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Donald J. Benkendorf

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**OMNIVORE DENSITY AFFECTS COMMUNITY STRUCTURE  
THROUGH MULTIPLE TROPHIC CASCADES**

A Thesis  
Presented to  
The Faculty of the Department of Biology  
Murray State University  
Murray, Kentucky

In Partial Fulfillment  
of the Requirements for the Degree  
of Master of Science

by Donald James Benkendorf  
March 2018

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## ABSTRACT

Omnivores can dampen trophic cascades by feeding at multiple trophic levels, yet few studies have evaluated how intraspecific variation influences the effect of omnivores on community structure. The Speckled Dace (*Rhinichthys osculus*) is an omnivorous cyprinid that consumes algae and invertebrates and is abundant throughout the western United States. I sought to identify the effects of size and size structure on top-down control by dace and learn how these effects scaled with density. Dace were manipulated in a mesocosm experiment and resulting changes in invertebrate and algal communities and measures of ecosystem function were monitored. Omnivores affected experimental communities via two distinct trophic pathways (benthic and pelagic). In the benthic pathway, dace reduced benthic macroinvertebrate biomass, thereby causing density-mediated indirect effects that led to increased benthic algal biomass. Dace also reduced pelagic predatory macroinvertebrate biomass (notonectidae and corixidae), thereby significantly increasing the abundance of emerging insects. The effect of dace and hemipterans on emerging insects was mediated by a non-linear response to dace density with a pronounced peak at intermediate density. Omnivore size and size structure had minimal effects, indicating that the small and large dace used in this experiment share similar functional roles, and contrasting with recent studies that support the differential effect of intraspecific size structure on communities. My results indicate that the degree to which omnivores dampen trophic cascades depends on their relative effect on multiple trophic levels. Availability of an abundant, high calorie food source in the form of macroinvertebrates, and the absence of top predators, may have shifted dace diets from primary to secondary consumption, strengthening density-dependent trophic

cascades. Thus, both omnivore density and dietary shifts are important factors influencing omnivore-mediated communities.

**TABLE OF CONTENTS**

Acknowledgements.....	iii
Abstract .....	v
Table of Contents.....	vii
List of Tables.....	viii
List of Figures.....	ix
Introduction.....	1
Materials and Methods.....	4
Results.....	9
Discussion.....	13
Literature Cited.....	19

**LIST OF TABLES**

1. Descriptive statistics of invertebrate abundance responses to mesocosm treatments  
over the eight week duration of the experiment.....35
2. Descriptive statistics of invertebrate biomass responses to mesocosm treatments over  
the eight week duration of the experiment.....36
3. Descriptive statistics of water quality responses to mesocosm treatments over the eight  
week duration of the experiment.....37



**LIST OF FIGURES**

1. Hypothesized food web interactions of size and size structure on community structure and biomass.....	27
2. Experimental size by density dace treatments.....	28
3. Mean benthic algae biomass as indicated by chlorophyll a concentration.....	29
4. Mean pelagic hemipteran abundance for each treatment.....	30
5. Mean benthic macroinvertebrate biomass (without chironomidae) over time.....	31
6. Mean insect emergence abundance over time .....	32
7. Dace $\delta^{15}\text{N}$ collected at the end of the experiment in each treatment.....	33
8. Mean small and large dace $\delta^{15}\text{N}$ across treatments collected at the end of the experiment.....	34

## INTRODUCTION

Top-down control occurs when predators affect the abundance and distribution of lower trophic levels via consumption and threat of consumption, and is strongly interconnected with ecosystem functionality (Carpenter et al. 1985, Hunter and Price 1992, Terborgh and Estes 2010, Gianuca et al. 2016, Östman et al. 2016, Breviglieri et al. 2017, Winnie and Creel 2017). Trophic cascades are a form of top-down control where predators cause a pronounced alternating positive and negative cascading effect down a food chain (Paine 1969, Power 1990, Ripple et al. 2016). This phenomenon has been documented, to varying degrees, across aquatic and terrestrial ecosystems (Carpenter et al. 1985, Estes and Duggins 1995, Pace et al. 1999, Schmitz et al. 2000, Terborgh et al. 2001, Sinclair 2003, Breviglieri et al. 2017, Winnie and Creel 2017). However, predator traits often affect the strength of trophic cascades, as well as the degree to which cascades dampen as they reach lower trophic levels (Gianuca et al. 2016, Brose et al. 2017, Start and Gilbert 2017).

Predator size, and resulting population size structure, can strongly influence the top-down role of a predator on lower trophic levels (Rudolf and Rasmussen 2013, Renneville et al. 2015, Brose et al. 2016, Stevenson et al. 2016). For example, Rudolf and Rasmussen (2013) experimentally manipulated the size of larval dragonflies (*Anax junius*) within experimental ponds and found cascading effects on primary production that varied in intensity with dragonfly size treatments. The functional role of the dragonflies was dependent on developmental stage and concomitant size and

differentially affected broad ecosystem processes such as respiration and net primary production (Rudolf and Rasmussen 2013). Research that elucidates predator size effects is particularly timely as climate change has been implicated in causing a shift toward smaller body size in many different species, but especially among ectotherms because their rate of metabolism scales directly with temperature (Genner et al. 2010, Sheridan and Bickford 2011). The ecosystem scale repercussions of this “body downsizing” are just starting to be explored (Estes et al. 2011).

In addition to size, feeding strategy produces additional complexity that must be accounted for if accurate predictions are to be made regarding top-down effects (Okun et al. 2008, Long et al. 2011, Wootton 2017). For example, omnivore consumption at multiple trophic levels makes predictions about interaction strength between trophic levels difficult (Pimm and Lawton 1978), as the feeding strategy (e.g. resource proportionality) of an omnivore may change markedly with other traits such as size and developmental stage (Kratina et al. 2012). Understanding how an omnivore regulates top-down control is necessary given that omnivores are ubiquitous within ecosystems (Williams and Martinez 2004, Thompson et al. 2007). Although, research suggests that omnivores generally dampen trophic cascades (Bruno and O’Connor 2005), identifying if and how cascade intensity changes with intraspecific trait differences (e.g. size) and density of an omnivore is largely unexplored.

Density can determine the intensity of top-down effects (Power 1992, Carter and Rypstra 1995, Katano 2007), yet interactions between density and factors such as size, size structure, and omnivory are less understood. Proportional resource utilization among omnivores is often dependent on omnivore density, which affects resource availability

(Krivan and Diehl 2005, Katano 2007). For example, Katano found that the percentage of algae in the diet of Japanese Dace (*Tribolodon hakonensis*) was positively related to density (Katano 2007), such that dace at higher densities consumed higher proportions of algae. Additionally, proportional resource utilization may vary based on size and related developmental stage (Wolfshaar 2006, Kratina et al. 2012). For example, most fish species undergo ontogenetic shifts where they consume smaller, lower trophic level prey early in life and transition to larger, higher trophic level food as they grow larger (Werner and Gilliam 1984).

In this study, size and size structure of an omnivore were manipulated at varying densities within mesocosms that mimicked natural ecosystem conditions. I sought to better understand effects of size and size structure on an omnivore's functional role and how these variables interact with density by monitoring community structure and ecosystem function. I hypothesized (1) that small omnivores (Fig. 1A) would consume a proportionally greater amount of algae and small invertebrates and that large omnivores (Fig. 1B) would consume more large invertebrates and this would cause algal concentrations to be reduced in the small omnivore treatments and be elevated in the large omnivore treatments due to enhanced suppression of larger herbivorous invertebrates. Following this logic, I predicted that size structure treatments (Fig. 1C) would have intermediate effects because both small and large dace were present. Additionally, I hypothesized that (2) increasing density would cause a proportional increase in trophic cascade effects as measured by algal and invertebrate biomass.

## MATERIALS AND METHODS

### *Focal organism*

The Speckled Dace (*Rhinichthys osculus*; hereafter dace) is a small omnivorous minnow that consumes algae and invertebrates, although its diet often changes with developmental stage and resource availability (Pilger et al. 2010, Seegert et al., 2014). Dace are naturally found at variable size structures (Moyle and Vondracek 1985, *personal obs.*) and densities (Moyle and Vondracek 1985, Propst and Gido 2004) throughout their range, which broadly encompasses the United States west of the Rocky Mountains and longitudinally from lower British Columbia down to Sonora, Mexico (Pfrender et al. 2003). For example, Propst and Gido (2004) reported densities in secondary channels of the San Juan River varying yearly from just below 0.1 dace/m<sup>2</sup> to just over 1 dace/m<sup>2</sup> and Moyle and Vondracek (1985) reported densities in Martis Creek, California ranging from 0 to just under 6 dace/m<sup>2</sup>. While dace are most commonly found in flowing water habitat (Quist et al. 2004), they are habitat generalists that have been observed within beaver ponds, such as those at our field site, Kimball Creek, a small third-order stream located in arid west-central Colorado, United States. The ecological role of dace within this less common habitat type is largely unknown.

### *Experimental design*

From March 19 - March 24, 2016, 35 mesocosms (1000 L cattle tanks) were arranged in a 7 × 5 blocking pattern (5 blocks) and then filled with well water and seeded with 45 liters of homogenized Kimball Creek benthos from beaver ponds that contained natural invertebrate communities. Additionally, six backswimmers (*Notonecta sp.*), three

water beetles (*Haliphus sp.*), and 15 mayfly larvae (*Baetis sp.*) were added to each tank. For the next two months, these tanks were left open to facilitate natural colonization by the fauna from adjacent Kimball Creek. In May 2016, shade cloth (55%) was hung over the tanks to mimic riparian shading and to ensure temperature variation similar to local beaver ponds. On May 25, 2016, each mesocosm was further inoculated with 250 ml of homogenized invertebrate slurry. The slurry was created by dip-netting (500 um mesh) Kimball Creek beaver ponds, aggregating invertebrates into a 5 gallon bucket, mixing thoroughly, and then distributing a 250 ml aliquot to each tank. On the day prior to dace addition (see below), four large-mesh leaf packs containing 5g of dried Gambel oak (*Quercus gambelii*) and four ceramic tiles were added to each tank (Hauer and Lamberti 2007). Tiles were hung vertically from the south facing wall of each mesocosm with the bottom of each tile resting on the benthos. Leaf packs were placed in the mesocosms opposite the tiles. The leaf packs were used to monitor decomposition rates and the ceramic tiles were used to measure benthic algal biomass.

In order to measure the effect of dace size, size-structure, and density on community structure, seven experimental treatments (5 replicates each) were randomly assigned within experimental blocks (1 replicate per treatment per block). Large, small, and additive size structured dace treatments were replicated at low and high densities (see Fig. 2), with an additional fishless control treatment. Densities ranged from 0 to 3 dace/m<sup>2</sup>. Large dace were  $101.23 \pm 0.57$  millimeters (mm) (mean  $\pm$  se) in length and weighed  $9.81 \pm 0.087$  grams (g). Small dace were  $69.32 \pm 0.47$ mm and weighed  $2.85 \pm 0.055$ . The experiment began with dace addition on June 3, 2016 and ran through July 30, 2016 (8 week duration), at which time all dace were captured and euthanized.

### *Sample collection*

One leaf pack and one ceramic tile were sampled from each mesocosm at week 2, 4, 6, and 8 of the experiment. The leaf packs were immediately placed in whirl packs and frozen until they could be processed. Leaf packs were later processed for ash free dry mass determination following standard methods (Hauer and Lamberti 2007). The entire front surface of the tile wall was scrubbed and rinsed into a 250 ml container. Pelagic algae were measured by collecting a 250 ml pelagic grab sample on similar dates. All algal samples (benthic and pelagic) were immediately filtered through 0.7  $\mu\text{m}$  microfiber filters, frozen, and analyzed within 48 hours of collection for chlorophyll a concentrations, a proxy for algal biomass, using a Turner Designs Aquafluor Fluorometer (Turner Designs, San Jose, California, USA) and following EPA protocol 445.0 (Arar and Collins 1997).

Two 3.8 cm diameter integrated water column samples were taken from each mesocosm at week 4 and 8 to sample zooplankton abundance. The water column samples were collected with a PVC tube sampler that sampled the entire water column of each mesocosm (Devries and Stein 1991). Both water column cores were combined for each mesocosm and rinsed through a 153 micrometer mesh sieve and preserved in 70% ethanol. Benthic stovepipe cores (20 cm diameter) were used to sample benthic invertebrates and were performed on day 0, 30, and 60 (Hauer and Lamberti 2007). At the end of the experiment, pelagic macroinvertebrates were destructively sampled from each mesocosm with a seine. Emergent insects were sampled every two weeks using floating  $0.45 \times 0.45 \text{ m}^2$  emergence traps made from fine mesh and PVC pipe (Malison et al. 2010). Benthic macroinvertebrates were stored in formalin solution and all other

invertebrates were stored in 70% ethanol. Benthic and pelagic macroinvertebrates were identified to a taxonomic resolution at which functional feeding group could be determined, generally genus or family, and then counted and measured for subsequent biomass determination. Emergent insects were also counted and measured for biomass determination.

Dace were euthanized and tissue samples were collected for stable isotope analysis (Post 2002). The samples consisted of one randomly selected dace per replicate for each treatment or two fish per replicate in the size structure treatments (1 large and 1 small dace). Stable isotope samples were sent to the Southern Illinois University-Carbondale Mass Spectrometry Facility where they were analyzed for  $\delta^{15}\text{N}$  with a ThermoFinnigan DeltaV mass spectrometer.

Water quality parameters including dissolved oxygen (DO), temperature, pH, and specific conductivity were measured once weekly (9 total) at a sequence of dawn, dusk, dawn using a YSI Professional Plus (YSI Incorporated, Yellow Springs, Ohio, USA). Net primary production (NPP) and respiration within each mesocosm were measured weekly. NPP was calculated as the difference between evening DO and the prior morning DO and respiration was calculated as the difference between evening DO and the following morning DO (Downing and Leibold 2002, Rudolf and Rasmussen 2013).

### *Statistical analyses*

Treatment effects on decomposition, algal biomass (benthic and pelagic), zooplankton abundance, macroinvertebrate biomass and abundance (benthic, benthic + pelagic, and emergent), NPP, respiration, and nutrient concentrations (nitrate/nitrite,



ammonia, soluble reactive phosphorous) were analyzed using linear mixed effects models (Bolker et al. 2009) using the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016) packages in R. If significant differences were observed, the lsmeans package (Lenth 2016) in R was used to test pairwise comparisons. Within each model, the blocking factor (mesocosm position) was considered to be a random effect and treatment (dace size  $\times$  density) and time (week) were fixed effects. Pelagic macroinvertebrate abundance was analyzed with a one-way ANOVA and Tukey's honestly significant difference test used for post hoc analyses. In order to improve normality and heteroscedasticity,  $\log_{10} + 1$  or  $\log_{10}$  transformations were performed on macroinvertebrate biomass and abundance and pelagic and benthic algae concentrations. A square root transformation was performed on the zooplankton abundance and emergence abundance data. To account for two missing replicates (in which dace died), the Satterthwaite approximation for degrees of freedom was used for all tests (Rudolf and Rasmussen 2013). An additional emergence replicate of the 4 dace treatment was lost because high wind blew the emergence trap off of the mesocosm during one of the sampling periods. A one-way ANOVA was performed on the stable isotope data with Tukey's honestly significant difference test used for post hoc analyses. In addition to stable isotope analysis among treatments, a Welch two-sample t-test was used to compare  $\delta^{15}\text{N}$  between small and large dace across treatments. Water quality parameters (DO, temperature, pH, specific conductivity) were averaged across all nine sampling dates for each replicate and were analyzed with a multivariate analysis of variance (MANOVA) (Cobbaert et al. 2010). All analyses were conducted using R version 3.2.4 (R Development Core Team, 2016).

## RESULTS

### *Decomposition and algal biomass*

Decomposition did not differ significantly among treatments ( $F_{6, 22.6} = 0.93$ ,  $P = 0.54$ ). There was a significant effect of time on benthic algal biomass ( $F_{3, 78} = 290.9$ ,  $P < 0.0001$ , Fig. 3) and each treatment increased significantly between week 2 and week 8 (all  $P < 0.05$ ). However, the rate of increase was different among treatments ( $F_{6, 26} = 9.4$ ,  $P < 0.0001$ ) and there was also a significant interaction with time ( $F_{18, 78} = 2.8$ ,  $P = 0.0009$ ). All dace treatments had significantly higher biomass of benthic algae than the fishless control treatment (all  $P < 0.05$ ), except for the lowest density dace treatment (1 dace;  $P = 0.53$ ). Additionally, the 8, 6, and 3 dace treatments had significantly higher benthic algal biomass than the 1 dace treatment (all  $P < 0.05$ ) and the 4 dace treatment had an increase in benthic algae compared to the 1 dace treatment, though not a significant increase ( $P = 0.07$ ).

Pelagic algal biomass also increased significantly between week 0 and week 8 for all treatments ( $F_{4, 104} = 153.2$ ,  $P < 0.0001$ ) and the rate of increase was significantly different among treatments ( $F_{6, 26} = 6.7$ ,  $P = 0.03$ ), but there was no significant interaction between treatment and time ( $F_{24, 104} = 1.3$ ,  $P = 0.21$ ). Post hoc comparisons revealed that the 8 dace treatment had significantly higher pelagic algal biomass than the 1 dace treatment ( $P = 0.016$ ).

### *Invertebrate biomass*

No significant differences existed for zooplankton abundance among the treatments ( $F_{6, 25} = 1.1$ ,  $P = 0.42$ ) or across time ( $F_{1, 25} = 0.88$ ,  $P = 0.36$ ).

Total macroinvertebrate biomass at week 8 (pelagic and benthic macroinvertebrates) varied significantly among treatments ( $F_{6, 21.7} = 24.8$ ,  $P < 0.0001$ ). The control treatment had significantly higher biomass than all other treatments (all  $P < 0.044$ ). Additionally, the 1 dace treatment had significantly higher biomass than all treatments, except the fishless control (all  $P < 0.05$ ). Total macroinvertebrate abundance at week 8 did not vary significantly among treatments ( $F_{6, 22.5} = 1.25$ ,  $P = 0.32$ ). Week 8 pelagic macroinvertebrate abundance (Fig. 4) followed a similar, and even more pronounced, trend as total macroinvertebrate biomass and varied significantly among treatments ( $F_6 = 20.8$ ,  $P < 0.0001$ ). The control treatment had a significant increase in pelagic macroinvertebrate abundance compared to all other treatments and the 1 dace treatment also had a significant increase in pelagic macroinvertebrate abundance compared to all other treatments, except the control treatment (all  $P < 0.05$ ). Tables 1 and 2 show the abundances and biomasses, respectively, of the major macroinvertebrate groups collected in each treatment from the week 8 benthic core.

In addition to week 8 total macroinvertebrate data (benthic + pelagic), total benthic macroinvertebrate and total primary consumer macroinvertebrate data were analyzed over time (weeks 0, 4, and 8). There was a significant difference in total biomass and abundance over time for total benthic macroinvertebrates (both  $P < 0.0001$ ). However, no significant differences were observed among treatments (biomass:  $F_{6, 26} = 0.66$ ,  $P = 0.68$  and abundance:  $F_{6, 26} = 0.43$ ,  $P = 0.85$ ). There was a significant difference in total primary consumer biomass and abundance over time ( $P < 0.0001$ ), but again there

was no difference in biomass or abundance among treatments ( $F_{6, 26} = 0.90$ ,  $P = 0.51$  and  $F_{6, 26} = 0.46$ ,  $P = 0.83$ , respectively). These analyses were repeated after removing chironomidae because the comparatively high proportion of chironomidae across treatments appeared to obfuscate observable differences among the other less abundant taxa. After removing chironomidae biomass, total benthic macroinvertebrate biomass was significantly different among treatments ( $F_{6, 78} = 3.8$ ,  $P = 0.002$ , Fig. 5A), with the control and 1 dace treatments having a significant increase in biomass compared to the 8 dace treatment ( $P = 0.015$  and  $P = 0.010$ , respectively). There was also a significant interaction between treatment and time ( $P = 0.048$ ). A similar trend was observed for the primary consumer biomass when chironomidae were removed, with a significant difference occurring among treatments ( $F_{6, 78} = 3.2$ ,  $P = 0.007$ , Fig. 5B). Again, the control and 1 dace treatments had a significant increase in biomass compared to the 8 dace treatment ( $P = 0.019$  and  $P = 0.022$ , respectively). There was no significant effect of time on either total benthic or primary consumer macroinvertebrate biomass after removing chironomidae (both  $P > 0.05$ ). After removing chironomidae, total macroinvertebrate abundance and total primary consumer abundance did not differ by treatment ( $F_{6, 26} = 0.82$ ,  $P = 0.57$  and  $F_{6, 26} = 0.77$ ,  $P = 0.60$ , respectively), but there was a significant effect of time for both ( $P < 0.001$ ).

A significant difference occurred over time for both emergent insect abundance and biomass, with a peak occurring at week 4 (biomass:  $F_{3, 75} = 28.9$ ,  $P < 0.0001$  and abundance:  $F_{3, 75} = 27.9$ ,  $P < 0.0001$ ). Significant differences in emerging insect abundance existed among treatments ( $F_{6, 25} = 3.2$ ,  $P = 0.019$ , Fig. 6), However no significant difference occurred among treatments for emerging insect biomass ( $F_{6, 25} =$

0.78,  $P = 0.60$ ) and there were no significant interactions between time and treatment for either abundance or biomass ( $P = 0.39$  and  $P = 0.47$ , respectively). Post hoc comparisons showed that the 3 dace and the 2 dace treatments had significantly higher abundance of emerging insects than the control treatment ( $P = 0.040$  for both). Total abundance of benthic macroinvertebrates with winged adult stages (primarily chironomidae and baetidae) was also analyzed to better elucidate trends in insect emergence and specific mechanisms controlling observed trends. There was no significant difference among treatments ( $F_{6, 26} = 0.52$ ,  $P = 0.79$ ), however, there was a significant effect of time ( $F_{2, 52} = 68.7$ ,  $P < 0.0001$ ), with a peak occurring at week 4.

#### *Stable isotope data*

Average  $\delta^{15}\text{N}$  across treatments was significantly lower for small dace than for large dace ( $t_{33.7} = 2.83$ ,  $P = 0.008$ , Fig. 8). Stable isotope values also revealed significant differences in  $\delta^{15}\text{N}$  enrichment among treatments ( $F_7 = 4.6$ ,  $P = 0.001$ , Fig. 7). Specifically, large dace in the 1 dace treatment had higher  $\delta^{15}\text{N}$  values than the small dace in the 3 dace treatment and the small dace in the 8 dace treatment ( $P = 0.006$  and  $P = 0.06$ , respectively). Additionally, large dace in the 2 dace treatment, large dace in the 8 dace treatment, and small dace in the 4 dace treatment all had higher  $\delta^{15}\text{N}$  values than the small dace in the 3 dace treatment ( $P = 0.012$ , 0.06, and 0.008, respectively).

#### *Water quality parameters*

A MANOVA revealed no significant differences among water quality parameters (DO, temperature, pH, specific conductivity;  $F_{24, 81.5}$ ,  $P = 0.60$ , Wilks'  $\lambda = 0.44$ ). Nutrient concentrations increased over time for all three nutrients measured (all  $P < 0.05$ ),

however there were no significant differences in nutrient concentrations among treatments. The treatment means and standard errors of the water quality parameters at week 8 of the experiment are presented in Table 3.

#### *Productivity and respiration*

NPP and respiration rate increased significantly over time ( $P < 0.0001$ ). However, only respiration rate was significantly different among treatments ( $F_{6, 25} = 2.8$ ,  $P = 0.031$ ). Pairwise comparison revealed that rate of respiration in the 8 dace treatment was significantly higher than in the 4 dace treatment ( $P = 0.014$ ).

## **DISCUSSION**

My experimental results suggest that Speckled Dace exerted top-down forces that affected the underlying invertebrate community and cascaded to benthic and pelagic algae. Changes in algal biomass were best explained by changes in dace density. At low dace densities, algae increased because dace were not effective at suppressing invertebrate herbivores. However, at high densities, dace were very effective at controlling herbivores (Fig. 5B) and this led to a dramatic increase in benthic algae (Fig. 3) and a moderate increase in pelagic algae. This particular pathway from fish to herbivorous invertebrates to algae has been documented in numerous studies (Carpenter et al. 1985, Power 1990, Richardson et al. 2016), but rarely with an omnivorous species that consumes both algae and invertebrates (Bruno and O'Connor 2005, Finke and Denno 2005, Long et al. 2011) and even more rarely with direct density manipulation of the top-predator (Katano 2007). My results highlight the importance of density in experiments

seeking to better understand trophic cascade dynamics and species-specific effects on top-down control. The range of densities used in my experiment was similar to natural populations, but my results show that the magnitude of trophic cascades varied greatly within this range, and might not have been detected without density manipulation.

Predicting top-down effects by an omnivore is difficult because omnivory is a dynamic feeding strategy and many factors affect its strength (Wootton 2017). The literature broadly indicates that Speckled Dace are generalist omnivores, feeding opportunistically as resource type and availability changes (Pilger et al. 2010, Seegert et al., 2014). Therefore, I had hypothesized that at high densities, dace would consume a commensurately higher proportion of algae and that this would dampen any cascading effects. In contrast, I saw an increase in top-down control of macroinvertebrates with dace density, and my algal results refute increased algal consumption with dace density. It is possible that even our highest dace density treatment ( $\sim 3$  dace/m<sup>2</sup>) was not high enough to trigger a dietary shift from macroinvertebrates to increased algal consumption. Indeed, optimal foraging theory predicts that animals will utilize the resource that maximizes net energy gain (Pyke et al. 1977, Marcarelli et al. 2011, Cachera et al. 2017), and macroinvertebrates were more energetically valuable than algae (Coll and Guershon 2002, Buck et al. 2003), regardless of dace density.

Emerging insect abundance results were also shaped by differences in dace density, however, the effects of density were non-linear in this case. My results indicated that the intermediate dace density treatments (2 dace and 3 dace) had a significantly higher abundance of emerging insects than the other treatments. These emergence results do not correspond with benthic macroinvertebrate abundance, where no significant

differences in total benthic abundance of macroinvertebrates with winged adult stages (primarily chironomidae and baetidae) occurred among treatments. This result supports the idea that variation in emergence does not merely reflect treatment differences in benthic macroinvertebrate abundance (i.e. fewer benthic macroinvertebrates in certain treatments would imply fewer emerging insects). One explanation for these emergence results is that at high dace densities (e.g. 4, 6, and 8 dace treatments), fewer emerging insects were able to evade direct predation by dace and at low dace densities (e.g. 0 and 1 dace treatments) fewer emerging insects were able to evade predation by abundant pelagic hemipteran predators. Indeed, corixidae and notonectidae were extremely prevalent in the absence of dace and comprised a high proportion of the animal biomass in the fishless control and 1 dace treatment (Fig. 4). Notonectids are formidable predators in fishless ponds and can cause pelagic trophic cascades yet have minimal effect on benthic invertebrates (Blaustein 1995). Therefore, the intermediate dace densities in the present experiment may have been sufficient to suppress hemipteran abundance but insufficient at suppressing emerging insect abundance.

Reduced densities of dace leading to high densities of intermediate hemipterans is an example of mesopredator release (Soulé et al. 1988). This phenomenon has been documented in terrestrial and aquatic systems (Ritchie and Johnson 2009) and describes the rise in abundance of intermediate predators that accompanies the decline in top predator abundance. Intraguild predation theory predicts this type of interaction in a stable system, where intermediate predators (pelagic predators) are competitors for a shared resource (herbivorous invertebrates) and the intraguild predators (dace) prey upon both groups (Polis et al. 1989). The stability of intraguild predator systems depends on



many factors such as defenses and refuges used by the intraguild prey and the population density of the intraguild predator (Finke and Denno 2006, Kratina et al. 2010, Anderson and Semlitsch 2016). I observed increased emergence in the presence of the intraguild predator (dace), but this was only true at intermediate dace densities. At high dace densities, the intraguild predator was numerous enough to suppress emergence directly. However, multiple predators often create unexpected predator-prey interactions. These interactions among predators can lead to variable prey responses that depart from additive predictions stemming from observations of independent predator effects (i.e. single predator systems) (Sih et al. 1998). For example, Peckarsky and McIntosh (1998) found that size of emerging *Baetis* mayflies was smaller in the presence of brook trout and stoneflies separately, yet there was no additive effect on mayfly size with both predators present. While Peckarsky and McIntosh (1998) attributed this to a behavioral change in stonefly foraging in the presence of trout, I observed a dace density threshold (2 dace), above which little difference occurred in pelagic invertebrate abundance, and dace were responsible for moderating the actual densities of pelagic invertebrate predators, not simply their behavior.

Omnivory can also be affected by size. Historically, food web theory has treated each species as a discrete unit, with all of the individuals within that species displaying a similar functional role within its ecosystem (Miller and Rudolf 2011). As a result, the majority of studies have focused on interspecific differences between predators and the differential role of these species on top-down control. This approach, however, has neglected intraspecific variation (e.g. size) and the variable ecological roles that result

within a species (Jansson et al. 2007, Bonaldo and Bellwood 2008, Albert et al. 2010, Bolnick et al. 2011).

My initial hypothesis concerning small dace feeding behavior (i.e. small dace would consume more algae and a narrower range of macroinvertebrates) was partially supported by the significantly lower  $\delta^{15}\text{N}$  values in small dace compared to large dace, which indicates small dace were feeding lower on the food web than large dace. However, both small and large dace consumed enough macroinvertebrates to produce a strong trophic cascade on algal biomass regardless of dace size treatment. Thus, in my experiment, small and large dace performed similar functional roles. This may indicate that factors related to size such as gape limitation and trait-mediated prey fear response were not limiting factors between small and large dace. Alternatively, it is possible that my hypothesized shifts in feeding strategy with dace size did occur, but the effects of these shifts were shrouded by consistently strong consumption of abundant herbivorous invertebrates. Also, top predators such as trout were absent from my mesocosms. Top predators may cause fear-induced shifts in feeding strategy that differentially affect small and large individuals of the same species such as dace. Therefore, differences in feeding strategy between small and large dace may be accentuated in the presence of natural predators, which were absent in my experiment.

Analyzing the strength of trophic links between an omnivore and its food resources provides a more quantitative means of predicting the extent to which an omnivore dampens trophic cascades (Williams and Martinez 2004, Wootton 2017). For example, Bruno and O'Connor (2005) found that the trophic links between an omnivore and its algal and herbivorous invertebrate resources were strong and this caused a

dampened trophic cascade compared to a trophic cascade produced by a non-omnivorous predator that primarily consumed herbivorous invertebrates. Indeed, when predicting omnivore effects on trophic cascades, it is necessary to consider proportional resource utilization of each lower trophic level by the omnivore (Kratina et al. 2012). While I did not quantitatively calculate link strength between each trophic level utilized by dace, my results indicated that the trophic link between dace (both small and large) and herbivorous invertebrates was relatively strong and that the link between dace and algae was relatively weak. Dace in my experiment exhibited a low degree of omnivory, and I found that trophic cascade dampening was minimal. My results contrast those of Bruno and O'Connor (2005), who used a strong omnivore and observed a strongly dampened trophic cascade as a result. These results suggest that the effect of omnivory on trophic cascades is highly dependent on the degree of omnivory exhibited by the predator: the more omnivorous, the more likely cascade effects will be dampened. Therefore, a thorough evaluation of omnivorous link strength among trophic levels will provide much more accurate predictions regarding omnivore effects on trophic cascades.

A growing body of literature exists that describes the variable effect that omnivores have on trophic cascades and ecosystem stability, however the specific factors responsible for these differences have gone largely unstudied (Kratina et al. 2011, Wootton 2017). This experiment provides empirical support for omnivorous trophic cascades that occur along multiple trophic pathways and are mediated by omnivore density and by the relative strength of consumption at multiple trophic levels. When my results are contrasted with similar studies (e.g. Bruno and O'Connor 2005, Katano 2007), it is clear that there is a high degree of variation among and within omnivores. While I

did not observe differential effects of omnivore size on trophic cascade intensity, I did observe a difference in feeding strategy between small and large dace. However, these feeding differences were not strong enough to overcome the strong consumption of herbivorous invertebrates by both size classes and produce size dependent trophic cascades. Predictions regarding omnivore effects on trophic cascades and top-down control in general can be improved by stronger consideration of specific trophic link strength and distribution among trophic levels (Long et al. 2011, Pujoni et al. 2016). Furthermore, in our quest to better predict trophic cascades and ecosystem functioning at large, attention should be given to the factors, both inter and intraspecific, that create variation in feeding strategy (Rudolf and Rasmussen 2013). In doing so, ecologists will be better equipped to forecast ecosystem responses to anthropogenic disturbance and to manage and restore degraded ecosystems (Estes et al. 2011, Sheridan and Bickford 2011, Brose et al. 2016, Stevenson et al. 2016).

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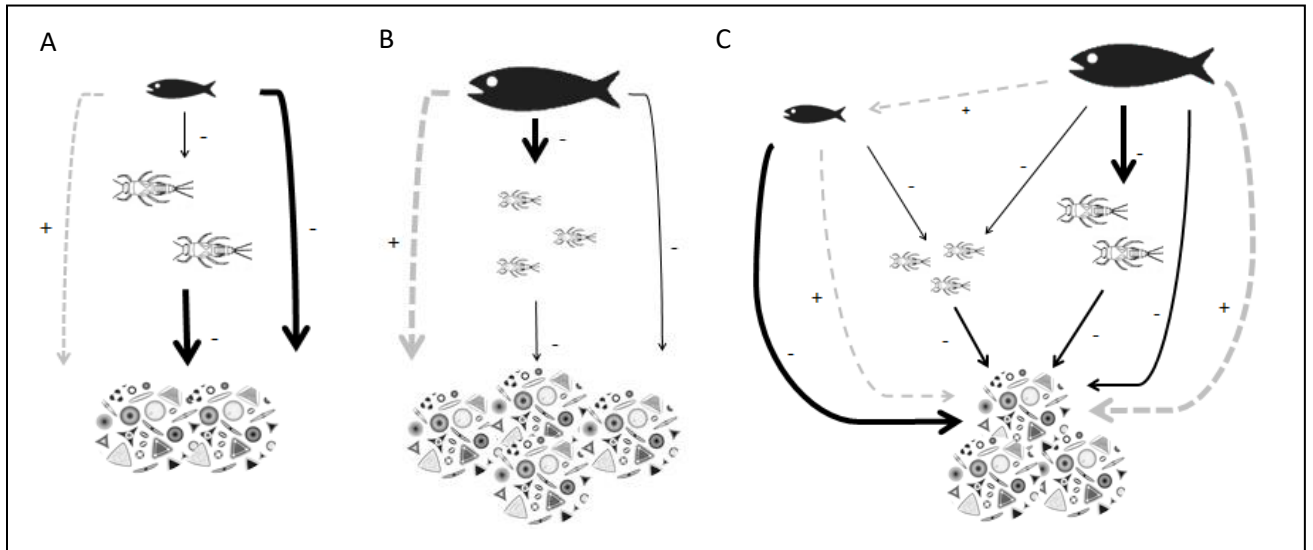
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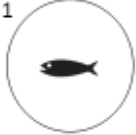
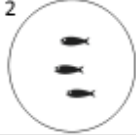
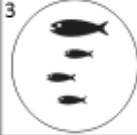
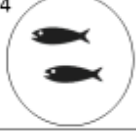
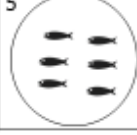

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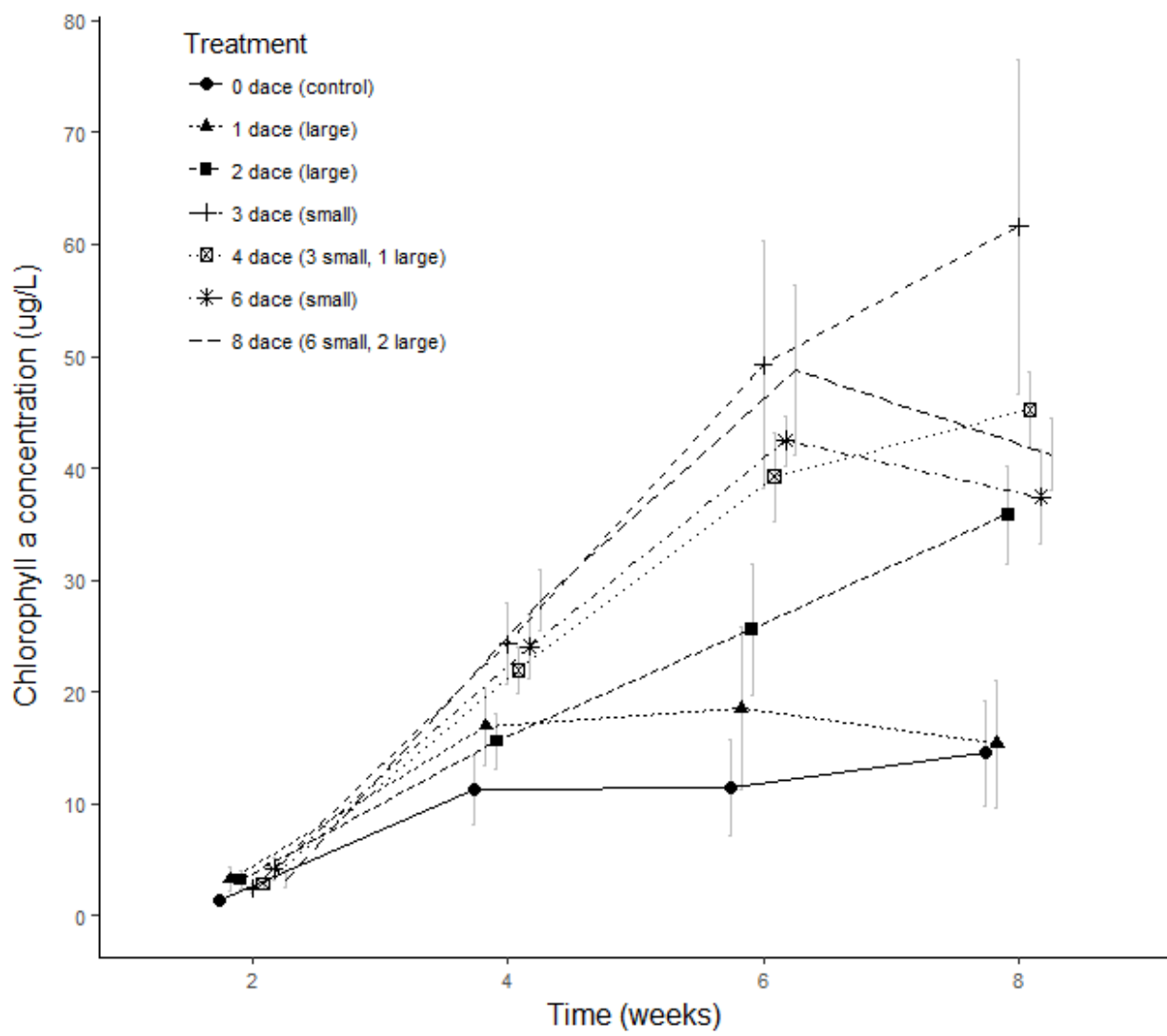
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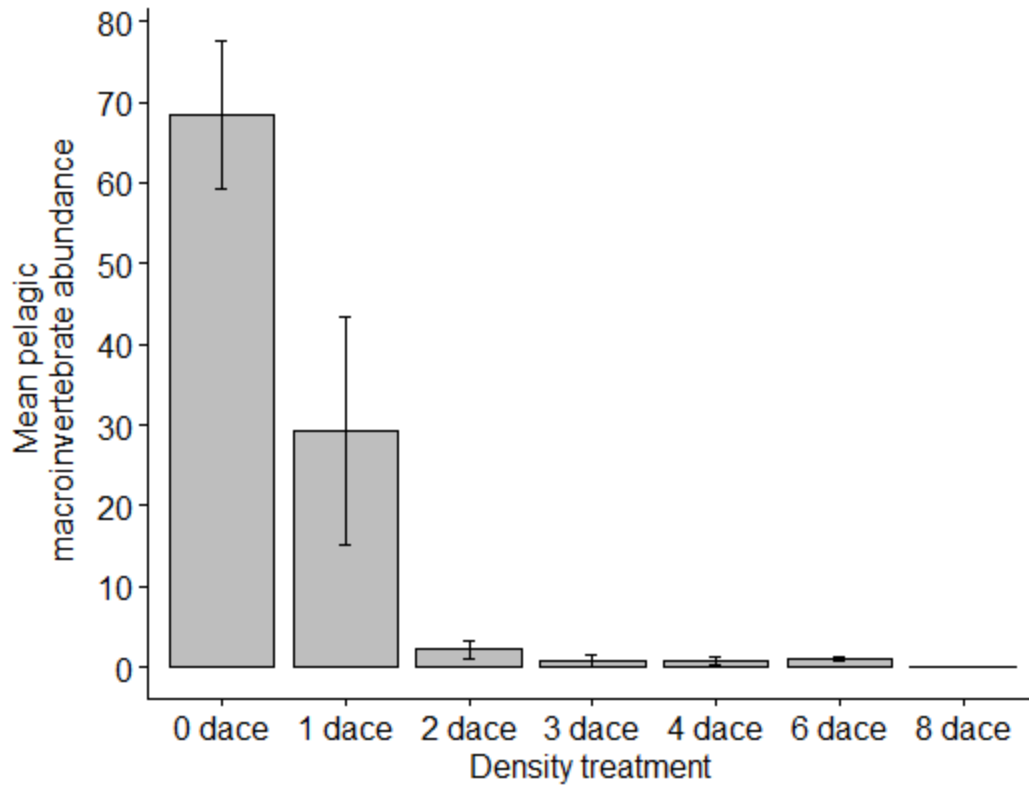
**Figure 1.** Hypothesized food web interactions of size and size structure on community structure and biomass. A) Small omnivores exert a direct negative effect on smaller sized herbivores, but also directly consumes appreciable amounts of algae. B) Large omnivores are able to consume a broader size range of herbivores, and also directly consume fewer algae. C) Size-structured omnivores exert an intermediate effect because interactions imposed by small and large omnivore are present. Solid black lines indicate direct negative effects and dashed grey lines indicate indirect positive effects. Width of lines represents hypothesized interaction strength.

	Large Dace	Small Dace	Size Structure
Low Density	1 	2 	3 
High Density	4 	5 	6 

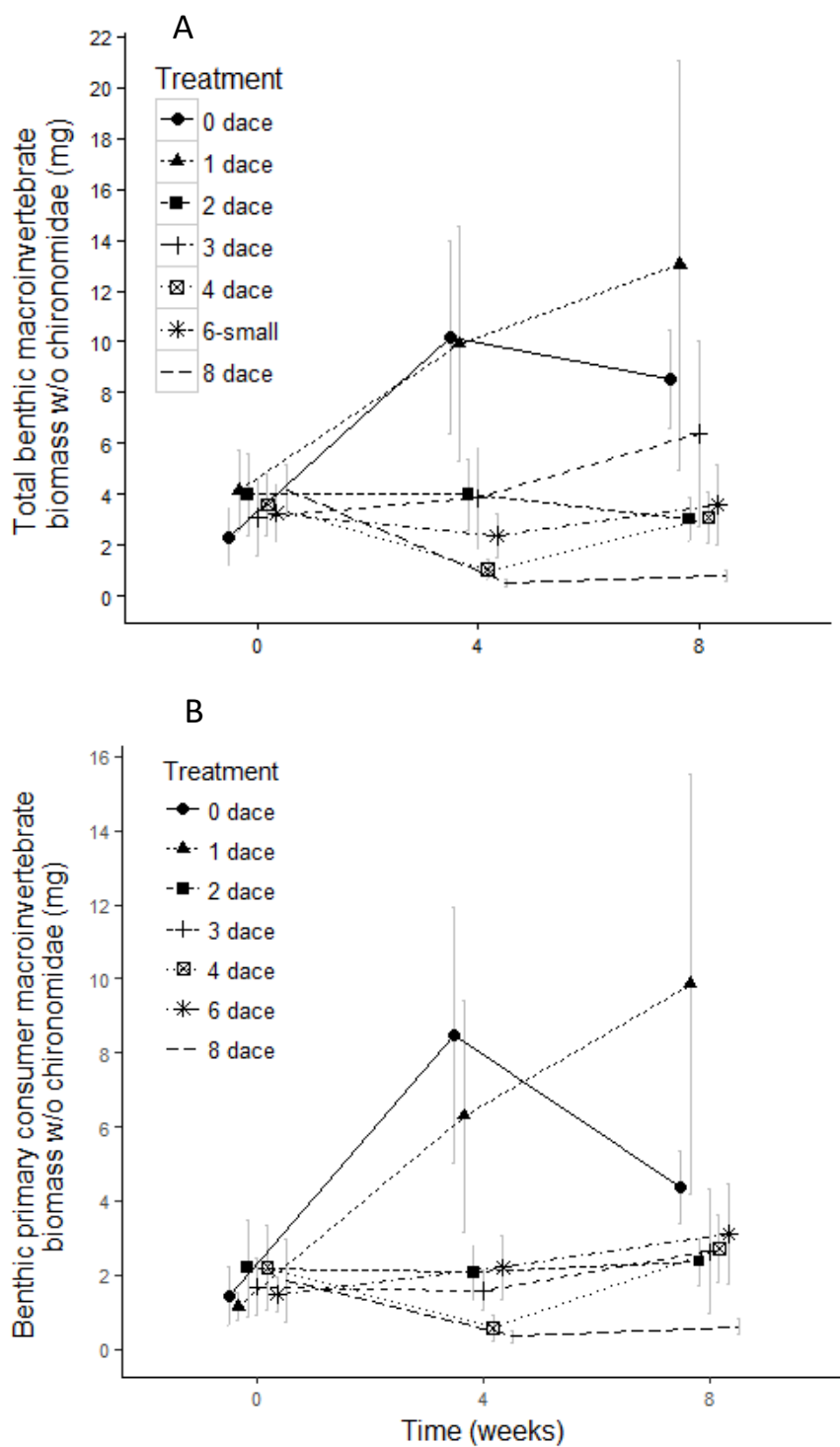
**Figure 2.** Experimental size by density dace treatments. Each treatment was replicated 5 times and each replicate occurred within one mesocosm (circle). The fishless control (treatment 7) is not shown.



**Figure 3.** Mean benthic algae biomass as indicated by chlorophyll a concentration  $\pm$  SE (gray vertical bars) over time.

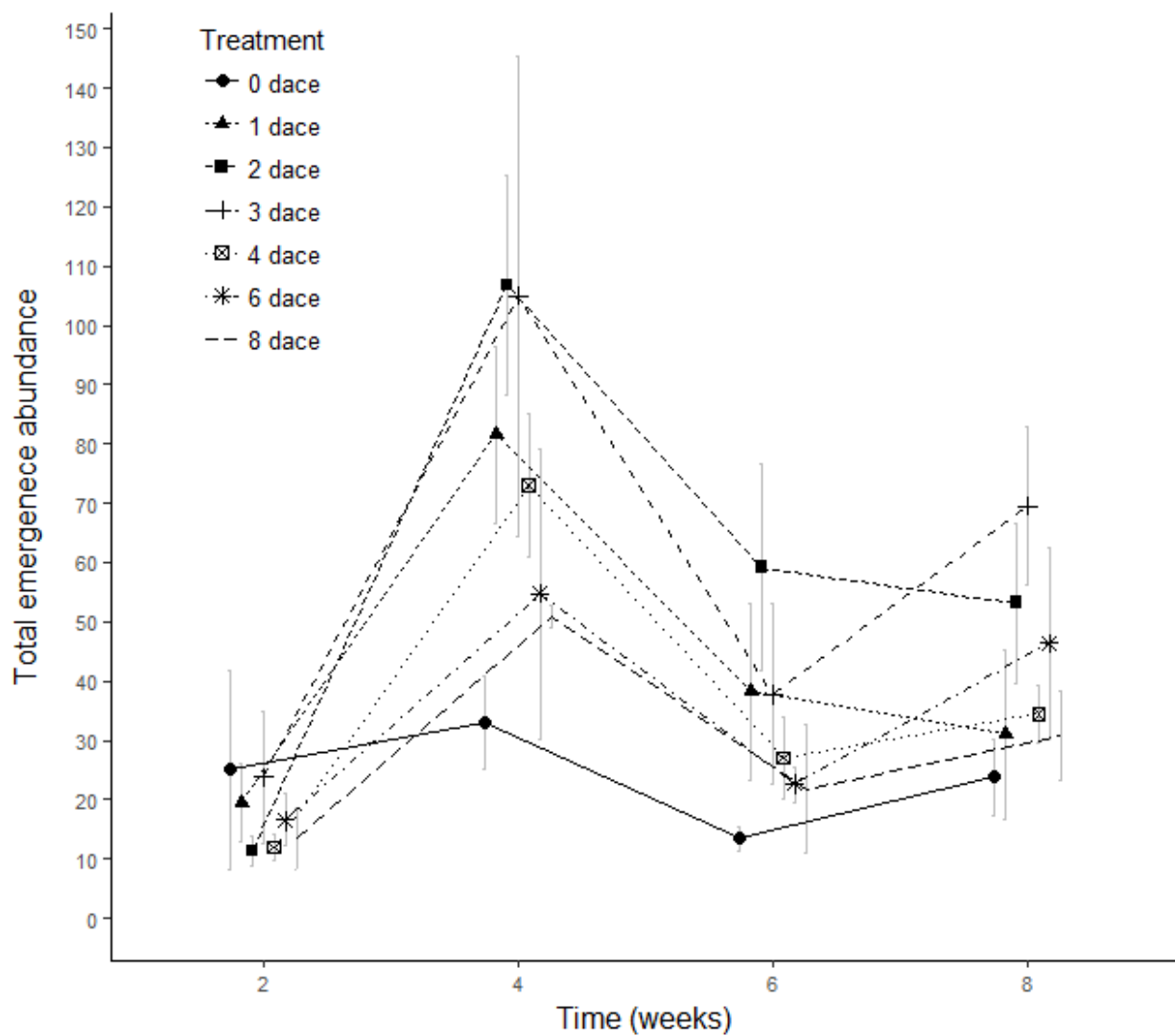


**Figure 4.** Mean  $\pm$  SE of pelagic hemipteran abundance for each treatment. Density is dace/mesocosm.

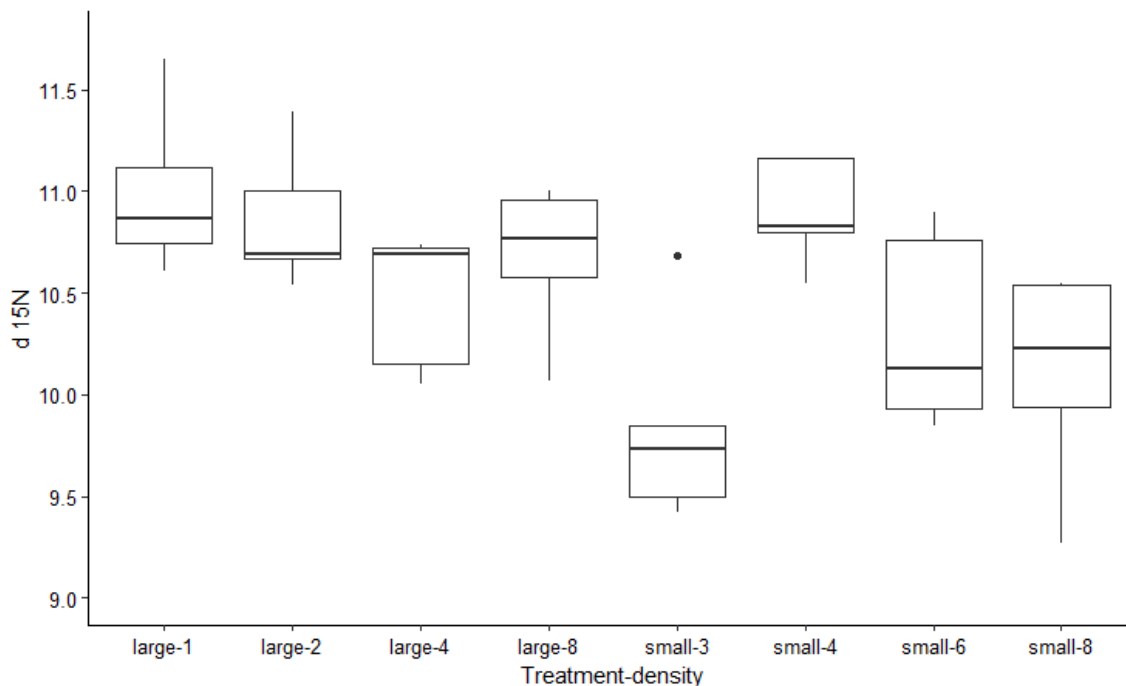


**Figure 5.** Mean  $\pm$  SE of A) total benthic macroinvertebrate biomass (without chironomidae) over time and B) benthic primary consumer macroinvertebrate biomass (without chironomidae) over time.

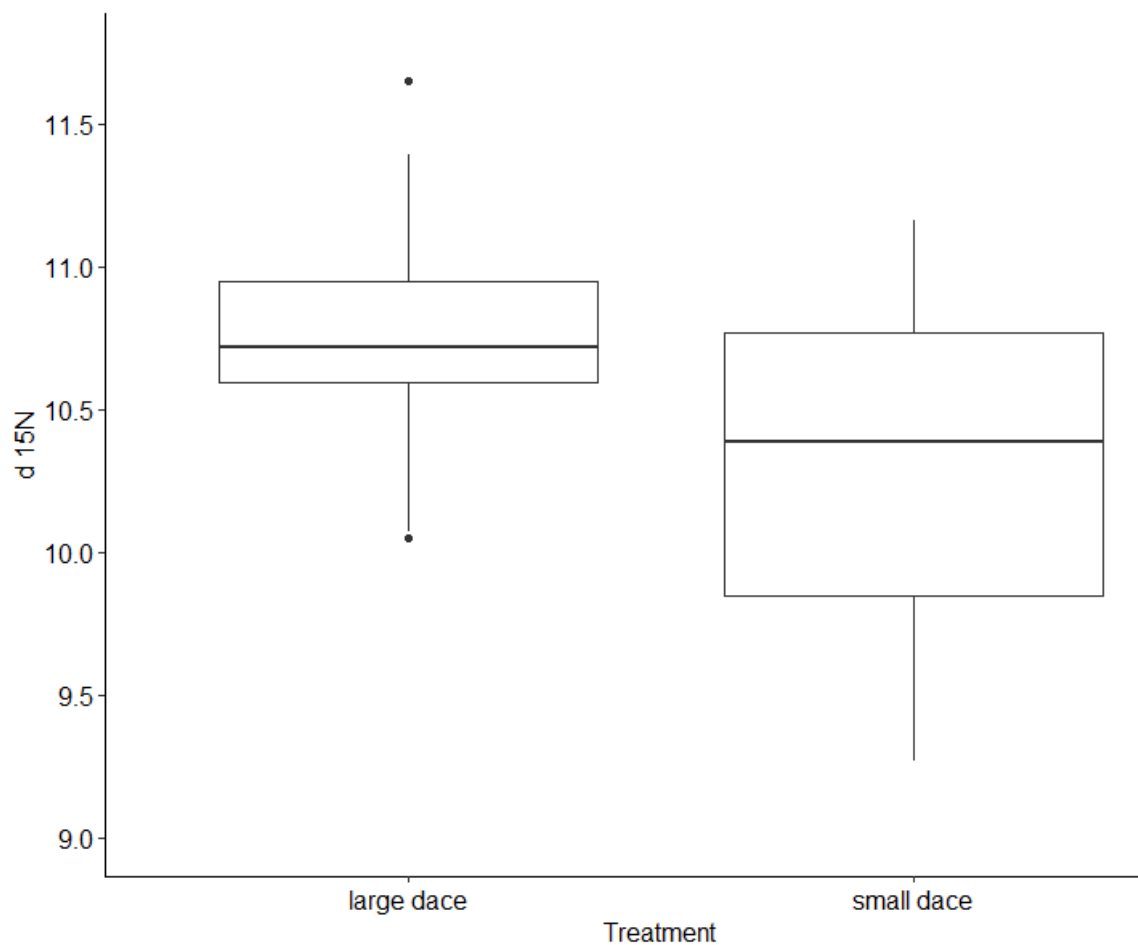




**Figure 6.** Mean insect emergence abundance  $\pm$  SE over time.



**Figure 7.** Dace  $\delta^{15}\text{N}$  collected at the end of the experiment in each treatment. Treatments along the x-axis are in the form size-density because size structure treatments had both small and large dace. The center line of each box is the median and the bottom and top of the box are 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The tails extend to the extremes of the data up to 1.5 times the interquartile range from the box. Extreme outliers are indicated with solid black circles.



**Figure 8.** Mean small and large dace  $\delta^{15}\text{N}$  across treatments collected at the end of the experiment. The center line of each box is the median and the bottom and top of the box are 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The tails extend to the extremes of the data up to 1.5 times the interquartile range from the box. Extreme outliers are indicated with solid black circles.

**Table 1.** Descriptive statistics of invertebrate abundance responses to mesocosm treatments over the eight week duration of the experiment. Data are from one 20 cm diameter benthic core collected from each mesocosm at week 8.

Taxa	Taxa Abundance by Treatment													
	0 dace	n = 5	1 dace	n = 4	2 dace	n = 5	3 dace	n = 4	4 dace	n = 5	6 dace	n = 5	8 dace	n = 5
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gastropoda	38	13.2	64.8	30.5	16.6	5.2	25.3	14.4	32	13.8	34.8	10.1	11.2	6.2
<i>Helobdella sp.</i>	9.6	2	8	2.1	6	1.9	1.3	0.9	3.2	0.7	2.8	0.7	1.4	0.4
Corixidae	15	4	14.8	11.1	0.6	0.6	0.8	0.8	0.4	0.4	0.2	0.2	-	-
<i>Notonecta sp.</i>	50.8	10.2	14	6.7	1.6	1.2	-	-	-	-	0.8	0.2	-	-
Dytiscidae	2.2	1.6	1	1	-	-	2.5	1.9	0.2	0.2	0.2	0.2	-	-
Baetidae	21.4	9.7	22.5	16.3	21.8	8.5	3.5	2	28.8	11.5	7.4	4	16	8.8
Oligochaeta	9.6	3.7	34.8	15.6	13	6.5	9.3	7.9	13	5.9	23.5	20.9	6.4	3.9
Chironomidae	199.8	34.7	302.8	158.7	413.8	154.1	417	76.7	262	114.9	256.8	73.4	176.2	27.3
Total macroinvertebrates	346.4	32.4	462.5	181.1	473.4	157.7	459.5	84.8	339.6	127.4	326.4	83.9	211.2	36.5
Chironomidae emergence	21.4	7	29.5	14.8	53	13.6	69.5	13.4	33.2	4	46.4	16.1	30.8	7.4
Baetidae emergence	5.3	2.1	1.2	1.5	0.2	0.2	-	-	-	-	-	-	-	-
Total emergence	23.8	6.5	31	14.4	53.2	13.5	69.5	13.4	33.2	4	46.4	16.1	30.8	7.4

**Table 2.** Descriptive statistics of invertebrate biomass responses to mesocosm treatments over the eight week duration of the experiment. Data are from one 20 cm diameter benthic core collected from each mesocosm at week 8.

Taxa	Taxa Biomass by Treatment													
	0 dace	n = 5	1 dace	n = 4	2 dace	n = 5	3 dace	n = 4	4 dace	n = 5	6 dace	n = 5	8 dace	n = 5
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gastropoda	0.3	0.1	1.2	0.4	0.8	0.5	1.9	1.5	0.5	0.2	2.1	1.3	0.4	0.2
<i>Helobdella sp.</i>	0.9	0.2	0.9	0.2	0.6	0.2	0.2	0.1	0.3	0.1	0.3	0.1	0.2	0.04
Corixidae	35.7	8	22.8	16.3	1.8	1.8	1.6	1.6	1.2	1.2	0.4	0.4	-	-
<i>Notonecta sp.</i>	537.4	112.3	139	72.1	13.2	9.1	-	-	-	-	7.3	1.9	-	-
Dytiscidae	3.2	2.7	2.3	2.3	-	-	3.6	3.4	0.04	0.04	0.2	0.2	-	-
Baetidae	3.5	0.8	7.4	5.9	1	0.5	0.3	0.2	0.7	0.3	0.3	0.1	0.2	0.1
Oligochaeta	0.6	0.3	1.2	0.6	0.5	0.2	0.4	0.2	1.5	0.9	0.7	0.2	0.003	0.003
Chironomidae	6.4	0.7	11.2	5.5	16.4	5.6	16.3	5	11.7	2.6	10.5	2.8	8.4	1.4
Total macroinvertebrates	588	107.1	185.9	76.7	34.4	13	24.2	5.3	15.9	3.8	21.7	3.7	9.2	1.5
Chironomidae emergence	4.2	1.2	4.7	2.2	8.2	2	8.8	1.6	5	0.4	10	2.6	7.6	1.9
Baetidae emergence	3.52	3.1	2.85	2.85	0.4	0.4	-	-	-	-	-	-	-	-
Total emergence	7.7	2.5	7.5	3.3	8.6	1.8	8.8	1.6	5	0.4	10	2.6	7.6	1.9

**Table 3.** Descriptive statistics of water quality responses to mesocosm treatments over the eight week duration of the experiment. Data are from each mesocosm at week 8.

Parameter	Water Quality by Treatment													
	0 dace	n = 5	1 dace	n = 4	2 dace	n = 5	3 dace	n = 4	4 dace	n = 5	6 dace	n = 5	8 dace	n = 5
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Temperature (°C)	19	0.3	19.2	0.3	19	0.3	18.7	0.3	18.9	0.3	18.9	0.3	18.9	0.2
Dissolved Oxygen (mg/L)	11.2	0.2	10.4	0.5	10	1	10.5	0.5	10.8	0.4	11.5	0.4	11	0.2
pH	9.1	0.01	9	0.04	9	0.02	9	0.03	9	0.02	9	0.03	9.1	0.03
Specific Conductance (µS/cm)	2997.5	38.2	2888.5	15.5	2988.5	33.3	2961.5	42.3	2992.6	26.8	2955.6	33.8	2951.1	27.3
NPP (mg/L)	2.9	0.1	2.9	0.3	2.8	0.3	3	0.1	3	0.1	3.5	0.2	3.3	0.1
Respiration (mg/L)	3.5	0.07	3.2	0.2	3.2	0.3	3.4	0.09	3.3	0.1	3.7	0.2	4.1	0.2
SRP	0.007	0.001	0.006	0.003	0.008	0.002	0.007	0.001	0.008	0.002	0.008	0.001	0.008	0.001
NH3	0.03	0.003	0.02	0.005	0.008	0.002	0.03	0.003	0.03	0.004	0.03	0.004	0.04	0.007
NO2/NO3	0.007	0.001	0.005	0.001	0.006	0.001	0.006	0.001	0.01	0.006	0.01	0.003	0.005	0.001