The effects of current and habitat on the shell morphology of the freshwater snail, *Elimia livescens,* in Northern Michigan streams

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ABSTRACT

In this study, I determined the effect of water current speed and habitat (riffle versus pool) on the shell morphology of the freshwater snail, *Elimia livescens*, in Northern Michigan streams. I predicted that snails in riffle habitats and areas of high current would have larger, thicker shells compared to shells of pools and low current areas. In addition, I predicted shells in riffles and high current areas would be narrower in shape. I measured snails from areas of pool and riffle habitats with different current speeds in Little Carp River near Bliss, Michigan and Wycamp Creek near Cross Village, Michigan. After measuring length, width and thickness of the shell, I calculated a size index and a shell shape proportion index. The results indicated there was no significant relationship between shell shape and habitat or current speed, disagreeing with my predictions. In addition, there was no significant relationship between shell size and habitat or current speed, also disagreeing with my predictions. There was a significant relationship between shell thickness and both habitat and current speed, agreeing with my predictions. In conclusion, snails in high current or riffle habitats are thicker than snails in low current or pool areas. Abiotic factors, such as water current, have an important effect on morphological traits of snail shells.

INTRODUCTION

Throughout the world, the dynamic environments of organisms have led to adaptations that allow survival in the harshest conditions. Within each environment, natural selection favors morphological traits that benefit organisms, increasing their fitness within particular populations and leading to higher frequencies of the traits within those populations. Both biotic factors and abiotic factors can produce selective pressures that can affect the morphology of organisms. Crowl and Schnell (1990) determined that biotic factors, such as levels of predation and availability of biomass, are most influential in the shell morphology of freshwater snails. In addition, Kemp and Bertness (1984) determined that population density also has an effect on shell morphology. Despite the focus on biotic factors, many other previous studies have indicated the importance of abiotic factors as selective pressures, such as habitat (pool versus riffle) and speed of water flow, on shell morphology (size, shape and thickness of the shell) (Raffaelli 1978, Hunter 1989, Crowl and Schnell 1990, Vermeij 1993, Johnson and Brown 1997, Trussell 1997, DeWitt et al. 1998, Rundle et al. 2004, Glass and Darby 2008, Minton et al. 2008).

Previous studies indicate that shell size is affected by current speed (Johnson and Brown 1997, Trussell 1997, Minton et al. 2008). According to Trussell's (1997) results, snails have larger shells in stream pools and smaller shells in riffle areas, and this difference is more exaggerated in conditions of increasing water flow, such that snails had even smaller shells in areas of higher current. Johnson and Brown (1997) also demonstrated that current affects snail shell size, but in contrast to Trussell's findings, their results indicated a positive direct relationship between shell size and current strength. In addition, Minton et al. (2008) found that larger snails have larger feet and therefore have a lower risk of dislodgement from their substrate, such that snails with larger feet will be more capable of maintaining niches within high current conditions. In addition, Minton et al. (2008) found similar morphological differences between snails in other areas of variable habitat and current strength, including lotic versus lentic environments, as well as upstream versus downstream environments.

In addition to shell size, current has also been shown to affect other traits of shell morphology, such as shell shape (Vermeij 1993, Trussell 1997). According to Vermeij (1993), smaller shells with sharper points in high flow riffles are more energetically favorable and selected for because of hydrodynamics that create a laminar flow of water.

In contrast to Vermeij's results, Trussell (1997) found that snails in higher current, wave exposed environments will have globular shaped shells in order to reduce drag. According to Raffaelli (1978), current and habitat also affect the thickness of snail shells. In areas of high current speed, where the risk of shell injury due to dislodgement or crushing by stones is higher, shells have been found to be thicker (Raffaelli 1978).

In addition to water current, calcium levels affect snail shell morphology; calcium levels in the environment act as limiting factors and selective pressures on snail shell morphology (Rundle et al. 2004). Higher levels of calcium allow snails to build thicker shells to protect against predation; in the presence of predator chemical cues and a high availability of calcium, a snail's shell is physically altered, becoming thicker and developing a narrower aperture (DeWitt et al. 1999, Rundle et al. 2004). Although snails primarily intake calcium from their food, a portion of the snail shell calcium is derived from the water column (Glass and Darby 2008), and water column calcium levels are directly related to pH level (Hunter 1989). In the presence of low pH levels (and subsequently low calcium concentrations), snail shells are more prone to erosion; however, low pH does not limit calcium uptake, and in experimental manipulations of calcium levels at fixed low pH, high levels of calcium have been shown to repair the erosion, indicating that calcium levels and pH are both important factors in snail shell morphology (Glass and Darby 2008).

In this study, I determined how water current and habitat (riffle versus pool) in Northern Michigan streams affect shell morphology of the freshwater snail, *Elimia livescens*. Based on the previous findings of Johnson and Brown (1997) and Minton et al. (2008), I predicted that snails in areas of higher current speed and in riffle habitats have larger shells in order to resist strong current flow. In addition, based on Raffaelli's (1978) findings of differential shell thickness in areas of varying current speeds, I predicted that snails in different habitats and current speeds to have different shell morphology; in riffles and high current areas, I expected the shells to be thicker in order to resist shell damage. Based on Vermeij's (1993) findings that current affects shell shape, I also predicted that snails in stream riffles and high current areas have more streamlined, narrow shells to counter the effect of the stronger current and laminar flow.

METHODS

I 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. I 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, I collected snails and measured current at six sites of varying current speeds, of roughly 8-16 m^2 in area. To measure current (m/s), I determined the time it took an orange to travel 1 meter downstream. I determined the sites within the streams by snail density and current speed. Using glass bottomed buckets, I 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, I measured three features with digital calipers: length, width at the widest point and thickness of shell at its aperture (Figure 2). I 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.

A t-test was used to compare the mean current speeds between the streams. To determine the significance of shell size, shell thickness and shell shape proportion versus current strength in riffles and pools of streams, two-way analyses of variance (ANOVA) were used. Linear regressions were used to establish the relationship of shell size, shell thickness and shell shape proportion with current speed.

RESULTS

The current levels between the streams were not statistically significant (t-test t=-.587, df=10, p=.570). In addition, the abiotic factors measured were similar in value, with the exception of conductivity, which was 49.6 µS higher in Little Carp River than Wycamp Creek (Table 1). Although both streams indicate similar relationships between shell size and thickness with habitat, shell size, thickness at the aperture and shape proportion were all significantly higher in Little Carp River than in Wycamp Creek (Table 2; Figure 3; Figure 5; Figure 7).

Snail shell thickness was significantly different between streams; the snails in Little Carp River had significantly thicker shells than those in Wycamp Creek (Figure 3; Table 2). Although the streams were significantly different, there was no interaction between stream and habitat (Table 2). In both streams, mean thickness at the shell aperture was significantly higher in riffle habitats than in pools (Figure 3; Table 2). In addition to habitat, shell thickness was significantly correlated with current speed (linear regression R^2=.63, df=11, p=.002). There was a positive direct relationship between current speed and shell thickness at the aperture and 63 percent of the variation in shell thickness is explained by current speed (Figure 4).

Snail shell size was significantly different between streams; the snails in Little Carp River had significantly larger shells than those in Wycamp Creek (Table 2; Figure 5). Although the streams were significantly different, there was no interaction between stream and habitat (Table 2). In both streams, the mean shell size was not significantly different in pool habitats versus riffles (Table 2). Also, there was no significant relationship between shell size and current speed (linear regression R^2=.05, df=11, p=.483; Figure 6).

The shell shape proportion was significantly different between the streams, and there was a significant interaction between the stream and habitat (Table 2); snails in Little Carp River had higher shell shape proportions in pools, whereas Wycamp Creek had higher shell shape proportion in Wycamp Creek (Figure 7). The shell shape proportion between riffles and pools was not significantly different (Table 2). In addition, there was no significant relationship between shell shape proportion and current speed (linear regression R^2=.048, df=11, p=.493; Figure 8).

DISCUSSION

Based on my results, the streams were not statistically different in current speed. In addition, the abiotic factors, except conductivity, were similar in both streams, including calcium concentration, indicating that differences in shell morphology were not influenced by calcium or other abiotic factors. The similarity of current and abiotic factors indicated that the streams can be considered replicates when analyzing current speed and shell morphology.

The difference in overall shell shape, thickness and size between the two streams can be attributed to the difference in conductivity levels between the streams; the conductivity of Little Carp River was 49.6 µS greater than that of Wycamp Creek (Table 1). Higher conductivity values indicate a higher availability of algal biomass and less competition among snails for nutrients; this greater availability of nutrients in Little Carp River would cause the snail shells to be larger in all aspects measured (Crowl and Schnell 1997, Chetelat et al. 1999). Another factor that may influence the competition for algal biomass and shell morphology is population density (Kemp and Bertness 1984); Wycamp Creek had a higher snail population density, which might have increased competition among snails and therefore decreased overall morphology.

Based on my results, shell thickness varied significantly with habitat; shell thickness also varied significantly with current speed, indicating that current speed is an important difference between riffle and pool habitats. Snails with thicker shells predominated in riffle habitats with high current speeds, while snails with thinner shells were more commonly found in pool habitats with low current speeds (Figure 3; Figure 4). These results supported my hypotheses. In addition, my findings were consistent with those of Raffaelli (1978), which indicated that snails in areas of higher current have thicker shells in order to resist shell damage and crushing if dislodged from their substrate. In previous studies, it was found that shell thickness was also affected by predation; Trussell's (1997) results indicated that shells are thicker in pools due to the higher density of predators. My results were inconsistent with the findings of Trussell (1997), indicating that current speed has a stronger influence on snail shell morphology than predation.

My results demonstrated that shell size was not significantly different in either stream habitat or in areas of different current speeds. My findings were inconsistent with previous findings of Minton et al. (2008), which suggested that snails with larger shells are found in areas of high current because they have larger feet and a better ability to resist dislodgement. In addition, my findings were inconsistent with Johnson and Brown (1997) and Trussell (1997) whose studies indicated the existence of a relationship between current and shell size, although Trussell's (1997) found an inverse relationship while Johnson and Brown's (1997) indicated a positive direct relationship. Results of previous studies might be incongruent with the results of this study due to the species of snail studied or regional effects on snail shell morphology. The results indicated that another selective pressure, such as predation or biomass availability, might be acting on shell size (Crowl and Schnell 1990).

Snail shell shape was not significantly related to stream habitat or current speed. There was a significant difference between the interactions of each stream with the habitats in relation to shell shape (Table 2): in Little Carp River, snails in pool habitats had higher shell shape proportions; whereas, in Wycamp Creek, snails in riffle habitats had higher shell shape proportions (Figure 5). This result did not agree with my hypothesis that snails with more streamline, narrower shells (higher shell shape proportion) would inhabit riffles, whereas, snails with shorter, fatter shells would inhabit pools due to the effect of energy efficiency and hydrodynamic pressures. The results were also inconsistent with the findings of Vermeij (1993) which suggested that shells with sharper points are more energetically favorable in high current riffles because of hydrodynamics and laminar flow, as well as with the findings of Trussell (1997), which indicated that snail shells are more globular shaped in high current areas in order to reduce drag. As with shell size, selective forces other than habitat and current speed might be acting on shell shape. Population density might affect shell shape through competition for resources and space; according to Kemp and Bertness (1984), snails in areas of high population density may have narrower shells than those in low population density. Additionally, predation or biomass availability may be affecting the shell shape (Crowl and Schnell 1990).

Possible errors might have affected my results. When collecting snails, there might have been biased selection for snails with larger shells; however, this would have affected all results equally. In addition, the data was collected over a week of time and weather might have affected biomass availability, current speed and snail distribution. It is unlikely that these errors affected the significance of the results.

In conclusion, snail shell morphology is affected by abiotic factors. Shell thickness has a positive direct relationship with current speed and thicker shells are more likely to be found in riffle habitats in order to reduce shell injury and risk of dislodgement. Other morphological factors, shell size and shape, were not affected by current speed or habitat, but may be influenced by a variety of both biotic and abiotic factors, including population density, competition, predation, conductivity and biomass availability (Kemp and Bertness 1984, Crowl and Schnell 1990, Chetelat et al. 1999). Future work should focus on the interaction of other factors such as predation, population density, competition, biomass and conductivity, and how these factors affect snail shell morphology.

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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).

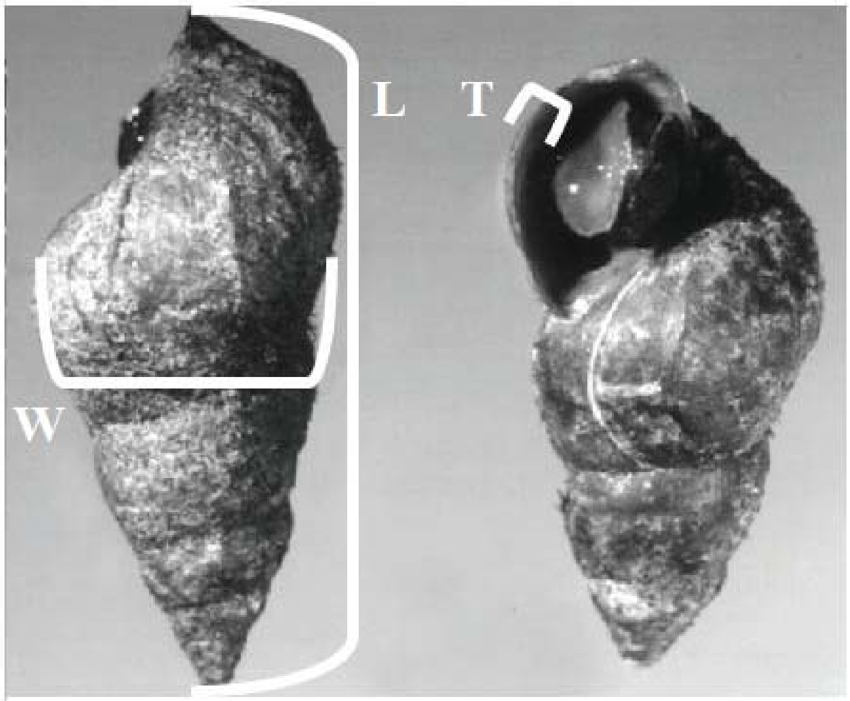

Figure 2: We measured the length (L), width at the widest point (W) and thickness at the aperture (T) of the snail shell.

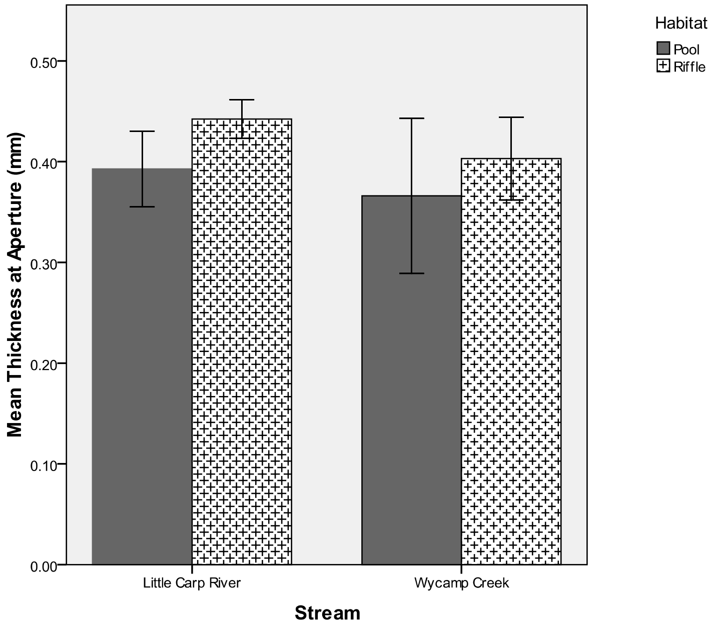

Figure 3: Mean shell thickness at the aperture in pools and riffles of Little Carp River and Wycamp Creek. Mean thickness of shells was significantly greater for Little Carp River than for Wycamp Creek; however, both streams demonstrated that snail shell thickness was significantly different between riffle and pool habitats (Table 2).

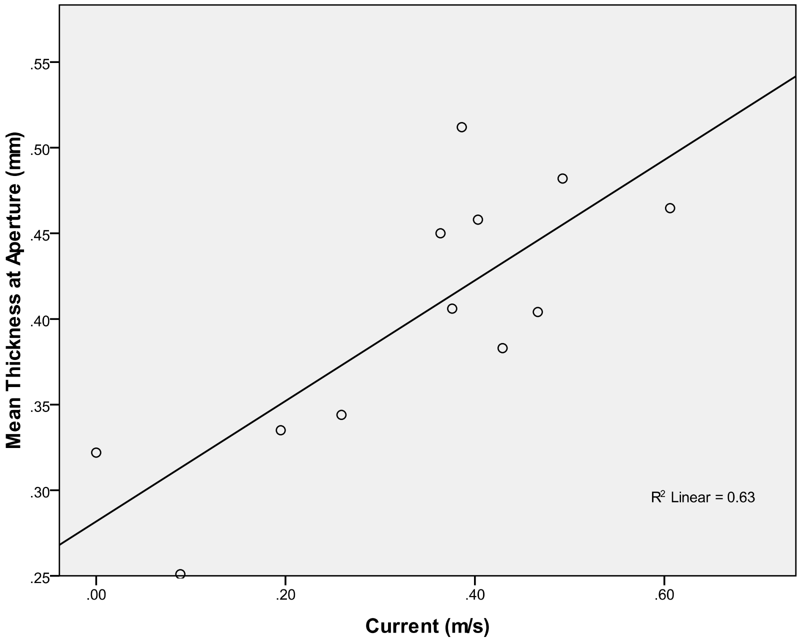

Figure 4: Relationship between mean shell thickness and current speed in pools and riffles in Little Carp River and Wycamp Creek. As current speed increases, shell thickness at the aperture also increases (R^2=.63, df=11, p=.002).

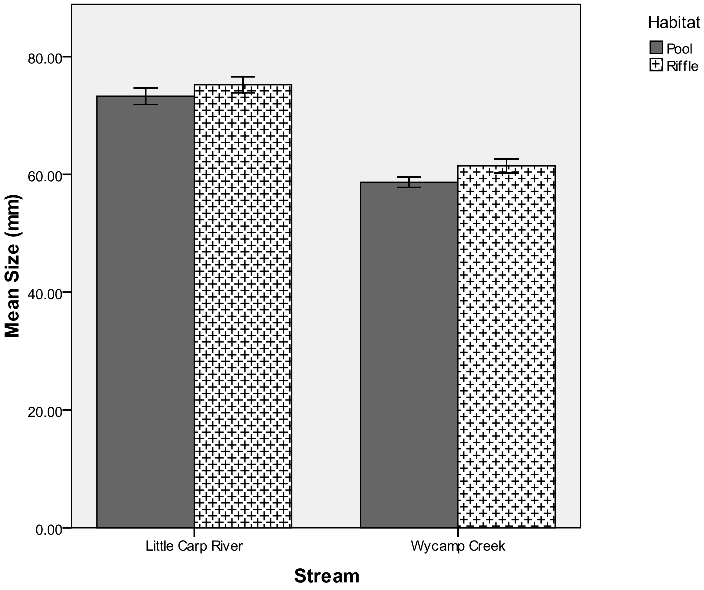

Figure 5: Mean shell size in pools and riffles of Little Carp River and Wycamp Creek. Mean thickness of shells was significantly greater for Little Carp River than for Wycamp Creek; however, both streams demonstrated that snail shell size was not significantly different between riffle and pool habitats (Table 2).

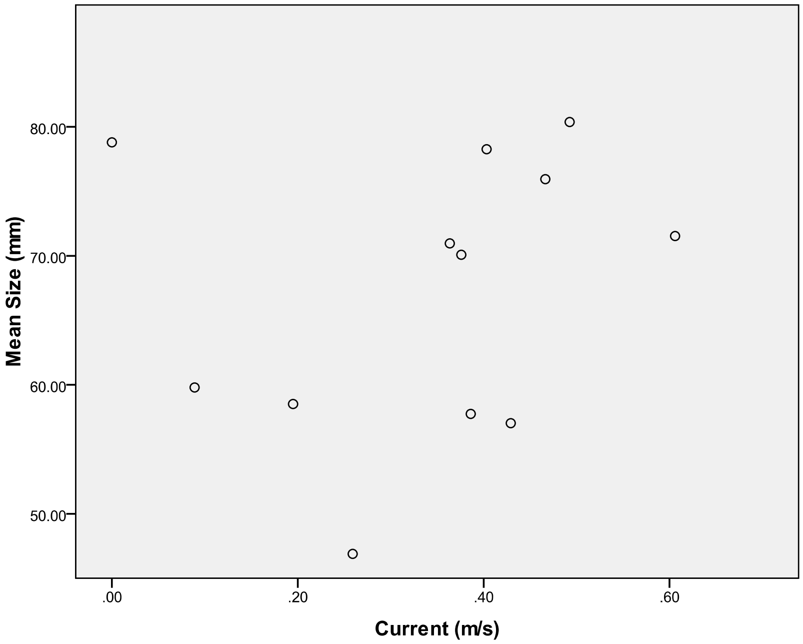

Figure 6: Mean shell size and current speed in pools and riffles in Little Carp River and Wycamp Creek are not significantly correlated (R^2=.05, df=11, p=.483).

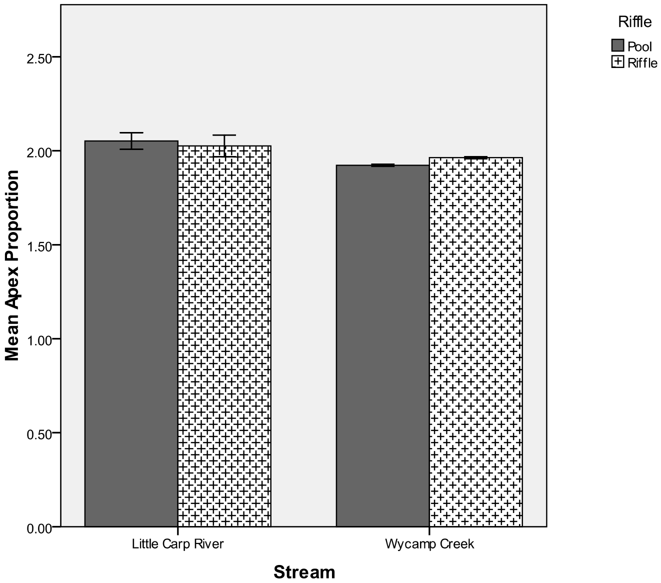

Figure 7: Mean shell shape proportion in pools and riffles of Little Carp River and Wycamp Creek. Mean shell shape proportion of shells was significantly greater for Little Carp River than for Wycamp Creek; in addition, both streams demonstrated that snail shell shape proportion was significantly different between riffle and pool habitats (Table 2).

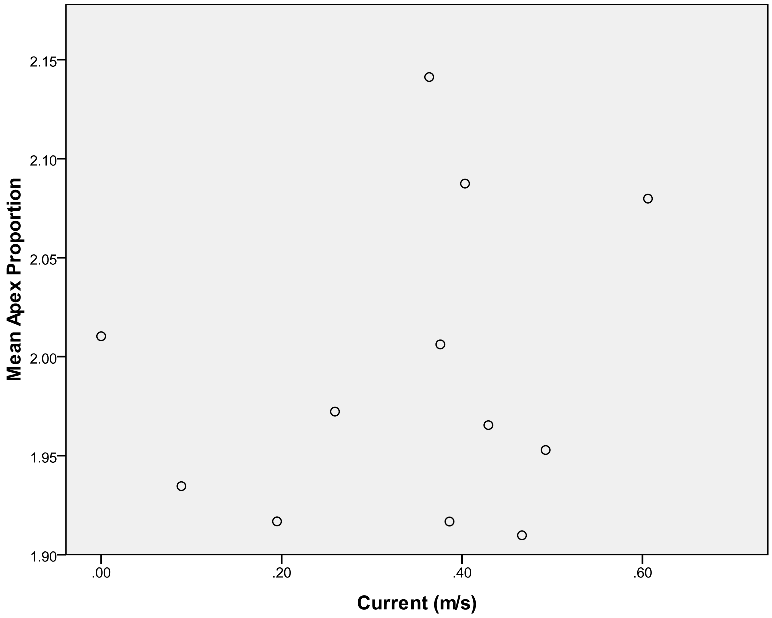

Figure 8: Mean shell shape proportion and current speed in pools and riffles in Little Carp River and Wycamp Creek are not significantly correlated (R^2=.048, df=11, p=.493).

Table 1: Abiotic factors (calcium ion concentration, pH, dissolved oxygen, conductivity and temperature) 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 higher 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 (°C)	22.2	27.2

Table 2: Statistics (F, df and p-values) from Two-Way ANOVAs, comparing the streams, the habitats and the interaction of stream and habitat for three variables: size, apex proportion and thickness at the aperture.

Size			
	F	df	p
Stream	127.787	1,896	>.001
Habitat	3.48	1,896	0.062
Stream*Habitat	0.103	1,896	0.748
Apex Proportion			
	F	df	p
Stream	59.703	1,896	<.001
Habitat	0.361	1,896	0.548
Stream*Habitat	7.084	1,896	0.008
Thickness at Aperture			
	F	df	p
Stream	9.006	1,896	0.003
Habitat	15.491	1,896	<.001
Stream*Habitat	0.346	1,896	0.557