The Effects of Resource Dilution on Zooplankton Communities in Lake Systems

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Abstract

Resource dilution may occur when terrestrial particulate organic carbon (t-POC) washes into lake systems and is consumed by zooplankton. T-POC is a poor quality food source for zooplankton because it lacks essential nutrients and fatty acids that are physiologically necessary for these organisms. This project used a dilution series of eight mesocosms to study the effects of potential resource dilution on the species composition, growth, and reproduction of zooplankton taxa *Daphnia*, calanoid copepods, and cyclopoid copepods. This dilution series used corn flour as a proxy for naturally occurring t-POC because of its similar nutrient content and small size. The results of the experiment suggest several trends accompanying increasing resource dilution: a shift from *Daphnia* dominated zooplankton community to copepod dominated communities, an increase in average cyclopoid biomass, and a likely decrease in *Daphnia* fecundity.

Introduction

Zooplankton are a significant component of lake food webs as they link the lowest trophic level of primary producers such as phytoplankton and algae (which zooplankton consume) to the higher trophic levels occupied by planktivorous fish and other secondary consumers. For this reason, any changes in zooplankton communities due to pressures on their environment or living conditions may have ramifications throughout an entire lake ecosystem.

Zooplankton play many important ecological roles in lakes: filter-feeding zooplankton are involved in the biocontrol of algal blooms as well as the maintenance of stable fish populations (Gliwicz 1990). The ecological role of zooplankton can also be commercially significant. Because alterations in a lake's zooplankton community can result in changes in fish productivity, collapses of zooplankton communities have had devastating effects on fisheries (Worm et al. 2006). Conversely, professionals in the fishing industry often use zooplankton

bioindicators to identify productive fishing grounds (Goswami 1991). The ability of zooplankton communities to perform these functions and maintain lake health is dependent on many environmental factors. This project focused on the pressures exerted on zooplankton communities by modifications in zooplankton diet due to resource dilution (influxes of terrestrial carbon) in lakes.

Generally, zooplankton prefer to consume autochthonous primary producers like algae and phytoplankton for biomass carbon and other necessary nutrients. However, when organic matter such as leaves and other allochthonous terrestrial particulate organic carbon (t-POC) wash into lakes, zooplankton will also consume this food (Kankaala et al. 2010). Previous studies have demonstrated that under such conditions, t-POC can come to comprise a significant component of zooplankton diets (Cole et al. 2011). Though it is commonly consumed by zooplankton, terrestrial POC is considered a poor quality resource because it is low in physiologically essential nutrients and polyunsaturated fatty acids like eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Brett et al. 2009). This project aimed to study resource dilution in order to determine whether or not increasing relative concentrations of a poor quality carbon resource would exert an influence on the growth, fecundity, and/or species composition of zooplankton communities in lake systems.

It was expected that resource dilution by additions of t-POC to lake systems would limit energy availability for zooplankton. Previous studies have suggested that the presence of fatty acids like EPA and DHA in phytoplankton and algae is closely and positively related to the growth rate of zooplankton species like *Daphnia magna* (Gulati and DeMott 1997). Meanwhile, allochthonous t-POC often comes from higher plant sources that lack the enzymes necessary to create EPA and DHA (Brett et al. 2009). Therefore, it would be expected that the consumption of

increasing amounts of t-POC by zooplankton (like *Daphnia magna)* may decrease the energy available to them for growth and eventually their biomass. In addition, if zooplankton growth is inhibited due to nutrient limitation and dietary fatty acid deficiencies, this could lead to a decrease in zooplankton reproduction. When nutrients are limited, zooplankton are known to allocate as little energy as possible to reproductive efforts (Tessier et al.1983).

These expectations may be overly general as different zooplankton taxa may react to the pressures of resource dilution differently. These differences in response could cause shifts in the overall community composition of zooplankton in a lake system. Previous studies have shown that the zooplankton species *Daphnia rosea* exhibits low dietary selectivity (DeMott 1982). Meanwhile, it is known that copepod zooplankton like calanoids and cyclopoids exhibit greater dietary selectivity for food containing higher quality nutrients (Cowles, 1988). Thus, we expected that copepods would be more competitively fit in lake systems undergoing resource dilution. Under these conditions, copepods should be better able to pick out higher quality food (algae) and bypass the t-POC at higher rates. At the same time, it has been found that *Daphnia magna* is able to cope well with unbalanced diets and maintain its stoichiometric balance in the face of differing levels of nutrients (DeMott 1982). This may mean that *Daphnia* could be well equipped to deal with conditions of low nutrient quality and are able to maintain their abundance and biomass even under resource dilution. Because of the different ways that zooplankton species react to dietary differences, resource dilution in lakes may shift zooplankton community composition.

Thus far, the interconnectedness of pelagic food webs and the difficulty of controlling whole lake experiments have made studies of resource dilution on zooplankton communities difficult (Cole et al. 2011). This project aimed to bypass these difficulties and study the effects of

t-POC influx on the community composition, growth, and fecundity of zooplankton through a controlled mesocosm experiment. It was expected that with increasing resource dilution, copepods would become the most prevalent taxa in the zooplankton communities, that the average individual biomass of all three taxa would decrease, and that fecundity (as will be observed in egg laying *Daphnia*) will decrease.

Materials and Methods

This project examined the effects of varying levels of allochthonous terrestrial particulate carbon on zooplankton communities through the use of eight mesocosm experimental units over a four week period. Each of these 190-L mesocosms were filled with water from Tenderfoot Lake (filtered to remove unwanted POC, zooplankton, and other possible confounding elements), 32.25mg of algae cultured in the lab, and zooplankton samples collected from Raspberry Lake using vertical tows with a zooplankton net (Aquatic Research Instruments, Hope, ID). All of the zooplankton samples were collected concurrently from the same location in Raspberry Lake at a depth of 1.5 meters in order to promote the initial community homogeneity across all eight mesocosms. The dominant taxa of zooplankton present in these samples were *Daphnia*, calanoid copepods and cyclopoid copepods.

A gradient of differing concentrations of corn flour were added to these mesocosm experimental units in order to simulate the allochthonous carbon inputs that comprise the poor quality POC food that zooplankton consume in lakes. The dilutions of corn flour used were 0x, 0.5x, 1x, 5x, 10x, 25x, 50x, and 100x of algal carbon present in the mesocosms. Over the course of the four week treatment period, corn flour was added to each mesocosm three times at the concentrations given in Table 1. Each mesocosm was then covered with a screen in an attempt to exclude *Chaoborus* larvae

Corn flour was chosen for this experiment because it is high in recalcitrant carbon and low in essential nutrients (including EPA and DHA). In addition, its small particle size makes it easily consumable by zooplankton organisms. Thus, corn flour was thought to be a reliable proxy material for natural t-POC in the study of the effects of differing levels of this poor quality food on zooplankton communities.

After the four week treatment period, zooplankton were sampled from each of the mesocosms. Within each mesocosm, the proportion of each zooplankton taxa, the biomass of each zooplankton taxa, as well as proportion and abundance of *Daphnia* eggs were determined. This was done using a *Leica* microscope (Solms, Germany). Proportions were determined by counting the zooplankton individuals in each sample. The average individual biomasses were calculated by taking the lengths of 50 individuals of each taxa from each mesocosm and converting the measurements to biomass using length-weight regressions (Zooplankton Counting Procedure 2011). Photographs for zooplankton measurements were captured with *Leica* imaging software and measured using the *imageJ* measurement tool (National Institutes of Health). The total number of egg-carrying *Daphnia* and the number of eggs carried by the *Daphnia* in each mesocosm were also counted. Systat was used to run regression analysis and determine how each of the above variables changed (or failed to change) with differing levels of allochthonous carbon across the eight mesocosm treatments. Regression analyses were run at $\alpha=0.10$. In the regressions used to analyze the changing proportions of each zooplankton taxa with changing corn flour concentration the 100x mesocosm was excluded so as not to bias the data. This was done because the sample from this mesocosm only contained four zooplankton individuals and was therefore unrepresentative of the trends in question.

Results

Regression analyses revealed several trends in zooplankton taxa proportions. First, they revealed that the proportion of *Daphnia* in each mesocosm was negatively correlated with corn flour concentration ($p = 0.099$, $r^2 = 0.45$) (Figure 1). The regression of the proportion of calanoid copepods in each mesocosm versus corn flour concentration revealed no significant relationship ($p = 0.38$, $r^2 = 0.15$) (Figure 2). In contrast to these two taxa, it was found that the proportions of cyclopoid copepods were positively correlated with increasing corn flour concentrations across the mesocosms ($p = 0.04$, $r^2 = 0.57$) (Figure 3).

A series of regressions were also used to characterize the relationship between the average biomass of individuals from each taxa and changing corn flour concentrations. These analyses revealed that the average biomass of *Daphnia* individuals was not significantly correlated with changing corn flour concentrations ($p = 0.20$, $r^2 = 0.25$) (Figure 4). The average biomass of calanoid copepod individuals was likewise not found to be significantly correlated to corn flour concentration at $\alpha = 0.10$ ($p = 0.53$, $r^2 = 0.07$) (Figure 5). Unlike the *Daphnia* and calanoid copepods, the average biomass of cyclopoid copepods was significantly and positively correlated to corn flour concentrations across mesocosms ($p = 0.02$, $r^2 = 0.69$) (Figure 6). With increasing amounts of corn flour, the average mass of cyclopoid individuals increased.

The relationship between *Daphnia* fecundity and corn flour concentration was also analyzed using regression tests. Two characteristics of the *Daphnia* populations were used as measures of fecundity across the eight mesocosms: the proportion of *Daphnia* carrying eggs in each mesocosm and the average number of eggs carried by each egg-carrying *Daphnia* individual. Regression analysis revealed that the proportion of egg carrying *Daphnia* was not significantly correlated with the corn flour concentration ($p = 0.13$, $r^2 = 0.33$) (Figure 7). The average number of eggs carried by each egg-carrying *Daphnia* was likewise not significantly

correlated with the corn flour concentration in each mesocosm (Figure 8). At the same time, respective R^2 values of 0.33 and 0.35 and respective p-values of 0.13 and 0.12 for each of these tests reveal that the negative slope of both regression lines may represent actual trends.

Unfortunately, despite efforts to exclude *Chaoborus* from the samples, some were present in the mesocosms. These carnivorous zooplankton may have had some influence on community composition and average biomass.

Discussion

Through use of a corn flour dilution series, this mesocosm experiment was able to demonstrate several things about the effects of resource dilution on the zooplankton communities composed of *Daphnia*, calanoid copepods, and cyclopoid copepods. Firstly resource dilution appeared to cause a shift in zooplankton taxonomic composition from *Daphnia* to copepod dominated. Additionally, cyclopoid copepods enjoyed an increase in biomass with resource dilution, reflecting their competitive advantage under these condtions. Finally, resource dilution may have acted as a suppressor of *Daphnia* fecundity due to nutrient limitation. This research demonstrated that the phenomenon of resource dilution may exert many pressures on the dynamics of these zooplankton communities.

As corn flour concentration increased, several trends emerged regarding the proportions of each zooplankton taxa in each mesocosm. The proportion of *Daphnia* in each mesocosm was found to be significantly negatively correlated with increasing corn flour concentration. This is likely due to the low dietary selectivity of this *Daphnia* (DeMott 1982). As the proportion of low quality t-POC increases by resource dilution, *Daphnia* continue to feed as largely unselective omnivores and thus decrease in proportion due to a lower intake of nutrients. The proportion of calanoid copepods seemed to exhibit a slight positive correlation with corn flour concentration,

but this relationship was found to be statistically insignificant. Despite the pressures exerted by resource dilution, the calanoids continued to make up a roughly constant proportion of each mesocosm zooplankton community. Meanwhile, the proportion of cyclopoid copepods was positively correlated to increasing corn flour concentration. Under conditions of increasing resource dilution, it seems that the high dietary selectivity of cyclopoids allowed them to thrive relative to *Daphnia* and calanoids (Cowles et al. 1988). The differential dietary selectivity of the three zooplankton taxa examined in this study resulted in a shift from *Daphnia* dominated to copepod (especially cyclopoid) dominated zooplankton communities under simulated increases of t-POC.

This experiment also began to characterize the relationship between resource dilution and the average individual biomass of each taxa. Neither the *Daphnia* nor the calanoid taxa demonstrated a significant relationship with increasing corn flour concentration. It thus appears that resource dilution does not exert a strong negative effect on these taxa of zooplankton as expected from the limiting of nutritional resources (Brett et al. 2009). This could suggest that the growth of these zooplankton taxa are more tolerant than expected to lower levels of essential nutrients like EPA and DHA than expected or that these taxa begin to demonstrate more dietary selectivity when higher concentrations of corn flour are present. In addition, cyclopoid individual biomass increased significantly with increases in corn flour concentration. Though it may seem counterintuitive that cyclopoids were able to grow larger as the mesocosms became more inundated with low quality food sources, it is likely reflective of their competitive advantage through high dietary selectivity (Cowles et al. 1988).

The examination of egg prevalence in *Daphnia* also revealed no significant relationship with increasing corn flour concentration. However, though not statistically significant, both the

proportion of egg-carrying *Daphnia* and the average number of eggs carried by egg-carrying *Daphnia* appeared to decrease with heavier resource dilution. Further studies would be needed to discover whether or not this negative relationship between *Daphnia* and t-POC exists, but this experiment suggests that it may.

An important consideration in analyzing the data gleaned from this project is the unintended presence of *Chaoborus* in the mesocosms. *Chaoborus* are known to exert predatory pressure on small copepods (Elser et al. 1987). Thus, it is possible that the presence of *Chaoborus* could have suppressed copepod proportions or resulted in higher average individual biomass for copepods in the mesocosms.

Overall, this experiment was still able to make suggestions for the possible effects of resource dilution on zooplankton communities in lake systems. The high dietary selectivity of copepods generally made them more competitively fit in conditions of higher t-POC than *Daphnia* which were more competitively dominant with lower levels of t-POC. This could prove to be highly useful information for the bio-manipulation of zooplankton communities to promote lake health. In addition, the diminishing deposition of acid and rising temperatures associated with recent environmental changes has contributed to long term DOC increases in waters worldwide (Evans et al. 2005). These increases in DOC likely indicate a corresponding increase in inputs of terrestrial carbon, which may result in resource dilution. This indicates the possible global significance of resource dilution in the future.

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Tables

Table 1. *Corn flour treatments.* During the four week experiment, corn flour was added to each of the mesocosms in three treatments. The amounts of corn flour added in each treatment (in miligrams) are given in the table.

	0x	0.5x	1x	5x	10x	25x	50x	100x
Treatment 1	0mg	20.156mg	40.31mg	201.56mg	403.125mg	1007.81mg	2015.0mg	4030.0mg
Treatment 2	0mg	20.156mg	40.31mg	201.56mg	403.125mg	1007.81mg	2015.0mg	4030.0mg

Treatment 3	0mg	80.624mg	161.23mg	806.24mg	1612.5mg	4031.24mg	8060.0mg	16120.0mg

Figures

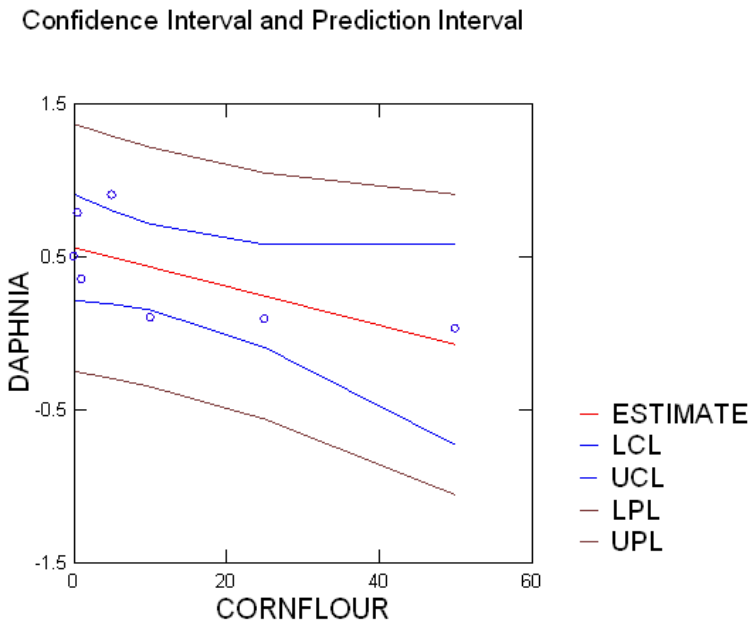

Figure 1. *Proportions of Daphnia decrease with increasing corn flour concentration.* Regression analysis revealed that at α=0.10, the proportion of *Daphnia* (shown on the y-axis) was significantly negatively correlated with the increasing concentrations of corn flour across mesocosms (p=0.099199, df = 1, F-ratio = 4.085865). The R^2 value of the regression revealed that roughly 44.9695% of the change in *Daphnia* proportion observed could be attributed to the changing corn flour concentration (Squared Multiple R = 0.449695).

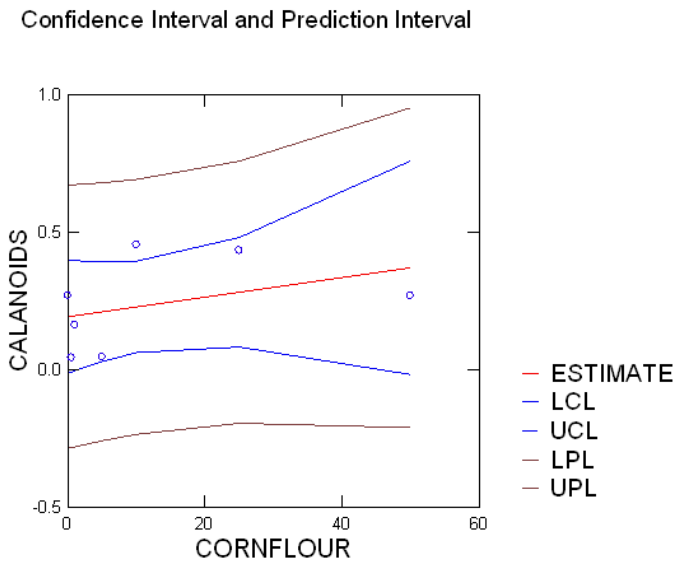

Figure 2. *Calanoid Copepod proportions reveal no significant change with increasing corn flour concentration.* Though the regression of *Calanoid* proportion (shown on the y-axis) versus corn flour concentration appears to reveal a positive relationship, this trend is not statistically significant (p = 0.382253, F-ratio = 0.916954, df = 1). Very little of the change in *Calanoid* proportion could be attributed to changes in corn flour concentration (Squared Multiple R = 0.154971).

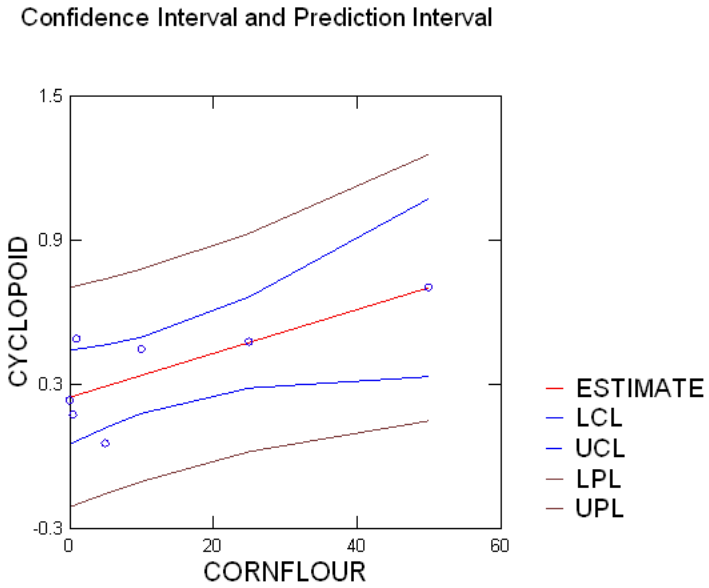

Figure 3. *Proportions of Cyclopoid Copepods are positively correlated with increasing corn flour concentration.* Regression analysis of the proportions of *Cyclopoid* zooplankton (shown on the y-axis) with increasing corn flour concentrations revealed a statistically significant positive correlation (p = 0.049695, df = 1. F-ratio = 6.633845). The R^2 value of the regression revealed that roughly 57.0219% of the change in *Cyclopoid* proportion observed could be attributed to the changing corn flour concentration (Squared Multiple R = 0.570219).

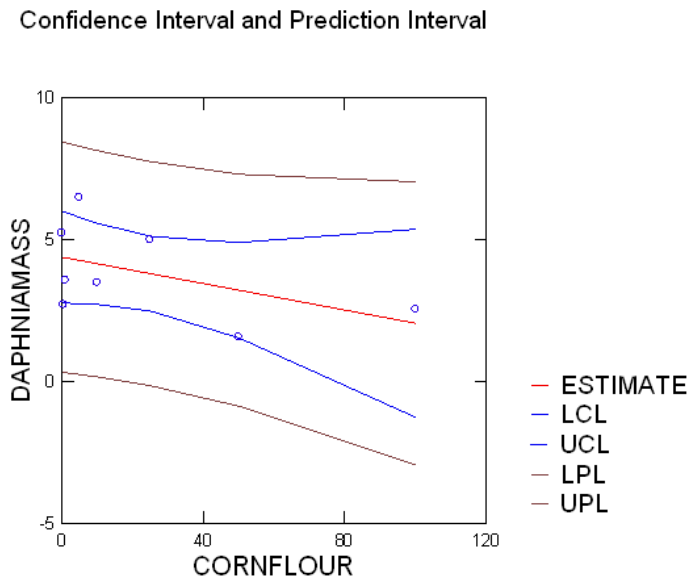

Figure 4. *Daphnia biomass is not significantly correlated with corn flour concentration.* Regression analysis revealed that there is no significant relationship between the concentration of corn flour and the average biomass of *Daphnia* zooplankton (shown in µg on the y-axis) in each mesocosm ($p = 0.203374$, $\alpha = 0.10$, df = 1, F-ratio = 2.037462, Squared Multiple R = 0.253496).

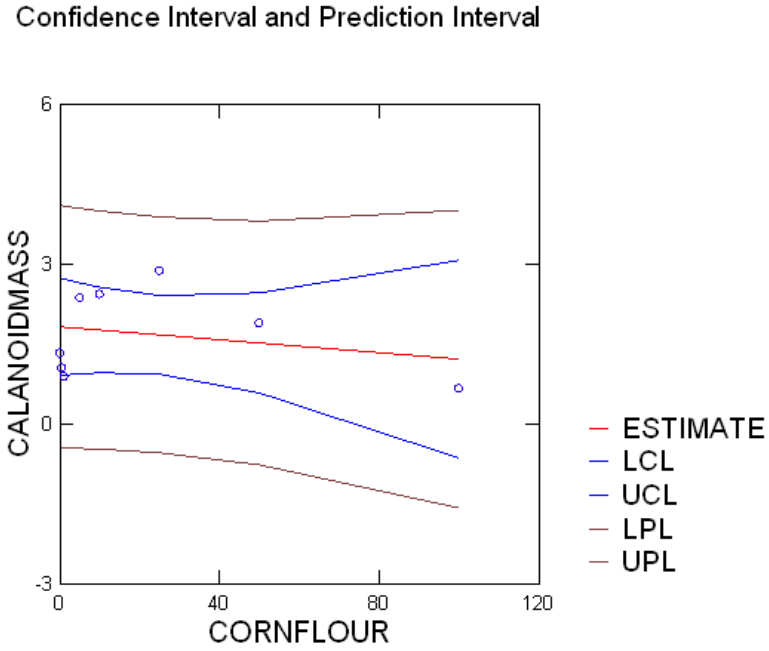

Figure 5. *Calanoid Copepod biomass is not significantly correlated with corn flour concentration.* Regression analysis revealed that there is no significant relationship between the concentration of corn flour and the average biomass of *Calanoid* zooplankton (shown in µg on the y-axis) in each mesocosm ($p = 0.532508$, $\alpha = 0.10$, df = 1, F-ratio = 0.438355, Squared Multiple R = 0.068086).

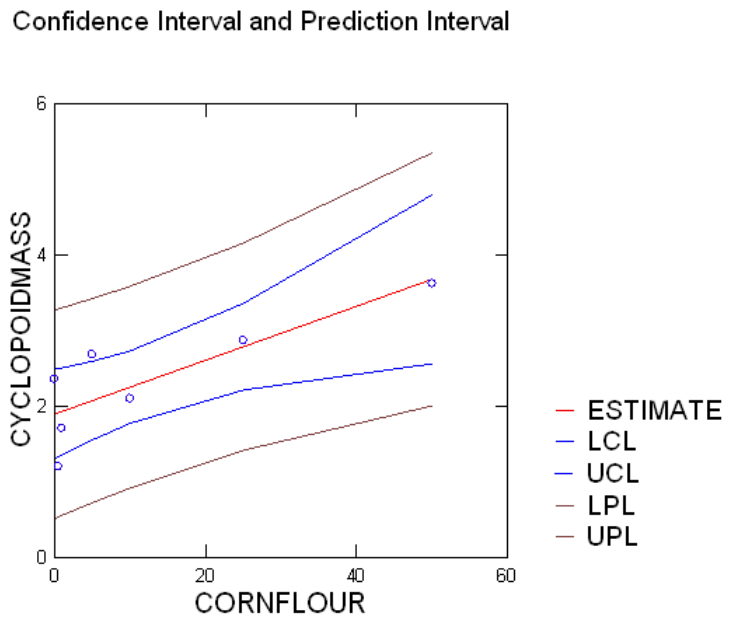

Figure 6. *The biomass of Cyclopoid Copepods increases with increasing corn flour concentrations.* Regression analysis revealed a statistically significant positive relationship between the average *Cyclopoid* biomass (given in µg on the y-axis) and the corn flour concentration in each mesocosm ($p = 0.020557$, F-ratio – 11.154181, $df = 1$). The R^2 value of this regression reveals that this relationship is relatively strong (Squared Multiple $R = 0.690483$).

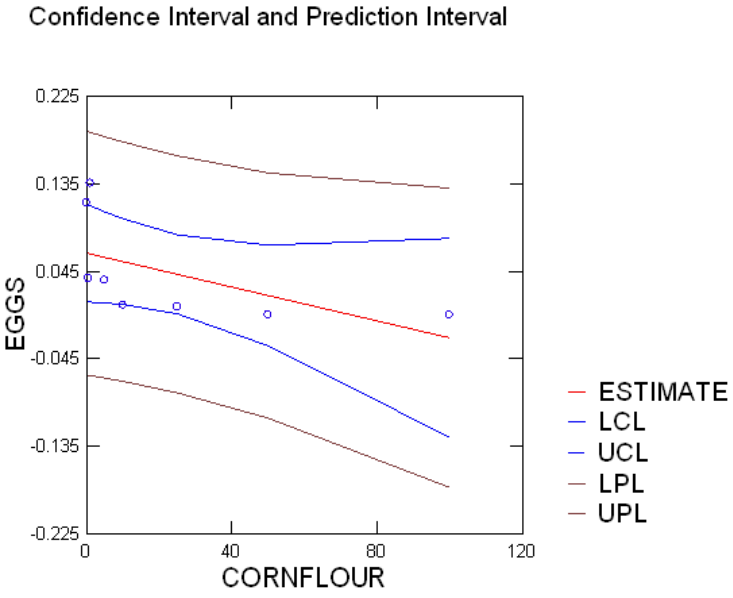

Figure 7. *The proportion of egg carrying Daphnia is not significantly correlated with corn flour concentration.* Though the regression analysis of the proportion of egg carrying *Daphnia* versus the corn flour concentration in each mesocosm appears to reveal a negative correlation, this relationship is not statistically significant ($p = 0.134968$, F-ratio = 2.981508, $df = 1$). Nonetheless, the R^2 value for the regression attributes roughly 33.1961% of the variation in egg carrying proportions to variation in the concentration in corn flour (Squared Multiple $R = 0.331961$).

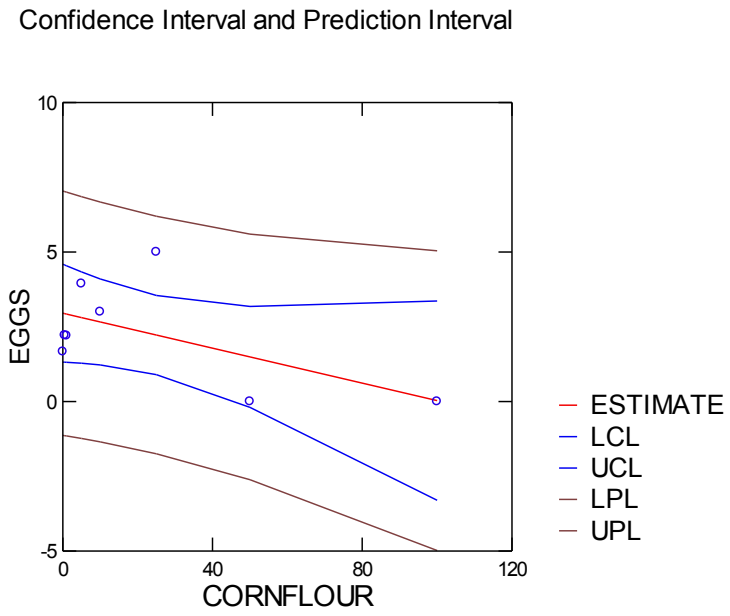

Figure 8. *The average number of eggs carried by an egg-carrying Daphnia is not significantly correlated with corn flour concentration.* Though the regression analysis of the average number of eggs carried by an egg-carrying *Daphnia* versus the corn flour concentration in each mesocosm appears to reveal a negative correlation, this relationship is not statistically significant ($p = 0.125568$, F-ratio = 3.164488, df = 1). Nonetheless, the R^2 value for the regression attributes roughly 34.5299% of the variation in egg carrying proportions to variation in the concentration in corn flour (Squared Multiple R = 0.345299).