

**The Relative Strength of Top-Down and Bottom-Up Trophic Dynamics  
in the Context of Habitat Isolation**

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**ABSTRACT**

Habitat isolation is rapidly increasing, due, in part, to habitat fragmentation. While isolation's effects on species richness, genetic diversity, predator:prey ratios, etc. have been well studied, little is known about isolation's effect on trophic dynamics. Isolation can potentially alter both top-down and bottom-up dynamics through its effects on local processes, such as predation and herbivory, that influence trophic dynamics. In order to investigate the impact of isolation on trophic dynamics, I conducted an experiment in aquatic mesocosms manipulating isolation and bottom-up and top-down dynamics, through the addition of nutrients and fish, respectively. The strengths of top-down and bottom-up dynamics were differentially affected by isolation. Generally, isolation weakened top-down processes relative to bottom-up processes, which were not significantly altered by isolation. I found predator communities to consist of less efficient predators at high isolation, while herbivore community composition was relatively unaffected by isolation. This suggests that a possible mechanism behind the differential shift in trophic dynamics over isolation may be a change in predator community composition. My experiment illustrated that isolation could indirectly affect communities through its effects on trophic dynamics and suggests further that top-down and bottom-up dynamics do not respond equally to isolation.

## INTRODUCTION

Habitat fragmentation is occurring at an increasingly high rate (Fahrig 2002), leading to increased habitat loss and isolation between habitat patches. Isolation directly impacts communities by reducing the flow of resources and organisms between habitats. The negative effects of isolation on species richness (MacArthur and Wilson 1967, Simberloff and Wilson 1969), population size (Ward 2005), and other measures of community health (reviewed in Debinski and Holt 2000) have been well studied. Notably lacking from past work concerning habitat isolation, however, is its effects on local, or within community, processes, especially trophic dynamics.

Trophic dynamics have historically been divided into two approaches: top-down and bottom-up. The theory of top-down dynamics is founded in Hairston et al.'s (1960) 'green world' hypothesis, which proposes that top-predators limit herbivores, allowing plants to grow relatively unrestrained by herbivory. These predator controls on herbivore growth can 'cascade' through lower trophic levels, resulting in alternating effects of opposite magnitude (i.e. a decrease in herbivores and increase in primary producers) (Carpenter et al. 1985, Power 1990). Generally, top-down dynamics rely primarily on predators to propagate because the predators initiate the cascade, but their consequences are most observable in herbivores (Hairston et al. 1960). Systems governed by bottom-up dynamics are restrained by resource availability, limiting plant growth and therefore all upper trophic levels (White 1978). In this instance, herbivores are not limited by predation from upper trophic levels but by the lower trophic levels (e.g. plants) on which they rely. Contrary to top-down, bottom-up dynamics originate in lower trophic levels; hence, they are more reliant on producers and herbivores for their propagation.

Trophic dynamics differ greatly in their relative strengths across ecosystems (Borer et al. 2005), often because of variation in the local processes on which they depend, such as herbivory or predation. Top-down processes originate from predation due to a top predator, which is vulnerable to both local abiotic and biotic changes. A change in habitat structure, such as increasing prey refuges (Beukers and Jones 1998), could increase or decrease predation. Biotic factors, such as disease (Holdo et al. 2009) or development of anti-predator behavior in prey (Sih et al. 1985, Lima 1998), could also affect predation. Furthermore, top-down dynamics can be influenced by bottom-up dynamics (Stiling and Rossi 1997). Predators are only able to exist in environments that are productive enough to support higher trophic levels and, as a result, the strength of top-down dynamics depends on productivity (Oksanen et al. 1981). Unlike top-down dynamics, bottom-up dynamics are primarily limited by local resource availability. Higher resource availability can increase plant quality and abundance, which then transfers to higher trophic levels (Hurd and Wolf 1974, Hunter and Price 1992). Plant community traits, such as the ability to extract resources and anti-herbivory traits, can affect the strength with which productivity may cascade upwards and therefore the propagation of bottom-up processes (Anderson 2010, Goheen and Palmer 2010). The local processes that are integral to trophic dynamics are not all robust to isolation; thus isolation can indirectly affect trophic dynamics through its effects on local processes.

Isolation's most substantial impact on local communities is, arguably, its effect on colonization. Local communities rely on colonization from other sites for the accumulation of new species and for the persistence of current populations through rescue effects (Brown and Kodric-Brown 1977). Isolation has been shown to decrease

overall colonization rates (MacArthur and Wilson 1967), thereby lowering species richness. Furthermore, isolation acts as an environmental filter by differentially limiting species' colonization. Species with limited dispersal abilities, for example, are hindered more by isolation than a species with a specific dispersal mechanism. By acting as an environmental filter, isolation does not stochastically lower species richness in a community, but preferentially reduces the populations and richness of species that are more limited by isolation, resulting in a community composition much different than that of a habitat with low isolation.

Through its effects on colonization rates, isolation may influence trophic dynamics in several ways. Top-down dynamics may be weakened in isolated habitats through a change in the predator:prey ratio or the predator community as a whole. Isolation has been shown to lower the predator:prey ratio (Shulman and Chase 2007), potentially decreasing the strength of a predator-initiated trophic cascade and resulting in weakened top-down effects at high isolation. The composition of a predator community is also affected by isolation, with less efficient predators often dominating more isolated habitats (Chase et al. 2010). This could in turn weaken top-down effects. Another hypothesis is that top-down dynamics may be unaffected by isolation. Contrary to above, many believe the predator:prey ratio to be controlled by local community assembly rules (Warren and Gaston 1992), leading to the prediction that isolation would not change the ratio, and therefore not affect top-down dynamics. Similarly, the predator community composition may not change with isolation, resulting in a similar strength of top-down dynamics across the isolation gradient. Less is known about the impact of isolation on bottom-up dynamics. Isolation may weaken bottom-up dynamics. The competition-

colonization trade-off predicts that species who are better colonizers are worse competitors (Levins and Culver 1971, Hastings 1980, Tilman 1994). Therefore, communities at higher isolation may consist of worse competitors who would not be able to utilize resources as efficiently as those in less isolated communities, resulting in a weakened bottom-up effect. Alternatively, bottom-up processes may increase in strength in response to weaker predation, and therefore higher growth rates, at high isolation. An additional hypothesis is that either bottom-up or top-down dynamics, or both, will not respond to isolation and will exhibit similar strengths at all isolation levels. This may be because, similar to predator:prey ratios, trophic dynamics may be held stable throughout an ecosystem by an underlying local mechanism that is robust or unrelated to isolation. While studies have considered top-down and bottom-up dynamics individually with respect to isolation, none have examined both in order to understand their relative strength in the context of isolation.

In the summer of 2010, I established an aquatic mesocosm experiment to measure the effect of isolation on bottom-up and top-down dynamics. Isolation has been shown to greatly alter species composition and richness of ponds (Jonsson et al. 2009, Cohen and Shurin 2003, Ostman et al. 2006, McCauley 2007). Additionally, trophic dynamics have been well studied in aquatic systems (Carpenter et al. 2001, Chase and Ryberg 2004), and have even been examined in the context of regional processes (Chase et al. 2010); however, no work has yet to examine both bottom-up and top-down processes in the context of isolation. By manipulating bottom-up and top-down dynamics, through nutrient and top-predator additions, respectively, over a range of isolation, we were able to study their relative strengths in the context of isolation.

## **METHODS**

### *Experimental Set-Up*

I chose three fishless ponds of similar size at Shaw Nature Reserve (Gray Summit, MO, USA) as replicate source ponds. Shaw Nature Reserve is a 2,400 acre public park with a range of land types from prairie to wetland. Over 30 ponds and lakes lie within its borders, supporting a diversity of aquatic life. Source ponds were between 300-400m<sup>2</sup>, although this varied throughout the duration of the experiment with rainfall and temperature. It was important to choose ponds that were large and of a similar size, so that the emigration rate of each source pond would be large enough to colonize pools and similar across source ponds. All ponds were surrounded partly by an area of minimal canopy cover (<5%), so that mesocosms could be placed in an open canopy to allow for optimal dispersal of organisms.

Mesocosms were established in early June, 2010. Each mesocosm consisted of a plastic pool filled with ~100L well-water, to which approximately 20 grams of dried leaf-litter was added. Pools had two small holes (5mm in diameter) located 5 cm below the top, allowing excess rainwater to drain while preventing loss of colonists. Isolation was manipulated by placing mesocosms at a distance of 5m, 50m, or 100m from the source pond, which acted as a natural source of colonists. Shulman and Chase (2007) found these distances to significantly impact the community structure of mesocosms through isolation. Seven mesocosms were placed at each distance, three controls, three nutrient

addition treatments, and one predator addition treatment to manipulate top-down and bottom-up trophic dynamics. Treatments were randomly assigned to each pool, with a total of three control treatments, three nutrient addition treatments, and one predator addition treatment at each distance. Distance and trophic treatments were replicated across three spatial blocks (i.e. source ponds), for a total of 63 mesocosms (Fig. 1).

Trophic dynamics were manipulated in two ways, through addition of nutrients and addition of top-predators. Nutrients were added in the form of phosphorus ( $\text{NaH}_2\text{PO}_4$ ) and nitrogen ( $\text{NaNO}_3$ ), the two most limiting nutrients in aquatic systems (Wetzel 2001). The pools' ambient P:N ratios ranged from 1:0.638 to 1:30.66, so the P:N ratio of each pool was corrected to 1:16, to avoid co-limitation of mesocosms. Nutrients were added to the experiment at two week intervals, beginning two weeks after the experiment was established, for a total of three nutrient pulses. Nutrient pulsing was used because it has been shown to have a stronger effect than a one-time addition (Butzler and Chase 2009). Each pulse raised the nutrient load 100 $\mu\text{g/L}$  P: 1600 $\mu\text{g/L}$  N.

One pool at each distance had the addition of a top-predator, *Gambusia affinis*, which preys on aquatic macroinvertebrates. 20 individuals were added to each pool two weeks after the experiment was established and were counted and restocked if necessary when nutrients were added to account for mortality.

### *Sampling*

Pools were sampled 10 weeks after the experiment began. Zooplankton were sampled by collecting 5L of water from each pool and concentrated to 50mL by filtering it through a 80 $\mu\text{m}$  mesh zooplankton net. Samples were preserved in Acid Lugols

solution until they were processed. 10ml of this solution was extracted and the zooplankton in it were identified to species using a dichotomous key and photographic library of known species and enumerated using an inverted microscope (Chase et al. 2009). The abundances were then extrapolated to give a total abundance of each pool.

Each pool was sampled completely for macroinvertebrates and amphibians using a 15cm rectangular net with 0.33mm mesh netting. Pools were sampled to completion, or until there were 10 empty sweeps. Macroinvertebrates were preserved in a 70% ethanol solution and amphibians were identified to species and counted on site.

Macroinvertebrates were identified using a dichotomous key and taxonomic library of known identifications from the area, with a dissecting microscope when necessary.

Biomasses of all organisms were calculated using standard length-weight measurements.

All species were divided into herbivores and predators based on classifications from Merritt and Cummins (1996). Species were organized further into functional groups based on Chase et al. (2010) (Table 1).

### *Analysis*

I analyzed species richness using a randomized block 3x3 ANOVA with isolation and trophic treatment as continuous and categorical factors, respectively, and source ponds as blocks. I conducted a MANOVA to test the effect of distance, treatment, and the interaction between them on herbivore and predator biomass. Fisher's LSD pair-wise tests were used to make specific comparisons between treatment and isolation distance. Permutational analyses of variance (PERMANOVA; Anderson 2001) were conducted to examine any changes in species composition. A 3x3 PERMANOVA using a Bray-Curtis

similarity matrix was used to compare the effects of isolation and treatment on community composition, blocking for source ponds. In order to determine which functional group was driving the change in community composition, I conducted a one-way ANOVA on the biomass of each functional group over isolation. This data was analyzed further with TukeyHSD post-hoc tests to test for significant differences in biomass between each level of isolation.

All statistics and graphing were conducted in R 2.12.1 (<http://www.r-project.org/>).

## RESULTS

### *Species Richness*

A total of 77 species were collected and identified, including 29 predator species and 48 herbivore species. The blocking effect of source pond was insignificant, allowing species richness to be analyzed over all ponds. Total species richness decreased with increasing isolation (Figure 2; ANOVA:  $df=2$ ,  $f=5.5113$ ,  $p<0.001$ ). Average species richness was significantly different for predators (mean  $\pm$  SD=  $4.30\pm 2.17$ ) and herbivores (mean  $\pm$  SD=  $9.83\pm 3.82$ ) (t-test:  $t=9.97$ ,  $df=98.362$ ,  $p<0.001$ ). However, the species richness of predators and herbivores were not differentially affected by isolation or treatment.

### *Biomass*

Overall, biomass significantly decreased with increasing isolation and was significantly affected by treatment and the interaction between treatment and isolation (Table 2). Although, when analyses were run separately for each trophic level, only

predator biomass was significantly affected by distance (Fig. 3; ANOVA:  $df=1$ ,  $f=18.043$ ,  $p<0.001$ ). Herbivore biomass was significantly affected by the interaction between distance and treatment, responding differently to isolation in the fish treatment (Fig. 4; ANOVA:  $df=4$ ,  $f=9.318$ ,  $p<0.0001$ ). Additionally, the variance for herbivore biomass in fish ponds at high isolation was much higher than at low isolation ( $SE=425.65$  at 100m and  $SE=90.32$  at 5m; Fig. 4).

### *Community Composition*

Community composition was significantly affected by isolation (PERMANOVA:  $F=2.2964$ ,  $p<0.005$ ), treatment (PERMANOVA:  $f=2.7128$ ,  $p<0.005$ ), and the interaction between the two (PERMANOVA:  $f=1.9333$ ,  $p<0.005$ ). Predator and herbivore functional groups responded differently to isolation. Isolation negatively affected the biomass of dragonfly larvae (ANOVA:  $f=11.7293$ ,  $p<0.005$ ) and large beetles (ANOVA:  $f=4.9087$ ,  $p<0.05$ ) (Fig. 5). The only herbivore group significantly affected by isolation was large zooplankton (Fig. 6; ANOVA:  $f=11.8392$ ,  $p<0.005$ ).

## **DISCUSSION**

My results indicate that the relative strength of top-down and bottom-up dynamics differs greatly in the context of isolation. The presence of fish reduced predator biomass and increased herbivore biomass at near pools (Fig. 4), suggesting that top-down dynamics were present. Although herbivore biomass increased in fish pools relative to the control at high isolation, predator biomass was not significantly different (Fig. 4), indicating that top-down effects were not likely and that another mechanism is

responsible for the increase in herbivores at high isolation. While it is expected that bottom-up dynamics would increase in response to weakened top-down regulations, I found no significant change in bottom-up dynamics over isolation. This difference may be because predators and herbivores responded differently to isolation, with predators more susceptible to the effects of isolation.

I found species richness to decrease with increasing isolation, supporting many other studies (reviewed in Cadotte 2006). Several processes may be responsible for this decrease. Habitats with greater isolation tend to have lower colonization rates, both because dispersal-limited species are not able to disperse to them and because non-limited species may preferentially choose to colonize nearer habitats (McCauley 2007). Isolation can also influence species diversity by lowering the rescue effect, when colonizing individuals allow otherwise shrinking population to exist (Brown and Kodric-Brown 1977). If the rescue effect is lower, populations that rely on colonists to exist have a higher probability of going extinct. Lower species richness at isolated sites is often attributed to the lower colonization and higher extinction rates present (MacArthur and Wilson 1967), which could explain my findings of decreased species richness with increased isolation.

A community with lower species richness may be lacking functional groups, and therefore may be less efficient or productive than a more complete community with higher species richness. Furthermore, less complete communities can weaken interspecific actions, such as predation or herbivory, which would weaken trophic dynamics (Otto et al. 2008, Wojdak 2005). While lower species richness can explain an overall weakening in trophic dynamics, it does not explain the different responses of top-

down and bottom-up dynamics to isolation. If isolation affected predator richness more, it could explain why top-down dynamics were mediated by isolation while bottom-up dynamics were unchanged. In this case, predators would be a less complete community than herbivores at isolated sites, leading to reduced predation (Charnov et al. 1976) and weakened top-down dynamics. However, I found herbivore and predator richness to be affected similarly by isolation, so this explanation is not likely. This supports several studies that found predator:prey ratios unaffected by environmental change (Jeffries 2002, Urban 2004), but is contrary to results from the same aquatic system as my study, that found predator richness to decrease more than herbivore richness with increasing isolation (Shulman and Chase 2007). I argue, however, that this difference may be due to a difference in predator identity. Shulman and Chase's (2007) predator community was dominated by smaller diving beetles (Dytiscidae) and Notonectidae, while my predator community was predominantly Odonata (dragonfly larvae). This difference may be a result of the difference in canopy cover, which greatly influences colonization of aquatic invertebrates (Binckley and Resetarits 2009). My mesocosms were placed in open canopy prairie (<5% canopy cover), but Shulman and Chase's (2007) were in oak-hickory forest, a more closed canopy. Odonata prefer open canopy (Bried and Ervin 2005) and would be more likely to colonize my pools.

Although predator and herbivore species richness were not differentially affected by isolation, predator and herbivore biomass did respond differently to isolation (Fig. 3) and this could partially explain my results concerning trophic dynamics. Similar to species richness, biomass decreased with increasing isolation, but this decrease was driven by a decrease in predator biomass alone. There are several explanations why

predator biomass would decrease with isolation while herbivore biomass remained unchanged. Herbivore species tend to be less dispersal limited than predators and therefore less impacted by isolation (Komonen et al. 2000, Golden and Crist 1999, Faeth and Simberloff 1981). Additionally, a loss of predators at high isolation may have transferred to a lower predation rate. Predation pressure is directly influenced by the richness of the predator pool, with higher richness leading to higher predation pressure (Charnov et al. 1976). Because they were partly removed from predation pressure at high isolation levels, herbivore populations could have had a higher growth rate than at low isolation levels, counterbalancing any loss in biomass due to isolation. Top-down dynamics rely on upper-trophic level species (e.g. predators) to propagate through the food chain and the loss of predator biomass at high isolation could have weakened top-down dynamics. Herbivore biomass did not decrease over isolation and, accordingly, bottom-up dynamics did not change with isolation.

An anomaly in the described pattern is the dramatic increase in herbivore biomass in the fish treatment at high isolation relative to the other treatments. Were predator biomass to be significantly lower than other treatments, this could indicate a trophic cascade initiated by the top predator, fish. I found predator biomass to be similar across all treatments at high isolation, however, so another mechanism is likely driving this increase. The variance in biomass at fish pools at high isolation was much greater than that at low isolation. Higher variance in herbivore biomass could indicate that stochasticity is playing a larger role in more isolated ponds. Because there are fewer predators, colonists may not be as limited by more deterministic processes such as predation and any colonist that stochastically arrives at the pool is able to colonize and

grow. This unconstrained growth would explain cases of high biomass found in some high isolation fish treatments. Extremely low biomass would be due to the stochastic probability that some habitats receive little to no colonists. An increase in stochastic processes as described could imply a weakening of trophic dynamics in general, as they tend to consist of more deterministic processes.

Another mechanism that may be responsible for the change in trophic dynamics is the apparent shift in community composition over isolation. Top-level predators (e.g. Odonota, Dysticidae, Hemiptera) significantly decreased over isolation, but lower-level predators were not affected (Fig. 5). This caused an overall shift in predator community composition from one dominated by larger, more efficient predators at low isolation to one dominated by smaller, less efficient predators at high isolation. Weaker predator communities of more isolated pools may not have been able to convey top-down dynamics as well as those at less isolated pools. Contrary to predator composition, herbivore composition did not experience a shift to smaller, less efficient herbivores. With the exception of large zooplankton, herbivore community composition was relatively stable over an isolation gradient (Fig. 6).

A possible reason bottom-up dynamics did not respond to isolation in the same way as top-down dynamics is because bottom-up processes were too insignificant at low isolation to be weakened further. In the closest pools, adding nutrients did not affect herbivore or predator biomass relative to control pools. According to bottom-up theory, it is predicted that herbivore or predator biomass, or both, would increase with increased nutrient additions (White 1978) and a lack of an increase at low isolation could signify bottom-up dynamics were weak to begin with. If bottom-up processes were already too

low to detect at low isolation, any decrease in response to increasing isolation would not have been observable.

Only a small number of studies have examined bottom-up and top-down processes simultaneously over an environmental gradient, generally finding top-down dynamics more responsive to varying gradients, such as temperature (Hoekman 2010, Barton et al. 2009), altitude (Hillyer and Silman 2010), and environmental stress (Alberti et al. 2010). Very few studies have examined top-down or bottom-up dynamics specifically in the context of isolation. In a metacommunity context, isolation weakens top-down controls on an ecosystem (Chase et al. 2010), supporting my findings. Similar to my results, Terborgh et al. (2001) found top-down dynamics to be weaker on isolated islands, allowing bottom-up dynamics to increase in the absence of predator regulation.

My experiment was able to examine isolation explicitly because of the nature of the study system, but this limits the applicability of my results. Aquatic systems are an ideal study system for trophic dynamics in the context of isolation because aquatic trophic dynamics have been well studied (Carpenter et al. 2001, Sabo et al. 2009, Power and Dietrich 2002, Chase and Ryberg 2004) and isolation is relatively easy to define and control. Terrestrial trophic interactions, however, are often weaker than aquatic interactions (Shurin et al. 2002, Halaj and Wise 2001); future research conducting a similar study in a terrestrial system could better determine how broadly applicable my conclusions are. Furthermore, the species in my study system differ greatly in their dispersal abilities and so were affected disproportionately by isolation. A study that more strictly controlled dispersal rates would have been able to account for such differences in

dispersal abilities, but would not have had as realistic environmental conditions and results.

Previous studies on the effects of isolation on communities tend to overlook its effects on trophic dynamics. By integrating isolation and trophic dynamics, I was able to examine how these processes interact with each other to shape ecological communities. My study was the first to examine both bottom-up and top-down dynamics over isolation, allowing me to compare their relative strength in the context of isolation. I found isolation to alter the relationship between bottom-up and top-down dynamics, generally reducing the strength of top-down controls relative to bottom-up. In the context of fragmentation, this means more isolated patches may undergo an ‘ecological meltdown’ (Terborgh et al. 2001) as herbivores experience increased growth in the absence of predator control leading to unchecked exploitation of resources. Isolation has both direct and indirect effects on communities, and, in order to fully understand its potential consequences, future work must consider its ability to alter processes within communities.

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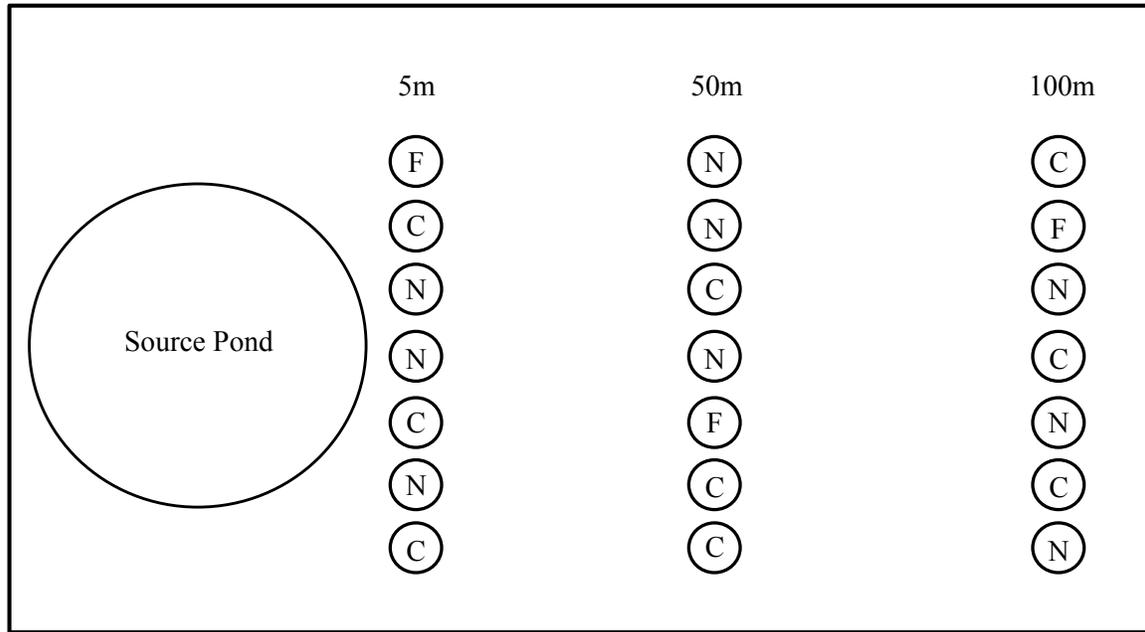
## TABLES AND FIGURES

<b>Predators</b>	<b>Herbivores</b>
Dragonfly larvae (Odonata)	Large grazers
Large beetles (Dysticidae)	Small grazers
Hemiptera	Large Zooplankton
Damselfly larvae	Small Zooplankton
Small beetles	

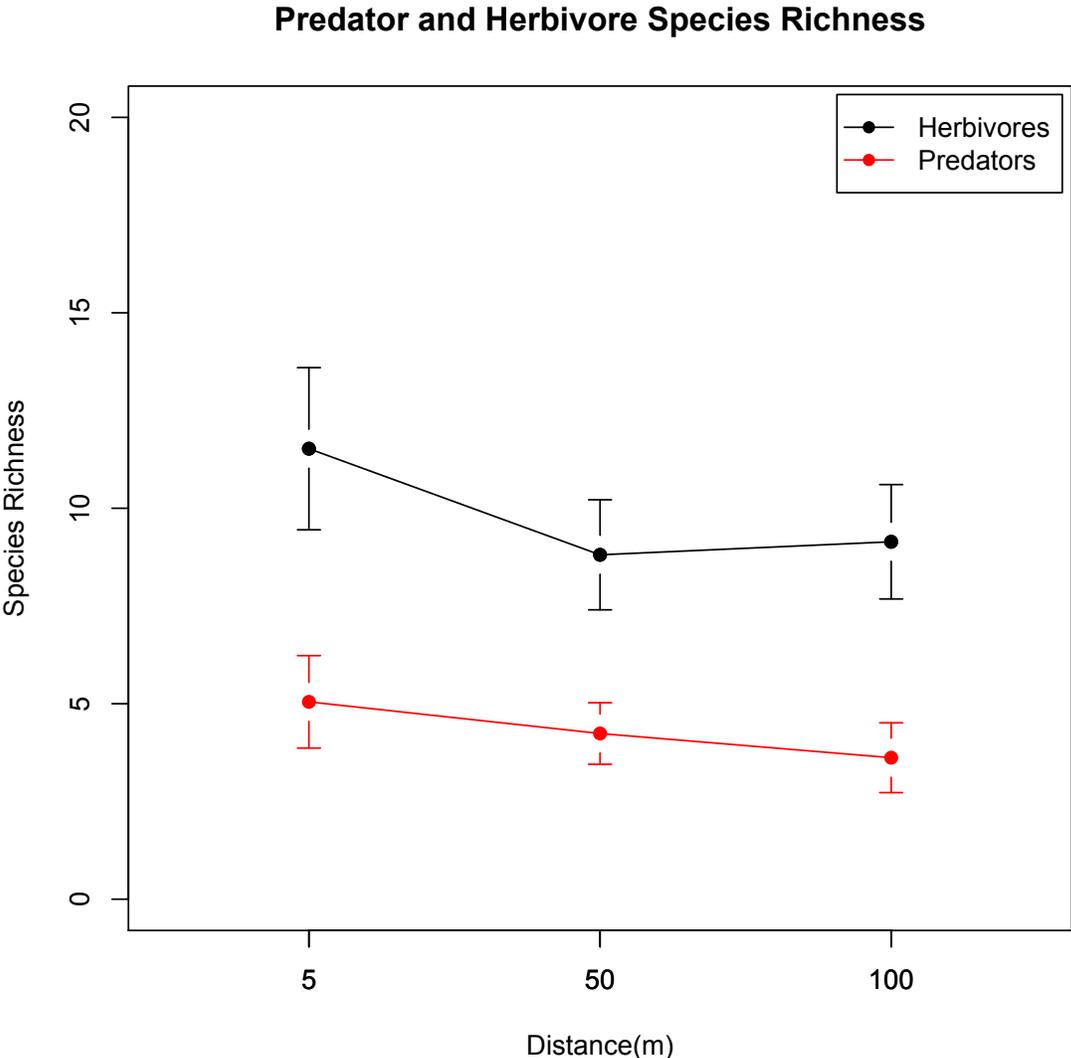
**Table 1.** Table of functional groups of predators and herbivores. Groups are listed in descending order of size and efficiency (i.e. groups consisting of larger, more efficient species listed first). Categorizing is based on Chase (2010).

<b>Variable</b>	<b>df</b>	<b>Wilks <math>\lambda</math></b>	<b>Mean Sq</b>	<b>f-value</b>	<b>p-value</b>
Isolation	2	0.78352	197741	7.7363	<b>0.00108</b>
Treatment	4	0.61931	240224	7.5798	<b>0.00002</b>
Isolation * Treatment	4	0.73055	293047	4.7592	<b>0.00139</b>

**Table 2.** MANOVA test on effect of isolation and treatment on predator and herbivore biomass. Significant p-values are bolded .

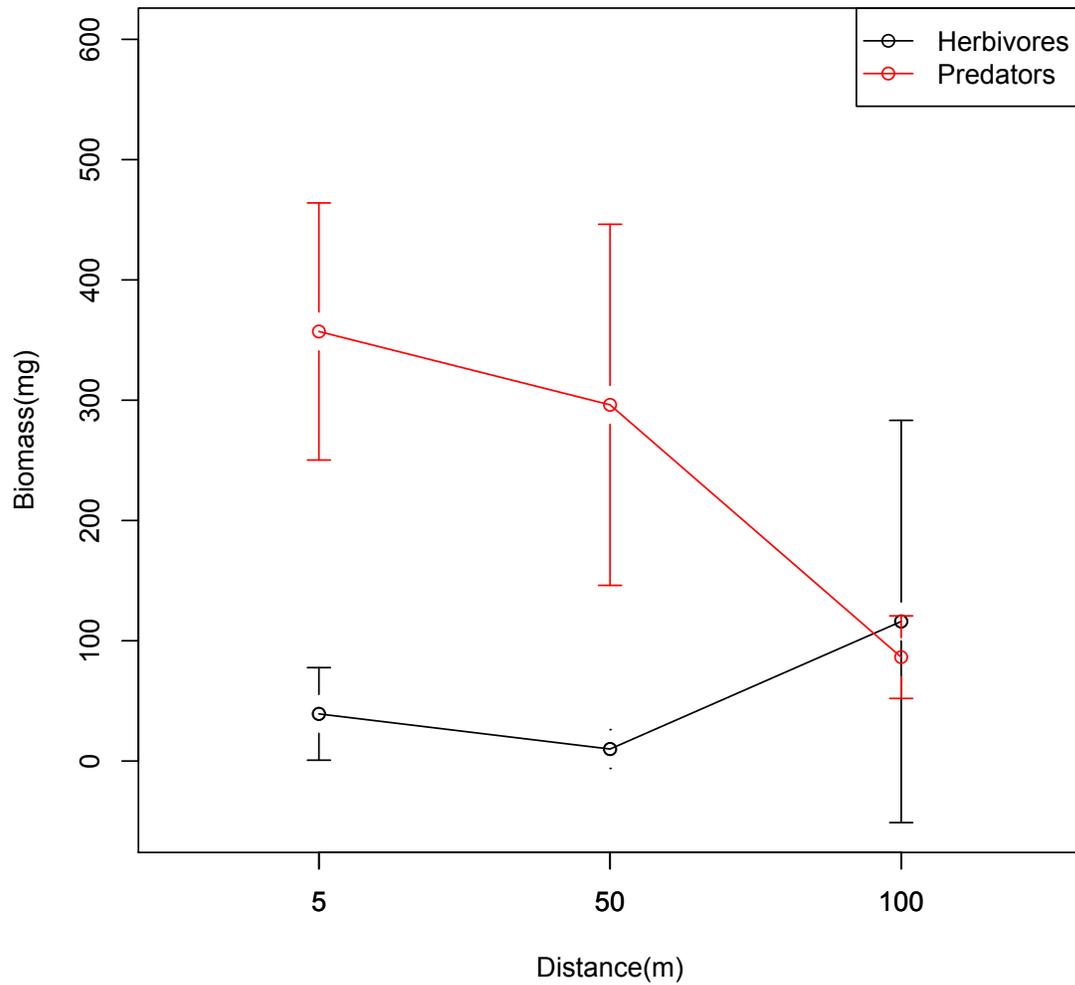


**Figure 1.** Example layout of experiment. Letters in pools represent treatments: control (C), nutrient (N) and fish (F). Treatments were randomized within each distance.

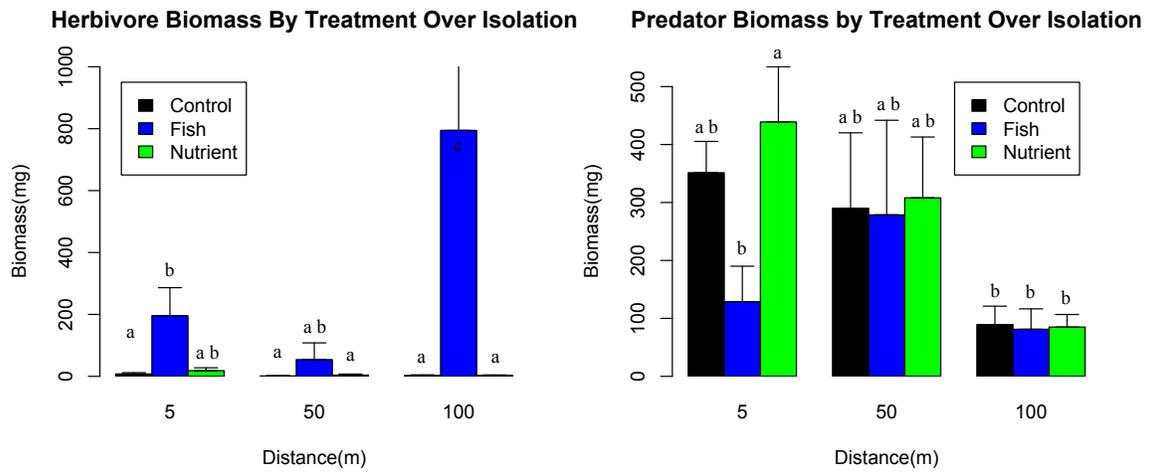


**Figure 2.** Mean herbivore and predator species richness across all treatments. Error bars represent 95% CI.

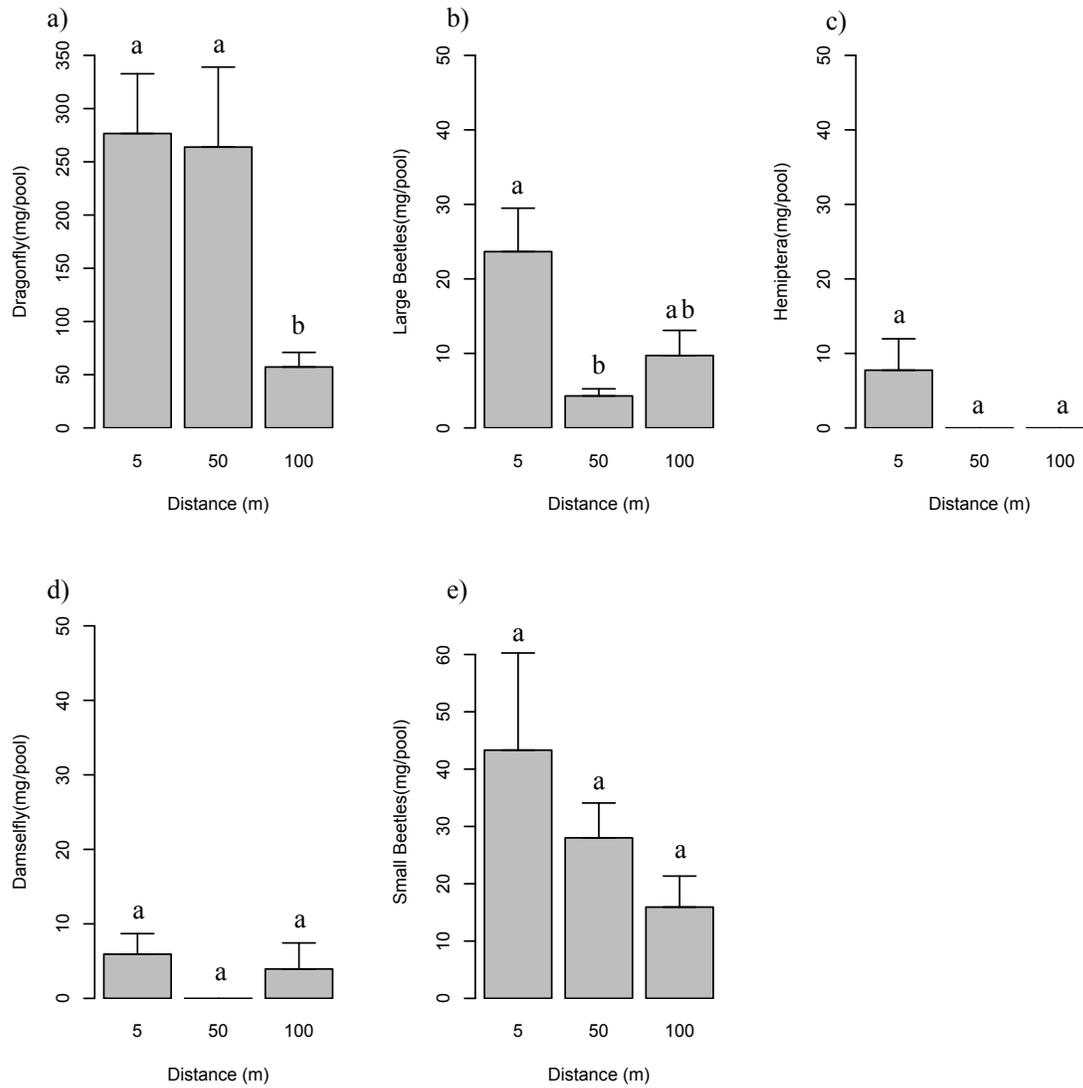
### Herbivore and Predator Biomass Over All Treatments



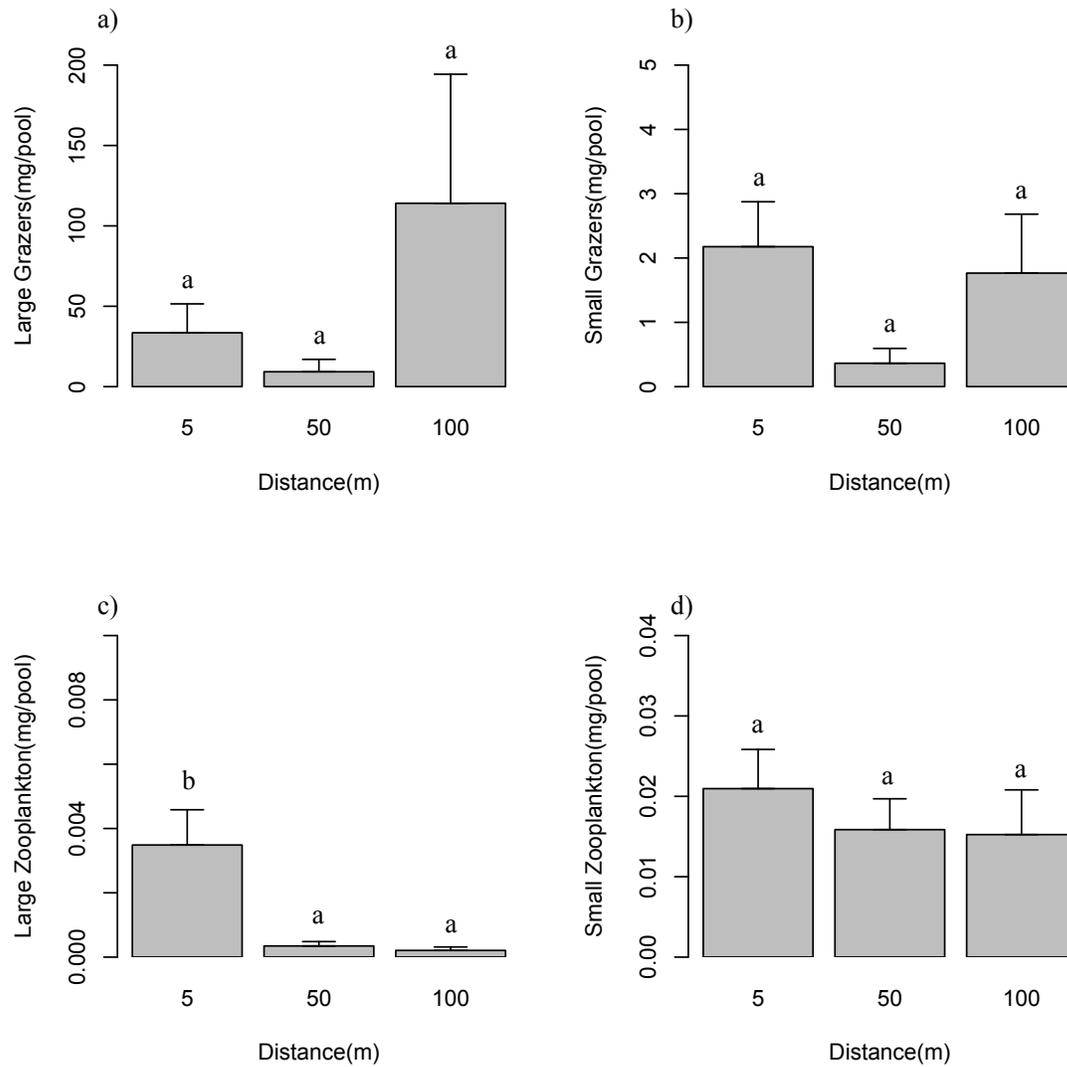
**Figure 3.** Mean predator and herbivore biomass across all treatments over distance from the source pond. Error bars represent 95% CI.



**Figure 4.** Mean herbivore and predator biomass grouped by treatment over isolation. Error bars represent standard error. Letters represent significance ( $p < 0.05$ ) based on Fisher's LSD pair-wise comparisons.



**Figure 5.** Effect of isolation on mean biomass (mg) of a) dragonfly larvae, b) large beetles, c) hemiptera, d) dragonfly larvae, and e) small beetles. Error bars represent standard error. Letters represent significance ( $p < 0.05$ ) based on TukeyHSD post-hoc tests.



**Figure 6.** Effect of isolation on mean biomass (mg) of a) large grazers, b) small grazers, c) large zooplankton, and d) small zooplankton. Error bars represent standard error. Letters represent significance ( $p < 0.05$ ) based on TukeyHSD post-hoc tests.