

The effects of the northern clearwater crayfish, *Orconectes propinquus*, on early and late successional leaf litter decomposition from a northern temperate stream in northern Michigan and a tropical stream in the Puerto Rican rainforest

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ABSTRACT

Decaying leaves that fall into a stream from overhanging trees provide a significant amount of allochthonous energy that is passed downstream. Shredders play a crucial role in this energy flow by tearing up decomposing leaves and sending particles downstream. Shredders can have preferences for the types of leaves they consume, and if the dynamics of the forest around a stream were changed, leaf decomposition within the stream would be effected. This study investigated whether species succession or foreign leaves had an effect on leaf decomposition by *Orconectes propinquus*. Three north temperate leaf species from Michigan, *Amelanchier arborea*, *Betula alleghaniensis*, and *Acer saccharum* representing different successional stages were studied along with three tropical species from Puerto Rico, *Schefflera morototoni*, *Cecropia schreberiana*, and *Spathodea campanulata*. Results showed that level of succession had a negative impact on rate of decomposition by *O. propinquus* for north temperate species. Tropical species *S. morotoni* and *C. schreberiana* did not show any significant decomposition by *O. propinquus*, but *S. campanulata* showed decomposition at a rate that was similar to that of *A. arborea* and *B. alleghaniensis*. To explain the preferences of *O. propinquus* it was hypothesized that leaf toughness or secondary compounds in the leaf caused the late successional and tropical species to be unappealing to the crayfish. Leaf toughness was seen to have a slight correlation to overall consumption, but there may also be a behavioral aspect of the crayfish that prevents them from consuming foreign leaves.

INTRODUCTION

A major source of energy in headwater stream systems comes from allochthonous organic matter that falls into the water from overhanging trees and vegetation (Grubbs and Cummins, 1994). This leaf matter is broken down by bacterial and fungal colonization as well as predation by aquatic invertebrates. Shredders, which are generally most abundant in headwaters of low-order streams (Graca 2001), are the first to prey on leaf material and do so by scraping and shredding leaf debris, sending smaller particles down the stream gradient to provide an energy source for collectors and grazers. The northern clearwater crayfish, *Orconectes propinquus*, is found in shallow riffle areas of freshwater streams throughout the northern temperate region of North America. *O. propinquus* is an important detritivore in stream communities, with a diet consisting of

algae and leaves from common riparian northern hardwood species (Corey 1987, Hobbes and Jass 1988).

It has been shown that shredders can discriminate among the type of leaves they choose to feed on due to leaf toughness, nutrient content, secondary compounds such as tannins, and microbial communities present in or on the leaves (Graca 2001, Campbell and Fuchshuber 1995). Early successional species put most of their energy into growth and energy production and not as much into chemical defense mechanisms. In contrast, late successional species are slower growing and have a tough texture and higher tannin content, as they put more energy into defensive mechanisms to avoid being preyed on by herbivores. It can be inferred that late successional leaves will have higher C/N and C/lignin ratios when compared to early successional leaves due to the increased tannin content and toughness quality, and this will most likely affect their rate of decomposition (personal interview, Todd Crowl). Disturbances that cause a rapid influx of leaves and growth of early successional species have been seen to affect stream system dynamics (Covich 1988). Forest succession alongside a stream may negatively affect leaf processing rates of shredders if new species of later succession begin to replace early successional species, as the main source of allochthonous input becomes species with higher C:N and C:lignin ratios that are less appealing to shredders.

In this study, three native deciduous species of northern Michigan representing different successional stages were fed to *O. propinquus* to determine which type they preferred based on their processing rates. Downy Serviceberry (*Amelanchier arborea*), a small tree or shrub often found in Aspen forests represented an early successional species. Yellow Birch (*Betula alleghaniensis*) is a mid to late successional species found

throughout the area, and may be known to carry several tannins and anti-herbivore chemicals in the leaves (personal interview, Gary Belovsky, Dan Botkin). Sugar Maple (*Acer saccharum*) is a very common late-successional hardwood and was the third north temperate species used in the study.

Leaf litter quality and chemical composition in leaves also differs by region. Tropical leaves can have higher levels of condensed tannins (Campbell and Fuchshuber 1995) as well as tougher leaves, as they are preyed on year-round by many insect herbivores and have evolved many forms of defense chemicals (personal interview, Todd Crowl). In riparian environments that are becoming substituted with exotic trees with different physical characteristics than native trees, leaf-processing dynamics from the leaf litter will be affected (Albarino and Balseiro 2002). In this study, the processing rates by *O. propinquus* of native species of the northern temperate region in Michigan's Upper Peninsula were compared along side exotic tropical species from the Luquillo Experimental Rainforest in Puerto Rico. The same three north temperate species were compared to three riparian species from Puerto Rico. *Schefflera morototoni* is a mid to late successional species that grows along tropical stream beds, *Cecropia schreberiana*, is a fast-growing early successional tropical plant and *Spathodea campanulata*, is a very fast growing and rapidly processed leaf in tropical streams (personal interview, Todd Crowl).

Studies have shown that replacement of native species by exotic species has a negative effect on leaf decomposition by shredders. This is often due to higher C:N and C:lignin ratios found in exotic leaves compared to native species (Albarino and Balseiro 2002, Mathuriau and Chauvet 2002). This series of experiments was run to see if

succession of different leaf species predicts their decomposition rate and whether tropical leaves differ from temperate leaves in the rates consumed by *O. propinquus*. A toughness analysis of the leaves used was performed in order to find any trends with leaf toughness and amount consumed. Any significance found would shed light onto leaf processing rates and the function of *O. propinquus* in northern temperate stream systems. It was predicted that *O. propinquus* would prefer the early successional *A. arborea* to the later successional *B. alleghaniensis* and *A. saccharum*. For the comparative experiments with Puerto Rican leaves, two outcomes were hypothesized—either the crayfish would follow a similar pattern of preference to the native species, preferring the early successional species to the later successional ones, or they wouldn't eat the Puerto Rican leaves at all, preferring the native temperate species to the exotic tropical species.

MATERIALS AND METHODS

Experiment 1: Decomposition of Northern Temperate Leaves

Twelve *Orconectes propinquus* crayfish were collected from a riffle area in Tenderfoot Creek on UNDERC property, Gogebic Co., Michigan. Each were randomly placed in individual 15”x 11” x 6” plastic containers each with a PVC tube, air-stone, and plastic lid with two 1 cm sized holes drilled through it. Crayfish were starved for 48 hours before adding the leaf treatments. Two crayfish that died during this period were replaced with crayfish caught in a trap on Tenderfoot Lake.

Eight leaves from each tree species, *Amelanchier arborea*, *Betula alleghaniensis*, and *Acer saccharum* were collected fresh off the branches. All leaves were cut to approximately the same size and set out on paper towels to air-dry at room temperature (20° C). An initial dry weight of each leaf was recorded before starting the experiment.

The experiment was set up in a lab with natural lighting. Twenty-four containers were lined up in two rows and a group of four containers with crayfish alternated with a group of four empty control containers (Figure 1). Each container had an air-stone and lid, and one leaf was placed in each container. Each crayfish and control treatment had four replicates for each species. The containers were filled with well water to a level of 3.5 cm. The water was kept at room temperature, which ranged from 18-22° C.

The experiment ran for 8 days with the leaves being measured every 48 hours. After 48 hours, each leaf would be removed and dried for a few hours on paper towels at room temperature and then be placed in the drying oven overnight. The dry weights were then recorded, and leaves were placed back in the containers for another 48-hour cycle. All shredded leaf pieces greater than 1 cm in diameter were weighed. When a leaf was completely consumed, it was recorded and the container was cleaned and given fresh water, and the crayfish was fed leaf particles until the end of the experiment.

Experiment 2: Decomposition of Northern Temperate Leaves vs. Tropical Leaves

Since the experiment comparing decomposition rates of tropical versus temperate leaves was run immediately after Experiment 1, the set up was similar. The three Northern temperate leaf species were collected the same way as in Experiment 1. Three species of Puerto Rican leaves, *Schefflera morotoni*, *Spathodea campanulata*, and *Cecropia schreberiana* were collected fresh from trees in the Luquillo Experimental Forest, Puerto Rico. They were placed in airtight plastic bags to minimize water loss and flown in immediately. The leaves were cut, dried and weighed in the same fashion as Experiment 1.

The same crayfish were used in this experiment, haven been given fresh water and starved for 48 hours upon completion of Experiment 1. The containers stayed exactly the same (Figure 2) with only two replicates of crayfish and control treatments to compensate for limited space and the doubled amount of leaf species tested. The methods for drying and re-weighing the leaves stayed the same from Experiment 1.

Data Analysis

To analyze the results for both experiments, the weights of each leaf recorded were converted to percentages of mass remaining. An exponential regression analysis of the log weight proportions of each treatment for each species was run using a computer statistics program (SYSTAT 10, 2000). A t-test ($p \leq 0.05$) was run to compare the k values from the exponential equations $y = xe^{-kt}$. The mean percent loss of crayfish versus control treatments were graphed for each species as well as a graph comparing crayfish decomposition alone for each species. This was found by adding the average amount decomposed by bacteria alone in the control treatments to the percent mass remaining of the crayfish treatments. To assess variation among *O. propinquus* size and amount consumed, the carapace length of each crayfish was measured using calipers, and a plot of carapace length versus percent consumed was made to see if any size trends were found.

Leaf Toughness Analysis

To find an estimate for the relative toughness of each leaf used in the experiment, a random leaf of each species was chosen and dried for approximately 24 hours at room temperature. Toughness was measured by using a model FT 01 (1 Lb x .010 Lb/ 500 gr. x 5 gr) Penetrometer from the International Ripening Co. A 1 mm diameter metal pin

was run horizontally into three random spots on the leaf, excluding any vein areas. The puncture pressure recorded on the dial was then converted to g/mm^2 . A graph of average toughness versus average percent consumed for each species was plotted to determine if there were any trends.

RESULTS

Crayfish Processing vs. Controls

In Experiment 1, *O. propinquus* processed all three species at a faster rate than decomposition by bacteria alone in the control treatments (Figure 3). A t-test was not run for the k values for each line showed clear differences (Table 1). However, in the second experiment comparing the crayfish and control processing rates of tropical species, only *S. campanulata* showed any consumption. The t-test ($p \leq 0.05$) results of the k values (Table 2) showed that *S. morototoni* had highly insignificant processing rates ($p > 0.8$, $t = 0.236$, $df = 8$) as did *C. campanulata* ($p > 0.9$, $t = 0.001$, $df = 8$). Processing rates between crayfish and control treatments for *S. campanulata* also didn't appear to be significant, but by a smaller margin than the other two species ($p = 0.08$, $t = 2.03$, $df = 8$).

Leaf Succession vs. Crayfish processing rate

For the three north temperate species studied in Experiment 1, a negative correlation was found between succession and processing rate. Figure 5A shows a significant difference in total percent consumed between *A. saccharum* (late successional) and both *A. arborea* and *B. alleghaniensis* (early and mid successional), but not much of a difference in total percent consumed between *A. arborea* and *B. alleghaniensis*. In the regression analysis (Table 1), there was a significant difference found in the rates of crayfish processing of *A. saccharum* and both *A. arborea* ($p < 0.01$, t

= 3.485, $df = 18$) and *B. alleghanensis* ($p < 0.01$, $t = 3.830$, $df = 18$). The average processing rate of *A. arborea* was faster than *B. alleghanensis* (Figure 6A), however, no significance was found between the processing rates of the two ($p > 0.35$, $t = 0.493$, $df = 18$).

No correlation between leaf succession and percent consumed was found among the tropical species studied. *S. campanulata* was consumed with the fastest rate, while the other two tropical species were hardly consumed at all (Figure 5B, Figure 6B). Regression analyses showed that the processing rate of *S. campanulata* was statistically significant from *S. morototoni* ($p < 0.01$, $t = 3.34$, $df = 8$) and *C. schreberiana* ($p < 0.01$, $t = 3.30$, $df = 8$). The crayfish processing rates of *S. morototoni* and *C. schreberiana* were not significant from each other ($p > 0.9$, $t = 0$, $df = 8$), and these were both a mid and early successional species.

Tropical vs. Temperate Leaves

Experiment 2 showed a significant difference in the processing rates of the tropical leaves compared to the crayfish processing rates of the north temperate leaves (Figure 6B). *S. campanulata* was the only Puerto Rican species that physically showed any significant consumption by crayfish (Table 2), and it was consumed in a rate that was not significant from either *A. arborea* ($p > 0.75$, $t = 0.329$, $df = 8$), *B. alleghaniensis* ($p > 0.5$, $t = 0.698$, $df = 8$) or *A. saccharum* ($p < 0.03$, $t = 2.66$, $df = 8$). *O. propinquus* consumption of *S. morototoni* was significantly different from consumption of *B. alleghaniensis* ($p < 0.01$, $t = 3.20$, $df = 8$) and *A. saccharum* ($p < 0.04$, $t = 2.68$, $df = 8$), but it was borderline insignificant to consumption rate of *A. arborea* ($p = 0.06$, $t = 2.19$, $df = 8$). The same pattern followed for *C. schreberiana* which showed significant results in

decomposition rates compared to *B. alleghaniensis* ($p < 0.01$, $t = 3.19$, $df = 8$) and *A. saccharum* ($p < 0.05$, $t = 2.30$, $df = 8$) but slightly insignificant results compared to *A. arborea* ($p = 0.06$, $t = 2.17$, $df = 8$).

Size vs. Amount Consumed

Both experiments showed no significant trends among crayfish size and amount of leaf consumed (Figure 7). For a few species, there was some upward trend in carapace length and percent consumed, but these results were not enough to base a complete analysis.

Leaf Toughness Analysis

In the first experiment, a somewhat negative correlation between leaf toughness and average percent consumed was observed (Figure 8A). However, due to a low sample size, these results were not significant enough to make any real judgments. In Experiment 2, a negative relationship between leaf toughness and percent consumed was also seen (Figure 8B), with the exception of *S. campanulata* which showed a high rate of consumption for its tough leaf exterior. Once again, due to the low sample size and variability of penetrometer readings, the toughness was merely an estimate and no significant results could be tabulated.

DISCUSSION

In the first experiment comparing early and late successional species of the northern temperate region, a correlation was found between succession and rate of decomposition. *A. saccharum*, a late successional species, had the slowest rate of consumption compared to both *A. arborea* and *B. alleghaniensis*. *A. arborea*, the early

successional species, had the fastest processing rate, although the results were not statistically significant from the processing rate of mid-successional *B. alleghaniensis*. It can be concluded from this data that there is some quality to the late successional Sugar Maple leaves that makes them unappealing to *O. propinquus*. Studies have shown that leaves with high tannin (C/N ratios) and hard texture (C/lignin ratios) have slower rates of decomposition in streams (Mathuriau and Chauvet, 2002). Toughness analysis showed that *A. saccharum* had tougher leaves than either *A. arborea* or *B. alleghaniensis*, and this could possibly be a reason. A chemical analysis of tannins in the leaves was not done, but this might also provide information that would explain *O. propinquus* preference to early and mid successional leaves.

Crayfish consumption of the tropical leaves in the second experiment did not follow a successional pattern. It was seen clearly that *O. propinquus* preferred the temperate leaves over the tropical leaves, as all three north temperate species showed consumption by crayfish, but only *S. campanulata* showed any crayfish processing out of the three tropical species studied. Both *S. morotoni* and *C. schreberiana* didn't show any significant decomposition by crayfish.

All of the tropical leaves were found to be tougher than northern temperate leaves. If *O. propinquus* prefers species that have a softer texture, it would explain why the leaves were not eaten. However, *S. campanulata* was the leaf that had the toughest texture, yet it was consumed at a rate that was not significant from the processing rates of both *A. arborea* and *B. alleghaniensis*. Being a very early successional species in the tropics, there may be some quality in the leaves that makes it very appealing to shredders. Studies with the tropical shrimp from Puerto Rico, *Xiphocaris elongata*, have shown

rapid consumption of *S. campanulata* that obliterate the leaf within the span of one hour (personal interview, Todd Crowl). However, *O. propinquus* did not follow the pattern of consumption as seen by *X. elongata* with the other Puerto Rican species. It may be simply a behavioral aspect that keeps *O. propinquus* off the tropical leaves, because they have not evolved to be able to handle tropical leaves; they reject them as foreign and will not consume them.

Many studies have shown shredder rejection of foreign or exotic species (Ablarino and Baslerio 2002, Royer, Monaghan and Minshall 1999). Neither study was able to pinpoint a specific reason to their findings; Royer, Monaghan and Minshall found C/N ratios an inaccurate indicator of decay rate. For this experiment, it may be that tropical leaves carry more tannins in their leaves as they are preyed on year round by insect herbivores (personal interview, Todd Crowl). A study of tropical and temperate leaf decomposition showed that tannin concentration was not different between the two types, but it was indicative of processing rate overall. However, it was noted that in a previous study by Stout in 1989, it was suggested that the higher levels of tannins present in tropical leaves would correlate with a slower processing rate overall. (Campbell and Fuchshuber, 1995).

Overall, the experiment showed that leaf processing rates in streams would be affected by substitution by exotic species. Tropical trees would be unable to grow in the north temperate region, but nevertheless it can be concluded that leaf processing in the north temperate region differs significantly from leaf processing in the tropics. Tropical streams receive a continuous influx of allochthonous energy from leaf litter caused by year round rain and wind disturbances. In contrast, north temperate streams receive a

large influx of leaves every fall and not as much during the summer or winter months (Covich, 1988). This may lead shredders like *O. propinquus* to act more as scavengers than primary leaf shredders. If they are not used to having leaves as a primary food source, they may easily reject leaves from species that are foreign to them.

There were several limitations to this experiment that should be noted. There were not many replicates done for each species--four for the temperate leaf studies, and only two of each for the tropical versus temperate study. This lack of replication was due to limits in time, space, and number of crayfish collected and may have led to discrepancies in results. Also, the leaves tested were not of the quality that normally falls into the streams, as mentioned previously, abscised leaves in the fall are the primary leaf litter energy source for north temperate leaves. Conditions in the lab were also not equal to conditions that are found in the streams, and variation in crayfish size may have also led to biased results, although no trends were found in crayfish size and amount consumed. Several of the crayfish molted during the time of the experiment, and because crayfish do not eat while they molt (personal interview, Todd Crowl), it may have led to results that were not entirely indicative of processing rates.

Future experiments on this question would include studying more north temperate species to determine any more correlations between succession and processing rate. A study taking place in the fall would also provide processing information on abscised leaves that would mirror natural conditions better. An investigation of C/N and C/lignin ratios might give a better idea of crayfish preference to certain species, and mixed leaf treatments would also provide valuable information on the leaf preferences of *O. propinquus*. Currently, experiments are underway in the Luquillo Experimental Forest in

Puerto Rico to study *X. elongata* response to the north temperate leaves used in this study. This data would provide a comparison between the two shredders as well as stream processing dynamics for both regions.

ACKNOWLEDGEMENTS

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AMAR CF	AMAR CF	AMAR CNTL	AMAR CNTL	BEAL CF	BEAL CF	BEAL CNTL	BEAL CNTL	ACSA CF	ACSA CF	ACSA CNTL	ACSA CNTL
AMAR CF	AMAR CF	AMAR CNTL	AMAR CNTL	BEAL CF	BEAL CF	BEAL CNTL	BEAL CNTL	ACSA CF	ACSA CF	ACSA CNTL	ACSA CNTL

Figure 1. Set up of containers. Four replicates of each species were run for each treatment with a single leaf being placed in each container. CF= crayfish, CNTL= control, AMAR= *A. arborea*, BEAL = *B. alleghaniensis*, ACSA = *A. saccharum*

ACSA CF	BEAL CF	ACSA CNTL	BEAL CNTL	AMAR CF	CESC CF	AMAR CNTL	CESC CNTL	SPCA CF	SCMO CF	SPCA CNTL	SCMO CNTL
ACSA CF	BEAL CF	ACSA CNTL	BEAL CNTL	AMAR CF	CESC CF	AMAR CNTL	CESC CNTL	SPCA CF	SCMO CF	SPCA CNTL	SCMO CNTL

Figure 2. Set up of containers in Experiment 2. Two replicates of each species were run for each treatment with a single leaf being placed in each container. CF= crayfish, CNTL= control, AMAR= *A. arborea*, BEAL= *B. alleghaniensis*, ACSA= *A. saccharum*, CESC= *C. schreberiana*, SPCA= *S. campanulata*, SCMO= *S. morotoni*

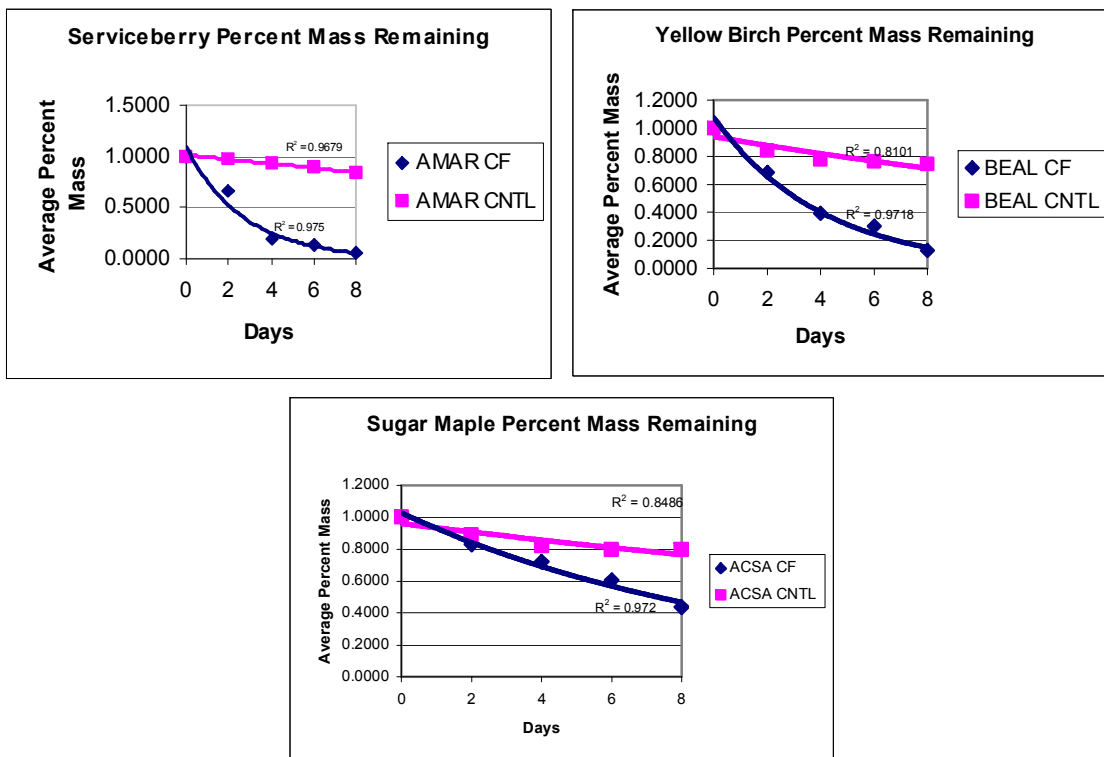


Figure 3. Plots of average percent mass lost by crayfish consumption against control treatments and exponential regression lines for north temperate species in Experiment 1. There is a greater loss in mass and rate of decomposition in crayfish treatments for all three species when compared to control treatments with bacteria alone. CF= crayfish, CNTL= control

	Regression Analysis				t-test values (p≤0.05)		ACSA
	k	Se	R ²	p	df	BEAL	
AMAR	-1.037	0.258	0.473	0.001	180.493	(p=0.35)	3.485 (p=0.01)
BEAL	-0.879	0.219	0.473	0.001	18		3.830 (p=0.01)
ASCA	-0.132	0.036	0.427	0.002	18		
AMAR CNTL	-0.023	0.001	0.934	0.0001			
BEAL CNTL	-0.035	0.004	0.789	0.0001			
ASCA CNTL	-0.029	0.004	0.773	0.0001			

Table 1. Table showing k values of the exponential regression analysis for each treatment and results of a t-test (p≤0.05) comparing crayfish treatments of each species in Experiment 1. The processing rates of *A. arborea* did not differ significantly from *B. alleghaniensis*, but significance was found in the processing rates of *A. saccharum* when compared to both *A. arborea* and *B. alleghaniensis*.

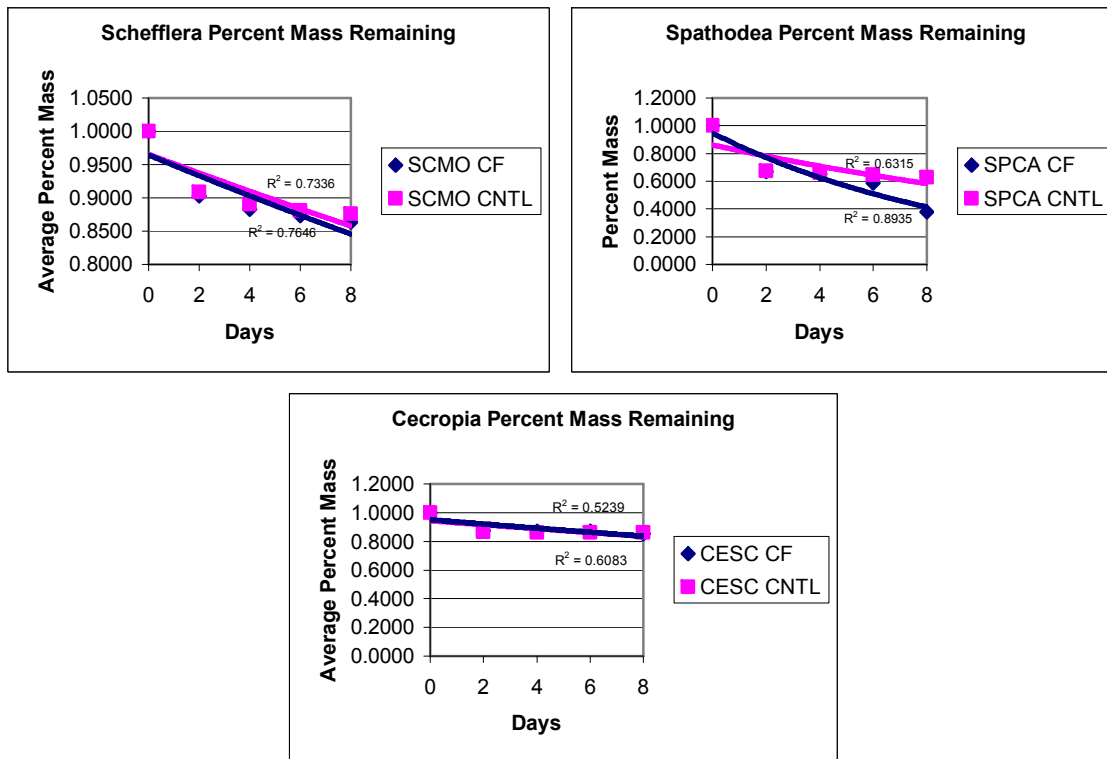
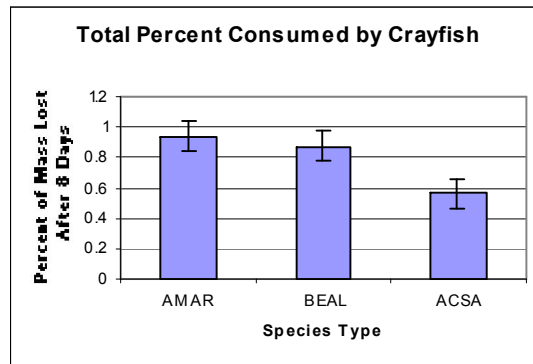


Figure 4. Plots of average percent mass lost by crayfish consumption against control treatments and exponential regression lines for tropical species in Experiment 2. Only *S. campanulata* showed any difference in processing rate over time, both *S. morotoni* and *C. schreberiana* showed little to no difference in processing rates. CF= crayfish, CNTL= control

	Regression Analysis				t-test values ($p \leq 0.05$)						
	k	se	R ²	p	n	SCMO	SPCA	CESSC	AMAR	BEAL	ACSA
SCMO	-0.016	0.003	0.764	0.001	8	0.236 (p=0.8)	3.34 (p=0.01)	0 (p=0.9)	2.19 (p=0.06)	3.30 (p=0.01)	2.68 (p=0.04)
SPCA	-0.110	0.028	0.657	0.004	8		2.03 (p=0.08)	3.30 (p=0.01)	0.329 (p=0.75)	0.698 (p=0.5)	2.66 (p=0.03)
CESSC	-0.016	0.005	0.606	0.008	8			0.141 (p=0.9)	2.17 (p=0.06)	3.19 (p=0.01)	2.30 (p=0.05)
AMAR	-0.095	0.036	0.470	0.029	8						
BEAL	-0.144	0.040	0.635	0.007	8						
ACSA	-0.034	0.006	0.779	0.001	8						
SCMO CNTL	-0.015	0.003	0.720	0.002	8						
SPCA CNTL	-0.049	0.013	0.631	0.006	8						
CESSC CNTL	-0.015	0.005	0.523	0.010	8						

Table 2. Table showing k values of the exponential regression analysis for each treatment and results of a t-test ($p \leq 0.05$) comparing crayfish treatments of each species and individual crayfish vs. control treatments of tropical species in Experiment 2. For *S. morototoni* and *C. shreberiana*, crayfish processing did not differ significantly from bacterial decomposition in control treatments. The crayfish vs. control rate test for *S. campanulata* was also not significant, but only by a slight margin of 0.03. Between the tropical leaves, the processing rates were only significant between *S. campanulata* and both *C. shreberiana* and *S. morototoni*. As for the comparisons between temperate and tropical leaves, only the rates between *S. campanulata* and both *A. arborea* and *B. alleghaniensis* were not significant. The rates between *S. morototoni* and *A. arborea* were also not significant, but only by a slight margin of 0.01.

A.



B.

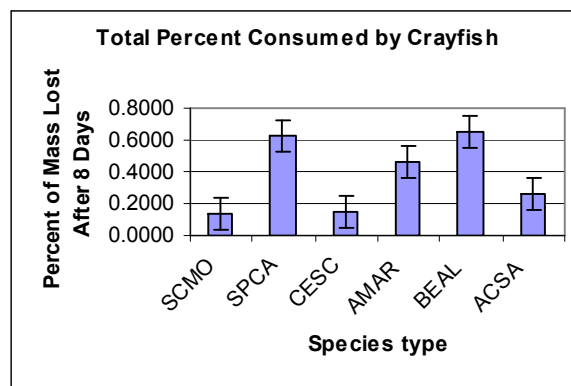
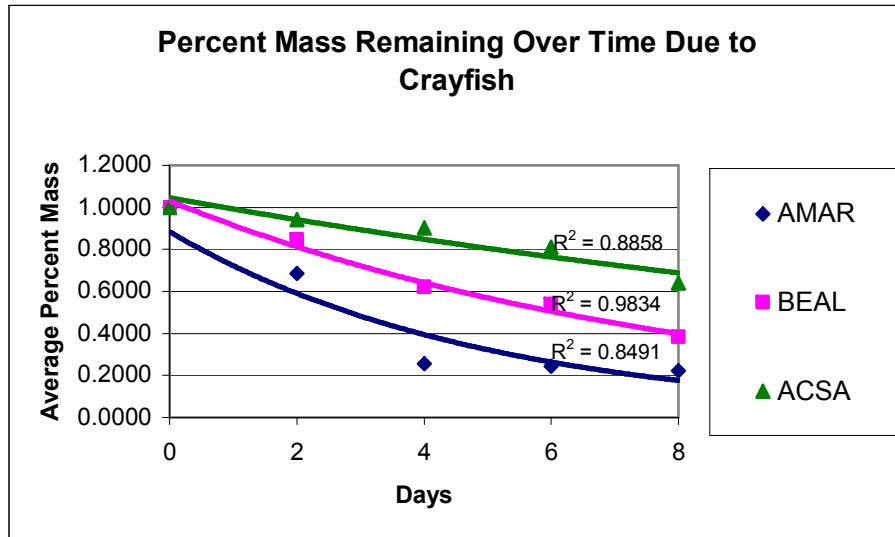


Figure 5. Average total percent consumed by of all species in crayfish treatments in Experiments 1 and 2. (A) In Experiment 1, total percent consumed of *A. saccharum* was significantly less than percent consumed by *A. arborea* and *B. alleghaniensis*. Total percent consumed by *A. arborea* and *B. alleghaniensis* did not significantly differ from each other, however. (B) In Experiment 2, the total amounts consumed by *S. campanulata*, *A. arborea*, and *B. alleghaniensis* was significantly more than the total amounts consumed by the other three species. *S. campanulata*, *C. schreberiana*, and *A. saccharum* all did not show significant rates as neither did *S. campanulata*, *A. arborea*, and *B. alleghaniensis*.

A.



B.

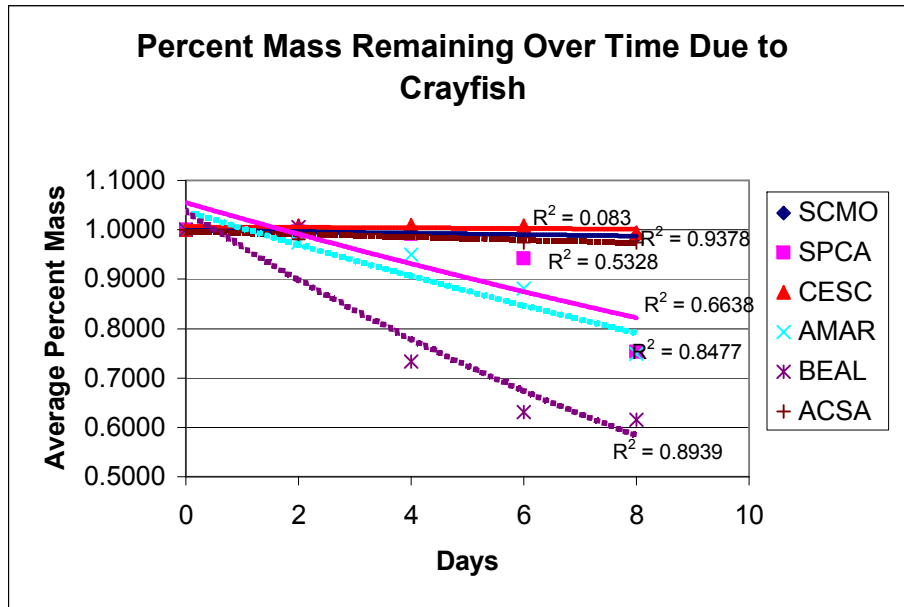
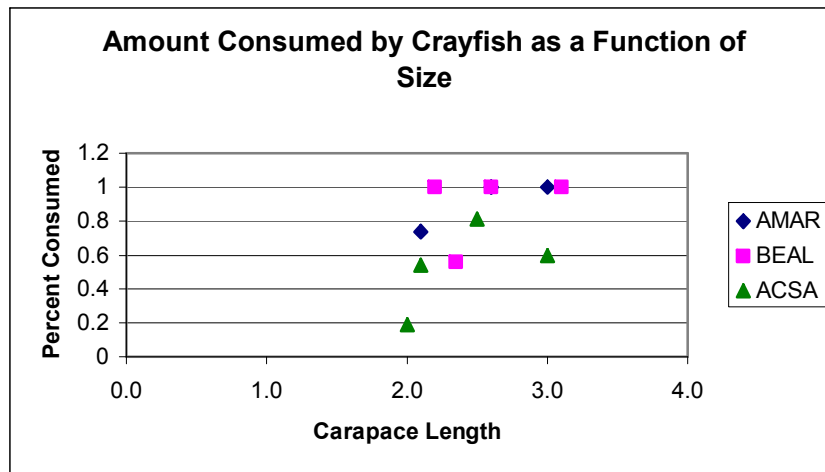


Figure 6. Graph of the average percentage consumed over time of crayfish alone for each species and exponential regression lines. (A) Experiment 1. *A. arborea* had the fastest processing rate, followed by *B. alleghaniensis*, while *A. saccharum* had the slowest processing rate of the three. (B) Experiment 2. *S. morotoni*, *C. schreberiana*, and *A. saccharum* showed the slowest processing rates of the six species studied. *B. alleghaniensis* was consumed fastest in this experiment, followed by *A. arborea* and *S. campanulata* which both had similar processing rates.

A.



B.

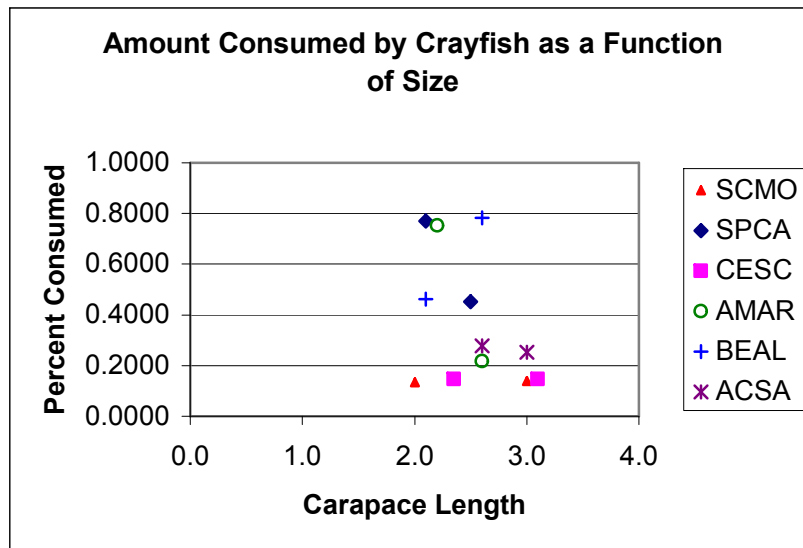
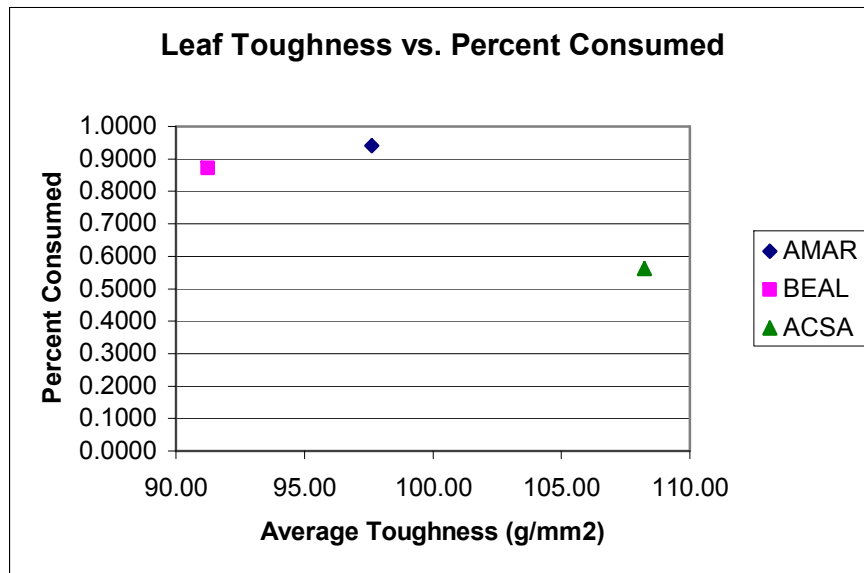


Figure 7. Scatter plot of carapace length vs. total percent consumed by crayfish. (A) Experiment 1; no significant correlations were found (B) Experiment 2; no significant correlations were found.

A.



B.

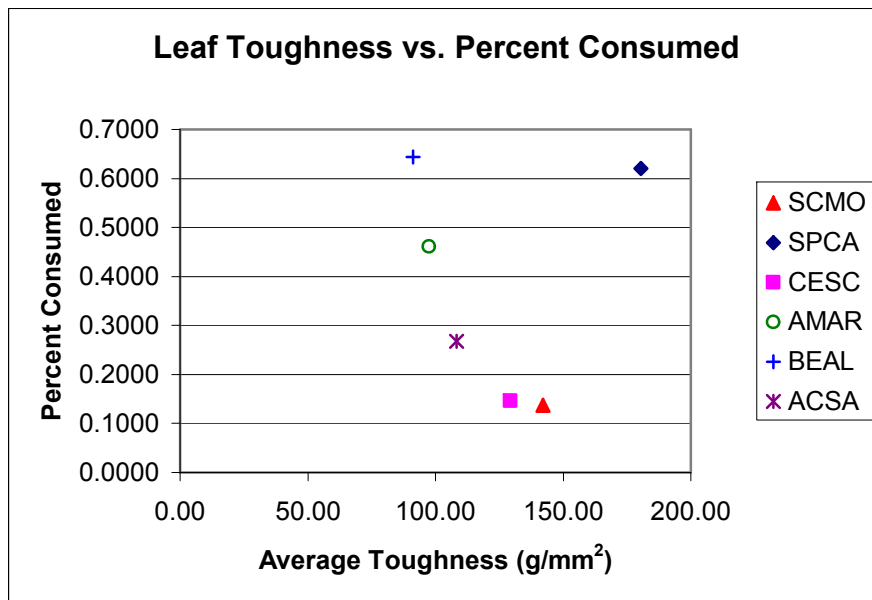


Figure 8. Graphs showing average leaf toughness for each species vs. percent consumed. (A) Experiment 1; a negative relationship is somewhat evident based on toughness and percent consumed. (B) Experiment 2; a negative relationship is also seen with the exception of *S. campanulata* which was consumed rapidly based on its tough exterior.