though chance and favorable conditions play an important role. Examples of intentional introductions are usually associated with the stocking of game fish to enhance a sport fishery (Allan and Flecker 1993). Howells (1992) reports that of 40 exotic fish species and 2 hybrids released or recovered in Texas, approximately 68% were originally introduced by state or federal agencies. Stocking animals for use as a biological control agent as in the use of grass carp for the control of aquatic macrophytes is another example of intentional introduction by man (Chilton and Muoneke 1992). Unintentional introductions into aquatic habitats may arise from activities in the pet (aquarium) trade (Allan and Flecker 1993, Horne et al. 1992, Hunt 1958), aquarists, and bait sources (Howells 1992). The impacts of introduced species on natives include predation, habitat alterations, hybridization (see Garrett 1991, Edwards 1979, Hubbs 1971), and the introduction of diseases (Garrett et al. 1992, Taylor et al. 1984, Ono et al. 1983).

Habitat modification through groundwater withdrawals may enhance the negative impact of exotics on endemic species. Bowles and Arsuffi (1993) list the over-pumping of the Edwards Aquifer due to expanding populations in central Texas as a major factor further endangering native and endemic species. As the level of the aquifer drops and hydrostatic pressure within the aquifer decreases, springflows decline which in turn lead to a decrease in the area potentially inhabited by endemic and other native species (Hubbs 1995). The environmental stresses (e.g., decrease in dissolved oxygen content or decreases/increases in water temperature) created by lowered springflows would tend to favor further invasion by nonnatives and exotics by increasing competition with already stressed natives and endemic species.

The exotic giant ramshorn snail, *Marisa cornuarietis* (Pilidae), was introduced into central Texas in the early 1980's and spread to several springfed river systems (Neck 1984). The introduction was believed to be accidental, the result of naive aquarists dumping this herbivore into local bodies of water (Neck 1984, Horne et al. 1992). Its appetite for aquatic macrophytes has raised questions concerning its impact on the habitat of the endangered fountain darter, *Etheostoma fonticola* (Horne et al. 1992). In Florida, where its introduction occurred in the 1950's, *M. cornuarietis* has been used for the control of aquatic macrophytes and can completely denude vegetated areas (Seaman and Porterfield 1964, Hunt 1958). The tendency for the snail to clear bodies of water of their macrophytes has alarmed authorities as to the potential impact to the habitat of endangered species in Central Texas. A U.S. district court judge has ruled that springflows (Comal Springs-Landa Lake, New Braunfels, Comal Co., TX) must be maintained above 5.66 m^3/s (200 cfs) in order to prevent "take" of the fountain darter (Edwards et al. 1995). Spring discharge less than 60 m^3/s (200 cfs) could lead to a net loss of vegetation (fountain darter habitat) due to the snails' preference for feeding in lower velocity currents, thereby negatively impacting fountain darters.

In a preliminary study, I found that *M. cornuarietis* macrophyte attachment and subsequent grazing behavior was negatively affected by increased water velocity. Dussart (1987) reported significant negative relationships with respect to detachment velocities on size and on types of shell profiles (especially for planispiral snails, e.g., *Planorbis planorbis*). Moore's (1964) study on the effect of water velocity on 2 species of snails, *Stagnicola palustris* and *Physa propinqua*, suggests that increased water velocity also may be a factor in increased detachment of *M. cornuarietis*. In a study of *Littorina obtusata*, an intertidal snail, Trussell (1997) found "the probability of dislodgment by a given flow is determined, in part, by shell size and shape, and by the attachment strength of the foot".

The purpose of this study is to determine the relationship between *M. cornuarietis* abundance and water velocity. Here, I describe the effect of current velocity on habitat suitability for *M. cornuarietis* in Landa Lake over a four month period. I also investigate the effect of the "partitioning velocity", i.e., current velocity above which *M. cornuarietis* is intolerant, on four size classes of *M. cornuarietis* in the laboratory. The results can be used to guide future control efforts of the snail. Management officials will be able to pinpoint areas favorable for infestation by examining velocity profiles within the lake with respect to springflows. If populations of *M. cornuarietis* are shown to be increasing, control efforts can begin before substantial negative impact to the ecosystem occurs, thereby protecting critical habitat of the fountain darter.

Materials and Methods

Study Area

The Central Texas (Edwards) Plateau is defined as the ecoregion corresponding to the Balconian biotic province (Omernik 1987, Gould 1975, Blair 1950). Its major geologic feature is a group of Cretaceous carbonates that make up the karstic Edwards Aquifer. The aquifer is composed of the Comanche Peak Limestone, Edwards Limestone, and Georgetown Limestone (Ogden et al. 1986). Thickness of the aquifer ranges from 122-183 m and extends from Brackettville in Kinney Co. to Kyle in Hays County. It is considered to be the most productive aquifer in the United States and is the sole source of water for nearly 2,000,000 people, including the city of San Antonio (Crowe and Sharp 1997).

Recharge to the aquifer occurs primarily through stream piracy events west and south of San Marcos, Hays County, and New Braunfels, Comal County. Surface water in the streams flows across the impermeable Glen Rose Formation until it encounters the locally exposed Edwards Aquifer (recharge zone) in the vicinity of the Balcones Fault zone. Once in the aquifer, water flows in a general east to northeast direction until it meets major discharge points at Comal, San Marcos, and Hueco Springs (in order of decreasing discharge). Rivers flowing from these springs course for short distances over the limestone of the Central Texas (Edwards) Plateau and then onto the clays and clay loams of the Blackland Prairie ecoregion on the way to the Guadalupe River (Ogden et al. 1986, Gould 1975).

The eastern edge of the freshwater aquifer is defined by the Balcones Fault Zone and its associated "bad water line". Total dissolved solids (TDS) concentrations associated with the bad water line exceed 1000 mg/l (non-potable) due to poor circulation and subsequent longer residence time of water in this area of the aquifer (Ogden et al. 1986).

The Comal Springs group discharges an average of 8.31 m^3/s (300 cfs) annually and is the largest spring system in Texas. They emerge from the base of the Comal Springs fault along a 372 meter stretch at the base of the Balcones Escarpment (Ogden et al. 1986). Four major springs and their associated spring runs, two large springs without spring runs and springs and seeps on the bottom of the lake supply the water flowing through Landa Lake (Figure 1, Crowe and Sharp 1997). The original river channel was dammed in 1847 (to supply water to a new channel to power a mill) to form the 21 acre lake (USFWS 1995).

Crowe and Sharp (1997) report on the uniform hydrochemistry found within the spring runs, lake, and river immediately downstream of the lake. They attribute this to the uniform hydrochemistry of the spring waters and the small local recharge component (small fluctuations were noticeable immediately after storm events).

It is the constancy of hydrochemical parameters that enable the existence of so many endemic species within the spring systems of central Texas (Hubbs 1995, Ono 1983). Hubbs (1995) notes that large springs often have an associated biota very different from the downstream biota. The downstream conditions of streams fed by springs are greatly impacted by ambient air temperature. Hubbs (1995) attributes the uniqueness of spring and springrun biota to the constant water temperatures found near springs. He also suggests that areas near springs are less impacted than downstream reaches by storm events that can substantially increase flow and turbidity. The constant conditions found near springs potentially enable a rich endemic population to exist, and may also be the hallmark of an easily invaded habitat. Highly variable flows (as during a major flood event) are known to negatively impact the abundance of nonnative fishes. Conversely, constant conditions may provide the additional leverage needed by an exotic species to become established in a particular system. Such conditions exist in San Marcos and Comal Springs (US Fish and Wildlife Service 1995, Hubbs 1971).

Field Observations

Field work was conducted at Landa Lake (Comal Springs), New Braunfels, Comal Co., Texas (29°42.86' N, 98°8.13' W). Data were collected monthly on the following dates - 28 Feb 98, 4 Apr 98, 9 May 98, and 12 Jun 98. Numbers of snails, macrophyte type, water velocity found at the maximum height of the macrophytes, substrate type, depth to substrate, and springflows were recorded. All observations were made at night due to the snail's diel vertical migration behavior, i.e., they move to the top of macrophytes at night to feed and down to the sediments during the day.

Water temperature during this study ranged from 23.4 to 23.6 °C. Specific conductance ranged from 536 to 552 uS/cm. The values for pH ranged from 7.0 to 7.4. These values were obtained from the Edwards Aquifer Research and Data Center (EARDC) Bad Water Line Monitoring Station located in spring run three. Crowe and Sharp (1997) documented dissolved oxygen ranges of 1.00 to 10.27 mg/l in the spring system. The USGS monitoring station (08169000) located downstream of Landa Lake reported similar readings during this study (10.2 - 1.6 mg/l).

Twenty-three sites within the lake (Figure 1) were chosen using a stratified random design. The sites were chosen according to the dominant macrophyte present and the number of sites per plant type was based upon overall percent coverage. Ten sites were placed in stands of *Vallisneria americana* (the most dominant macrophyte), four were placed in *Hygrophilla polysperma*, three in *Sagittaria platyphylla*, three in bare/filamentous algae areas, two in *Cabomba caroliniana*, and one in *Nuphar*. Numbered buoys were placed at the sites to allow for rapid identification of a particular sampling location.

Enumeration of snails was accomplished by using a 1 m^2 frame centered over the site buoy. The number of snails observed within the frame was recorded. The macrophyte type associated with the site was recorded and any temporal change in either the type or size of the stand noted. Water velocity was determined using a Marsh-McBirney flow meter. The flow meter was positioned to record the current velocity found at the top of the macrophyte stand within the frame. Springflows were obtained from the U.S. Geological Survey monitoring station (no. 08169000) located in the Comal River at New Braunfels, just downstream of Landa Lake. Average springflows for the four sampling dates are shown in Tables 1 and 2.

Geographic Information System (GIS) coverages of the lake were also created to aid in visualization of the data. The sampling sites were plotted on the map and linked to a database containing all of the recorded information obtained in the field.

Field Statistics

Simple linear regression was used to determine the relationship between the number of snails found at sites with *V. americana* and the observed current velocities over the sampling period.

Laboratory Experiment

Laboratory experiments were conducted at the Southwest Texas State University Aquatic Station Wet Lab, San Marcos, Texas. A velocity chamber was constructed to test *M. cornuarietis'* mobility performance. A rectangular (3.1 m x 0.6 m x 0.6 m) fiberglass holding tank was customized by inserting a fiberglass divider (2.4 m x 5.1 cm x 5.1 cm) into the center of the tank. A small, variable speed electric boat motor was used to generate consistent current velocities within the tank. The motor was oriented on the opposite side and as far downstream (approximately 5 m) of the snail attachment platform as possible so that turbulent flow would be minimized. Baffles were constructed of 0.6 cm mesh hardware cloth and inserted upstream of the attachment platform to further minimize turbulence. To smooth the flow of water around the square corners of the holding tank, curved fiberglass inserts were positioned at the downstream (from the motor) corners of the tank. A snail attachment platform was constructed of a sheet of plexiglass cut to fit the width of the channel and suspended halfway between the bottom of the tank and the water surface.

The tank was filled with spring water from the artesian well fed by the Edwards Aquifer located behind the SWT Aquatic Station (21°C, pH 6.9, conductivity 624 uS/cm, dissolved oxygen 5.2 mg/l). A drain was fitted in the tank that allowed a constant supply of freshwater to circulate through the system. Prior to the experiment, snails were kept in a separate tank filled with water from the same source and maintained on a diet of *V. americana.*

Mobility performance was defined as the ability of snails to move when exposed to current. It was measured by allowing the snails to attach to a substrate and measure the distance traveled after a two minute time period. Before initiation of the mobility performance experiments, the snails were divided into four size classes: 0.5 cm- 1.5 cm, 1.51 cm - 2.5 cm, 2.51 cm - 3.5 cm, and >3.51 cm (size class 1, 2, 3, and 4, respectively). A total of 20 snails for each size class was used for each experiment; 10 for the treatment (flowing conditions) and 10 for control (static conditions). A velocity of 0.18 meters per second (mps) was used, because this was found to be near the partitioning velocity (upper tolerance limit) where the snails were observed in the lake. T-tests were used to determine if a significant difference existed between the control and treatment units with respect to distance moved under the two flow regimes.

Results

Field Observations

During this study, *M. cornuarietis* was observed primarily in stands of *V. americana* (Figure 1). On two occasions two individuals were noted in *S. platyphylla* beds. No snails were observed in other macrophyte stands. Ten of the twenty-three sites were covered by *V. americana*. Of the forty observations made within *V. americana* beds, twenty contained snails (Table 1). The maximum current velocity where snails were found was 0.18 mps (Table 1). The greatest velocity recorded within *V. americana* beds (recorded at the maximum height of the plant) was 0.26 mps. This velocity was also the maximum velocity recorded at the top of the plants for all sites on all dates (Table 2). Pathways of greatest water movement, i.e. areas of highest water volume exchange were also determined based on data collected 4 April 1998 (Figure 2). Pathways were determined using the discharge equation $Q=VA$, where Q is discharge, V is the mean current velocity, and A is the cross-sectional area under examination. The pathways show the main channels of flow in Landa Lake.

Of the 22 of 87 quadrat observations with snails, 37.4% had velocities less than 0.03 mps; 27.3% had velocities between 0.03 and 0.06 mps; 22.7% had velocities between 0.06 and 0.09 mps; 9.1% had velocities between 0.09 and 0.12 mps; none were recorded with velocities between 0.12 and 0.15 mps; and 4% had velocities between 0.15 and 0.18 mps.

A total of 223 snails (*M. cornuarietis*) in 22 quadrats were counted during the study. In velocities less than 0.03 mps, 46.2% of the snails were observed; 34.1% were observed in velocities between 0.03 and 0.06 mps; 11.7% were observed in velocities between 0.06 and 0.09 mps; 6.7% were observed in velocities between 0.09 and 0.12 mps; none were observed in velocities between 0.12 and 0.15 mps; and 1.3% were observed in velocities between 0.15 and 0.18 mps.

The depths recorded for each of the sites ranged from 0.3 m and 2.6 m (Table 3). No snails were reported in depths greater than 2.4 m or less than 0.9 m. Depths of 0.9 to 1.2 m yielded 16.1% of observed snails; 1.21 to 1.5 m, 10.8%; 1.51 to 1.8 m, 39.7%; 1.81 to 2.1 m, 7.6%; 2.11 to 2.4 m, 26.0%. The analysis between depth and the number of snails did not show a significant correlation ($r = -0.206$), though a weak negative relationship was noted. Depths between 0.91 and 2.44 m did not appear to have any significant effect on snail abundance in this study.

Linear regression analysis showed a negative relationship between current velocity and snail counts ($r = -0.335$, Figure 3) over the four month sampling period. The predicted maximum tolerance velocity was 0.17 mps, i.e., habitats with current velocities above 0.17 mps were avoided by snails.

Laboratory Experiment

Mobility performance experiments conducted in the laboratory showed velocity to have a significant effect (class 1 p=0.01, class 2 p=0.008, class 3 p=0.02) on the three smaller size classes of *M. cornuarietis* (Figure 4). The largest size class (class 4 p=0.08) was less affected by velocity.

Discussion

Marisa cornuarietis shows more preference with respect to selection of habitat. The snails were previously observed in all major macrophyte types in the lake prior to this study, but were observed only in *V. americana* during this study (Howard 1998 , USFWS 1995, T.L. Arsuffi unpublished). The two individuals seen traversing a bed of *S. platyphylla* that bulged into a bed of *V. americana* were probably migrating to another patch of *V. americana.* Correll and Correll (1972) report that *V. americana* is an excellent source of nutrition for many aquatic vertebrates and invertebrates. I have observed in aquaria that *V. americana* was the first choice of adult *M. cornuarietis* when feeding. The snails actually traversed other macrophytes to feed on *V. americana.* This suggests that there is some nutritional requirement found in *V. americana* that is not found in the other macrophytes associated with Landa Lake (Howard 1998, Grantham et al. 1993).

The maximum current velocity found in habitats with snails compares favorably with the results from the mobility performance experiments. Distribution data from the field revealed larger size classes of snails were generally more abundant than smaller size classes at higher current velocities. For example, snails observed at sites 5 and 6 were all size class 4 (3.5 to 4.5 cm). Smaller size classes were generally restricted to areas of lower current velocities. Eighty-five percent of the snails observed in site 15 and 65% observed in site 3 on 12 June 98 were less than 2.5 cm in length (size class 2 or smaller). Shell morphology is a major factor in gastropod movement or detachment under high flow conditions (Dussart 1987). Moore (1964) showed that snails' ability to remain attached to the substrate under high current velocities was related to a combination of biological factors such as foraging behavior or the amount of mucus secreted by the foot by different age classes of snails. He further hypothesized that detachment could also be related to the ratio of foot to shell size, i.e., the larger the foot, the greater the snails capacity to remain attached. Further refinement of this idea was proposed by Dussart (1987) who suggested a relationship between index of foot size to shell profile that was modified by the mass of the snail. With a smaller profile or a larger foot, a snail could withstand higher current velocities. Greater mass of the snail could relate to greater muscle volume thereby allowing for greater attachment potential. In a separate investigation, I measured the surface area of the foot and shell of *M. cornuarietis* (n=30) and *Elimia comalensis* (n=30), a river snail found in areas of high current velocities. A ratio of foot to shell surface area was calculated to establish an index for comparison between the 2 species. *Marisa cornuarietis* had a significantly ($p < 0.05$) smaller index than *E. comalensis* when analyzed with a t-test. This suggests that *M. cornuarietis* is adversely affected due to its foot's inability to supply sufficient adhesion/suction in response to increased drag caused by its larger shell profile in current velocities greater than 0.18 mps.

The effects of macrophytes on current is well known in stream ecology, but their effect on circulation within lake ecosystems is much less studied (Carpenter and Lodge 1986). In experiments designed to examine the effect of macrophytes on micro-current velocity in the Portneuf River, Idaho, Watson and Rose (1982) showed that macrophytes affect current velocity and "obstruct the flow of water and cause a compensatory increase in current velocity above them". This would move boundary layer velocities (near zero velocities) to the top of the macrophytes. Velocity measurements taken near the substrate in macrophyte stands were near zero and did not increase until the tops of the plants were encountered. This allows *M. cornuarietis* the freedom to move easily to other suitable habitat, even though currents just above may be above their current velocity tolerance levels.

Low current velocities within the macrophyte stands should also have an effect on the dissolved oxygen content of the water, especially at night during plant respiration (Rothermel and Ogden 1987, Watson and Rose 1982). *Marisa cornuarietis* is tolerant of low dissolved oxygen content (Robins 1971, Hunt 1958). This factor could allow the snail to thrive during times of lowered springflows when naturally occurring (endemic) species are forced into smaller refugia habitats near the springs to avoid fluctuating hydrochemical conditions (Hubbs 1995).

Marisa cornuarietis' overwhelming preference for velocities less than 0.06 mps (80.3%) underscores the importance of maintaining springflows above 60 mps within the Comal Springs ecosystem (USFWS 1995). In areas of low current velocity where *V. americana* beds were present, I observed a greater accumulation of periphyton on the leaves of plants and a greater abundance of very small (<0.5 cm) snails. The combination of low current velocity and an abundant food supply for smaller snails suggests these areas are potential "nurseries". As springflows decline, the amount of habitat for use as nurseries will increase.

Regression analysis between current velocity and snail counts exhibited a negative relationship (r = -0.335). Although this explains only 10% of the variability, I believe that the collection of more data would show a stronger relationship. Of 40 *V. americana* areas sampled, only 20 had snails. However, this study ended at a time when snail populations appeared to be growing rapidly. A stronger relationship may also emerge with the use of a more accurate flow meter. The device used in this study yielded some conflicting results. All things being equal, it would be expected that the dates with the greatest springflows should produce the highest current velocities, whereas the lowest springflows would produce the lowest. The first sampling date shows this not to be the case (Tables 1 and 2). This fact may be attributed to extreme weather conditions. Ambient temperatures were below freezing the entire night, possibly affecting the battery or circuitry adversely.

The results of the laboratory experiments correspond well with the trend found in the field observations. In Landa Lake, the predicted partitioning velocity was 0.17 mps, whereas the 0.18 mps treatment velocity used in the lab experiments produced the effect of significantly inhibiting mobility (at least for the 3 smaller size classes - Figure 4). The largest size class was also affected by the 0.18 mps treatment, though to a lesser degree. Trussell (1997) reported that as foot size of *Littorina obtusata* increases, the dislodgment forces required to remove them from the substrate increases. Though no experiments concerning the force required to break the suction of the snail's foot were performed, I noted that considerably more effort was required to remove larger snails from the substrate.

Conclusions

In summary, current velocity does influence habitat suitability for *M. cornuarietis* in Landa Lake. Lowered springflows due to natural or anthropogenic causes produce a decrease in the current velocities found in Landa Lake (Crowe and Sharp 1997, Hubbs 1995). Under diminished springflow conditions, I found that decreases in current velocities within *V. americana* stands led to increases in *M. cornuarietis* abundance. Areas found to have velocities less than 0.18 mps within *V. americana* require monitoring for rapid outbreaks of *M. cornuarietis* populations so that management efforts can be more efficiently directed, and thus avoid the loss of vegetation within the lake. The observed partitioning velocity of 0.17 mps found in the lake corresponds with the 0.18 mps mobility inhibition velocity experienced by snails in the laboratory. Shell morphology and foot size are the probable explanations for the snails' preference for lower velocity areas. Studies have revealed that shell morphology does have a direct effect on the flow regimes preferred by different snail species (Trussell 1997, Dussart 1987, Moore 1964), i.e., more streamlined snails should be better adapted for higher current velocities than snails with discoidal or planispiral shells. Another reason for the partitioning effect observed relates to the ratio of foot area to surface area of the shell. In the velocities typically observed within the *V. americana* beds in the lake, a larger foot surface area would provide a heightened chance of adherence to the substrate under flowing conditions given the large discoidal shape of *M. cornuarietis'* shell. Reasons for the shift in macrophyte preference from virtually all major macrophyte types to the exclusive use of *V. americana* requires further investigation. A possible explanation would be that *V. americana* provides some nutritional benefit not provided by the other macrophytes found in Landa Lake.

The need for more data concerning the abundance and distribution of *M. cornuarietis* in Landa Lake is clear. Although the findings in this study show a negative relationship between current velocity and snail abundance within *V. americana* stands, the collection of data over 1 or more life cycles (500+ days) is needed to validate conclusions reached thus far. In the laboratory, experiments with habitat partitioning and velocity need to be of longer duration and include various current velocities in the experiment, thereby allowing snails to seek preferential habitat.

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List of Tables

Table 1 - Snail abundance and current velocities (mps) of sites with *M. cornuarietis*. The solid bars are scaled to represent the number of snails found and the unfilled bars are scaled to represent the current velocity (mps) found at a site on a particular date.

Site	Plant	02/28/98	04/04/98	05/09/98	06/12/98
2	*S. platyphylla*	1 0	1 0	0 0	0 0
3	*V. americana*	2 0	0 0.15	9 0.08	25 0.01
4	*V. americana*	2 0	2 0.08	10 0.07	43 0.05
5	*V. americana*	0 0.09	0 0.21	3 0.16	12 0.06
6	*V. americana*	1 0.04	0 0.18	0 0.23	0 0.09
7	*V. americana*	1 0.04	5 0.12	10 0.12	20 0
8	*V. americana*	1 0.08	4 0.09	3 0.06	16 0.04
15	*V. americana*	0 0	0 0.04	6 0	47 0
	Springflow	9.3 m^3/s	9.4	8.2	6.2

Explanation

10 Scale bar (actual number of snails)
0.12 Scale bar (actual velocity in mps)

Table 2 - Current velocities (mps) recorded for sites without *M. cornuarietis*.

Site	Plant	02/28/98	04/04/98	05/09/98	06/12/98
1	*S. platyphylla*	0	0	0	0
9	*V. americana*	0.08	0.12	0.26	0.01
10	*V. americana*	0.12	0.12	0.26	0.04
11	*H. polysperma*	0.08	0.12	0	0.03
12	*Bare/fil. algae*	0	0.03	0	0
13	*Bare/fil. algae*	0	0	0	0
14	*Nuphar sp.*	0	0	0	0.01
16	*H. polysperma*	0	0	0	0
17	*C. caroliniana*	N/A	0.04	0	0.03
18	*H. polysperma*	N/A	0.04	0	0.04
19	*H. polysperma*	N/A	0.09	0	0.04
20	*C. caroliniana*	N/A	0.08	0.04	0.03
21	*V. americana*	N/A	0.06	0.14	0
22	*S. platyphylla*	0.14	0	0	0
23	*Bare/fil. algae*	0.18	0.06	0.23	0.07
	Springflow	*9.3 m^3/s*	*9.4*	*8.2*	*6.2*

Explanation ▭0.12 -- Scale bar (actual velocity in mps)

Table 3 - Depth and sediment composition of sampling sites.

Site	Depth (m)	*Macrophyte*	Sediment
1	2.01	*Saggitaria platyphylla*	silt/cobble
2	1.86	*Saggitaria platyphylla*	silt/cobble
3	1.62	*Vallisneria americana*	silt/cobble/mud
4	2.41	*Vallisneria americana*	silt/mud
5	2.04	*Vallisneria americana*	cobble/sand
6	2.19	*Vallisneria americana*	silt/cobble
7	0.94	*Vallisneria americana*	silt/cobble
8	1.25	*Vallisneria americana*	silt/cobble
9	2.59	*Vallisneria americana*	mud/gravel
10	2.50	*Vallisneria americana*	mud/gravel
11	0.85	*Hygrophilla polysperma*	mud
12	1.71	*Bare/filamentous algae*	gravel/sand
13	1.65	*Bare/filamentous algae*	gravel/sand/mud
14	1.62	*Nuphar sp.*	mud/sand
15	1.77	*Vallisneria americana*	mud/cobble
16	1.04	*Hygrophilla polysperma*	mud/cobble/sand
17	1.19	*Cabomba caroliniana*	mud/cobble/sand
18	1.37	*Hygrophilla polysperma*	gravel/sand
19	0.52	*Hygrophilla polysperma*	cobble/sand
20	0.73	*Cabomba caroliniana*	cobble/sand
21	2.29	*Vallisneria americana*	mud
22	1.04	*Saggitaria platyphylla*	cobble
23	0.30	*Bare/filamentous algae*	limestone/cobble

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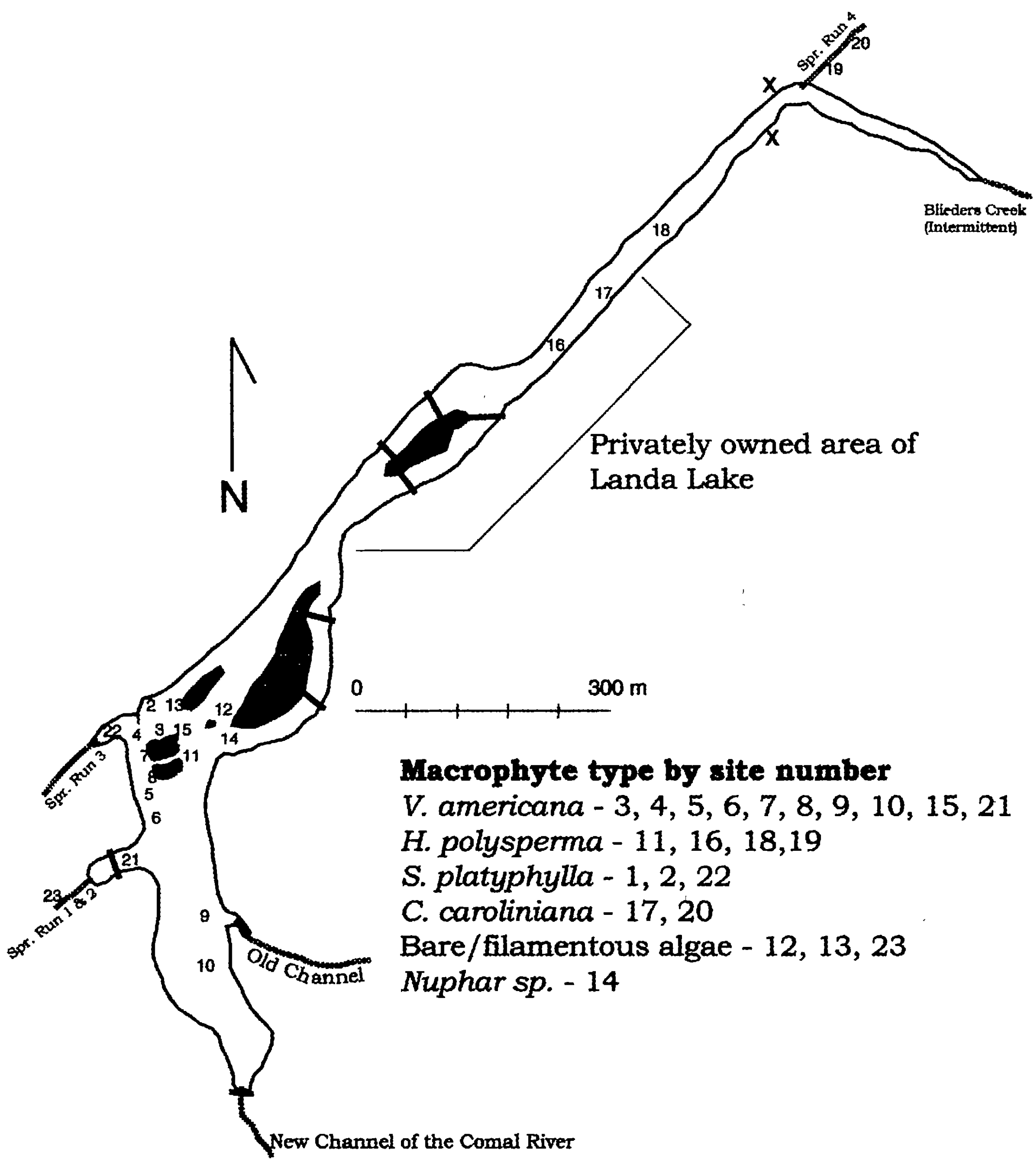

Figure 1 - Map of Landa Lake (Comal Springs), New Braunfels, Comal Co., TX. Individual sampling sites are marked by numbers. X's denote large springs without springruns.

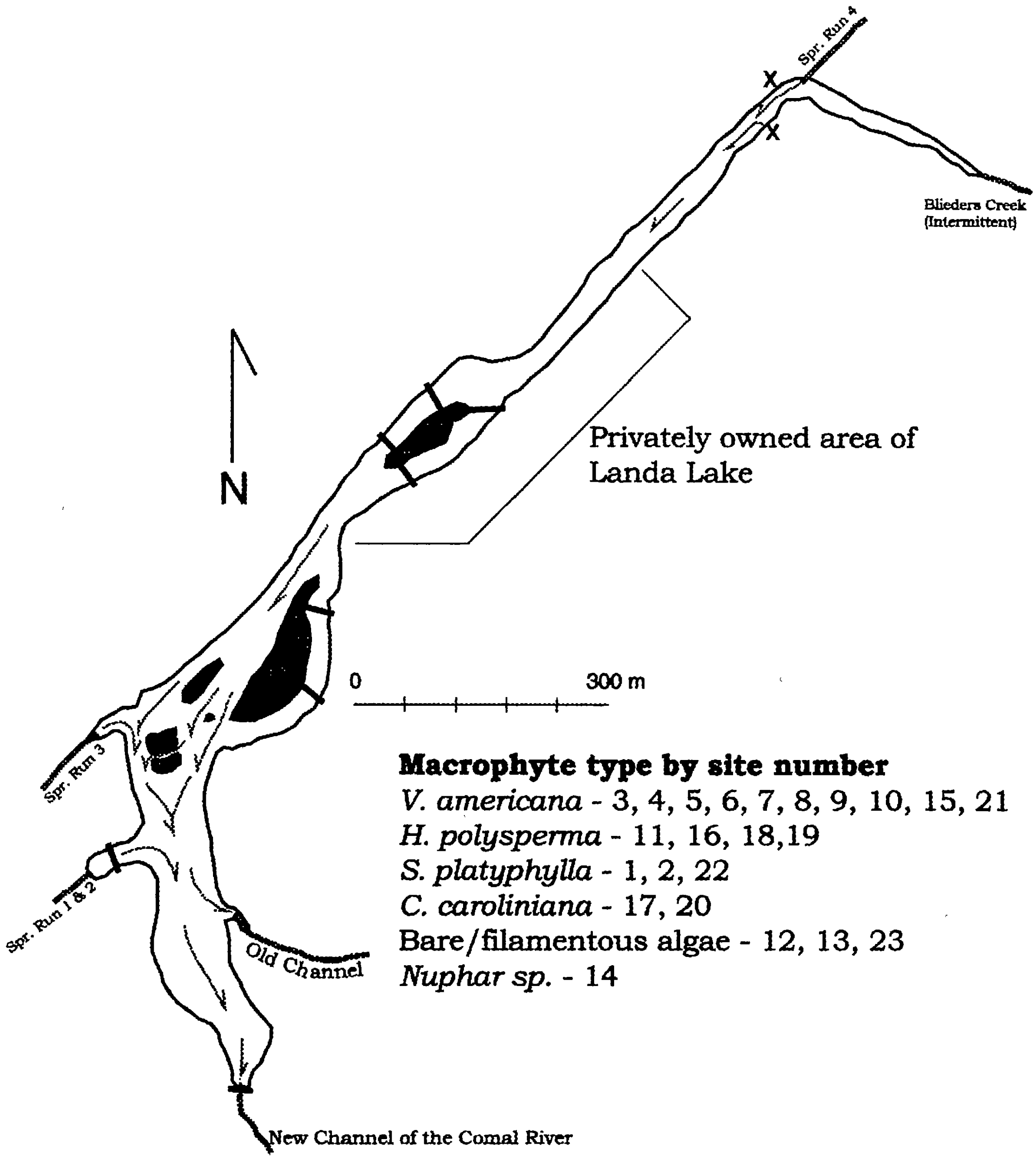

Figure 2 - Water flow through Landa Lake. Arrows denote channels of greatest average discharge.

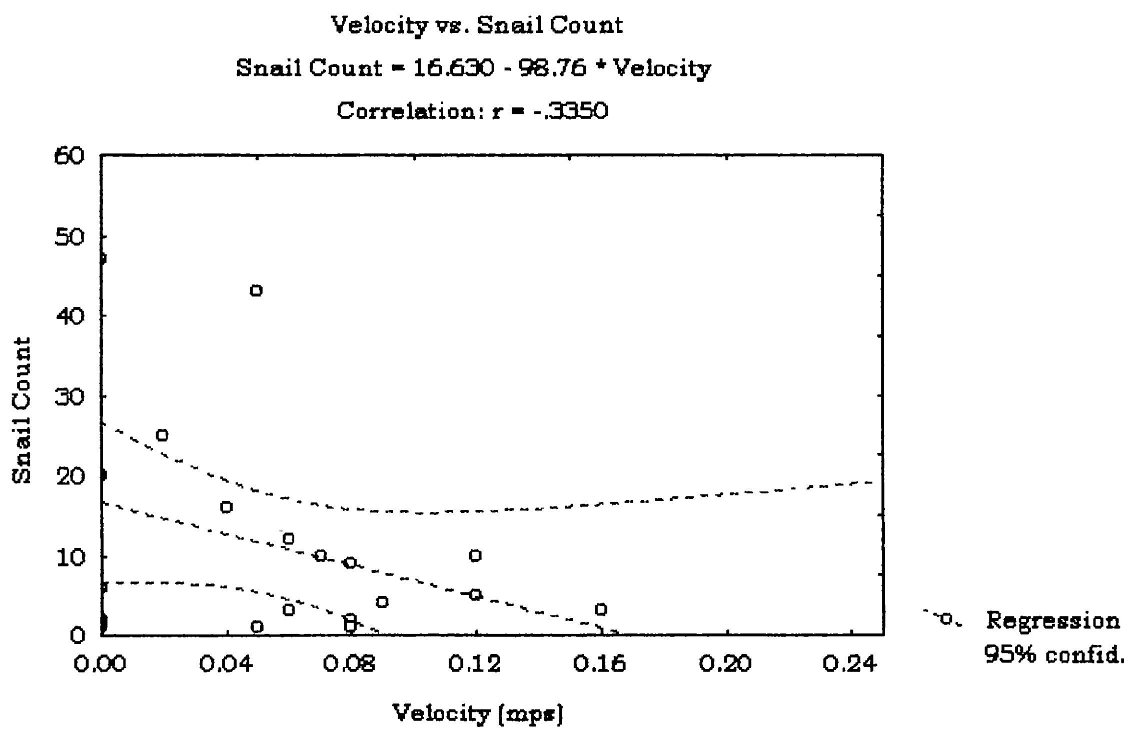

Figure 3 - Linear regression of the relationship between current velocity and number of snails observed in Landa Lake over a four month period.

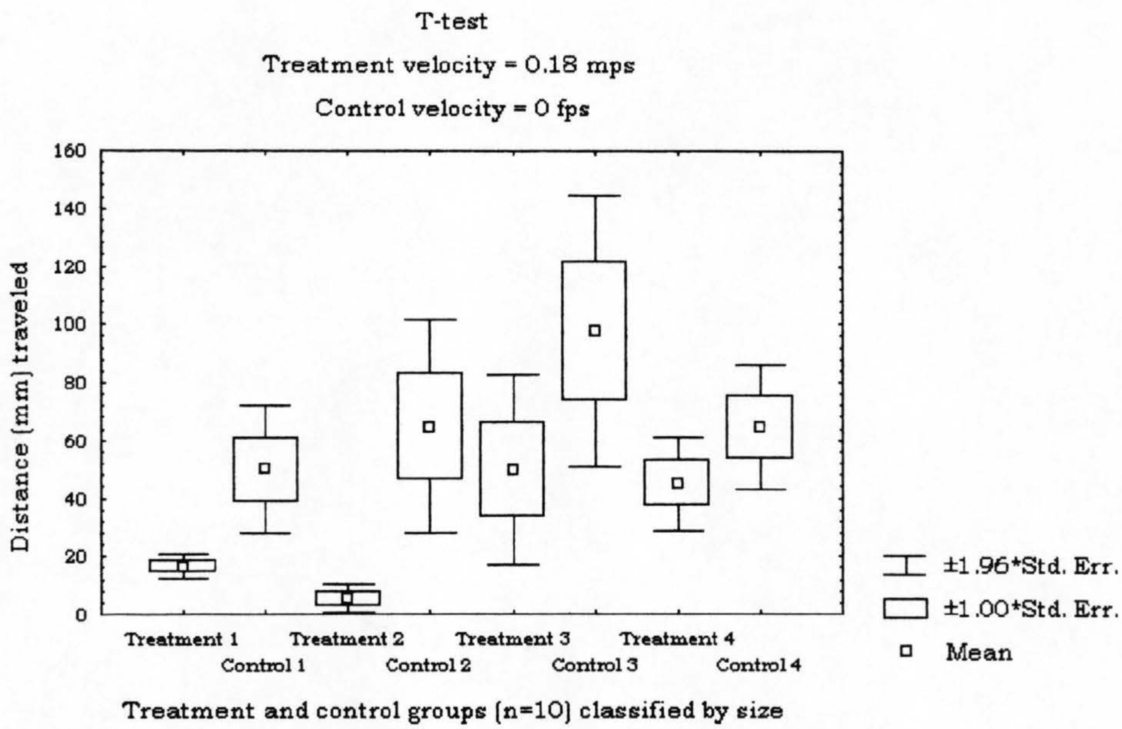

Figure 4 - T-tests for effects of static and a current velocity of 0.18 mps on four size classes of snail. Size class (treatment and control) 1 = 0.5-1.5 cm, 2 = 1.51-2.5 cm, 3 = 2.51-3.5 cm, 4 = 3.51-4.5 cm.