

**PREY DENSITY EFFECTS ON PREDATOR FORAGING:  
A COMPARISON OF PREY LOSS AND IMPLICATIONS FOR A NATURAL  
INSECT COMMUNITY**

A Final Report of the Tibor T. Polgar Fellowship Program

Katherine Guild

Polgar Fellow

Department of Ecology and Evolution  
SUNY Stony Brook University  
Stony Brook, NY 11790

Project Advisor:

Dr. Jeffrey Levinton  
Department of Ecology and Evolution  
SUNY Stony Brook University  
Stony Brook, NY 11790

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## ABSTRACT

Aquatic insect community composition and diversity are strong indicators of stream health; these aspects were examined in the context of disturbance along Wappinger Creek, a lower Hudson River tributary, in order to evaluate changes in community trophic structure. Wappinger Creek was sampled at three locations in late June and early July 2014 to observe diversity changes caused by weather disturbances. Stream health increased with decreasing stream order; the highest stream order site had the lowest diversity. Community diversity and density peaked at the medium stream order site; whereas the headstream site had the most unique insects. Diversity did not generally change between sampling times.

The effects of varying prey density on predator foraging efficiency were studied. The two aquatic insect predator taxa studied were Sialidae (alderflies, Megaloptera) and Perlidae (stoneflies, Plecoptera), chosen for their similar diets, body size and prey recognition methods. Macroinvertebrates for the predator-prey experiments were collected from Wappinger Creek and sorted into containers designated for six treatments with two variable factors: prey density and predator type. While the predators caused prey loss, neither predator's foraging efficiency was significantly affected by changes in prey density. The lack of predator response to prey density ('null numerical response') implies that the predators are limited by intra-predator competition. Predation was not the only factor operating to remove individuals from the experimental communities; intra-guild predation within typically herbivorous larvae may have resulted in density-dependent losses due to excess resource competition within each container. In regard to the Wappinger Creek diversity changes and the reduction of predator abundance, the self-

regulatory actions of low trophic level intra-guild individuals observed in the foraging experiment support the natural community's continued stabilization.

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## INTRODUCTION

Lotic ecosystems are predominantly unobserved or overlooked, in part, because their erratic responses to weather and flow across the landscape create variable spatial and temporal heterogeneity across relatively short reaches. Extensive observation, dedication and expense would be necessary to evaluate these systems thoroughly (Barbour et al. 1999; Flotemersch et al. 2006). In contrast, lakes have uniform responses to environmental factors and are evaluated more frequently than streams and rivers. Due to the irregularity of a stream, across its width and along its length, many more samplings of numerous biological, chemical, and physical aspects are needed in an effort to accurately comprehend the aquatic ecosystem, its biodiversity, and ecological niches available (Blocksom and Johnson 2011). Although rivers, such as the Hudson River and other streams in its watershed, are more complicated to assess than lakes, lotic systems fulfill a vital function in the environment that ought not to be overlooked as a result of the challenge that they pose (Limburg et al. 1986).

Biological assessments are utilized by government agencies as well as non-governmental organizations (NGOs) in order to analyze potential sources of pollution and to assess water quality. Based on an aquatic insect's sensitivity to pollution and the community species richness and abundance, the health of the stream ecosystem can be determined through bioassessment. Macroinvertebrates are ideal indicators of stream health due to their strict feeding behaviors, habits and dissolved oxygen requirements which instigate quick responses to environmental changes. Such responses can be utilized to infer a categorical representation of stream health, and the macroinvertebrate community composition can suggest the degree to which the stream is stressed by

pollution (Hilsenhoff 1988; Voshell 2002; Merritt et al. 2008). In order to assist with the correlation between stream health and macroinvertebrates, Hilsenhoff (1987, 1988) classified each genus of common North American freshwater invertebrate species with an empirical value along a scale (0-10) of tolerance. High levels of biodiversity and the presence of especially sensitive families of aquatic insect larvae (Ephemeroptera, Plecoptera, and Trichoptera) are, also, essential factors for stream quality assessments (Hilsenhoff 1987).

In addition to being valuable indicators for bioassessment due to their presence in certain environments, aquatic insects have an intriguing community-level interactions network. Aquatic insects fill crucial ecological niches within the stream ecosystem. For example, most caddisfly larvae (Trichoptera) are filter-feeders or collect fine particulate organic matter from rock surfaces, whereas, dragonfly and damselfly larvae (Odonata) are predaceous (Voshell 2002; Peckarsky et al. 1990). These ecological guilds fill important and distinct roles in the lotic ecosystem. According to the nutrient spiraling concept and river continuum concept, invertebrates are pivotal elements that shred allochthonous coarse particulate organic material (CPOM), which, in increasing stream order, reduces CPOM to fine particulate organic material (FPOM) available for a myriad of invertebrate species, which in turn recycle detritus and decomposing organic matter (Newbold et al. 1982; Vannote et al. 1980). All in all, the aquatic insect niches support a diverse community across long distances and through stream orders.

Many scientists have examined the predator-prey interactions between insectivorous fish and choice prey items (Heck 1981; Ioannou et al. 2009; Baxter et al. 2005; Wesner 2010), but studies of the intra-order aquatic insect predator-prey dynamics

are few. These studies are essential to determine the overall efficiency of predation and effect of predation on the community, specifically whether some prey species are more affected than others, or if the collective prey community is significantly depleted by predators (Benke 1976; Townsend and Hildrew 1978). Peckarsky (1982) stated that the reverse interaction, how prey affects predators, has not been thoroughly examined. A community with high prey density may affect factors such as prey detection, selection of food items, and the success of attacks. The term *confusion effect* is defined as “the reduced rate or success of attacks on prey groups as multiple targets overload the information-processing capacity of predators” (Ioannou et al. 2009). This response has been demonstrated to be dependent on prey density with increasing number of failures as prey density expands and the predator becomes unable to distinguish a vulnerable prey item (Milinski 1977).

In order to test whether the *confusion effect* influences aquatic insect predators; an experiment was designed that compares two common predators’ foraging behavior at different prey densities. The common stonefly (Plecoptera: Perlidae) and alderfly (Megaloptera: Sialidae) larvae have many similarities allowing them to occupy similar niches. Both are known to be voracious generalists and actively hunt their prey. They eat similar prey items, typically small mayfly (Ephemeroptera) and true fly (Chironomidae) larvae (Azam 1969; Peckarsky and Wilcox 1989). These predators choose prey based on an allometric body size relationship. Throughout their development, their prey’s body size directly increases with instar development (Klecka and Boukal 2013). Generalists have strong effects on the community structure and stability of the food webs because they have the ability to switch prey types almost effortlessly depending on the

optimization of their foraging response to varying prey quality and quantity (Murdoch and Oaten 1975).

Community structure is affected by factors such as the environment's productivity and biological interactions. Peckarsky and Dodson (1980) observed the effects of predator-prey interactions on prey recruitment and their aversion to some habitats based on predator and competitor presence; however, they failed to investigate the effects of prey density on predator foraging responses.

### **Study Objectives**

For the purposes of experimentation, there were three major study objectives:

- (1) Assess differences in Wappinger Creek's community structure and species diversity across stream order and time caused by small disturbances,
- (2) Evaluate the prediction that top predators have a major effect in a structurally complex experimental environment; and
- (3) Determine whether aquatic insect predator foraging responses are affected by prey density.

Community structure in the context of stream order was assessed by field sampling. Laboratory experiments were used to understand the role of predator effects as a function of prey density. In the predator-prey density experiment, the preliminary prediction was that neither Sialidae nor Perlidae would be affected by varying prey densities. Considering that both predators respond to hydrodynamic cues, higher prey densities ought not to confuse them, thereby foraging efficiency should remain constant across any prey density. Laboratory tests of these hypotheses were interpreted in order to

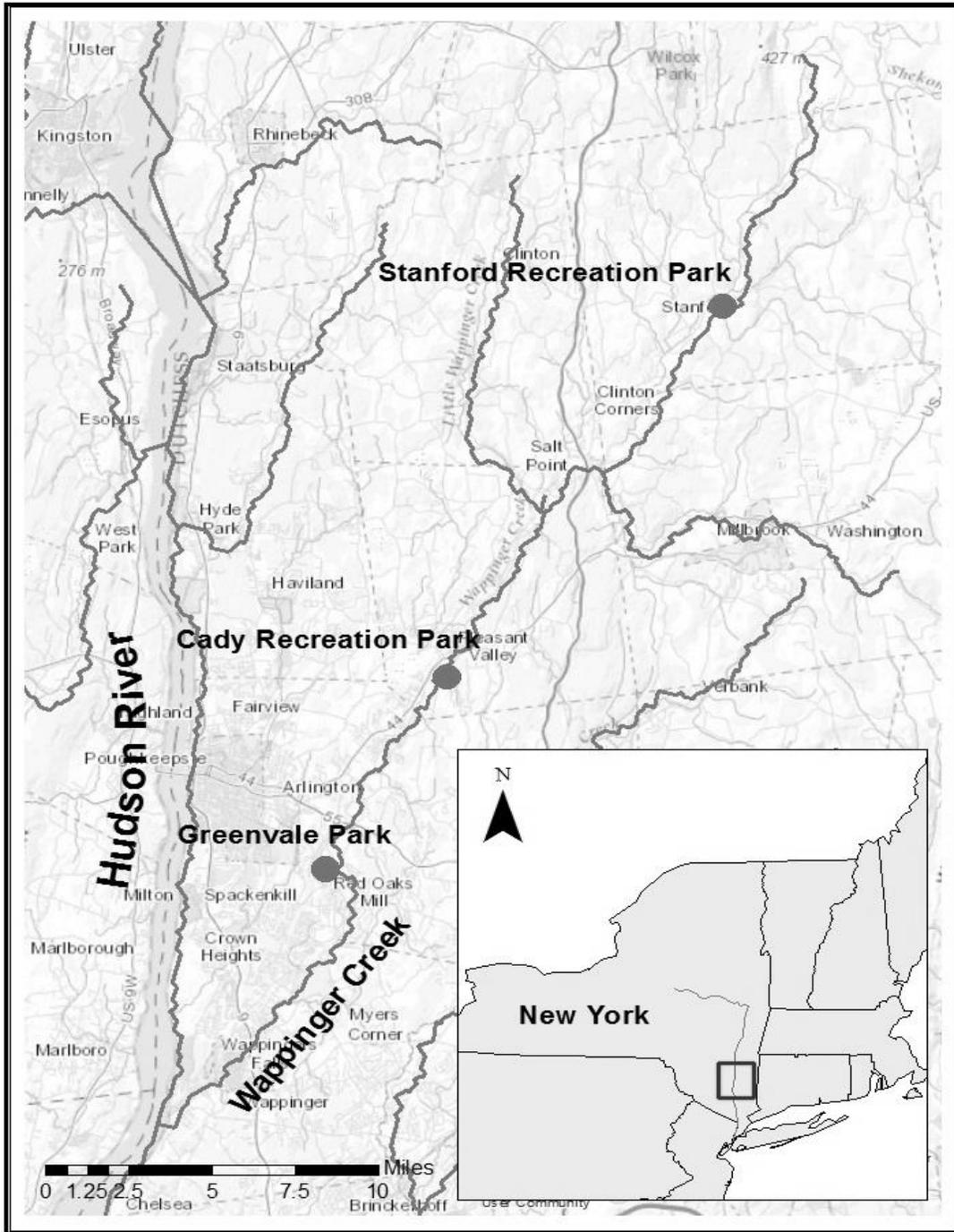
predict the persistence of Wappinger Creek's community structure during periods of disturbance.

## **METHODS**

### **Site descriptions**

Wappinger Creek originates from lakes and wetlands in Eastern New York and joins the Hudson River at Wappingers Falls, New York. Three sites along Wappinger Creek (Fig. 1; Table 1) were observed for two consecutive weeks during late June and early July. The sites were accessed through public use lands. The following sites were visited and are listed by increasing stream order: the Town of Stanford Recreation Park in Stanfordville (SRP), Cady Recreation Park in Pleasant Valley (CRP) and Greenvale Park in Poughkeepsie (GVP). The sites displayed physical properties appropriate to increasing stream order (Vannote et al. 1980).

The SRP site is a shallow, calmly moving stream with 90% shade cover; whereas, the GVP site is a meter-deep, slow moving stream with 5% shade cover. In order to perform the predator-prey density experiment, it was necessary to choose a healthy stream that supported a diverse resident community of insect larvae. The SRP and CRP sites can be characterized as fast-flowing lotic-erosional zones containing many riffles and high dissolved oxygen content, and the GVP site is a lotic-erosional zone with low discharge and exhibits the presence of algal mats.



**Figure 1:** Wappinger Creek site locations for aquatic insect collections. **1A.** Stanford Recreation Park at Stanfordville. **1B.** Cady Recreation Park at Pleasant Valley. **1C.** Glenvale Park at Poughkeepsie. Map courtesy of ESRI ArcMap Online.

**Table 1:** Wappinger Creek site information including site name, abbreviation, town name, relative stream order and GPS coordinates. Wappinger Creek is located in Dutchess County, New York.

Site Name	Abbr.	Town Name	Relative Stream Order	GPS Coordinates
Stanford Recreational Park	SRP	Stanfordville	Low	41°87'24.40'' N, 73°71'06.67'' W
Cady Recreational Park	CRP	Pleasant Valley	Medium	41°74'20.85'' N, 73°82'87.06'' W
Glenvale Park	GVP	Poughkeepsie	Medium-High	41°66'09.56'' N, 73°87'71.64'' W

### Field Sampling

The aquatic insect community was sampled during two consecutive weeks in late June and early July. The macroinvertebrate community was sampled using a dip net with 500 micrometer mesh. Positioning the net facing upstream, approximately one square foot of the stream bottom was agitated by foot in front of the net's mouth, and the contents were placed in a 1-gallon plastic jar filled with 95% ethanol preservation (NYSDEC 2012). This process was repeated three times in order to amass a single kick sample. Three kick samples were collected across a transect line perpendicular to stream flow. The kicks across the transect line were replicated three times for a total of nine composite collection samples per site. All individuals were picked from the samples and identified to family ordination using a dissecting microscope and high intensity illuminator.

Hilsenhoff Biotic Index (HBI), Simpson Diversity Index (SDI), percent Ephemeroptera, Plecoptera and Trichoptera (% EPT), percent individuals based on feeding strategy and species densities were calculated for the composite macroinvertebrate samples at each site.

## Prey Density Experiment

Insect samples were collected from the GVP and CRP sites five times during July, August and September 2014. The insects were collected using a dip net and were stored in a 16-quart plastic storage bin. All insects were transported in bins with air pumps and air stones to the laboratory for sorting. Stream water was collected in two liter containers. Four collections were gathered from the CRP site, and two were collected from the GVP site. The predators were collected, separated and kept in solitude within 4 dram snap cap vials until the beginning of the experiment.

In the laboratory, six 4-quart plastic containers were filled with five centimeters of substrate and stream water collected from Wappinger Creek filled to five centimeters above the rock substrata (Fig. 2). The substrate was a mixture of medium-sized cobbles, small pebbles, and sand to increase heterogeneity. A six-outlet commercial air pump was used to aerate the

containers; an air stone was placed in the center of each container.

Additionally, two layers of mosquito netting covered the openings in order to collect any individuals that emerged as adults.

The containers were



**Figure 2:** Predator-prey experiment set-up

given labels based on treatment. The treatments were ‘high prey density – Sialidae predator’(HD-S), ‘low prey density – Sialidae predator’(LD- S), ‘high prey density – Perlidae predator’(HD-P), ‘low prey density – Perlidae predator’(LD-P), ‘high prey density – no predator’(HD-N) and ‘low prey density – no predator’(LD-N). Based on insect densities and species composition observed from the field samples, the prey densities and composition for the prey density experiment was determined. The low prey density containers had 20 individuals: 10 Chironomidae, 5 Ephemeroptera and 5 Trichoptera. The high prey density containers had 60 individuals: 10 Chironomidae, 30 Ephemeroptera and 20 Trichoptera. The total prey remaining was counted after a week. The six treatments were performed simultaneously and repeated a total of five times. Average prey consumed by both predators at each density was calculated from the five ‘no predator’ treatment replicates. The ‘no predator’ treatments were used as a control for predation effects.

The insect samples were sorted by hand accordingly. For the final three replicates, the prey body size was divided into size ranges. Large body size individuals were longer than one centimeter, medium body size individuals were between 0.99 centimeters and 0.5 centimeters, and small body size individuals were smaller than 0.49 centimeters. The body length was measured for each predator as well.

At the beginning of the experiment the predators were placed in their designated arenas. The arenas remained undisturbed for seven days. After a week, the water was carefully decanted and replaced with 95% ethanol. The insects were recovered from their containers and those that remained were picked, identified and recorded.

## Statistical Analysis

In order to determine the number of individuals lost to predation, the total individuals lost in the five replicates of the HD-N and LD-N treatments were averaged and the standard deviation was calculated. This number was subtracted from the treatments with predators. The additional losses that could not be contributed to the designated predators' activities were observed in all treatments and considered to be lost for other reasons.

Standardized *t*- tests were used to determine the significance of the prey density based on prey consumed for both predators. The null hypothesis was that there was no difference in the proportion of prey consumed at high and low prey density. A one-way Analysis of Variance (ANOVA) determined whether prey consumption was different between the predator treatments. In this case, the null hypothesis was that prey consumption was not significantly different as a function of predator type. Additionally, the relationship between predator body size and prey consumed was graphically represented and fit using linear regression. The relationship between predator body size and proportion of prey lost were also graphed and fit by linear regression.

The changes to the community composition and diversity due to the predator-prey density experiment were quantified by calculating Simpson's Diversity Index (1 - *D*) of the community.

$$D = \sum(n/N)^2$$

The significance of the difference between these diversity values was calculated across the factors, prey density and predator type, using a two-way factorial ANOVA. The proportions of the abundant prey taxa lost (Hydropsychidae, Heptageniidae, Baetidae and

Chironomidae) were calculated, and a two-way factorial ANOVA design was used to calculate the significant differences in proportions between prey density or predator type and the loss of certain taxa. Tukey's HSD *post-hoc* test was performed to identify which taxa were affected more than others.

## RESULTS

### Wappinger Creek Community

From the samples collected at Glenvale Park (GVP) in Poughkeepsie, Cady Recreational Park (CRP) in Pleasant Valley and Stanford Recreational Park (SRP) in Stanfordville, various descriptive metrics were calculated to describe the aquatic insect community's diversity and indications of stream health during two consecutive weeks in midsummer (Table 2). Notably, due to substantial rainfall between 30 June 2014 and 7 July 2014, the diversity metrics indicated changes. For example, species richness at all sites declined slightly; however, the GVP site's diversity increased from the first observation ( $1 - D = 0.5088$ ) to the second ( $1 - D = 0.7922$ ). The other sites exhibited no change in diversity. The Hilsenhoff Biotic Index remained relatively similar between the observations. Stream health increased with decreasing stream order. Overall, the CRP site had the highest diversity ( $1 - D = 0.8254$ ;  $SR = 36$ ), as well as the most consistent density (1028.1 - 1338.4 individuals per square meter). The other sites experienced more drastic changes related to the weather conditions. The SRP site's density strongly declined, but the taxa present did not change. In the GVP site, the density increased slightly, yet the species present were radically different. After the rainfall, there were

more individuals present from the pollution-sensitive families Ephemeroptera, Plecoptera and Trichoptera.

**Table 2:** Descriptive community statistics across the three Wappinger Creek sites. The table includes comparisons of species richness (SR), density (individuals / meter squared), Simpson Diversity Index (1 - D), percent Ephemeroptera, Plecoptera and Trichoptera (% EPT) and Hilsenhoff Biotic Index (HBI).

Site	GVP (Poughkeepsie)		CRP (Pleasant Valley)		SRP (Stanfordville)	
	30 June	7 July	30 June	7 July	30 June	7 July
Metric						
SR	26	21	36	35	29	26
Density	454.54	602.45	1028.1	1338.4	2153.7	577.2
1 - D	0.5088	0.7922	0.8254	0.7955	0.8234	0.8005
% EPT	17.36	59.95	68.19	45.14	53.96	56.2
HBI	5.62	6.01	5.06	4.79	4.55	4.79

### Prey Density Experiment

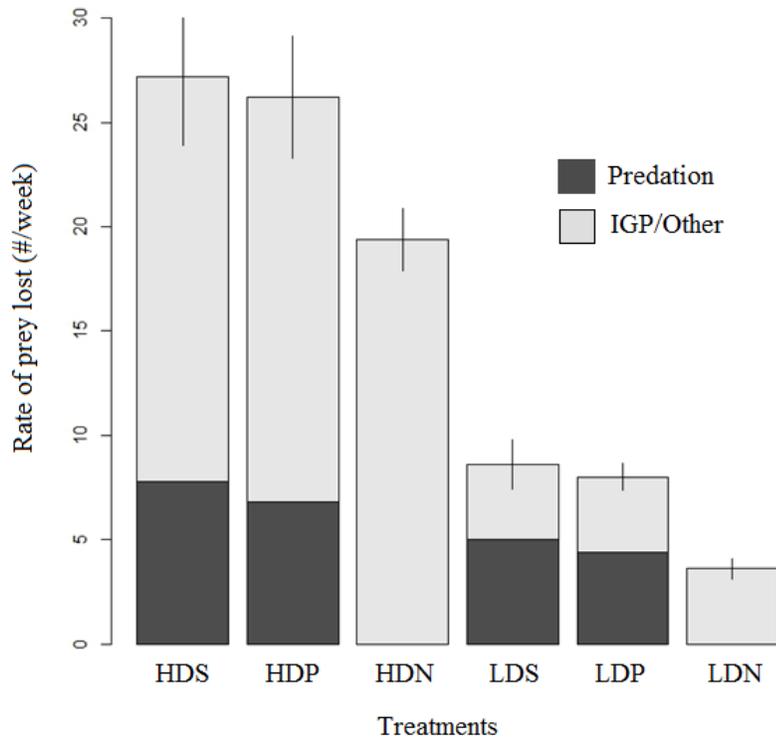
The estimates for the average prey consumption accounted for a small percentage of the total number of prey lost during the experiment (Table 3; Fig. 3). In the low prey density treatments (N = 20), predation accounted for about 55% of total prey loss. Predation contributed to 30% of total prey loss in the high prey density treatments (N=60). The residual prey loss was attributed to other community dynamics.

Statistical analysis of the different treatments yielded significant results for certain factors (Table 4). Prey loss did not change across high and low density treatments for either predator ( $t_{5.03} = 1.59$ ,  $P = 0.172$ ;  $t_{4.57} = 1.60$ ,  $P = 0.178$ ); however, the differences in prey consumption across Sialidae, Perlidae and absent-predator treatments was significant in high ( $F_{2, 12} = 9.93$ ,  $P = 0.0029$ ) and low density ( $F_{2, 12} = 43.0$ ,  $P < 0.001$ ).

Comparisons between Sialidae or Perlidae and the absent-predator treatments were all significant ( $P < 0.01$ ); however, neither Sialidae nor Perlidae had a greater effect on prey loss than the other. These trends applied to both high and low prey density treatments.

**Table 3:** A comparison of the average predator foraging rate (number of prey consumed per week) and average rate of prey loss for all reasons including predation, intraspecific competition and intra-guild predation during each of six experimental treatments.

Treatment			
Prey Density	Predator	Average Rate of Predator Consumption	Average Rate of Prey Loss
High	Sialidae	7.8 ± 3.7	27.2 ± 3.7
	Perlidae	6.8 ± 3.27	26.2 ± 3.27
	None	-	19.4 ± 1.67
Low	Sialidae	5.0 ± 1.34	8.6 ± 1.34
	Perlidae	4.4 ± 0.71	8.0 ± 0.71
	None	-	3.6 ± 0.55



**Figure 3:** Representation of prey loss rate. The stacked bar plot separates the number of prey lost to predator consumption per week and prey lost to intra-guild predation and for other reasons. The treatments are abbreviated by high (HD) and low (LD) density, and by predator type: Sialidae (S), Perlidae (P) and no predator (N).

The differences between prey loss rates were highly significant between high and low density ( $P = 0.001$ ; Table 4). This alludes to the presence of strong density-dependent losses that are unrelated to the effects of either Sialidae or Perlidae predator additions.

**Table 4:** Statistical analysis of differences in mean rates of predator foraging **A)** between high and low density using Standardized t tests, **B)** among all predator types using One-way ANOVA and **C)** between two predator types using Standardized t tests. **D)** Differences in mean rate of prey loss between high and low prey density.

Test	Prey Density	Predator	Statistic	<i>P</i>
<b>A)</b> Differences in predator foraging means for high and low density		Sialidae	$t_{5.03} = 1.59$	0.172
		Perlidiae	$t_{4.37} = 1.60$	0.178

<b>B) Differences in predator foraging means among all predator treatments</b>	High		$F_{2,12} = 9.93$	0.0029	**
	Low		$F_{2,12} = 43.0$	<0.001	***
<b>C) Differences in predator foraging means between predator treatments</b>	High	Sialidae vs. None	$t_{5.57} = 4.29$	0.0061	**
	High	Perlidae vs. None	$t_{5.96} = 4.14$	0.0062	**
	Low	Sialidae vs. None	$t_{7.53} = 7.72$	<0.001	***
	Low	Perlidae vs. None	$t_{5.3} = 11.0$	<0.001	***
<b>D) Differences in prey loss rates means between high and low density treatments</b>			$t_{18.8} = 3.75$	0.001	***

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### Prey Community

The effects on the prey community were calculated through changes to the Simpson Diversity Index ( $1 - D$ ) after the experiment (Table 5). The Two-way ANOVA yielded no significant change to the prey diversity as a result of prey loss. Neither predator type ( $F_{2,26} = 0.98$ ,  $P = 0.389$ ) nor prey density ( $F_{1,26} = 2.2$ ,  $P = 0.15$ ) had significant effect on the species richness or species abundance of the prey community.

In order to determine whether some taxa were negatively affected more than other taxa in the treatments, the proportions of prey consumed for the four most abundant taxa in the prey communities were calculated. The differences in proportions of lost individuals within taxa were evaluated using a Two-way Factorial ANOVA in order to determine whether prey density and predator type had significant effects (Table 5). Prey

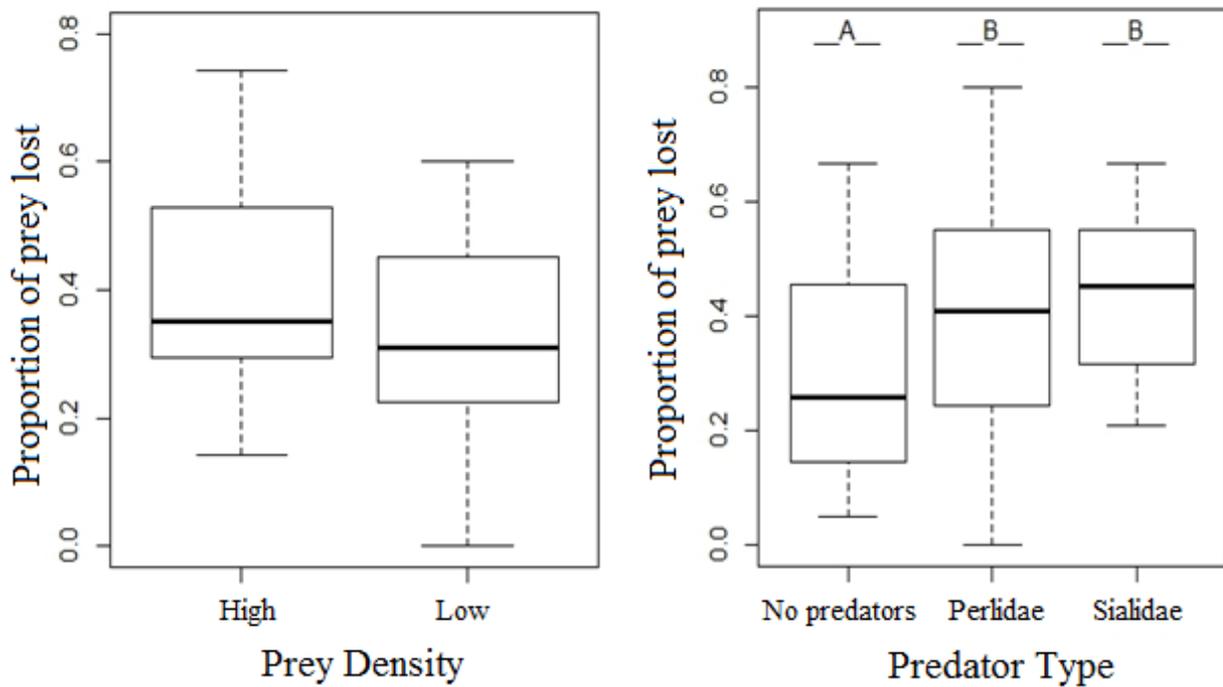
density ( $F_{1,32} = 4.79$ ,  $P = 0.036$ ) and predator type ( $F_{2,48} = 6.3$ ,  $P = 0.0037$ ) had significant results; however, the interaction between prey taxa and prey density was not significant ( $F_{3,32} = 0.78$ ,  $P = 0.512$ ). The interaction factor between prey taxa and predator type was highly significant, though ( $F_{6,48} = 5.25$ ,  $P < 0.001$ ). Prey density had a slight effect on the proportions of taxa lost, which relates to the total number of prey lost since more prey were removed in higher density than in lower density (Fig. 3; Fig. 4a). Predator type displayed an effect as a result of the ‘no predator’ treatments being included (Fig. 4b), which further demonstrates that Perlidae and Sialidae contributed to prey loss, but they did not differ in their effect. The prey community experienced heavier losses in the presence of active predators; however, Tukey’s test revealed that Baetidae and Chironomidae experienced higher proportions of loss than Heptageniidae and Hydropsychidae in the presence of both predators, Sialidae and Perlidae (Fig. 5). Baetidae and Chironomidae had higher mean proportions of prey loss than the two other prey families. Baetidae differed most from the other three taxa (all  $P < 0.01$ ).

**Table 5:** Statistical analysis of prey loss effects on community by assessing **A**) the difference between the Simpson Diversity Index values ( $1 - D$ ) before and after the prey density experiment. The differences between mean prey loss by taxa in regards to **B**) prey density and **C**) predator type as factors were interpreted using a Two-way Factorial ANOVA design. The  $p$  values were calculated in R program.

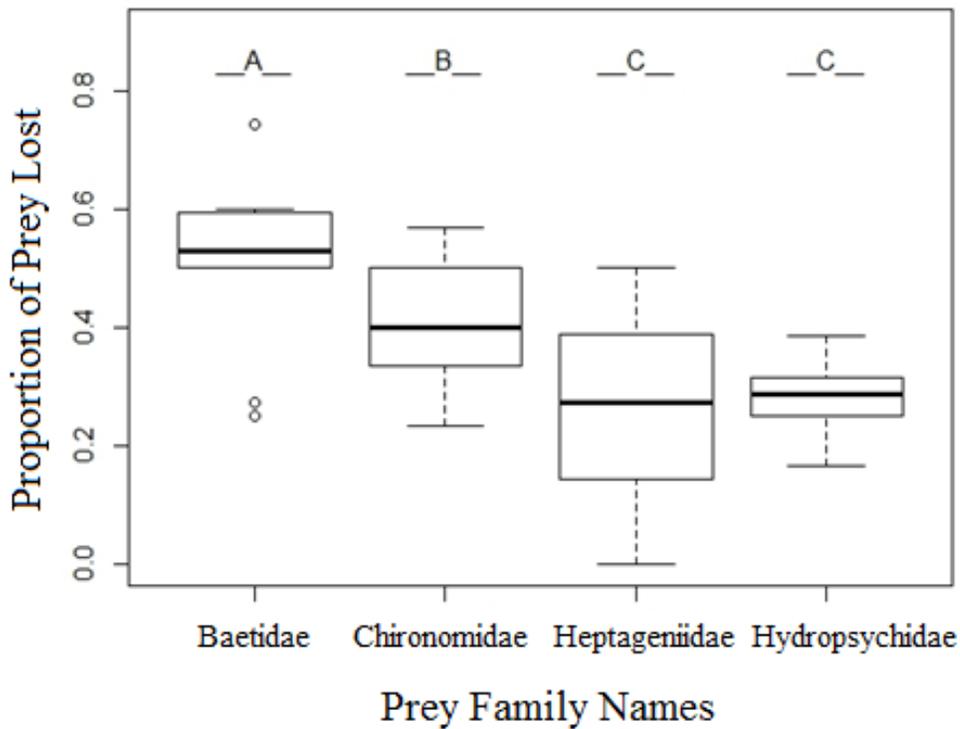
Test	Factor	$F$	$P$	
<b>A</b> ) Differences among $\Delta(1-D)$ without factor interaction	Predator	0.98	0.389	
	Density	2.2	0.15	
<b>B</b> ) Differences in mean loss proportions among prey taxa and density with factor interaction	Prey Taxa	10.16	<0.001	***

	Density	4.79	0.036	*
	Interaction	0.78	0.512	
C) Differences in mean loss proportions among prey taxa and predator type with factor interaction	Prey Taxa	17.27	<0.001	***
	Predator	6.3	0.0037	**
	Interaction	5.25	<0.001	***

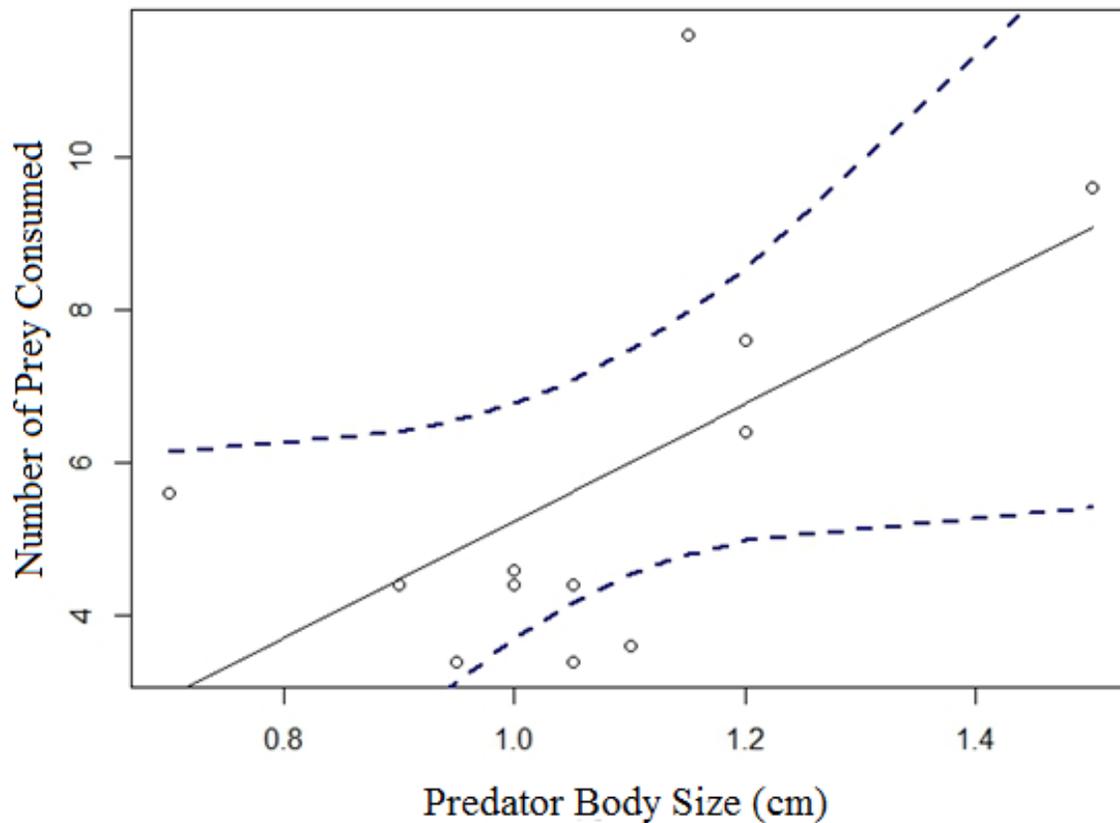
The proportion of Chironomidae lost was different from all other taxa, yet only the comparisons of the proportions of Chironomidae lost to proportions of Baetidae and Heptageniidae lost had statistically significant differences. Heptageniidae proportional loss was similar to that of Hydropsychidae ( $P = 0.98$ ). Predator body size relative to the number of prey consumed was graphed in order to determine the differences in prey consumption between treatment replicates (Fig. 6). The number of prey consumed increases with predator body size ( $P = 0.053$ ,  $r^2 = 0.326$ ). More Baetidae and Chironomidae were consumed by larger predators. For example, in an arena with a perlid predator (body size = 1.15 cm), Baetidae had a 75% loss and Heptageniidae had a 37% loss; however, in a container with a smaller perlid predator (body size = 0.7 cm), Baetidae had only a 53% loss and Heptageniidae had no loss. Predator body size and the proportions of prey consumed from all possible prey had a positive but statistically non-significant relationship ( $y = 0.72x + 0.92$ ;  $P = 0.55$ ,  $r^2 = 0.32$ ; Fig. 7).



**Figure 4:** Boxplots showing a) proportions of prey lost in high and low prey density treatments and b) proportions of prey lost in Sialidae, Perlidae and no predator treatments. Significant differences are identified using letters above the boxplots.



**Figure 5:** Boxplots showing proportions of prey lost for the prey families Baetidae, Chironomidae, Heptageniidae and Hydropsychidae. Significantly different family means are labeled with letters above each boxplot.

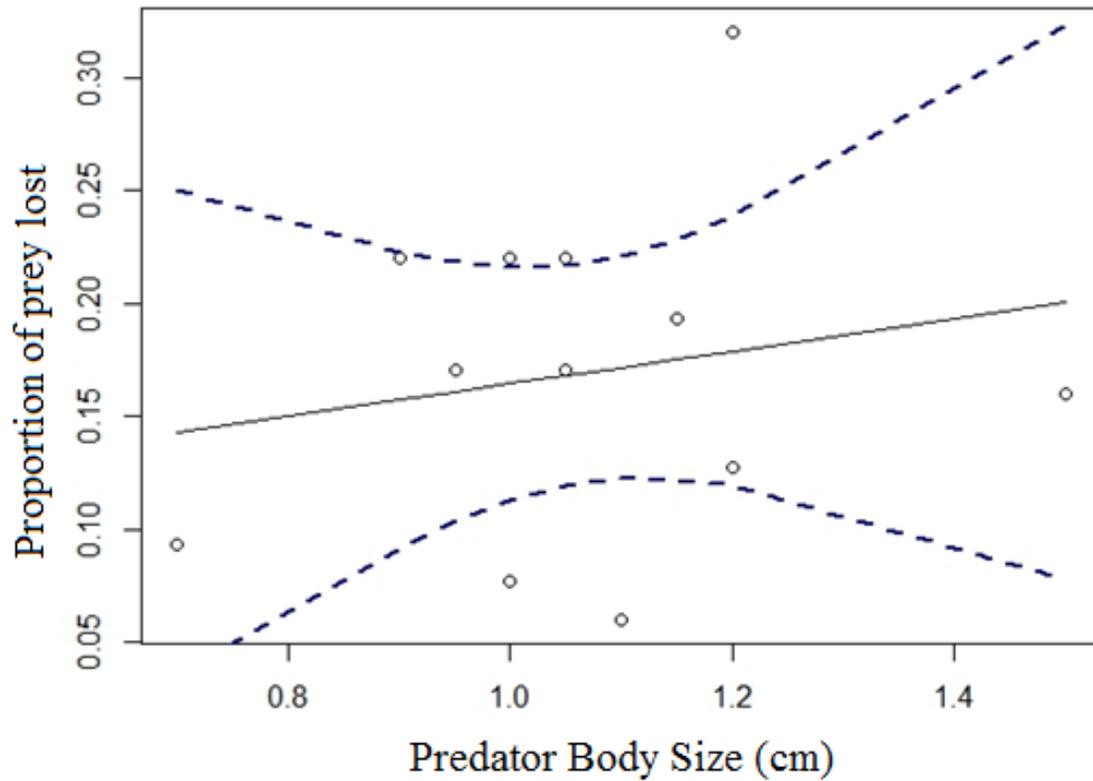


**Figure 6:** Linear regression representation of predator body size (cm) and number of prey consumed. Linear regression data:  $Y = 7.68x - 2.44$ ,  $P = 0.053$ ,  $r^2 = 0.326$ .

In a container with a smaller perlid predator (body size = 0.7 cm), Baetidae had only a 53% loss and Heptageniidae had no loss. Predator body size and the proportions of prey consumed from all possible prey had a positive but statistically non-significant relationship ( $y = 0.72x + 0.92$ ;  $P = 0.55$ ,  $r^2 = 0.32$ ; Fig. 7).

Prey body sizes were recorded into three ranges: greater than one centimeter, 0.5 centimeters to 0.99 centimeters and less than 0.5 centimeters. The body sizes of the 55% of the prey individuals were less than 0.5 cm and considered to be ‘small’. Seventy-nine percent of the consumed prey was within the ‘small’ body size range. Of the most abundant prey taxa incorporated in the experiment, both Baetidae and Chironomidae

were the smallest taxa and experienced the highest consumption rates (Fig. 5). Prey and predator body size allometry may partially explain the community interactions and losses observed in the predator-prey density treatments.



**Figure 7:** Linear regression representation of predator body size (cm) and proportion of prey community lost. Line of best fit:  $Y = 0.92 + 0.072x$ ,  $P = 0.55$ ,  $r^2 = 0.039$ .

## DISCUSSION

The Wappinger Creek sites resembled the community changes explained by the River Continuum Concept (Vannote et al. 1980) and Nutrient Spiraling Concept (Newbold et al. 1982). These concepts combine insect community's fundamental niches and the cycle of organic nutrients to predict the types of insects and nutrients available throughout all orders of a stream. They predicted that CPOM would be more available in

lower orders with higher shade coverage, like the SRP site, and there would be more organisms that can reduce this larger matter into FPOM. Due to the actions of the insects in the lower orders and inflow of allochthonous nutrients, the middle stream orders, like the CRP site, have a highly diverse stream community. Also, a mixture of insects that disassemble large plant material and filterers and collectors of FPOM become prominent features. In the higher orders, like the GVP site, the nutrient load has increased to a point that algal mats ('aufwuchs') cover most of the substrate and little vegetation grows around the stream. At these reaches, the community has reduced diversity becoming composed mainly of filter-feeders. They predict that predator abundance will be congruent throughout the stream orders. The Wappinger Creek sites correspond with these theoretical predictions before the rainfall events between 30 June 2014 and 7 July 2014. The aquatic macroinvertebrate feeding guilds present at the sites changed with increasing stream order based on the availability of coarse and fine particulate organic matter. However, the rainfall caused a disturbance that diminished the diversity of the GVP site in the lower reaches of the creek.

Along with the transformation of the insect functional groups, taxa diversity is maximal at the CRP site where dissolved oxygen and nutrient levels should be the greatest within the stream. Since taxon diversity changed substantially after the rainfall only in the deep, slow-moving water at the GVP site, this location seemed to benefit from the intermediate natural disturbance. The diversity of the SRP site did not benefit nor suffer from the rainfall, but drastic changes to density were noticed. Considering the number of unique species at this site, frequent disturbances may actively remove them. Percent predators within the community remained constant at all sites, which speaks to

the dependence of these communities on their presence acting as a stabilizing factor for community structure across stream order.

In the predator-prey density experiment, all treatments endured losses of prey individuals from the assembled communities. Further losses from the prey community were noticed in all treatments with intentionally-added predators compared to the absent-predator control treatments. This indicates that the predators had a significant, negative effect on the prey community; however, fixed experimental differences in prey density had no effect on either Sialidae or Perlidae consumption rates. According to Peckarsky and Dodson (1980), the lack of predator reaction to shifting prey density is termed a *null numerical response*.

When this response is observed, it is considered that the predator is limited more substantially by factors other than prey availability (Holling 1961; Crawley 1975). Such a factor may be interference competition between conspecific and interspecific predators that occupy the same patch. Since neither Perlidae nor Sialidae encountered other large predators, their foraging response was not reduced between treatments.

Additionally, Sialidae and Perlidae exhibited comparable prey consumption rates. Given their similar body size, voracity and the hydrodynamic sensory cues used to distinguish their desired prey items, the predators' feeding rates were expected to be comparable. In prey recognition experiments, Peckarsky and Wilcox (1989) determined that *Kogotus modestus* (Plecoptera: Perlodidae) was able to distinguish its preferred prey through mayfly wave patterns made while swimming. This ability allows the predators to identify viable prey items, pursue and attack them after an encounter. The number of prey consumed increased with predator body size, which is supported by Klecka and Boukal's

(2013) predator body size allometry results. Furthermore, the proportion of prey lost had no relationship to Sialidae or Perlidae body size. Since the number of prey consumed correlated with predator body size but total prey loss was not, predation most likely is not the main influence on the final proportions of prey loss.

The comparison of predator-inclusion treatments to the absent-predator control treatments showed that large predators only contributed to a partial increase in total prey loss. In other words, factors that were unrelated to predation by introduced Sialidae and Perlidae had either an equal or more substantial influence on determining the prey abundance at the end of the experiment. Since predation by larger predators was not entirely responsible for the disappearance of the larvae, smaller-sized resource competitors may have participated in predator-prey behaviors. This prospective cause of prey loss is called intra-guild predation (IGP). The observation that the predator control treatment-related losses increased from 45% in low density to 70% in high density suggested that the negative interactions between prey led to density-dependent losses.

It has been shown that herbaceous aquatic insects are more likely to colonize available patches with lower competitor densities than those with higher prey densities when predators are present; thereby indicating that their aversion to intra- and interspecific competition is greater than their response to large-bodied predators (Peckarsky and Dodson 1980). In the predator-prey density experiment, the presence of potential competitors within the same guild had a heavier influence on prey individuals than did the presence of either the Sialidae or Perlidae predators.

The prey taxa that experienced the highest losses were Baetidae and Chironomidae, which belonged to the small prey category (body size < 0.5 cm). This

differed from Hydropsychidae and Heptageniidae that, usually, belonged to the medium and large prey categories (body size > 0.5 cm). In addition to the differences in their body size, the prey taxa with greater losses tended to have similar reactions when physically encountered by predators. In streams, Baetidae and Chironomidae (when they are not hidden in self-created organic particle tubes or algal mats) swim in undulating motions that attract undesired predator attention (Peckarsky and Wilcox 1989; Merritt et al. 2008). The other prey taxa do not have this reaction; rather, their habits are to cling to and crawl between rocks in order to escape larger predators. These other prey taxa may not be as efficient competitors as their more active counterparts. Overall, in environments where there are reduced, normal predation pressures on the better competitors, intra-guild predation may have been a way to regulate the frequency of superior prey and influence top-down control to maintain a nutrient-rich ecosystem and reduce the abundance of dominant competitors, which increases aquatic insect species richness and persistence of the community during disturbances.

Holt and Polis's (1997) intra-guild predation module describes the requirements for the coexistence of intra-guild competitors. First, the actions of the intra-guild competitors that predate upon other competitors are inversely correlated with autotrophic productivity, and second, the intra-guild competitors that are consumed in IGP relationships are superior exploiters of shared resources. Therefore, when productivity is low, better competitors outcompete worse competitors. In order to compensate for the loss of desired resources and to obtain enough energy for their continued survival, the worse competitors tend to become selectively omnivorous and will prey upon the superior competitors. Facultative omnivory, as explained by the IGP module, is a staple

in communities with limited resources and numerous competitors of varying exploitative aptitudes (Polis et al. 1989).

In the predator-prey density experiment, small (<0.5 cm) prey were lost with more frequency as a result of regular predation or intra-guild predation. These smaller and faster prey individuals may have been better competitors over resources within the arenas, and were, therefore, consumed by larger, more tentative intra-guild competitors. This would increase the probability of the larger individuals' survival. Due to the lack of allochthonous water inputs such as particulate organic matter during the experiment, resources would have been limited within the treatment containers and would have provoked heightened intra-guild predatory behaviors. Also, the presence of a single Sialidae or Perlidae predator removing dominant competitors may have increased the degree of intra-guild predation, which would act as an additional stabilizing factor within the experimental prey community and allow the survival of some species that are less prone to predation (Gilinsky 1984).

The implications of the predator-prey density experiment can be applied to the communities observed at the Wappinger Creek sites. As noted previously, the large Sialidae and Perlidae predators did not respond to changes in prey density; however, their non-response implied that their foraging efficiency is probably limited by competition for prey. The Wappinger Creek sites had higher densities of predators (~ 30 individuals/sq. meter) than the density of predators in the experiment. Therefore, an aquatic insect predator's foraging response may change with the interactions with other predators. The experiment supported that a single predator has a slight effect on the prey community; however, the intra-guild predation involving predators of much smaller body size was the

dominant cause of prey loss. In a natural community like that of Wappinger Creek, aquatic insect density changed after the rainfall. The GVP and CRP sites increased in density after the rain, and the percent predators decreased; however, the community at the SRP site decreased in density and the percent predators increased. When changes like this occur, predation and IGP are important factors leading towards the restoration of community equilibrium.

Predation acts to organize the community structure and increase diversity. Intra-guild interactions such as competition and predation become important in community organization when obligate predators are few (Hairston et al. 1960; Polis et al. 1989). Severe disturbances like urbanization and pollution instigate trophic cascades throughout the community structure. An upstream shift of slightly poorer water quality, like that of the GVP site, would occur in the lower orders of the stream. Aquatic insect densities and diversity decline, and for some less abundant or vulnerable species, local extirpation is a possibility (Smith and Lamp 2008). Predators, like Perlidae and others that are highly sensitive to pollution, would be removed, and less sensitive predators like Sialidae would replace them. In extreme circumstances the loss of predator diversity will cause a trophic cascade that limits the diversity of the prey community and photosynthetic productivity. For example, in the GVP site, there was lower predator diversity which corresponded with decreased density and species diversity. In comparison, the CRP site displayed the opposite trends; greater predator richness corresponded with higher site density and diversity. Therefore, predators are crucial to aspects that stabilize the aquatic insect community, especially during disturbances.

Further inquiries about the aquatic insect predators and community structure stem from the predator-prey density experiment. Suggested future investigations include 1) focusing on the actual number and species of prey consumed by the predators through radiometric tagging, 2) testing the foraging responses of other predators found in Wappinger Creek like dragonfly (Odonata: Gomphidae) and dobsonfly (Megaloptera: Corydalidae) larvae, and 3) examining the predator response to increasing predator density in both intraspecific and interspecific competition treatments. Since the prey density did not change the foraging efficiency of the predators, the addition of conspecific individuals and other predator species may affect the focal predator's foraging efficiency. Moreover, further intra-guild predation experiments would provide important information about community structure and stability. If intra-guild predation effects decline in environments with higher proportions of predators to prey individuals, at what predator density or from which combination of predators would this happen?

In order to explore these questions in the future, a similar experimental design to the foraging experiment can be utilized. By setting up multiple treatment arenas simultaneously, the effects to the experimental community can be compared and analyzed under varying predator densities and different organizations of competing predators in the arenas. Accordingly, a series of revised macroinvertebrate foraging experiments can delve further into understanding the shift from primarily standard predation by obligate predators to intra-guild predation by facultative omnivores in disturbed stream systems.

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