The relationship between current speed and shell morphology in the freshwater snail, *Elimia livescens*, in two Northern Michigan streams

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Abstract

In this study, we examined *Elimia livescens*, a freshwater snail, in two Northern Michigan streams to determine the relationship between current speed and shell morphology. Because of environmental selective pressures, differences in morphology can be attributed to either phenotypic plasticity (morphologic changes in individuals not attributed to genes) or ecotype formation (existence of genetic variation and trait heritability among populations within a species). We predicted that there would be no relationship between shell thickness and length or width, that there would be a positive direct relationship between current speed and shell thickness and size, and that snails in high current areas would have narrower shells than those in low current areas. Sites of variable current speed were sampled in Wycamp Creek near Cross Village, Michigan and in Little Carp River near Bliss, Michigan. For each snail collected, we measured length, width at the widest point and thickness at the aperture. From these measurements, we calculated indices for shell size and shape. Our results indicated that shell thickness is independent of both shell length and width, supporting our prediction and suggesting that an outside selective force is acting on shell thickness. Additionally, there was a significant positive relationship between current speed and shell thickness, but not between current speed and size or shape. Overall, we determined that current speed is an important selective force on snail shell thickness, indicating either phenotypic plasticity in individual snails or the existence of ecotypes within the species.

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ABSTRACT

In this study, we examined *Elimia livescens*, a freshwater snail, in two Northern Michigan streams to determine the relationship between current speed and shell morphology. Because of environmental selective pressures, differences in morphology can be attributed to either phenotypic plasticity (morphologic changes in individuals not attributed to genes) or ecotype formation (existence of genetic variation and trait heritability among populations within a species). We predicted that there would be no relationship between shell thickness and length or width, that there would be a positive direct relationship between current speed and shell thickness and size, and that snails in high current areas would have narrower shells than those in low current areas. Sites of variable current speed were sampled in Wycamp Creek near Cross Village, Michigan and in Little Carp River near Bliss, Michigan. For each snail collected, we measured length, width at the widest point and thickness at the aperture. From these measurements, we calculated indices for shell size and shape. Our results indicated that shell thickness is independent of both shell length and width, supporting our prediction and suggesting that an outside selective force is acting on shell thickness. Additionally, there was a significant positive relationship between current speed and shell thickness, but not between current speed and size or shape. Overall, we determined that current speed is an important selective force on snail shell thickness, indicating either phenotypic plasticity in individual snails or the existence of ecotypes within the species.

INTRODUCTION

Environmental selective pressures can influence a variety of morphological traits within a species. Different populations adapt to unique selective pressures of the changing environment, leading to gradients of phenotypes within a species (Lortie and Aarssen 1996). Phenotypic variation within a population can be due to induced individual adaptation to changing environmental conditions; this is called phenotypic plasticity (Stearns 1989). Genetic dissimilarities can also cause phenotypic variation within a species; genetically distinct populations within a species that are adapted to different ecological niches are called ecotypes (Konstantinidis and Tiedje 2005, Lande 2009). The gradient of traits present in ecotypes is maintained by assortative mating and heritability of the trait; however the integrity of the species as a whole is maintained by gene flow (Guerra-Varela et al. 2009).

The water current speed within a stream is an example of a local environmental gradient and selective pressure; in general, areas in the middle of the stream have higher current speeds than areas near the shore, with a range of speeds between the two extremes. In addition to current, many other environmental factors, such as predation, biomass availability and population density, are variable within a stream and act as selective pressures (Kemp and Bertness 1984, Crowl and Schnell 1990). Freshwater snails inhabit all areas within a stream; however, shell morphology is not constant in varying environments, and snail shell character traits differ within a population due to selective pressures acting on the size, thickness and shape of the shell (Raffaelli 1978, Kemp and Bertness 1984, Crowl and Schnell 1990, Vermeij 1993, Johnson and Brown 1997, Trussell 1997, DeWitt et al. 1998, Minton et al. 2008).

Predation is a selective pressure affecting the morphological traits of snail shells. According to Trussell (1997), snails in areas of high predation have larger, thicker shells in order to reduce crushing and narrower apertures to prevent removal of the organism from the shell; DeWitt et al. (1998) also found that snails have narrower apertures in areas of high predation. Another selective pressure affecting shell morphology is biomass availability; Crowl and Schnell's (1990) results suggest that shell size is larger in areas of higher biomass availability due to its nutritional content. In addition to predation and biomass availability, population density may also affect shell shape. According to Kemp and Bertness (1984), snails in areas of high population density have narrower shell shapes, whereas snails in low population density areas may have wider, more globular shells.

Current strength varies along a gradient within a stream and is also an important selective pressure that affects shell morphology. Previous studies have indicated conflicting results on the effect current speed has on shell size. According to Trussell (1997), in order to reduce drag, snails have smaller shells in high current environments; however, Johnson and Brown's (1997) results indicate a positive direct relationship between current speed and shell size due to the stress of high current environments.

In addition to Johnson and Brown's (1997) study, the results of Minton et al. (2008) suggest that snails with larger shells also have larger feet and therefore a better ability to resist dislodgement by high current. Shell thickness is also affected by current strength; shells have been found to be thicker in areas of high current speed, where the risk of shell injury due to dislodgement is higher (Raffaelli 1978). Additionally, shell shape is affected by current speed, but the effect has been debated. Vermeij (1993) found that in high current areas smaller shells with sharper points are more energetically favorable and selected for because of hydrodynamics that create a laminar flow of water, while Trussell (1997) suggests that a short and wide shell is more advantageous in high current environments due to reduced drag.

In this study, we examined the effect that current speed has on the shell morphology of the freshwater snail *Elimia livescens* in two Northern Michigan streams. *Elimia livescens* are found crawling on rocks in shallow streams (Burch and Jung 1992). Based on Raffaelli's (1978) findings, we predicted that shell thickness will be independent of both length and width of the shell, indicating that different selective pressures, rather than strictly growth, are acting on thickness. In addition, we predicted that shell thickness and current speed will have a positive direct relationship because there is selection for thicker shells in areas of high current due to the high risk of dislodgement and shell injury (Raffaelli 1978). We also predicted that shell size and current speed will have a positive direct relationship because larger snails with larger feet will be less prone to dislodgement in areas of high current (Minton et al. 2008). Finally, we hypothesized that snails in high current areas will have sharper points in order to be hydrodynamic, and therefore more energy efficient than globular shaped shells (Vermeij 1993).

METHODS

We measured snails at Little Carp River on Munger Road in Bliss, Michigan and at Wycamp Creek off Wycamp Road near Cross Village, Michigan (Figure 1). The locations are approximately 13.1 km apart, and the source of Little Carp River is Lake Paradise while the source of Wycamp Creek is Wycamp Lake. In each location, water samples were collected and calcium ion concentrations were measured through chemical analysis in Lakeside Lab at the University of Michigan Biological Station. We also measured pH with a pH meter (Fisher Scientific, Accumet Portable AP10, fishersci.com), dissolved oxygen level with a dissolved oxygen meter (YSI Incorporated, model 50B, YSI.com), conductivity and temperature with a salinity/conductivity/temperature meter (YSI Incorporated, model 30, YSI.com) to control for these variables between the different rivers. Within each river, we collected snails and measured current at six sites of varying current speeds, of roughly 8-16 m^2 in area. We determined the sites within the streams by snail density and current speed. To measure current (m/s), we determined the time it took an orange to travel 1 meter downstream. Using glass bottomed buckets, we collected 50 snails per site at Little Carp River and 100 snails per site at Wycamp Creek due to different densities of snails at each stream and time constraints. For each snail collected, we measured three features with digital calipers: length, width at the widest point and thickness of shell at its aperture (Figure 2). We used the product of length and width to establish a size index and the quotient of length and width to establish a hydrodynamic current resistance, or shell shape, index. T-tests were used to compare the mean current speeds between the streams, and to compare the mean shell size, shape and thickness between streams. Linear regressions were used to test whether or not shell thickness varied with shell length and shell width. Linear regressions were also used to test whether or not mean shell size, thickness and shape varied with current speed per site.

RESULTS

The difference in current speeds between the two streams was not statistically significant (t-test, $t=-.587$, $N=6$, $p=.570$). Other abiotic factors measured, including calcium ion concentration, pH, dissolved oxygen level, conductivity and temperature, in Little Carp River and Wycamp Creek (Table 1) were similar between the streams, but we did not conduct statistical analyses to compare them. Based on these similarities, we did not distinguish between streams in subsequent analyses.

The p-value of the linear regression indicates that snail shell thickness varied significantly with shell length; however, the coefficient of determination suggests there is little relationship between the variables (linear regression, R^2=.099, N=900, p<.0001; Figure 3). In addition, the p-value of the linear regression indicates that snail shell thickness varied significantly with shell width; however, the coefficient of determination suggests there is little relationship between the variables (linear regression, R^2=.075, N=900, p<.0001; Figure 4).

Shell thickness at the aperture was significantly dependent on current speed (linear regression, R^2=.63, N=12, p=.002); snails in higher currents had significantly thicker shells (Figure 5). In contrast, snail shell size was not significantly dependent on current speed (linear regression, R^2=.05, N=12, p=.483; Figure 6), and snail shell shape was not significantly dependent on current speed (linear regression, R^2=.048, N=12, p=.493; Figure 7).

DISCUSSION

Based on the similarities in abiotic factors and current speeds between both streams, it was unlikely that the small differences would contribute to differences in shell morphology. However, there was a difference in shell size and thickness between the two streams, with Little Carp River having larger and thicker snail shells, which might be due to the 49.6 μS increase in conductivity in Little Carp River; conductivity influences biomass availability, which affects shell morphology by increasing size and thickness (Crowl and Schnell 1990, Chetelat et al. 1999).

There was a significant relationship between shell thickness at the aperture and both shell length and width; however, based on the low coefficients of determination for both relationships, shell thickness did not have a strong relationship with either length or width of the shell, which was consistent with our predictions. It is improbable that shell thickness is completely dependent on growth rate, and it is likely influenced by outside selective pressures. Based on our findings, current speed was a selective force on snail shell thickness because there was a significant, positive direct relationship between current speed and shell thickness at the aperture (Figure 5); our results were supported by Raffaelli's (1978) study, which found that snails had thicker shells in areas of higher wave action to prevent shell damage and crushing if dislodged. Our results indicated that in areas of high current, shells are thicker than shells in low current areas, with a gradient of thickness corresponding to the gradient of current speed. The differences can be attributed to phenotypic plasticity of this trait (Stearns 1989); however, the gradient of phenotypic variation can also be attributed to genetic differences within the species, called ecotypes (Konstantinidis and Tiedje 2005, Lande 2009). Ecotypes are maintained by heritability of the trait and assortative mating of snails based on shell thickness; however, speciation fails to occur due to gene flow along the gradient of the trait (Guerra-Varela et al. 2009). Based on the findings of Trussell (1997), it was expected that predation would increase shell thickness, but our results indicated that current speed is a stronger selective force on shell thickness. If predation was the most important selective force, there would be an inverse relationship between current speed and shell thickness due to the higher likelihood of predators, such as crayfish, being found in areas of low current (Rabeni 1985).

Based on our findings, snail shell size is independent of current speed (Figure 6), disagreeing with our prediction that there would be a positive direct relationship between current speed and shell size. Previous studies have suggested mixed results of the relationship between the two variables. Crowl and Schnell's (1990) results indicated an inverse relationship between shell size and current strength, while Johnson and Brown (1997) found that there was a positive direct relationship between the two factors. In addition, Minton et al. (2008) suggested that snails with larger shells would have larger feet and be able to resist dislodgement better than smaller snails; therefore, snails with larger shells would be found in areas of high flow. Our results disagreed with these studies and indicated no relationship between current speed and shell size. Selective pressures other than current, such as predation or biomass availability, might be acting upon size, and a gradient of shell size might exist along a different cline other than current speed (Crowl and Schnell 1990). Other explanations for the incongruence in results between our study and previous studies can be attributed to the use of different snail species, and the use of diverse geographic regions of study. Different snail species might have different growth patterns, and varying geographic regions might experience differential climate and water current speed distributions, which might affect shell growth.

In addition, our results indicated no significant relationship between shell shape and current speed (Figure 7), disagreeing with our prediction that snails in high current environments would have more pointed shell shapes. The results disagreed with the findings of Vermeij (1993), which suggested that snails in areas of high flow have more pointed shells due to hydrodynamic selective pressures and energy efficiency. The results also disagreed with the findings of Trussell (1997), which indicated that short and wide shells are more advantageous and selected for because they reduce drag in high current environments. Other selective pressures, such as population density, predator density and biomass availability, might be establishing a gradient of variation in shell shape proportion (Kemp and Bertness 1984, Crowl and Schnell 1990). The incongruence in the results between our study and previous studies might be attributed to the use of different snail species; growth rates might vary between snail species. Also, differences in snail shell shape might be due to geographic variations among studied streams, such as water current speed distribution within a stream and climate.

Possible errors might have occurred during data collection. There might have been bias for larger sized snails during collection from the streams; however, similar bias would have occurred at all sampled sites. Additionally, the sites sampled were chosen by availability of snails within the streams, limiting the variability in current speed. Snails were collected over a week of time and differences in weather might have affected current flow and snail distribution within the streams. Despite possible sources of error, it was unlikely the results were significantly affected.

In conclusion, we found that current speed is an important selective force on snail shell thickness; shell size and shape were not dependent on current speed, but other selective forces, such as predation, population density and biomass availability, might be acting on them, creating a phenotypic gradient of variation along a different cline of selective pressure (Kemp and Bertness 1984, Crowl and Schnell 1990). Based on our results, which indicated a gradient of shell thickness co-occurring with an environmental gradient of stream current strength, we predicted that either individual snails are adapting to their environment through phenotypic plasticity, or an ecotype gradient has been established within the species. Future research should include the use of molecular markers to focus on the heritability of morphological traits such as thickness, as well as the genetic differences among snails living in streams with varying current speeds. In addition, cross fostering experiments on snails, where snails originating in one current environment are reared in a second current environment, could indicate whether differences in thickness can be attributed to genetic or environmental effects.

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FIGURES AND TABLES

Figure 1: Our two study sites were located 13.1 km apart in Northern Michigan (A): Wycamp Creek off Wycamp Road near Cross Village, Michigan (B) and Little Carp River on Munger Road in Bliss, Michigan (C).

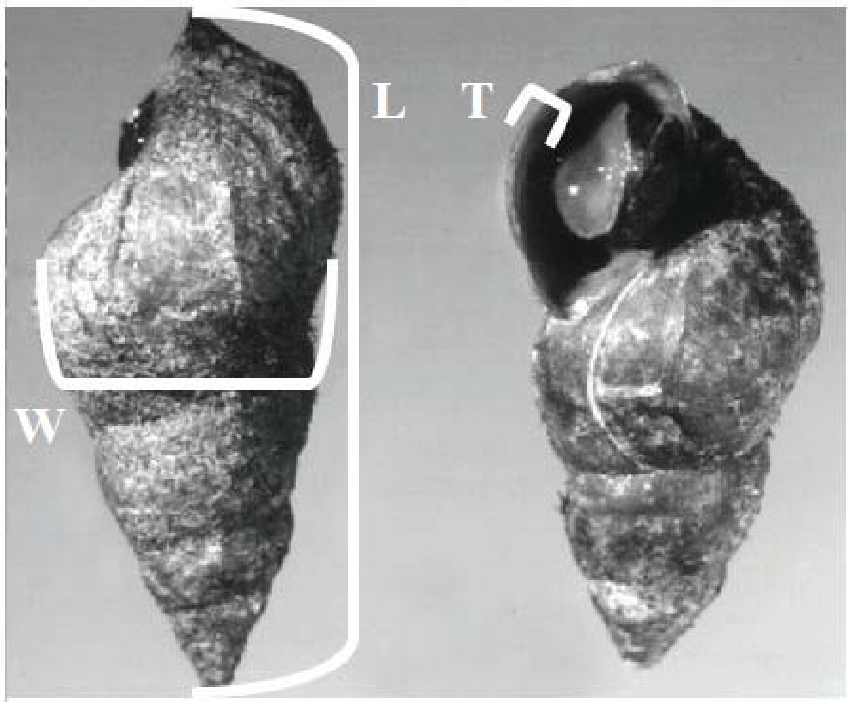

Figure 2: We measured the length (L), width at the widest point (W) and thickness at the aperture (T) of the snail shell.

Table 1: Abiotic factors measured at Little Carp River and Wycamp Creek. The results for each factor between the streams are similar, with the exception of conductivity which was 49.6 µS greater in Little Carp River.

Factor	**Little Carp River**	**Wycamp Creek**
Calcium ion conectration (mM)	1.4	1.7
pH	7.68	7.61
Dissolved oxygen (%)	39.2	40.1
Conductivity (µS)	286.2	236.8
Temperature (^{o}C)	22.2	27.2

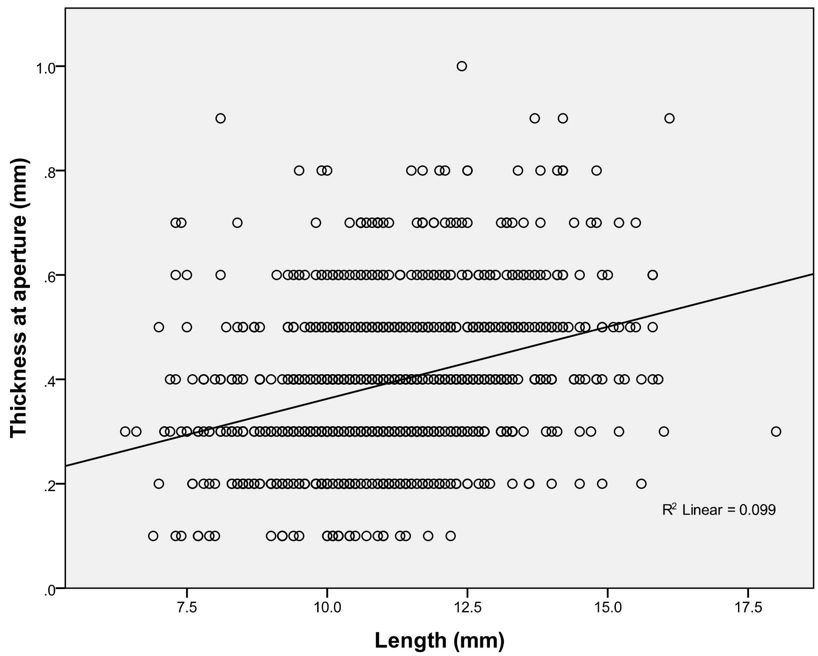

Figure 3: There was significant relationship between shell thickness at the aperture and shell length measured at each site (linear regression, R^2=.099, N=900, p=<.0001).

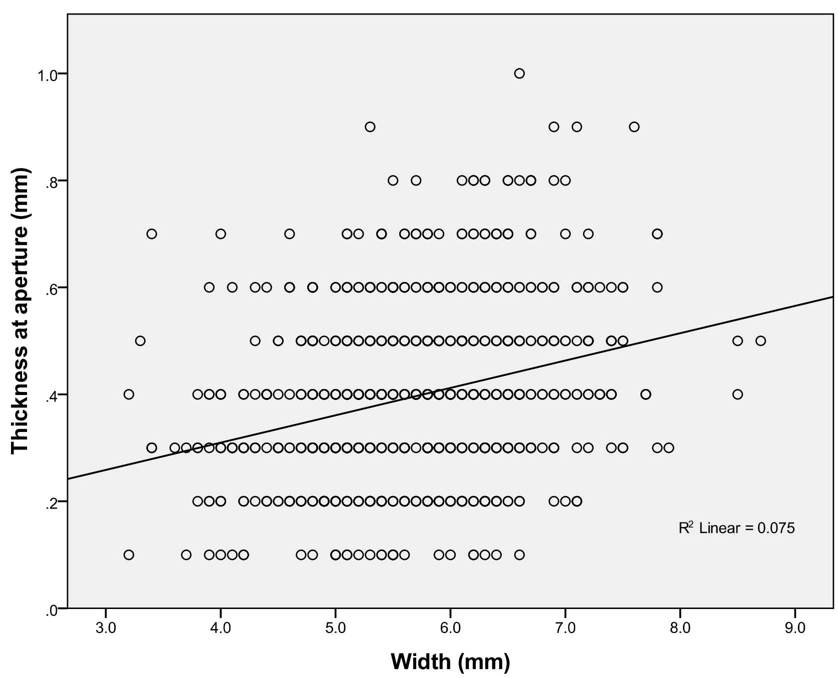

Figure 4: There was a significant relationship between shell thickness at the aperture and shell width measured at each site (linear regression, R^2=.075, N=900, p<.0001).

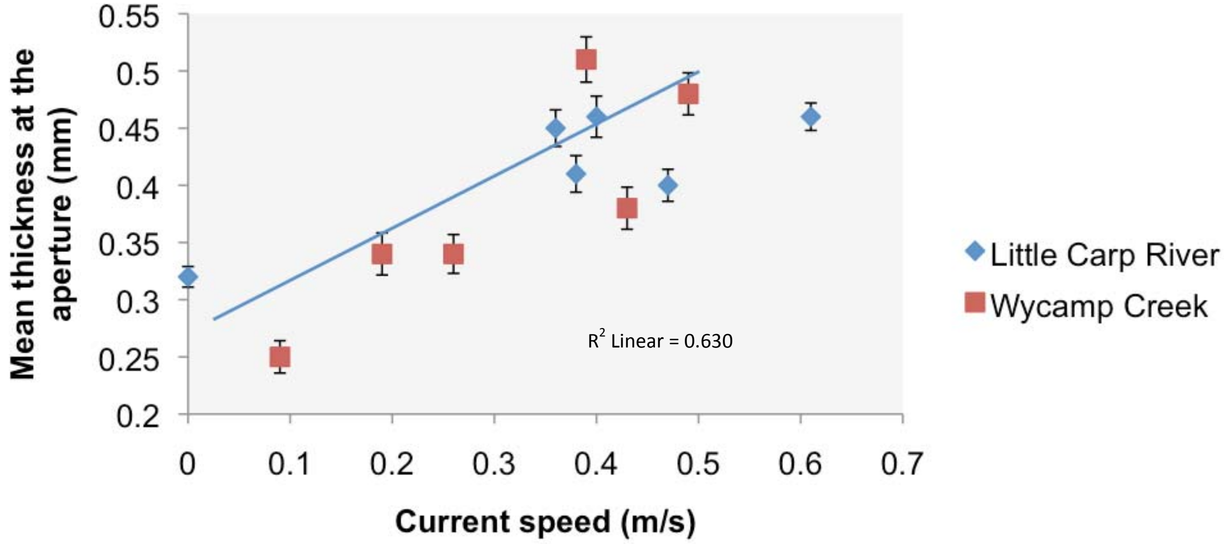

Figure 5: Mean (±SE) shell size of snails as a function of current speed at 12 locations (N=50 for Little Carp River, N=100 for Wycamp Creek). As current speed increases, shell thickness at the aperture also significantly increased (linear regression, R^2=.63, N=12, p=.002).

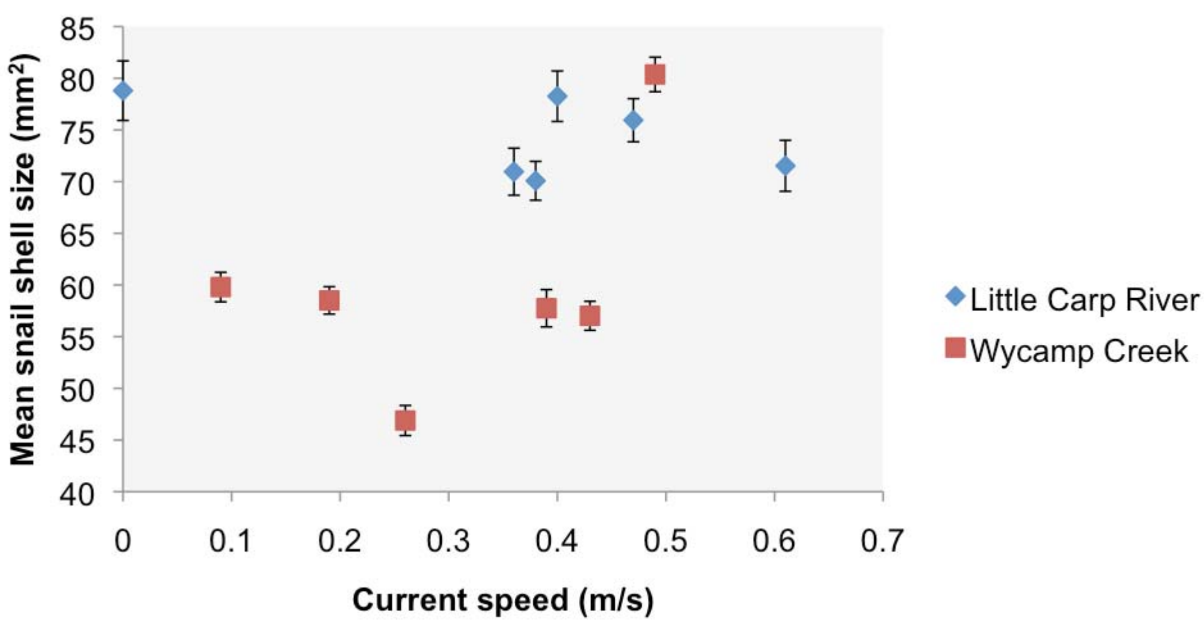

Figure 6: Mean (±SE) shell size of snails as a function of current speed at 12 locations (N=50 for Little Carp River, N=100 for Wycamp Creek). There was no significant relationship between mean shell size and current speed (linear regression, R^2=.05, N=12, p=.483).

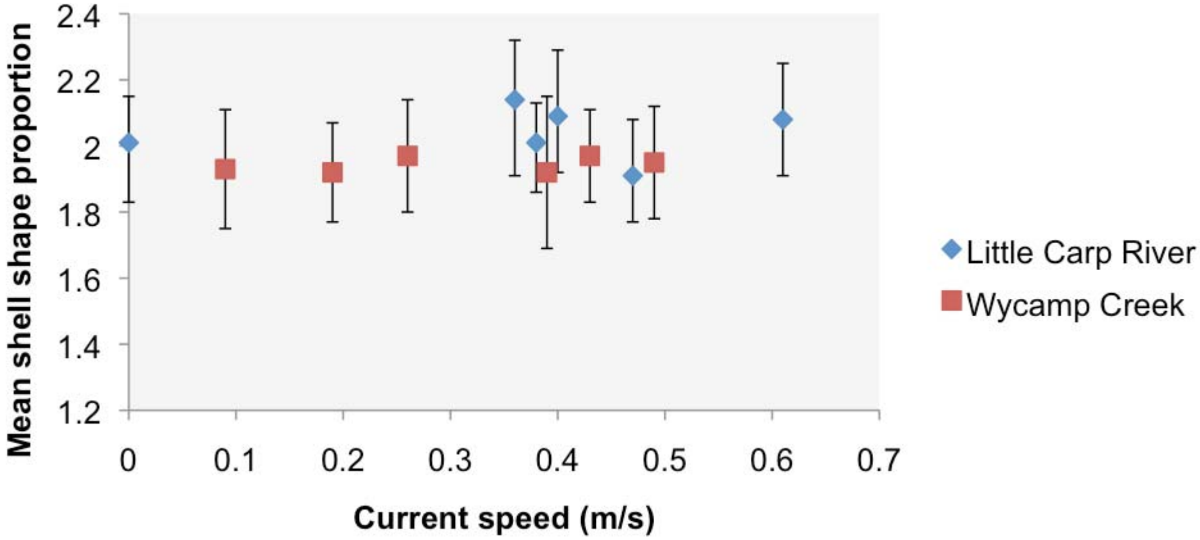

Figure 7: Mean (±SE) shell size of snails as a function of current speed at 12 locations (N=50 for Little Carp River, N=100 for Wycamp Creek). There was no significant relationship between shell shape and current speed (linear regression, R^2=.048, N=12, p=.493).