**EFFECTS OF AN INVASIVE CONSUMER ON ZOOPLANKTON COMMUNITIES ARE
UNALTERED BY NUTRIENT INPUTS**

by

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Abstract

Interactions between multiple anthropogenic stressors can have unexpected synergistic or antagonistic effects, making it difficult to predict their combined effect using single stressor studies. The interaction between invasive consumers and nutrient enrichment is particularly important as both of these stressors frequently co-occur and their respective bottom-up and top-down effects have the potential to interact across multiple trophic levels. We conducted a mesocosm experiment that crossed an increasing nutrient addition gradient against an increasing zebra mussel invasion gradient. Native zooplankton communities were added to the mesocosms, and after three months we examined how the single stressor effects on available resources and the zooplankton community were altered by their multiple stressor interaction. Added nutrients had no effect on primary producer abundance, but increased the abundance and dominance of the top consumer, which likely increased predation pressure on the producers and so prevented their response to increased nutrients. Zebra mussels reduced total phytoplankton abundance by ~75%, rotifer abundance by ~80%, and shifted communities towards dominance of cladocerans and adult/juvenile copepods. When combined, the top-down control exerted by the mussels interacted antagonistically to prevent any bottom-up influence of nutrient enrichment on the zooplankton community. These results provide insight into the potential outcomes of nutrient and invasive consumer stressor interactions, and illustrate the need for researchers to consider single stressor problems in a multiple stressor context.

Co-Authorship

This thesis conforms to the manuscript format as outlined by the School of Graduate Studies and Research.

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Chapter 1

General Introduction

Multiple stressors in ecology

Though multiple stressor interactions have been studied in medicine, physiology, and agriculture for decades, only recently has their role in ecology been considered. For the purposes of this paper we will use the same definition of an ecological "stressor" as outlined in Vinebrooke et al. (2004): "...an abiotic or biotic variable that exceeds its range of normal variation, and adversely affects individual physiology or population performance in a statistically significant way." Due to the growing human population and progression of climate change, terrestrial and aquatic communities worldwide are frequently becoming exposed to multiple simultaneous anthropogenic stressors (such as overharvesting, acidification, pollution, nutrient enrichment, invasive species, and habitat destruction), resulting in a variety of potentially damaging multiple stressor interactions (e.g. Yan et al. 2008, Schweiger et al. 2010). Paine et al. (1998), Breitburg et al. (1998), and Folt et al. (1999) were three of the first publications to recognize the issue of multiple stressors in ecology. Experimental ecological work involving multiple stressors had been performed prior to this, primarily in coral reef systems (e.g. a study by Lessios in 1988 found that mass sea urchin die-offs around Caribbean coral reefs were due to a combination of disease and overharvesting of fish), but these experiments were designed to explore potential reasons behind species loss, and did not pose specific multiple stressor questions about how anthropogenic stressors could interact. Paine et al. (1998) and Breitburg et al. (1998) highlighted the growing need for ecological multiple stressor experiments, as research up to that point had focused on the effects of individual stressors, and had largely ignored how these effects might be altered by their inevitable interaction with other, co-occurring stressors. Paine et al. (1998) described the growing inevitability of "ecological surprises", which were the unexpected consequences of interactions between both natural and anthropogenic disturbances, a clear parallel to what would currently be

termed “multiple stressor” interactions. Communities whose assemblage was dictated by disturbance, such as in areas of large, recurrent climatic events, could be dramatically altered by interactions between these historical disturbances and new anthropogenic disturbances. Paine et al. (1998) illustrated the inevitability of multiple stressor interactions and their inherent unpredictability by suggesting that "... ecologists must begin to prepare themselves for novel and unanticipated consequences of previously well-understood phenomena". Of particular importance to the development of multiple stressor experiments was the hypothesis by Breitburg et al. (1998) that the most damaging combinations of stressors would be those that interact to affect different species in a community. Species diversity plays an important role in ecosystem and community stability (Tilman 1996, Yachi and Loreau 1999), and systems become more unstable as species are removed. Combinations of stressors that affect multiple species would therefore be the most likely to destabilize affected communities or ecosystems. This concept provided the basis for understanding how multiple stressor interactions could alter single stressor effects, and for designing studies by first identifying which combinations of stressors may be the most harmful based on the number of potentially impacted species.

Folt et al. (1999) took a more quantitative approach to studying multiple stressor interactions by applying models developed for agricultural research to ecological communities. Interactive effects of stressors had historically been classified as additive (an interactive effect equal to the sum of the effects of the individual stressors), synergistic (greater than the sum of the individual stressors), or antagonistic (less than the sum of the individual stressors) based on their combined impacts on crop yield. However, how to apply this classification method to ecological interactions had yet to be clearly defined. Folt et al. (1999) helped to set the theoretical groundwork for classifying ecological interactions using three different multiple stressor models:

- i) The "simple comparative effects" model which defined additivity as the effect of the single worst stressor, and synergism or antagonism as anything less than or greater than this effect.
- ii) The "additive effects" model, wherein additivity was equal to the sum of the effects of both

individual stressors, and synergism or antagonism as anything greater than or less than this sum. Finally, iii) the "multiplicative effects" model which assumed that additivity was equal to the product of the individual stressors, and synergistic or antagonistic effects were anything greater than or less than this product. The most applicable model was chosen based on the mechanisms by which the individual stressors interacted, and then the model dictated how the interactive effect was classified. Based on these models, Folt et al. (1999) proposed using measured change in species growth and abundance to determine whether stressor interactions were additive, synergistic, or antagonistic.

Vinebrooke et al. (2004) used the theories on stressor impact introduced by Breitburg et al. (1998), and the concepts of additivity, synergism, and antagonism synthesized by Folt et al. (1999), to further develop predictive methods of how communities might respond to two different stressors. Community structure was predicted to be a function of species co-tolerance, whereby the combined effect of two stressors on biodiversity would be determined by whether tolerance for one stressor made a community more (positive co-tolerance) or less (negative co-tolerance) likely to tolerate the other. This also allowed for predictions about which interactions could be non-additive. Stressor combinations that led to positive co-tolerance would likely be antagonistic, while negative co-tolerance would be synergistic (Vinebrooke et al. 2004). This was especially relevant when considering the role played by ecological history in determining community response. If communities had prior exposure to a stressor then there was a higher probability that the species of that community could exhibit positive co-tolerance, and novel combinations of stressors would therefore have the greatest potential for harm (Vinebrooke et al. 2004). In addition to the idea of co-tolerance, Vinebrooke also further developed the concept, introduced by Breitburg et al. (1998), that the worst stressor interactions would be those that removed multiple species. Often the loss of multiple species can be replaced by others that fill a similar functional role (Yachi and Loreau 1999), mitigating the impacts of stressor interactions. However, the loss of an entire functional group is less easily managed, and could be more important to ecosystem

stability than species diversity (Balvanera et al. 2006). Therefore, multiple stressor studies should focus on interactions that affect multiple functional groups as these stressor combinations are the most likely to have whole community consequences (Vinebrooke et al. 2004).

Though the total number of studies researching multiple stressor interactions in natural communities remains low, adopting a multiple stressors perspective in ecological research is becoming more common. Examples of such work can be found in studies by Christensen et al. (2006) and Yan et al. (2008), who found that stressors such as climate change, acidification, nutrient enrichment, and invasion interacted together to dictate the plankton communities in their respective study regions. Meta-analyses by Crain et al. (2008) and Darling and Côté (2008) on the frequency of non-additive stressor interactions found that these were as common as additive interactions, and sometimes more so, highlighting the difficulty of predicting the outcome of multiple stressor interactions with single stressor research. Finally, more attention is being given to how interactive effects could change based on stressor order. Breitburg et al. (1998) first suggested that stressors could be sequence dependent, whereby stressors may have to occur in a certain order for interactive effects to result. Further support for this idea has been provided by work on disturbance order by Fukami (2001), and multiple stressor studies by Flöder and Hillebrand (2012) and MacLennan and Vinebrooke (personal communication), which found that community response to combined stressors could change depending upon stressor sequence.

Nutrient loading as a single and multiple stressor

If the most damaging stressor interactions will be those that result in the loss of multiple species or whole functional groups, then individual stressors with whole community impacts could be the most likely to result in severe stressor interactions. Anthropogenic enrichment of limiting nutrients, particularly nitrogen (N) and phosphorus (P), from agricultural fertilization, fossil fuel combustion, and human wastewater is an enduring global issue (Matson et al. 1997, Smith et al. 1999, Bennett et al. 2001, Schindler 2006). As an individual stressor, increasing

limiting nutrients can have repercussions for multiple species and trophic levels, leading to shifts in community abundance and structure. The influence of nutrient enrichment on both terrestrial and aquatic ecosystems has been recognized since the 1800's (reviewed by Smith et al. 1999). In any system, an increase in nutrients generally results in an increase in primary productivity and a change in producer community composition (Smith et al. 1999). This increase in producer abundance can support a larger and potentially more diverse herbivore community, which in turn can increase biomass and shift composition of the top predators (Oksanen et al. 1981, Polis et al. 1997). This "bottom-up" influence of nutrient enrichment, whereby the overall community biomass and structure at all trophic levels can be altered by the lowest trophic group, has been frequently observed in natural systems. Studies by Ginzburg and Akçakaya (1992) and Chase et al. (2000) on abundance, and work by Dodson et al. (2000) and Siemann (1998) on diversity concluded that changes in producer productivity can result in bottom-up shifts in whole community abundance, richness, and composition. While nutrient loading can enhance productivity and increase biodiversity, higher nutrient levels can have some potentially adverse effects. On land, nutrient enrichment can lead to the replacement of native species unsuited to high nutrient conditions, often causing a decline in biodiversity (Smith et al. 1999). Added nutrients can often disproportionately benefit species better able to utilize the increase in resources (Leibold 1989, 1991), or better able to survive stress conditions that can occur in high-nutrient environments (e.g. cyanobacteria proliferating in turbid or low CO₂ conditions resulting from eutrophication, Downing et al. 2001). Additionally, nutrient enrichment in terrestrial systems can acidify and increase soil leeching, drought susceptibility, and grazing pressure (Jefferies and Maron 1997). In freshwater and marine environments nutrient inputs can lead to toxic cyanobacteria blooms, increase fish kills due to severely depleted oxygen levels from decomposing algae, and loss of species diversity due to declining water quality (Smith 2003).

Interactive effects of consumer invasion

A stressor with the potential to interact with the bottom-up effects of nutrient enrichment is the opposing "top-down" impacts of consumer invasion. The idea of top-down control was first described by Hairston, Smith, and Slobodkin (1960). It referred to the process by which a top predator could regulate the abundance and composition of the trophic levels below, beginning the debate between the relative importance of top-down and bottom-up effects on community structure. Prior to this it was believed that the bottom-up influence of producer groups was solely responsible for dictating community abundance and diversity, however more recent reviews have identified many examples of top-down predator control in both aquatic (Strong 1992) and terrestrial (Pace et al. 1999) communities. However, it has become clear that there is no consistent dominance of one process over the other. Communities are simultaneously limited by interactions between both predators and resources, and the relative importance of each is variable (Mittelbach 2012). For example, often the level of bottom-up influence exerted upon a community is dependent on the strength of top-down processes. Productivity can determine potential growth and diversity in a community, while top-down predation can determine realized growth and diversity (Gutierrez et al. 1994). Changes in the strength of bottom-up influences through nutrient enrichment can lead to increased top-down predation (Oksanen et al. 1981, Power 1992), and increasing the abundance of a top-consumer can alter how a community responds to changes in the resource pool (McQueen et al. 1986, Carpenter and Kitchell 1993, Wollrab et al. 2012).

Invasive species are a major, global driver of species extinctions (Mack et al. 2000, Simberloff et al. 2013), the recognition of which began in 1958 with "The Ecology of Invasions of Animals and Plants" by Charles Elton. This book took a grim view of the consequences of species invasion, and actively sought to portray this issue as a growing global problem for biodiversity. For several decades afterwards ecological focus moved back and forth between viewing invasions as a conservation issue, or as an opportunity to apply and advance our understanding of ecological theory (Davis 2006). This continued until the 1990's, when public

and scientific knowledge of the problems caused by invasion species, and a greater need to justify the social benefits of scientific research, brought the field back to a focus on conservation (Davis 2006). The concern for invasive species as a biodiversity threat was well founded as there are numerous examples throughout the literature of their population, community, and ecosystem level impacts (Lockwood et al. 2007). Not all invasives are transported by humans, but some of the worst cases of ecosystem destruction and biodiversity loss come from anthropogenically transferred, non-native species, which then became invasive after establishment. For example, Nile perch (*Lates niloticus*) were intentionally introduced to Lake Victoria in the 1950's, which by the late 1970's had a native cichlid community comprised of ~500 different species (Witte et al. 1992), as a potential source of food and economic revenue. Between 1978 and 1999, bottom trawl catches showed a dramatically reduced diversity of native cichlids (Witte et al. 1992), and though there has been some recovery the fish community, cichlid diversity remains low (Hecky et al. 2010). This loss of native diversity was attributed to the boom in the introduced perch population around 1980, which went from constituting less than 1% of the yearly fish harvest to 97% by 1987 (Witte et al. 2000).

Invasive consumers, such as the Nile perch, often have large impacts on community function, resource use, and biodiversity due to their strong top-down influence on invaded communities. Invasion of a top consumer frequently leads to top-down control because they often reach high abundances (usually attributed to the 'enemy release hypothesis', but the link between high abundance and enemy release isn't yet clear, Coautti et al. 2004), they tend to be generalists (Romanuk et al. 2009), and the prey community is often naïve to their predatory behavior (Sih et al. 2010, Paolucci et al. 2013) which increases the number of potentially vulnerable prey and can cause invasive consumers to have twice the consumptive effect on prey population size compared to native consumers (Salo et al. 2007, Paolucci et al. 2013). The post-invasion reduction of multiple prey species or functional groups can lead to top-down trophic cascades, where the effect of predation at one trophic level cascades downwards to all trophic levels below (Pace et al.

1999, Shurin et al. 2002). For example, introduced brown trout (*Salmo trutta*) in New Zealand can regulate the algal community through predation on native invertebrate grazers (Townsend 1996), the introduced Asian lady beetle (*Harmonia axyridis*) has improved pecan crop growth in North America by preying heavily upon the native herbivorous aphids (Mizell 2007), and the invasive little red fire ant (*Wasmannia auropunctata*) can alter litter decomposition rates and nutrient cycling through predation on herbivorous invertebrate communities (Dunham and Mikheyev 2010).

Nutrient loading and consumer invasion are both common, global stressors, their bottom-up/top-down influences have the potential to interact, and their multi-trophic and species level effects meet the criteria set forth by Vinebrooke et al. (2004) for identifying stressor interactions with potential whole community impacts. The co-occurrence of these stressors is therefore both likely, and possibly a powerful structuring force in affected communities. In addition, examples from natural communities illustrate how the single stressor effects of both nutrient enrichment and invasive consumers can be altered by their interaction. For example, the introduction of Nile perch to Lake Victoria did little to change the native community until the 1980's, a time lag of 30 years (Hecky et al. 2010). This delay was due to the lake conditions, which continued to favor cichlid dominance until nutrient inputs from urbanization and agriculture lowered lake visibility, making conditions more favorable for perch, and increased productivity which further increased perch predation on the native cichlids (Hecky et al. 2010). Nutrient loading and perch invasion would have had little individual effect on the native community (Hecky et al. 2010), but when combined they interacted (arguably synergistically) to produce a greater effect than the sum of both single stressors. Salt marshes in the United States can experience periods of fertilization when large amounts of sediment are deposited by storms, floods, and hurricanes, resulting in increased plant biomass and decreased species diversity (Gough and Grace 1998). However, when herbivores are present in this area, the most abundant of which is the invasive nutria (*Myocastor coypus*), plant biomass can still increase, but diversity no longer declines. A final

example comes from a mesocosm experiment by Dzialowski (2013) on the interaction between the consumptive effects of the invasive zebra mussel (*Dreissena polymorpha*) and nutrient enrichment. In the absence of the mussels, the abundance of the zooplankton community increased with added nutrients, but when zebra mussels were present the response of the zooplankton community to added nutrients was delayed.

Predicted mechanisms of interaction between nutrient loading and zebra mussels

For our study we chose the North American Great Lakes basin as an example system with which to observe the interactions between nutrient loading and consumer invasion. The single stressor effects of nutrient loading are relatively well understood in this region as it has been a long-standing issue in the Great Lakes (Beeton 1965, Schindler 1974, Michalak et al. 2013) and other North American inland lakes (Nürnberg 1996), and classic eutrophication studies having been performed in the Experimental Lakes Area (Schindler 1974, Schindler et al. 2008) in northwestern Ontario. Additionally, zebra mussels are a wide-spread invader throughout the Great Lakes (U.S. Geological Survey 2013), and are a well-researched invasive consumer that we know can have potential interactions with nutrient loading (Dzialowski et al. 2009, Dzialowski 2013).

Zebra mussels first invaded the North American Great Lakes in the 1980's, likely transported from their native Ponto-Caspian range in ship ballast water (Hebert et al. 1989). Between then and now, they have spread into both lotic and lentic systems (Johnson and Carlton 1996) eastward to the St. Lawrence River, south as far as the Gulf of Mexico, and north to the northern shore of Lake Superior (U.S. Geological Survey 2013). They can produce up to 30,000-40,000 eggs per female per year (Stańczykowska 1977) and have a three-stage life-cycle. The first stage is a planktonic veliger (Stańczykowska 1977), the primary mechanism by which zebra mussels are transported anthropogenically across oceans and passively downstream (Johnson and

Carlton 1996), followed by the post-veliger and settling stages as the mussel shell begins to form and the organism attaches to a solid substrate (Stańczykowska 1977). Adult zebra mussels can survive between 3-5 years (Stańczykowska 1977), can attach to almost any moderately-hard submerged surface (even macrophytes, wood, small pebbles, inflow/outflow pipes, and native unionids), can live out of water for several days (Ricciardi et al. 1995), and can tolerate temperatures up to 30°C for extended periods (Spidle et al. 1995). These characteristics allow the adult mussels to easily disperse on floating debris, or overland attached to boat hulls (Johnson and Carlton 1996).

There have been numerous studies on the effects of zebra mussels in invaded systems (reviewed by Higgins and Vander Zanden 2010). Zebra mussels are voracious filter feeders, capable of consuming large quantities of particulate matter, phytoplankton, and microzooplankton (MacIsaac et al. 1991, 1992). Per gram of shell-free dry weight zebra mussels can filter ~33 L day⁻¹ (Zaiko and Daunys 2012), up to ten times higher than other freshwater bivalves. Their filtration of the water column can increase clarity (Effler et al. 1996), increase macrophyte growth (Zhu et al. 2006), cause toxic cyanobacteria blooms (Vanderploeg et al. 2001), and transfer nutrients and organic matter from the pelagic zone to the benthos and littoral zones (Karatayev et al. 1997, Hecky et al. 2004, Higgins and Vander Zanden 2010). Changes in nutrient concentrations and transfer of nutrients due to mussel filtration and excretion can alter established nutrient ratios (Johengen et al. 1995, Arnott and Vanni 1996, Naddafi et al. 2008), change the composition of the planktonic community (Heath et al 1995, Arnott and Vanni 1996), and increase benthic biomass and productivity (Johannsson et al. 2000, Higgins and Vander Zanden 2010).

The most likely mechanism of interaction between nutrient loading and zebra mussels would be through their effects on phytoplankton, as this is the only group upon which both stressors have direct effects. Zebra mussels can consume most phytoplankton, but preferentially feed on the small, palatable species as they are more easily consumed and digested (Wu and

Culver 1991, Heath et al. 1995). This greater loss of small phytoplankton can result in blooms of larger phytoplankton species, such as cyanobacteria, due to reduced competition (Raikow et al. 2004). Nutrient loading can also directly affect phytoplankton biomass and composition. Though both nitrogen and phosphorus are important limiting nutrients in aquatic environments (Elser et al. 1990), phytoplankton growth is primarily phosphorus limited as their physiological demand for phosphorus is much higher than its natural supply (Hecky and Kilham 1988) compared to nitrogen. In addition, experimental manipulations of phosphorus and nitrogen concentrations have repeatedly shown that phosphorus more frequently limits phytoplankton growth (Schindler 1974, Schindler et al. 2008). Anthropogenic phosphorus loading generally occurs through runoff from agricultural and urban land use (Downing and McCauley 1992), as well as through atmospheric deposition (Kalff 2002). The N:P ratio of these sources tends to be much lower than non-anthropogenically altered sources (Downing and McCauley 1992), resulting in anthropogenic aquatic stress since the primary limiting macronutrient is occurring in concentrations that far exceed its natural levels. Phosphorus loading can increase phytoplankton biomass (Hecky and Kilham 1988) and shift the size composition of the phytoplankton community. At low nutrient levels small phytoplankton species tend to dominate, and in more eutrophic conditions the size structure shifts towards larger species (Watson et al. 1997, Irwin et al. 2006).

Though we can hypothesize about the potential mechanism by which these stressors interact, the variability in their single stressor effects and the unpredictability of their bottom-up and top-down interactions highlights the difficulty in using single stressor research to predict the outcome of a multiple stressor interaction. Depending upon the studied system, nutrient loading can increase or decrease phytoplankton productivity and diversity (Smith et al. 1999). Zebra mussels tend to reduce phytoplankton biomass, but this can be dependent upon mussel density (Mellina et al. 1995), water depth and mixing (Mellina et al. 1995, Bastviken 1998), food concentration (James et al. 2001), temperature (Descy 2003), amount of zooplankton consumed (Descy 2003), or the species composition of the phytoplankton community (Bastviken 1998).

Additionally, the predictability of the interaction between their respective bottom-up and top-down processes is dependent upon community complexity, strength of trophic interactions, and prevalence of omnivory (Pace et al. 1999). Preliminary work by Dzialowski (2013) provided some insight into this stressor interaction, concluding that zebra mussel consumption could delay the response of the zooplankton community to increased productivity, however there were some issues with the study design that limited its predictive use. Only a single nutrient concentration and mussel treatment density were used, and both concentrations were towards the highest level of what is generally observed in North America (Mellina et al. 1995, Nürnberg 1996). Rotifers were not included in the zooplankton community analysis, despite their higher vulnerability to zebra mussel predation (MacIsaac et al. 1995), and their inclusion could have altered the community response to the treatments. Finally, zebra mussel impact is dependent upon water mixing and mussel density, and the mesocosms were not mixed, and dead mussels were not replaced for the duration of the experiment.

Thesis objectives

The purpose of this thesis was to further the ecological work on anthropogenic multiple stressors, as there are few studies exploring these commonly occurring interactions. Specifically, our objectives were to study the interactions between two widespread stressors that could interact to alter community composition. We chose to study the interaction between nutrient loading and an invasive consumer as these stressors are both common, have impacts at multiple trophic levels, and their opposing bottom-up and top-down processes are likely to interact. The primary objectives were:

- i) Determine the bottom-up effects of nutrient addition on producer and consumer community composition.
- ii) Determine the top-down effects of an invasive consumer on producer and consumer community composition.

- iii) Study how these two stressors interact to affect overall community composition, and classify this interaction as either additive, synergistic, or antagonistic

Chapter 2

Effects of an invasive consumer on zooplankton communities are unaltered by nutrient inputs

Introduction

The expansion of the human population and progression of climate change has dramatically increased the probability of interactions between multiple anthropogenic stressors. A “stressor” is defined as an abiotic or biotic variable that exceeds its range of normal variation, and adversely affects individual physiology or population performance in a statistically (and biologically) significant way (Vinebrooke et al. 2004). Research on individual anthropogenic stressors, such as acidification, climate change, and invasive species, has provided important insight into single stressor effects, but is often not useful for predicting the outcome of multiple stressor interactions. Reviews of stressor interactions in marine, terrestrial, and freshwater environments found that the vast majority of outcomes (~75%) were non-additive (Crain et al. 2008, Darling and Côté 2008), such that the effect sizes of interacting stressors were generally greater (synergistic) or less than (antagonistic) the response predicted based on combining their individual stressor effects. Experimentation involving multiple stressors is therefore critical for detecting potentially non-additive interactions, and for providing better predictions to inform the management and restoration of communities affected by co-occurring stressors.

Two of the primary stressors driving recent global environmental change and biodiversity loss are nutrient enrichment (Smith et al. 1999) and invasive species (Mack et al. 2000). Though it is likely these stressors commonly co-occur, and there is a substantial body of literature exploring their individual effects (Smith et al. 1999, Schindler 2006, Lockwood et al. 2007), relatively few studies have investigated their potential interaction. Those that have were primarily focused on invasive plants (e.g. Dukes and Mooney 1999, Rao and Allen 2010, Gennaro and Piazzini 2011) since the addition of unexploited food resources from nutrient loading can increase

invasibility and invader growth (Davis et al. 2000, Zedler and Kercher 2004), but less attention has been given to interactions between nutrient addition and invasive consumers. The wealth of literature on bottom-up-top-down (BUTD) interactions suggests that it is likely consumer invasion and nutrient enrichment can interact. Increasing primary production through nutrient addition can result in a bottom-up increase in primary and secondary consumer abundance, which can in turn increase their top-down predation pressure on trophic levels below (Oksanen et al. 1981, Power 1992). If the affected higher-level consumer is an invader, nutrient enrichment may increase their top-down impacts on the invaded community. Introducing a higher trophic level predator can result in a “trophic cascade” (top-down reciprocal predator-prey effects, Pace et al. 1999), which can alter how lower trophic levels (McQueen et al. 1986, Carpenter and Kitchell 1993), and the entire food web (Wollrab et al. 2012) respond to added nutrients.

There are also some examples of additive and non-additive interactions in experiments that simultaneously manipulated both nutrients and consumption pressure. Nitrification and herbivore removal synergistically increased primary producer abundance in benthic marine habitats (Burkpile et al. 2006), increasing grazing pressure on seagrasses reduced the positive growth effects of nutrient enrichment (Hughes et al. 2004), and removal of grazing snails increased the positive effects of nutrient enrichment on periphyton biomass (Rosemond et al. 1993, Hillebrand 2002). Despite the extensive literature on BUTD interactions, it does not sufficiently address how simultaneous stress effects resulting from nutrient enrichment and consumer invasion may interact to influence community structure. BUTD studies frequently group producers into a single trophic level, which does not account for changes in producer community composition that may result from nutrient stress (Leibold et al 1997, Gruner et al. 2008). Non-native consumers can also have a two times greater effect on prey population size compared to native consumers (Salo et al. 2007, Paolucci et al. 2013) since native prey usually have not evolved the proper anti-predator behavior (Sih et al. 2010), and the foraging strategies of an invasive consumer may differ from native consumers (McIntosh and Townsend 1996, Simon

and Townsend 2003). Investigation into the interaction between nutrient and invasive consumer stressors is therefore needed since we cannot reliably predict the outcome based on predicted BUTD effects, and we need a better understanding of the potential for non-additive interactions between these commonly occurring stressors.

The North American Great Lakes basin provides an ideal system with which to study this interaction. Nutrient stress in the Great Lakes region and other inland lakes has been a continuing problem for decades (Schindler 1974, Nürnberg 1991, Nürnberg 1996, Michalak et al. 2013). In addition, one of the most widespread and economically/ecologically damaging invasive consumers is the zebra mussel (*Dreissena polymorpha*), a benthic invertebrate filter-feeder whose impacts have been carefully studied since the beginning of its North American invasion (reviewed by Higgins and Vander Zanden 2010), and subsequent expansion throughout the Great Lakes region (U.S. Geological Survey 2013). In addition to co-occurring in the same region, both of these stressors can have a strong structuring influence on native phytoplankton and zooplankton communities.

Based on studies of individual stressor effects, we expect that nutrient enrichment would increase aquatic primary productivity (Schindler 2006), subsequently increasing zooplankton abundance (Leibold et al. 1989, Steiner et al. 2001), while zebra mussels would selectively consume phytoplankton and rotifers (MacIsaac et al. 1991, 1995, David et al. 2009). When combined, the added productivity from nutrient enrichment may help offset the increased grazing pressure from zebra mussel invasion, or mussel grazing may reduce the effects of nutrient enrichment. However, as mentioned above BUTD predictions for this study system are problematic because assuming increasing productivity following nutrient enrichment doesn't account for changes in producer composition or edibility, and invasive zebra mussels may have a larger than expected consumptive effect on native zooplankton and phytoplankton abundance. Further unpredictability also arises since zebra mussels are omnivorous, which can alter expected trophic relationships (Pace et al. 1999) and trophic responses to nutrient enrichment (Diehl and

Feissel 2000), and they can disrupt the nutrient cycle by increasing available nutrients through excretion, or shunting nutrients to the benthos (Hecky et al. 2004, Higgins 2010), which can reduce or enhance top-down consumer effects on producers (Vanni and Layne 1997). For example, Dzialowski et al. (2013) found that despite high phosphorus additions (+200 μ g/L), zebra mussel grazing was strong enough to temporarily suppress any effect of nutrient addition on phytoplankton and crustacean zooplankton. Additionally, although nutrient enrichment and zebra mussel invasion can individually promote the growth of large, inedible *Microcystis* phytoplankton (by respectively alleviating phosphorus limitation and increasing nutrient cycling, Downing et al. 2001, Vanderploeg et al. 2002), Sarnelle et al. (2012) found that when these stressors were combined *Microcystis* abundance declined.

The purpose of this study is to examine the interaction between nutrient enrichment and invasive consumer stressors, and how this interaction changes over a range of stressor intensities. Although similar experiments using our chosen study system were performed by Dzialowski et al. (2013) and Sarnelle et al. (2012), these studies only examined this interaction over a narrow range of nutrient concentrations and invader densities, and their community analysis only involved crustacean zooplankton. However, the influence of nutrient enrichment and mussel invasion can vary over a range of nutrient concentrations and mussel densities (Mellina et al. 1995, Arnott and Vanni 1996, Sarnelle et al. 2012), and non-crustacean zooplankton, such as rotifers, are often the group most affected by mussel invasion (MacIsaac et al. 1995, Pace et al. 1998, David et al. 2009) and can significantly contribute to total zooplankton production (Herzig 1987) and nutrient cycling (Makarewicz and Likens 1979). Therefore, we examined this interaction over a gradient of oligotrophic to eutrophic nutrient concentrations, a range of low, medium, and high zebra mussel densities, and with a more complete native zooplankton community. Further examination of this stressor interaction over a gradient of intensities will provide additional analysis into a complex and variable system, as well as a better assessment of the potential for non-additive

interactions between two important, global stressors that frequently co-occur, and have the potential for complex interactions across multiple trophic levels.

Methods

Experimental design

To examine the interactive effects of zebra mussel invasion and nutrient loading we conducted a mesocosm experiment at Queen's University Biological Station, Canada (QUBS 44.5653N, -76.3240W) from 09-May-2012 to 23-Aug-2012. This experiment used a regression design in which the nutrient enrichment and mussel treatments were applied as crossed gradients. Regression experiments can allow for finer ecological gradients without sacrificing statistical power or having to dramatically increase replication since fewer parameters are required to estimate intercept and slope compared to estimating the mean for all treatment categories in ANOVA designs, and power in regression comes not from the number of treatments or replicates, but from the number of factors and experimental units (Cottingham et al. 2005). Our nutrient addition gradient consisted of ten phosphorus addition levels, increasing from +0 to 85µg/L above ambient. This phosphorus range was selected to reflect observed phosphorus concentrations throughout the Great Lakes and southern Ontario (Nürnberg 1991, Nürnberg 1996). Our mussel treatment gradient consisted of four densities of 0.0, 0.25, 0.5, and 1.0 mussel(s)/L. These levels were chosen to approximate low, medium, and high zebra mussel densities based on our own estimated volumetric calculations using lake survey data from southern Ontario, Quebec, and the northeastern United States (Mellina et al. 1995, Naelpa et al. 1995, Ricciardi et al. 1996, Bailey et al. 1999, Burlakova et al. 2000, Spada et al. 2002, Hunter and Simons 2004, Evans et al. 2011), and previously used experimental volumetric densities (Mellina et al. 1995). The 10 nutrient enrichment and 4 mussel density treatment levels were then crossed against each other over a total of 40 mesocosms, such that each mesocosm represented a unique nutrient and mussel density treatment.

From May 9th to 10th forty 378 L cattle tanks (132x78x63cm) were filled with 350L of water from nearby Lake Opinicon filtered through a 50µm mesh to remove zooplankton, but allowing most phytoplankton and small rotifers to pass through. The tanks were placed in a sheltered location and arranged in two rows of 20 tanks each, then covered with 1mm mesh to protect from insects and debris. Tanks were then haphazardly assigned nutrient and mussel treatment levels. Precipitation was sufficient to maintain water levels within 10cm of initial height for the duration of the experiment.

On May 16th, the nutrient gradient treatment was established by adding phosphorus (as KH₂PO₄; Fisher Scientific, Pittsburgh, Pennsylvania) to the mesocosms. This increased the baseline phosphorus concentration of the mesocosms, ~10.6±1.4µg/L (determined using Lake Opinicon water samples from May 2012, Arnott unpublished data), by +0, 5, 15, 25, 35, 45, 55, 65, 75 and 85µg/L. After the initial phosphorus additions, two additions of 20µg/L phosphorus and 500µg/L nitrogen (as equal parts NaNO₃ and NH₄Cl; Fisher Scientific, Pittsburgh, Pennsylvania) were made to all tanks on June 16th and August 1st to account for potential losses that typically occur to periphyton on tank walls in mesocosm studies (Downing 2005). Since our mesocosms were closed systems, all phosphorus additions remained in the system throughout the experiment, albeit likely in different food web components across treatments.

Regional zooplankton and phytoplankton were collected from five oligotrophic, uninvaded lakes (Table A1.1) and added to the mesocosms on May 22nd. This ensured that the experimental community was diverse, and that both the nutrient and mussel treatments were outside of the normal range experienced by the communities. In each lake a 35cm diameter net with a 50µm mesh was hauled vertically through 2886L of water at the deepest point of the pelagic zone, and was towed horizontally through 770L of water in the littoral zone. Zooplankton samples collected from the 5 lakes were condensed into cooled containers, transported to the mesocosm site, and pooled in a 200L container. We then dispensed 1.15L aliquots, divided over three additions, from the constantly mixed inoculum into each tank to stock our 350L mesocosms

with a mean ambient zooplankton density based on the volume of water sampled from the 5 lakes.

Zebra mussels were collected from Lake Opinicon on May 20th and 21st. All mussels had their byssal threads cut from rocks using razor blades, they were then stored in coolers with lake water and transferred to fibreglass aquarium tanks on the same day. All mussels were lightly scrubbed, measured, and separated into three size classes of small (<10mm), medium (10-20mm), and large (>20mm). Treatment densities were standardized by size, such that each mussel addition was comprised of 35% small, 60% medium, and 5% large mussels. In the aquarium, the number of mussels for each mesocosm were first placed onto circular plastic mesh supports 8 centimetres high and 20cm in diameter and weighed down with a 13 cm² ceramic tile (including supports without mussels). Supports were used to raise the mussels above the bottom of the tanks and provide an easy attachment surface. All mussels were kept on the supports in the aquarium tanks for at least 10 days prior to their addition to the mesocosms. During this time they were fed with a continuous flow of Lake Opinicon water, in addition to 2g of *Chlorella spp.* algae powder (Glenbrook Farms, Cambellsville, Kentucky) per 1000 mussels drip-fed over 8 hours every two days (Nichols 1993). Aquarium tanks were supplied with constant airflow using 5 or 10cm air stones (depending on tank size). All forty supports with and without mussels were added to their respective mesocosms on May 31st. Supports were placed at the center of each tank (an approximate depth of 63.5cm), and a 4.5cm airstone was attached to each support near the zebra mussels. During the experiment a 51 LPM @ 10.3kPa diaphragm air pump (JEHM Co., Lambertville, New Jersey) was used to ensure a constant airflow to all mesocosms throughout the day and night. To maintain our density treatment, every three days all supports, including those with no mussels, were raised to the water surface and checked for dead mussels. Mussels were presumed dead if they were open and would not close after being touched with a plastic rod. Dead mussels were removed and replaced with live mussels of the same size class, all of which came from a stock that was maintained in the aquarium in the lab. Weekly mussel mortality was low for

the first 10 weeks of the experiment and similar between treatment densities (<10%, low compared to mortalities observed by Mersch and Pihan 1993 on river tiles and Bykova et al. 2006 in laboratory tanks), rising to ~20% in the final two weeks. Mortality rates within size classes and across treatment densities were also consistent with percent size compositions since small, medium, and large mussels always respectively contributed ~30-40%, 60-70% and 5-10% to weekly mussel mortality.

Sampling protocol

Mesocosms were sampled for zooplankton community composition, total/edible chlorophyll a, water temperature, pH, conductivity, dissolved oxygen, and total phosphorus. The initial zooplankton community samples were taken on May 23rd, and the final samples on August 23rd. Zooplankton were sampled from three different points in the tanks, with 3L of water taken each time using an 8cm diameter tube sampler. All three samples were passed through a 50µm filter, zooplankton were anaesthetized in carbonated water, then condensed into one sample for a total sampling of 9L of zooplankton from each 350L tank. All zooplankton samples were preserved in at least 70% ethanol for future analysis, and the tube sampler was rinsed between each mesocosm.

Identification and enumeration of cladoceran, copepod, and rotifer zooplankton was performed using a Leica MZ16 dissecting scope and a Leica DM E compound microscope. Cladocerans and copepods were identified to species using Edmondson (1966), Brandlova et al. (1972), and Witty (2004). *Daphnia pulex/pulicaria* and *Bosmina freyi/riedri* were grouped by genus because they are difficult to differentiate based on morphological characteristics. Immature copepods were identified as either cyclopoid or calanoid nauplii and copepodids. Rotifers were identified to species level using Stemberger (1979) and Aliberti et al. (2003), except for *Synchaeta* which were identified to genus. Samples were enumerated by subsampling a known volume and counting all individuals within a subsample. Subsamples were counted until three

subsamples in a row contained no new species, with a minimum of seven subsamples counted for each sample. Cladocerans and copepods were enumerated using dissecting trays containing 3mL subsamples, and rotifers were counted using a metal-rimmed slide containing 1mL of subsample.

Water chemistry and chlorophyll a samples were taken on May 30th, then June 6th, followed by samples at two week intervals. Total phosphorus samples were taken on May 30th. Phosphorus samples were not taken immediately following the initial additions on May 16th due to logistical constraints with the phosphorus analyzer. Conductivity, pH, temperature, and dissolved oxygen were recorded using a YSI 600R multiparameter probe (YSI Inc., Yellow Springs, OH), while total and edible chlorophyll a was collected from as a 1-L grab sample in brown nalgene bottles, 0.1 m below the water surface, from each mesocosm. Grab samples took approximately one hour to collect, after which they were transported to the lab to be filtered and frozen on the same day. Phytoplankton for total chlorophyll a was collected by filtering 250mL of the grab sample through a G4 glass fibre filter (1.2µm pore size; Fisher Scientific, Pittsburgh, Pennsylvania). The edible chlorophyll a sample was collected by filtering 250mL of the grab sample through a 30µm mesh, then passing the filtrate through a glass fibre filter. All filters were frozen, then later extracted in methanol for 24 hours and analyzed following methods from Welschmeyer (1994) using a TD-700 fluorometer (Turner Designs, Sunnyvale, CA). Phosphorus samples were collected by filtering 30mL of the grab sample through a 50µm mesh into culture tubes and refrigerating them overnight for analysis the next day. Phosphorus analysis methods followed those outlined by Eaton et al. (2005) for persulfate digestion and the ascorbic acid method, and was performed using a FIALab Phosphorus Analyzer (FIALab, Bellevue, Washington) calibrated to low phosphorus levels.

Statistical analyses

All analysis was performed in R 2.15.2 (R Core Team 2012) using packages 'MuMIn' v.1.9.5 (Bartoń 2013), 'glmmadmb' v0.7.2.4 (Fournier et al. 2012, Skaug et al. 2013), and 'vegan' v.2.0-7 (Oksanen et al. 2013) with $\alpha=0.05$.

We examined how the treatments affected zooplankton communities and available resources by analyzing zooplankton abundance, richness, and total/edible chlorophyll a. All tests were performed on data from the first and final sampling dates of the experiment, except total phosphorus as only the first sampling date was analyzed to ensure an increasing phosphorus gradient was maintained in the two weeks prior to the mussel additions. Comparisons of initial to final states in aquatic mesocosm experiments that last several months may miss transient changes in plankton abundance, and pulse nutrient additions can be less realistic than those applied gradually over time (Sarnelle et al. 2012). However, such experimental designs have been used to provide valuable insight to a diverse range of ecological questions (e.g. Horner-Devine et al. 2003, Hall et al. 2004, Declerck et al. 2007, Pedruski and Arnott 2011, Hamilton et al. 2012). Although plankton abundance may show large fluctuations over short duration experiments, establishment of stable states in mesocosm plankton communities can occur within six to eight weeks (Forrest and Arnott 2006, Howeth and Leibold 2008, Strecker and Arnott 2010). Additionally, strong treatment effects on community composition can appear within the initial weeks of the experiment, the trajectory of which remains consistent thereafter (Forrest and Arnott 2006, Strecker and Arnott 2010).

Following Crawley (2005), minimum adequate models were determined from the same full model with mussel treatment, the linear and quadratic terms for nutrients, and all interaction terms as the predictor variables. Statistical assumptions were checked using plots of residual vs. fitted values, normal quantile-quantile plots, standardized residual vs. fitted values, and constant leverage. In cases where abundance or richness model assumptions were violated the data was reanalyzed using generalized linear models (GLMs) with Poisson, quasi-Poisson, or Negative

Binomial distributions with a log link function. Significance of terms for linear models was determined using either analysis of covariance (ANCOVA), analysis of variance (ANOVA), or linear regression, depending on the number and type of predictor variables in the best model. Significance of GLM terms was evaluated using F-ratio tests, with a chi-squared test used for Poisson and Negative Binomial distributions. R^2 values for GLM tests were calculated using the pseudo- R^2 methods described in Zuur et al. (2009). Post-hoc analyses were performed using tests of Tukey's Honest Significant Differences (Tukey HSD) or regression analysis. Benjamini-Hochberg False Discovery Rate corrected p-values were used for all non-Tukey HSD post-hoc analyses.

Significant shifts in total zooplankton community composition were detected with the non-parametric MANOVA method described by Anderson (2001) using the function 'adonis' from the 'vegan' package with mussel density as the categorical predictor and nutrients as the continuous covariate. Rare species (<10% occurrence) were removed, and the community data was chord transformed. Post-hoc tests on community data were performed using linear regression and ANCOVAs on sites scores from axes 1 and 2 of a Principal Coordinates Analysis (PCoA) on the chord distance matrix to determine the effects of nutrients within mussel treatments, and differences in community location between mussel treatments.

Results

Chlorophyll a and phosphorus

All of the mesocosms began the experiment with no significant differences in total or edible chlorophyll a (Table A6.9 and A6.10). Established nutrient gradients were maintained two weeks after the initial phosphorus additions and the day before mussel additions; total phosphorus levels showed a significant increasing relationship with nutrient treatment for mesocosms at the 0.0 (Linear regression, $R^2=0.65$, $P=0.01$), 0.25 (Linear regression, $R^2=0.59$, $P=0.012$) and 1.0 (Linear regression, $R^2=0.79$, $P=0.002$) mussels/L density treatments (Fig. A3.1). Phosphorus

concentrations in the 0.5 mussels/L treatment showed a positive, but non-significant trend with increasing nutrients (Linear regression, $R^2=0.28$, $P=0.11$).

At the end of the experiment there was at least an 80% reduction in total chlorophyll a in all treatments with mussels (ANCOVA, $F_{3,36}=8.01$, $P=3.2 \times 10^{-4}$) compared to the 0.0 mussels/L treatment (Table A2.3). Concentrations decreased from $\sim 12 \mu\text{g/L}$ without mussels to $1\text{--}3 \mu\text{g/L}$ with mussels. There was, however, no effect of nutrients, nor was there an interactive effect of nutrients and zebra mussels (Table A5.9).

Zooplankton abundance and richness

Zooplankton abundance and richness for all taxa across treatments was similar at the start of the experiment, except cladoceran abundance, which showed some variation across nutrient treatments owing to a significant interaction between the linear and quadratic nutrient terms (Fig. A6.1, $F_{1,36}=7.78$, $p=0.008$). This was primarily driven by high cladoceran abundance in a single, uninvaded mesocosm at the lowest nutrient concentration, and low average abundance in all mesocosms at the $+35 \mu\text{g/L}$ nutrient treatment level (Fig. A6.1). We do not believe this had any impact on our final results since this pattern could not be detected by the conclusion of the experiment (Fig. 3, Table A5.2).

At the end of the experiment, there was a significant effect of the mussel treatment on total zooplankton abundance (ANOVA, $F_{3,36}=3.74$, $P=0.019$), but we didn't detect an effect of nutrients. Total zooplankton abundance was four times lower in the 0.5 and 1.0 mussels/L treatments compared to the 0.0 mussels/L (Fig. 2a), a loss of ~ 300 individuals/L, and the 0.25 mussels/L treatment was $\sim 46\%$ lower than the 0.0 mussel/L treatment. Although none of the mussel addition treatments were significantly different from each other, the difference between the 0.0 and 0.5 treatments was only marginally non-significant ($P=0.057$, Table A2.3), and the difference between 0.0 and 0.25 was non-significant ($P=0.12$, Table A2.3).

Total zooplankton abundance declines in mussel addition treatments were primarily driven by a ~94% decrease in rotifer abundance (ANOVA, $F_{3,36}=4.04$, $P=0.014$) from ~400 to 20 individuals/L, specifically in the 0.25 and 1.0 mussels/L treatments compared to the 0.0 mussels/L (Fig. 2d). However, removal of a 0.0 mussel/L mesocosm with particularly high rotifer abundance reduced this effect size to ~75% (a reduction from ~100 to 20 individuals/L) and resulted in marginal non-significance of the overall mussel effect (ANOVA, $F_{3,35}=2.78$, $P=0.055$). There were no detectable effects of zebra mussel additions on cladoceran or copepod abundance (Table A5.2 and A5.4). Across all treatments, nutrients were never retained in the minimum adequate models for cladocerans, copepods, or rotifers (Tables A5.2-A5.4). However, planned comparisons between mussel treatments revealed a significant positive effect of nutrients on copepod abundance in the 0.0 mussels/L treatment (Linear regression, $R^2=0.6$, $P=0.0001$, Fig. 3e), but no effect of nutrients on rotifers, cladocerans, or total zooplankton abundance in any mussel addition treatments (Fig. 3).

There was no significant treatment effect on zooplankton richness for cladocerans and copepods (Tables A5.6 and A5.8), but we did detect a significant effect of the zebra mussel treatment on total richness (ANOVA, $F_{3,36}=3.08$, $P=0.039$). However, this difference was not supported by post-hoc analysis (Table A2.3), and was likely driven by a small decline in rotifer richness (Fig. A6.2, ANOVA, $F=8.38$, $P=0.039$) between the 0.0 and 0.5 mussels/L treatments (Table A2.3) of ~2 species (Fig. A5.1).

Zooplankton community composition

Community composition was similar across all treatments at the beginning of the experiment before treatments were established (Table A2.6). At the end of the experiment we found a significant interaction between the mussel and nutrient treatments (non-parametric MANOVA, $F_{\text{model } 3, 32}=1.58$, $P=0.048$), along with a strong significant main effect of the mussel treatment (non-parametric MANOVA, $F_{\text{model } 3, 32}=2.53$, $P=5.7 \times 10^{-4}$) on zooplankton

community composition. In order to tease apart this interaction between mussel density and nutrients we used a PCoA of our mesocosm communities to calculate change in community position with nutrients within each mussel treatment category.

Within our mussel density treatments, we found correlations between community position and nutrient treatment along PCoA axis 2 in the 0.0 mussels/L treatment (Linear regression, $R^2=0.37$, $P=0.062$, Fig. 4e, 6a), and along PCoA axis 1 in the 0.5 mussels/L treatment (Linear regression, $R^2=0.35$, $P=0.07$, Fig. 4c, 6b). Although these P -values were marginally non-significant when calculated using only the first 2 dimensions of a PCoA, these treatments are the likely source of the significant interaction between our mussel and nutrient treatments detected by the multidimensional, non-parametric MANOVA analysis. In the 0.0 mussels/L treatments nutrient additions resulted in a shift from small rotifers in low nutrient treatments towards adult cyclopoids, juvenile calanoids, and small cladocerans (e.g. *Bosmina spp.* and *Chydorus sphaericus*) in high nutrient treatments (Fig. 6a). In the 0.5 mussels/L treatments community dominance shifted away from pelagic cladocerans and adult copepods in low nutrients towards juvenile cyclopoids and large rotifers in high nutrients (Fig. 6b). The 0.25 and 1.0 mussels/L treatments showed no relationship between nutrients and community position on either PCoA axis (Fig. 4 and 6c).

Compared to uninvaded communities, mussel addition significantly shifted invaded communities along PCoA axis 1 (Fig. 6a vs. 6c, ANCOVA, $F_{3,32}=7.35$, $P=0.00069$), but not PCoA axis 2, in all three invaded densities (Table A2.3). This equated to a community shift away from small rotifer species, such as *Polyarthra remata* and *Keratella spp.*, to large rotifers (e.g. *Lecane mira*), adult (e.g. *Mesocyclops edax*) and juvenile copepods, and small pelagic (*Bosmina spp.* and *Ceriodaphnia quadrangula*) and littoral cladocerans (e.g. *Alona spp.* and *Chydorus sphaericus*)(Fig. 6a vs. 6c).

Discussion

As evidenced by copepod abundance and our community analysis there was a clear interaction between our resource and consumer stressors. Individually, the bottom-up influence of added resources in uninvaded mesocosms led to gains in copepod abundance and a shift in community composition away from rotifer dominance, while the invasion of an omnivorous consumer resulted in heavy predation on primary producers and rotifers in all invaded treatments. The consequences of our stressor interaction varied based on invader density. When stressors were combined in the low and high invasion treatments, only the invasive consumer effect on our univariate and multivariate metrics remained as there was no longer any change in zooplankton abundance or community composition with increased resources. However, in the medium invader density treatment there was an additive effect of both invasion and nutrient stress on the zooplankton community, but not on any measures of abundance or richness. These differences in multiple stressor response showed that generally increased consumption from our invasive consumer was antagonistically reducing the effects of nutrient enrichment, but this effect changed depending upon invader density and whether univariate or multivariate analyses were used.

Energy transfer in uninvaded and invaded communities

To better understand the mechanisms behind our univariate stressor impacts we simplified our uninvaded and invaded zooplankton communities to the major energy pathways (Fig. 5, an "end-to-end" model, Fulton 2010), with available resources as the lowest level in the food web (similar to Wollrab et al. 2012). Experimental communities consisted of two primary producer groups: small phytoplankton and large phytoplankton. Previous work on diets of small cladocerans (Fryer 1968, Geller and Müller 1981), adult and juvenile copepods (Fryer 1957, Hopp et al. 1997, Sommer and Sommer 2006), and rotifers (Pourriot 1977) suggested that in our uninvaded treatments small phytoplankton was consumed by both cladocerans and rotifers, and large phytoplankton primarily by copepods. The top consumers in our mesocosms were

copepods, and they likely fed on phytoplankton, rotifers, and small cladocerans (Fryer 1957, Hopp et al. 1997) as there was a variety of small herbivorous and large carnivorous copepod species. The energy links created by zebra mussel introduction were inferred based on observed community changes, and previous work on zebra mussel diet preferences for phytoplankton (Lavretyev et al. 1995, Bastviken et al. 1998) and zooplankton (MacIsaac et al. 1991, 1995).

Single stressor effects of nutrient enrichment

Nutrient addition in uninvaded mesocosms did not affect producers, but did increase the abundance (copepods, Fig. 3e) and community dominance (cladocerans and copepods, Fig. 6) of higher level consumers. The lack of effect on producers could have resulted if top-down predation was preventing the lower trophic levels from responding to the bottom-up influence of increased resources. This has been previously observed in zooplankton communities, for example by Leibold (1989) and Steiner (2001), where added nutrients also elicited no change in the primary producers, but significantly increased zooplankton consumer abundance. The end-to-end model of our uninvaded experimental community (Fig. 5) supported this proposed mechanism. Added resources would have increased top consumer (copepod) abundance, which in turn could have increased the grazing pressure on the trophic levels directly below (Wollrab et al. 2012), preventing the rotifers, cladocerans, and large phytoplankton from responding to added nutrients. Under these assumptions the small phytoplankton would have been released from consumptive control, however increases in small phytoplankton abundance could have been offset by shared predation between the cladocerans, rotifers, and potentially by consumption from smaller copepod species (Fryer 1957). Another possible reason there were no nutrient effects on producers is that the added nutrients were entirely absorbed by the periphyton that grows readily on mesocosm walls and can have similar nutrient uptake rates as phytoplankton (Hansson 1990, Chen et al. 2000). The nutrient-induced shift in community composition towards littoral cladocerans (Fig. 6a), which can consume periphyton (Fryer 1968), suggested that higher

nutrients may have favored periphyton growth. However, this would not explain why copepod abundance was higher in nutrient enriched mesocosms three months following the nutrient addition, and why there was no significant change in littoral cladoceran abundance. Although periphyton was not measured in this experiment, visual observations of attached algae cover on the sides and bottom of the mesocosms suggested no differences between mussel treatments, and no trends with increasing nutrients.

The nutrient-induced shift in community composition from rotifers to cladocerans and copepods (Fig. 6a) was indicative of how nutrient enrichment can benefit the growth of some consumers, yet be detrimental to others. There are a few possible explanations for why added resources in the uninvaded mesocosms favored dominance of cladocerans and copepods over rotifers. Rotifers feed on small-sized phytoplankton, while cladocerans and copepods are able to feed on larger-celled species. Nutrient enrichment can lead to dominance of larger phytoplankton due to increased predation pressure from added resources (Downing et al. 2001, Irwin and Finkel 2006) or better capability of cyanobacteria to compete in low light environments (Downing et al. 2001). This suggests that rotifers may have had a more difficult time feeding on the higher abundance of larger celled phytoplankton species in our higher nutrient mesocosms. For example, Miracle et al. (2007) found that planktonic rotifer abundance declined as algae dominance shifted towards larger-celled species. Though we attempted to capture phytoplankton size shifts by measuring total and edible ($<30\mu\text{m}$) chlorophyll a, it is possible that more subtle size shifts occurred within these categories that would have been better detected with species specific data. Changes in N:P food quality may also be a likely explanation of the community shift away from rotifers with increased nutrients. Rotifers may have been favored when experimental phosphorus additions were low (a high N:P ratio) as rotifer growth rates can be more limited by nitrogen availability (Hessen et al. 2007), while small cladocerans and copepods may have been favored when nutrient additions were high (a low N:P ratio) as their growth is generally more limited by phosphorus availability (Hessen et al. 1992, Carrillo et al. 2001, Hall et al. 2004). It is unlikely

this shift was due to the superior competitive abilities of large cladocerans (Gilbert et al. 1988) whose abundance is favored at higher phosphorus levels (Elser et al. 2001, Hall et al. 2004) since only small cladoceran abundance was affected by increasing nutrients (Fig. 6a), and small cladocerans generally do not competitively suppress rotifers (Gilbert et al. 1988). Whichever mechanism was responsible, the overall result was a nutrient-induced shift in the consumer community. This composition change, along with increased consumer abundance, indicated nutrient enrichment was having a strong bottom-up influence in our uninvaded communities.

Single stressor effects of an introduced consumer

Consumer invasion lead to sharp declines in preferred prey (rotifers and phytoplankton) and shifted community dominance towards macrozooplankton competitors (small cladocerans and copepods, Fig. A4.1). These effects are consistent with experiments and surveys on the consumptive effects of zebra mussels on phytoplankton and zooplankton (e.g. MacIsaac et al. 1991, 1995, Pace et al. 1998, David et al. 2009, Dzialowski 2013). Though we had anticipated possible declines in native competitor abundance due to reduced food resources, there was no significant loss of either cladocerans or copepods in invaded communities (Fig. 2b and 2c), possibly because they were able to exploit less preferred food resources that aren't as strongly affected by zebra mussel filtration, such as larger rotifers, more mobile phytoplankton, and periphyton. Studies by Pace et al. (1998) and Maguire and Grey (2006) also found little effect of zebra mussel invasion on cladoceran and copepod communities, attributing this to a possible diet shift towards consumption of bacteria, protozoans, detritus, or allochthonous material (though the mesh covering our mesocosms would have limited allochthonous inputs).

It was interesting to see no effect of the introduced consumer on the small, palatable producers (edible chlorophyll a, Fig. 1). Zebra mussels are filter feeders that can consume a wide size range of particles (0-750 μ m, Winkel and Davids 1982, Sprung and Rose 1988, Pires et al. 2004) and are known to drastically reduce phytoplankton abundances (Wu and Culver 1991,

Lavrentyev et al. 1995, Higgins and Vander Zanden 2010). If significant quantities of the larger primary producers were being filtered (total chlorophyll a, Fig. 1), then it is likely that the small phytoplankton were also being consumed. Some species of phytoplankton that are more mobile, difficult to digest, or have higher growth rates, can persist following zebra mussel invasion (Mellina et al. 1995), and could increase in abundance due to reduced competition (Lavrentyev et al. 1995), reduced zooplankton predation (Descy et al. 2003), or additional nutrients mobilized by mussel excretion (Gardner 1995, Heath et al. 1995, Mellina et al. 1995). Food quality can also be more important than size in determining filtering effects on phytoplankton (Vanderploeg et al. 1996). Some smaller phytoplankton can be a lower quality food source compared to larger phytoplankton (Naddafi et al. 2007), potentially causing zebra mussels to expel smaller phytoplankton species ($<7\mu\text{m}$ in the case of Naddafi et al. 2007) without digesting them. This selectivity for food quality over size was also observed by Winkel and Davids (1982) and Bastviken et al. (1998) who both found that zebra mussels could preferentially select between similarly sized phytoplankton species.

Multiple stressor interaction

In uninvaded communities there was a clear bottom-up transfer of resources into the highest level consumers (Fig. 3e and 6a), while native consumers in the invaded treatments showed little response to increased nutrients (Fig. 3 and 6c). This indicated that in invaded treatments the introduced consumer was counteracting our nutrient stressor. Indirect competitive effects between the invader and native competitors was the most likely mechanism preventing zooplankton from responding to increased nutrients (Fig. 5), though this was not directly tested in our experiment. Similarly, a survey by Johannsson et al. (2000) and a mesocosm experiment by Dzialowski (2013) both inferred that increased grazing on primary producers following mussel invasion subsequently controlled the realized productivity of the native zooplankton community. Although mussel densities used by Dzialowski (2013) were within the range used in our

experiment (0.33 vs. 0.25-1.0 mussels/L), he found that mussel invasion delayed the effects of nutrient enrichment on phytoplankton for one week, whereas our experiment showed these effects persisting for up to 12 weeks until termination of the experiment. This discrepancy could have resulted from differences in our experimental protocol. In our experiments, aeration likely allowed zebra mussels greater access to the full water column throughout the experiment due to greater water mixing. We also continually replaced dead mussels to ensure that consumer pressure was maintained throughout the experiment

The suppression of a nutrient effect by our introduced consumer was not consistent over all invaded treatments. Nutrient enrichment in the medium mussel treatment further shifted community composition towards juvenile copepods and large rotifers, an apparent exacerbation of the general effect of invasion on community composition (Fig. 6b vs. 6c), but not beyond that observed in invaded communities from the other mussel densities. It is difficult to say why the medium mussel density showed an effect of nutrients on community composition, and the low and high mussel treatments did not. Zebra mussel filtration is not always expected to increase linearly with mussel density. As mussel density increases and clusters become thicker the amount of refiltration (filtered water that isn't cleared of any particles, Yu and Culver 1999) also increases, which can dramatically reduce the clearance rate of higher density mussel clumps (Yu and Culver 1999, Elliot et al. 2008, Zaiko and Daunys 2012). Available literature on individual mussel clearance rates also varies greatly, from 5-574 ml mussel hr⁻¹, depending on mussel size, temperature, and food density (Elliot et al. 2008). For example, using averaged individual clearance rates of clumped mussels (as in our experiment) from Yu and Culver (1999) and Zaiko and Daunys (2012), we estimated that our low, medium, and high treatment densities were theoretically able to process approximately 46, 93, and 187 L/day respectively. However, this likely overestimates the change in total mussel clearance rates as the density treatment increases. Yu and Culver (1999), Elliot et al. (2008) and Zaiko and Daunys (2012) all observed their *lowest* individual and overall clearance rates at their *highest* mussel densities. Although there may be

some unexpected differences in clearance rates between our mussel treatments (e.g. a potential unimodal relationship between mussel density and clearance rate, similar to that proposed by Zaiko and Daunys 2012, and somewhat suggested by the lower rotifer richness in the medium mussel treatment, Fig. A6.2), we cannot determine the validity or cause of the community shift with nutrients in our medium mussel treatment since there was no effect of nutrients on any of our univariate metrics in invaded mesocosms, suggesting no differences in community function (based on abundance, biomass, or chlorophyll a) between all invaded treatments.

Quantitative classification of multiple stressor ecological interactions as additive, synergistic, or antagonistic is usually performed using changes in growth, productivity, biomass, mortality, or richness (Crain et al. 2008, Darling and Côté 2008). Based on these univariate metrics we found evidence for an antagonistic interaction between our stressors since copepod abundance increased with nutrients in uninvaded mesocosms, and showed no relationship with nutrients in invaded mesocosms (Fig. 3). However, few studies have quantitatively classified a multiple stressor interaction based on shifts in community composition. To do this we used an approach similar to how an interaction is assessed in an ANCOVA analysis, we calculated and compared the change in community position in both PCoA axes (illustrated by Fig. 4) due to nutrients (slope) and invasion (intercept) at all mussel densities. The uninvaded communities provided the baseline for a single stressor nutrient effect ($R^2=0.37$, Fig. 4e). Compared to the uninvaded communities, the slopes of community position against nutrients in the 0.25 and 1.0 mussels/L treatments were close to zero (Fig. 4), but were located in significantly different positions along PCoA axis 1 (Fig. 4a vs 4bd, post-hoc Table A2.3). We therefore classified these non-additive community interactions as antagonistic since the nutrient effect was no longer present (a decline in slope) at these mussel densities. The communities in the 0.5 mussels/L treatment showed the same magnitude of community shift with nutrients as the uninvaded treatments (Fig. 4c, $R^2=0.35$), in addition to exhibiting a similar shift in community position due to invasion along PCoA axis 1 (Fig. 4a vs. 4c, post-hoc Table A2.3). This stressor interaction was

determined to be additive, since the composition change caused by combining stressors was approximately equal to that expected based on their individual effects (positive slope of equal magnitude to uninvaded, equal change in intercept due to invasion). Interestingly, the trajectory of community change was consistent over all invaded treatments (a shift to the left, Fig. 6b and c), and nutrient addition in the 0.5 mussels/L treatment only added to this effect (as opposed to shifting downwards as it did in the 0.0 mussels/L treatment, Fig. 6a). This suggests that when these stressors were combined zebra mussels were the primary structuring force in the community, and nutrient stress further exacerbated their impacts.

Conclusions

Considering multiple stressor interactions as simple additions of individual stressor effects misses much of the complexity involved in community interactions. A simplistic view of nutrient and consumer stressor interactions based on their individual effects (e.g. a bottom-up increase in productivity from nutrient addition vs. a top-down reduction in primary or secondary biomass due to consumer invasion) might suggest that their interaction should effectively cancel their individual effects, or at least result in some reduction of both. However, we found that looking at stressor effects at a community level, and across a gradient of stressor intensities, could lead to different conclusions about the outcome of stressor interactions. The interaction between our nutrient and invasive consumer stressors was antagonistic at all treatment levels when looking at univariate metrics, such as abundance, while the community analysis showed an antagonistic or additive interaction that depended upon the density of the invader. Therefore, although the more simplistic view of multiple stressor interactions would suggest that stressor combinations are the sum of their individual components, in our experiment we observed a generally non-additive interaction between our nutrient and invasive consumer stressors.

Extrapolating the results of this study to natural communities and other regions should be done cautiously. Our experimental nutrient additions only corresponded to levels frequently

observed in oligotrophic to eutrophic lakes in North America, and likely did not capture the full range of stress effects that can result from phosphorus loadings an order of magnitude higher than those used in this experiment (e.g. levels encountered in some European lakes, Kristensen and Hansen 1994, Jeppesen et al. 2005). Additionally, mesocosm experiments are usually short duration and at a smaller scale than natural communities, and they create new, artificial structure for biotic growth (Chen et al. 2000, Englund and Cooper 2003). Also, though we did provide a small amount of constant mixing, zebra mussel studies using mesocosms may overestimate their filtration effects as the hydrodynamics of a natural lake system are not generally taken into account, and whether an interaction between nutrient and zebra mussel stressors is additive or antagonistic will likely depend upon water depth, residence time, and invader density (Conroy 2010). However, we believe we have provided some important insights on potential non-additive interactions between nutrient enrichment and consumer invasion, the difficulty of predicting the outcome of multiple stressor interactions using single stressor studies, and the need for further community-level multiple stressor experiments. Differing responses across a gradient of stressor intensities, the changes in one trophic level "masking" the changes in another, competitors potentially switching to unexploited food resources, and the tug-of-war between the relative bottom-up and top-down strengths of our individual stressors were just a few of the more complex and unpredictable interactions that we observed in an experiment using just two co-occurring stressors.

Figure 1 Values for total (grey boxes) and edible (open boxes) chlorophyll a from the final sampling date for each mussel treatment (n=10). Bottom and top edges of boxes represent the first and third quartiles respectively, with a dark, horizontal line as the median. Whiskers encompass data points that lie within 1.5 times the inner quartile range, data outside this range is shown as separate points. Different letters over boxes indicate mussel treatments with significantly different abundances ($P < 0.05$, Table A2.3). Note log-scale used on the y-axis.

Figure 2 Abundances of (a) total zooplankton (including rotifers), (b) cladocerans, (c) copepods, and (d) rotifers in each mussel treatment (n=10). Bottom and top edges of boxes represent the first and third quartiles respectively, with a dark, horizontal line as the median. Whiskers encompass data points that lie within 1.5 times the inner quartile range, data outside this range is shown as separate points. Different letters over boxes indicate mussel treatments with significantly different abundances ($P < 0.05$, Table A2.3). Note the break in the y-axis of (d).

Figure 3 Relationship between nutrient treatment and abundance (abund.) of rotifers (Rot.), copepods (Cop.), and cladocerans (Clad.) in the 0.0, 0.25, 0.5 and 1.0 mussels L⁻¹ treatment densities. Best fit lines are shown in the treatments for the zooplankton groups whose abundance is significantly correlated to nutrient level ($P < 0.05$). Note the break in the y-axis for rotifer abundance.

Figure 4 Change in community location (represented by PCoA Axis 1 and 2 scores) with increasing nutrients for each mussel treatment. Best fit lines are shown in the treatments whose PCoA location is correlated with nutrient level. Note log scale used on the y-axis.

Figure 5 End-to-end model of our predicted and observed impacts of nutrient enrichment and zebra mussel invasion on abundance of the phytoplankton and zooplankton community. Circles represent groupings at each trophic level, starting with the resource pool (R) utilized by the small phytoplankton (SP) and large phytoplankton (LP) producer groups. These producer groups would then be consumed by the herbivorous cladocerans (Cla) and rotifers (Rot), with copepods as omnivorous top consumers (Cop). Lines linking circles indicate which groups can utilize/consume those below, and arrows represent abundance changes in each group caused by the experimental treatments (horizontal arrows represent no change). Red arrows indicate observed abundance changes that were different from the predicted models, and bolded lines indicate pathways created due to zebra mussel (ZM) invasion.

Figure 6 Biplot of principal coordinates scores for PCoA axis 1 and 2 for community data from the final week of the experiment. Each point represents the zooplankton community from (a) uninvaded mesocosms (circles), (b) 0.5 mussels L⁻¹ (diamonds), and (c) 0.25 and 1.0 mussels L⁻¹ (squares and triangles). The increasing nutrient gradient is illustrated with an increasingly dark color fill. Colors transition from white to black in 10 equal increments representing the 10 nutrient treatments, with darker color equating to higher nutrient additions. Arrows and letters in (d) represent which species are associated with each community, with the direction and length of the arrow indicating the importance of that species to differentiating between communities. Color of abbreviations represents species belonging to the broader zooplankton groups of cladocerans (red), copepods (blue), and rotifers (green). Full species names that correspond to abbreviations can be found in Table A4.1.

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Appendix 1
Lake Characteristics

Table A1.1 Information for all lakes involved in the experiment. Data was collected from May 2012 to August 2012 (Arnott, unpublished data). Lake Opinicon was the source of all mesocosm water and zebra mussels, while zooplankton and phytoplankton samples were taken from the other five lakes.

Lake	Latitude (N) Longitude (W)	Area (ha)	Max Depth (m)	pH	DOC (mg/L)	Cond. (µS/cm)	Av. TP (µg/L)
Opinicon	44°55.94' 76°32.84'	788.0	11.3	8.17	6.37	192.0	13.3
Lindsay	44°53.72' 76°39.06'	31.5	10.9	8.09	6.65	230.5	8.6
Warner	44°52.86' 76°38.23'	9.2	6.4	8.03	7.05	246.0	10.4
Round	44°53.79' 76°39.99'	15.0	30.1	8.14	4.00	164.0	6.0
Long	44°52.78' 76°40.27'	15.5	26.0	8.23	4.30	182.0	5.0
Elbow	44°47.66' 76°42.82'	15.5	10.6	7.69	7.50	77.0	11.7

Appendix 2

Statistical Results

Table A2.1 Results of minimum adequate ANCOVA models conducted on the listed metrics to determine any differences in the zooplankton data collected from the first sampling week of the experiment. Analyzed metrics and model structure were based on the minimum adequate models from Tables A6.1-A6.10. Asterisk indicates significance ($P < 0.05$).

Metric	Nutrients (N)		Nutrient ² (N ²)		N*N ²	
	F	P	F	P	F	P
Cladoceran Abundance	0.29	0.59	1.86	0.18	7.78	0.0084*

Table A2.3 Results of Tukey HSD tests on the minimum adequate models for the listed metrics and PCoA post-hoc tests of community position. Asterisk indicates significance ($P < 0.05$).

Metric	<i>P</i> -values					
	0.0-0.25	0.0-0.5	0.0-1.0	0.25-0.5	0.25-1.0	0.5-1.0
Total Chlorophyll a	0.0015*	0.00036*	0.017*	0.95	0.81	0.51
Total Abundance	0.12	0.057	0.020*	0.98	0.85	0.97
Rotifer Abundance	0.022*	0.09	0.029*	0.93	1.00	0.96
Total Richness	1.00	0.11	0.25	0.11	0.26	0.97
Rotifer Richness	0.67	0.027*	0.52	0.30	0.99	0.43
PCoA axis 1 Position	0.0018*	0.0049*	0.0031*	0.98	0.99	0.99
PCoA axis 2 Position	1.00	0.99	0.99	0.99	0.99	0.98

Table A2.4 Results of the minimum adequate linear ANOVA models conducted on the listed metrics to determine any differences in the zooplankton data collected from the final sampling week of the experiment. Analyzed metrics and model structure were based on the minimum adequate models from Tables A5.1-A5.10, nutrient and interaction terms were excluded as these were never retained in the best models. Asterisk indicates significance ($P < 0.05$).

Metric	Mussels (M)		
	F	df	<i>P</i>
Total Chlorophyll a	8.01	3,36	0.00032*
Total Richness	3.08	3,36	0.039*
Rotifer Abundance	4.04	3,36	0.014*
Total Abundance	3.74	3,36	0.019*

Table A2.5 Results of the minimum adequate general linear ANOVA models conducted on the listed metrics to determine any differences in the zooplankton data collected from the final sampling week of the experiment. Analyzed metrics and model structure were based on the minimum adequate models from Tables A5.1-A5.10, nutrient and interaction terms were excluded as these were never retained in the best models. Asterisk indicates significance ($P < 0.05$).

Metric	Mussels (M)		
	χ^2	df	P
Rotifer Richness	8.38	3,36	0.039*

Table A2.6 Results of non-parametric MANOVA analysis conducted to determine any significant differences in zooplankton community composition caused by the mussel and nutrient treatments. Asterisk indicates significance ($P < 0.05$).

Metric	Mussels (M)			Nutrients (N)			M*N		
	F_{model}	df	P	F_{model}	df	P	F_{model}	df	P
Community Composition (1st week)	0.34	3,32	0.92	0.4	1,32	0.66	0.89	3,32	0.48
Community Composition (Final week)	2.53	3,32	0.00057*	1.63	1,32	0.11	1.58	3,32	0.049*

Appendix 3

Phosphorus Gradients

Fig A3.1 Relationship between phosphorus addition amount and measured phosphorus concentration two weeks following the initial addition date. Best fit lines are shown for treatments whose measured phosphorus concentration is significantly correlated to nutrient addition ($P < 0.05$). Note log scale used on the y-axis.

Appendix 4 **Zooplankton Community Data**

Table A4.1 Zooplankton species names and corresponding abbreviations for Fig. 6.

Species	Abbreviation
<i>Acroperus harpae</i>	A. H.
<i>Alona rectangula</i>	A. R.
<i>Alona guttata</i>	A. G.
<i>Alona quadrangularis</i>	A. Q.
<i>Bosmina lieferi/freyi</i>	B. L/F.
<i>Camptocercus rectirostris</i>	C. R.
<i>Ceriodaphnia quadrangula</i>	C. Q.
<i>Chydorus sphaericus</i>	C. S.
<i>Graptoleberis testudinaria</i>	G. T.
<i>Pleuroxus denticulatus</i>	P. D.
<i>Pleuroxus truncatus</i>	P. T.
<i>Polyphemus pediculus</i>	P. P.
Calanoid copepodid	CA. C.
Cyclopoid copepodid	CY. C.
Calanoid nauplii	CA. N.
Cyclopoid nauplii	CY. N.
<i>Cyclops scutifer</i>	CY. S.
<i>Cyclops vernalis</i>	CY. V.
<i>Mesocyclops edax</i>	M. E.
<i>Keratella cochlearis</i>	K. C.
<i>Keratella serrulata</i>	K. S.
<i>Lecane inermis</i>	L. I.
<i>Lecane mira</i>	L. M.
<i>Monostyla copeis</i>	M. CO.
<i>Monstyla closterocerca</i>	M. CL.
<i>Mytilina ventralis</i>	M. V.
<i>Polyartha remata</i>	P. R.
<i>Trichocerca rattus</i>	T. R.
<i>Trichocerca pusilla</i>	T. P.

Appendix 5

Abundance, Richness, and Chlorophyll Dredge Tables from the Final Week

Table A5.1. Dredge table for total zooplankton abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
2	2.507	+							5	-15.243	42.3	0.0	0.5
6	2.534	+		-1.10E-05					6	-15.131	44.8	2.56	0.139
4	2.524	+	-4.17E-04						6	-15.221	45	2.74	0.127
1	2.175								2	-20.665	45.7	3.4	0.091
8	2.445	+	6.57E-03	-8.42E-05					7	-14.723	46.9	4.69	0.048
5	2.201			-1.10E-05					3	-20.58	47.8	5.58	0.031
3	2.191		-4.17E-04						3	-20.649	48	5.71	0.029
40	2.501	+	-5.55E-03	2.98E-04			-3.02E-06		8	-14.403	49.5	7.2	0.014
7	2.112		6.57E-03	-8.42E-05					4	-20.27	49.7	7.43	0.012
39	2.168		-5.55E-03	2.98E-04			-3.02E-06		5	-20.028	51.8	9.57	0.004
12	2.414	+	2.30E-03		+				9	-14.614	53.2	10.98	0.002
22	2.483	+		9.96E-06		+			9	-14.786	53.6	11.32	0.002
16	2.335	+	9.28E-03	-8.42E-05	+				10	-14.1	55.8	13.53	0.001
24	2.394	+	6.57E-03	-6.33E-05		+			10	-14.37	56.3	14.08	0
48	2.391	+	-2.84E-03	2.98E-04	+		-3.02E-06		11	-13.77	59	16.72	0
56	2.45	+	-5.55E-03	3.19E-04		+	-3.02E-06		11	-14.045	59.5	17.27	0

32	2.218	+	1.97E-02	-2.09E-04	+	+		13	-12.931	65.9	23.61	0
64	2.274	+	7.53E-03	1.73E-04	+	+	-3.02E-06	14	-12.581	70	27.71	0
128	2.34	+	-6.69E-03	6.22E-04	+	+	-6.56E-06	+ 17	-12.296	86.4	44.16	0

Table A5.2. Dredge table for cladoceran abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
1	2.017								2	-16.37	37.1	0.0	0.516
3	1.986		7.70E-04						3	-16.299	39.3	2.2	0.171
5	2.004			5.49E-06					3	-16.343	39.4	2.29	0.164
7	1.947		4.21E-03	-4.14E-05					4	-16.186	41.5	4.45	0.056
2	2.14	+							5	-15.165	42.1	5.03	0.042
39	2.015		-1.06E-02	4.27E-04			-3.69E-06		5	-15.74	43.2	6.18	0.023
4	2.108	+	7.70E-04						6	-15.09	44.7	7.66	0.011
6	2.126	+		5.49E-06					6	-15.137	44.8	7.76	0.011
8	2.07	+	4.21E-03	-4.14E-05					7	-14.97	47.4	10.38	0.003
12	1.867	+	6.74E-03		+				9	-12.727	49.5	12.39	0.001
40	2.138	+	-1.06E-02	4.27E-04			-3.69E-06		8	-14.495	49.6	12.57	0.001
22	1.959	+		7.47E-05		+			9	-12.969	49.9	12.87	0.001
16	1.828	+	1.02E-02	-4.14E-05	+				10	-12.592	52.8	15.71	0
24	1.902	+	4.21E-03	2.77E-05		+			10	-12.783	53.2	16.09	0
48	1.896	+	-4.66E-03	4.27E-04	+		-3.69E-06		11	-12.056	55.5	18.48	0
56	1.971	+	-1.06E-02	4.96E-04		+	-3.69E-06		11	-12.252	55.9	18.87	0
32	1.86	+	7.34E-03	-7.23E-06	+	+			13	-11.815	63.6	26.57	0
64	1.928	+	-7.49E-03	4.61E-04	+	+	-3.69E-06		14	-11.258	67.3	30.25	0
128	2.002	+	-2.34E-02	9.64E-04	+	+	-7.66E-06	+	17	-10.997	83.8	46.75	0

Table A5.3. Dredge table for rotifer abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
2	1.831	+							5	-37.157	86.1	0.0	0.377
4	2.015	+	-4.54E-03						6	-36.278	87.1	1.02	0.226
6	1.953	+		-5.05E-05					6	-36.351	87.2	1.17	0.21
8	2.017	+	-4.75E-03	2.45E-06					7	-36.277	90.1	3.98	0.052
1	1.226								2	-42.959	90.2	4.16	0.047
3	1.41		-4.54E-03						3	-42.304	91.3	5.2	0.028
5	1.348			-5.05E-05					3	-42.358	91.4	5.3	0.027
40	2.006	+	-2.30E-03	-7.47E-05			6.09E-07		8	-36.273	93.2	7.11	0.011
7	1.412		-4.75E-03	2.45E-06					4	-42.304	93.8	7.67	0.008
22	2.136	+		-1.26E-04		+			9	-35.207	94.4	8.33	0.006
12	2.246	+	-1.03E-02		+				9	-35.466	94.9	8.85	0.005
39	1.401		-2.30E-03	-7.47E-05			6.09E-07		5	-42.301	96.4	10.29	0.002
24	2.2	+	-4.75E-03	-7.33E-05		+			10	-35.129	97.8	11.76	0.001
16	2.248	+	-1.05E-02	2.45E-06	+				10	-35.466	98.5	12.44	0.001
56	2.189	+	-2.30E-03	-1.50E-04		+	6.09E-07		11	-35.124	101.7	15.6	0
48	2.237	+	-8.02E-03	-7.47E-05	+		6.09E-07		11	-35.462	102.4	16.27	0
32	2.098	+	2.80E-03	-1.57E-04	+	+			13	-34.849	109.7	23.62	0
64	2.087	+	5.25E-03	-2.35E-04	+	+	6.09E-07		14	-34.844	114.5	28.41	0
128	1.901	+	4.55E-02	-1.51E-03	+	+	1.06E-05	+	17	-33.83	129.5	43.4	0

Table A5.4. Dredge table for copepod abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
1	0.5751								2	-17.507	39.3	0.0	0.452
3	0.5051		1.73E-03						3	-17.171	41	1.67	0.196
5	0.5331			1.74E-05					3	-17.255	41.2	1.84	0.18
7	0.4811		3.85E-03	-2.56E-05					4	-17.13	43.4	4.06	0.059
39	0.5929		-2.04E-02	7.38E-04			-6.02E-06		5	-15.976	43.7	4.38	0.051
2	0.7179	+							5	-16.404	44.6	5.24	0.033
4	0.6479	+	1.73E-03						6	-16.05	46.6	7.31	0.012
6	0.6758	+		1.74E-05					6	-16.139	46.8	7.49	0.011
8	0.6239	+	3.85E-03	-2.56E-05					7	-16.006	49.5	10.17	0.003
40	0.7357	+	-2.04E-02	7.38E-04			-6.02E-06		8	-14.783	50.2	10.87	0.002
22	0.4887	+		9.46E-05		+			9	-14.13	52.3	12.92	0.001
12	0.3989	+	7.88E-03		+				9	-14.333	52.7	13.33	0.001
24	0.4368	+	3.85E-03	5.16E-05		+			10	-13.983	55.6	16.21	0
16	0.3749	+	1.00E-02	-2.56E-05	+				10	-14.285	56.2	16.82	0
56	0.5486	+	-2.04E-02	8.15E-04		+	-6.02E-06		11	-12.625	56.7	17.34	0
48	0.4867	+	-1.42E-02	7.38E-04	+		-6.02E-06		11	-12.949	57.3	17.99	0
32	0.4837	+	3.72E-04	9.05E-05	+	+			13	-13.378	66.8	27.42	0
64	0.5955	+	-2.38E-02	8.54E-04	+	+	-6.02E-06		14	-11.978	68.8	29.42	0
128	0.5025	+	-3.69E-03	2.19E-04	+	+	-1.01E-06	+	17	-11.192	84.2	44.86	0

Table A5.5. Dredge table for total zooplankton richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
2	1.166	+							5	42.263	-72.8	0.0	0.41
1	1.126								2	37.697	-71.1	1.69	0.176
6	1.164	+		7.43E-07					6	42.272	-70	2.76	0.103
4	1.168	+	-5.28E-05						6	42.269	-70	2.77	0.103
5	1.124			7.43E-07					3	37.704	-68.7	4.02	0.055
3	1.128		-5.28E-05						3	37.701	-68.7	4.02	0.055
8	1.185	+	-1.53E-03	1.78E-05					7	42.662	-67.8	4.94	0.035
40	1.21	+	-7.00E-03	1.90E-04			-1.36E-06		8	43.835	-67	5.74	0.023
7	1.145		-1.53E-03	1.78E-05					4	38.014	-66.9	5.88	0.022
39	1.17		-7.00E-03	1.90E-04			-1.36E-06		5	38.938	-66.1	6.65	0.015
22	1.18	+		-5.99E-06		+			9	43.123	-62.2	10.52	0.002
12	1.186	+	-4.96E-04		+				9	42.656	-61.3	11.45	0.001
24	1.201	+	-1.53E-03	1.11E-05		+			10	43.531	-59.5	13.29	0.001
16	1.202	+	-1.97E-03	1.78E-05	+				10	43.057	-58.5	14.23	0
56	1.226	+	-7.00E-03	1.84E-04		+	-1.36E-06		11	44.757	-58.1	14.67	0
48	1.228	+	-7.44E-03	1.90E-04	+		-1.36E-06		11	44.254	-57.1	15.68	0
32	1.18	+	9.44E-06	-6.09E-06	+	+			13	45.842	-51.7	21.08	0
64	1.205	+	-5.46E-03	1.67E-04	+	+	-1.36E-06		14	47.224	-49.6	23.11	0
128	1.175	+	1.15E-03	-4.22E-05	+	+	2.84E-07	+	17	48.363	-34.9	37.85	0

Table A5.6. Dredge table for cladoceran richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N2	M:N	M:N2	N:N2	M:N:N2	df	logLik	AICc	delta	weight
1	0.9062								2	39.447	-74.6	0.0	0.42
2	0.8882	+							5	42.066	-72.4	2.2	0.14
3	0.9111		-1.19E-04						3	39.474	-72.3	2.29	0.134
5	0.9065			-9.86E-08					3	39.447	-72.2	2.34	0.13
7	0.9265		-1.49E-03	1.65E-05					4	39.766	-70.4	4.18	0.052
4	0.893	+	-1.19E-04						6	42.097	-69.6	4.92	0.036
6	0.8884	+		-9.86E-08					6	42.066	-69.6	4.98	0.035
39	0.9504		-6.66E-03	1.80E-04			-1.29E-06		5	40.669	-69.6	5.0	0.035
8	0.9085	+	-1.49E-03	1.65E-05					7	42.43	-67.4	7.21	0.011
40	0.9324	+	-6.66E-03	1.80E-04			-1.29E-06		8	43.465	-66.3	8.28	0.007
22	0.904	+		-6.51E-06		+			9	42.324	-60.6	13.92	0
12	0.9034	+	-3.76E-04		+				9	42.252	-60.5	14.07	0
24	0.924	+	-1.49E-03	1.01E-05		+			10	42.694	-57.8	16.77	0
16	0.9189	+	-1.74E-03	1.65E-05	+				10	42.588	-57.6	16.98	0
56	0.9479	+	-6.66E-03	1.73E-04		+	-1.29E-06		11	43.743	-56.1	18.51	0
48	0.9428	+	-6.92E-03	1.80E-04	+		-1.29E-06		11	43.631	-55.8	18.74	0
32	0.8744	+	2.20E-03	-3.10E-05	+	+			13	45.138	-50.3	24.29	0
64	0.8983	+	-2.98E-03	1.32E-04	+	+	-1.29E-06		14	46.328	-47.9	26.71	0
128	0.9062	+	-4.69E-03	1.86E-04	+	+	-1.72E-06	+	17	46.509	-31.2	43.37	0

Table A5.7. Dredge table for rotifer richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
2	1.482	+							4	-79.03	167.2	0.0	0.364
1	1.186								1	-83.223	168.6	1.35	0.186
4	1.554	+	-1.81E-03						5	-78.862	169.5	2.29	0.116
6	1.521	+		-1.67E-05					5	-78.926	169.6	2.41	0.109
3	1.258		-1.81E-03						2	-83.055	170.4	3.23	0.072
5	1.226			-1.67E-05					2	-83.119	170.6	3.36	0.068
8	1.597	+	-5.77E-03	4.83E-05					6	-78.796	172.1	4.93	0.031
7	1.302		-5.77E-03	4.83E-05					3	-82.989	172.6	5.44	0.024
40	1.678	+	-2.49E-02	6.59E-04			-4.85E-06		7	-78.47	174.4	7.24	0.01
39	1.383		-2.48E-02	6.59E-04			-4.85E-06		4	-82.663	174.5	7.26	0.01
12	1.788	+	-8.20E-03		+				8	-77.647	175.9	8.74	0.005
22	1.663	+		-8.26E-05		+			8	-77.937	176.5	9.32	0.003
16	1.816	+	-1.11E-02	3.68E-05	+				9	-77.609	179.2	12.01	0.001
24	1.726	+	-5.12E-03	-2.32E-05		+			9	-77.836	179.7	12.47	0.001
48	1.897	+	-3.01E-02	6.47E-04	+		-4.85E-06		10	-77.284	182.2	14.95	0
56	1.815	+	-2.50E-02	6.14E-04		+	-5.08E-06		10	-77.479	182.5	15.34	0
32	1.903	+	-2.03E-02	1.54E-04	+	+			12	-76.782	189.1	21.92	0
64	1.968	+	-3.77E-02	7.34E-04	+	+	-4.71E-06		13	-76.481	193	25.76	0
128	1.804	+	4.37E-03	-6.68E-04	+	+	6.65E-06	+	16	-75.211	206.1	38.87	0

Table A5.8. Dredge table for copepod richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	0.777								1	-60.138	122.4	0.0	0.504
3	0.7189		1.42E-03						2	-60.069	124.5	2.08	0.178
5	0.7396			1.52E-05					2	-60.078	124.5	2.1	0.176
7	0.7124		1.97E-03	-6.63E-06					3	-60.069	126.8	4.42	0.055
2	0.9555	+							4	-59.109	127.4	4.98	0.042
39	0.7195		4.82E-04	4.00E-05			-3.66E-07		4	-60.067	129.3	6.9	0.016
4	0.8974	+	1.42E-03						5	-59.041	129.8	7.47	0.012
6	0.918	+		1.52E-05					5	-59.05	129.9	7.48	0.012
8	0.8909	+	1.97E-03	-6.63E-06					6	-59.04	132.6	10.24	0.003
40	0.898	+	4.83E-04	3.99E-05			-3.65E-07		7	-59.039	135.6	13.2	0.001
12	0.5358	+	9.49E-03		+				8	-57.922	136.5	14.11	0
22	0.7432	+		7.97E-05		+			8	-58.201	137	14.67	0
16	0.5081	+	1.16E-02	-2.35E-05	+				9	-57.912	139.8	17.44	0
24	0.7008	+	2.89E-03	4.87E-05		+			9	-58.18	140.4	17.98	0
48	0.5153	+	1.00E-02	2.49E-05	+		-3.80E-07		10	-57.91	143.4	21.03	0
56	0.7125	+	2.29E-04	1.32E-04		+	-6.54E-07		10	-58.176	143.9	21.56	0
32	0.1053	+	3.97E-02	-3.40E-04	+	+			12	-56.65	148.9	26.47	0
64	0.09762	+	4.09E-02	-3.75E-04	+	+	2.67E-07		13	-56.649	153.3	30.92	0
128	-0.1854	+	8.28E-02	-1.58E-03	+	+	9.31E-06	+	16	-56.124	167.9	45.52	0

Table A5.9. Dredge table for total chlorophyll a. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
2	1.089	+							5	-24.299	60.4	0.0	0.317
4	1.251	+	-4.00E-03						6	-22.987	60.5	0.16	0.293
6	1.182	+		-3.87E-05					6	-23.394	61.3	0.97	0.195
8	1.325	+	-1.06E-02	7.90E-05					7	-22.691	62.9	2.52	0.09
12	1.502	+	-1.02E-02		+				9	-20.089	64.2	3.81	0.047
40	1.296	+	-4.33E-03	-1.18E-04			1.55E-06		8	-22.635	65.9	5.55	0.02
22	1.286	+		-8.14E-05		+			9	-21.112	66.2	5.86	0.017
16	1.576	+	-1.68E-02	7.90E-05	+				10	-19.746	67.1	6.72	0.011
24	1.428	+	-1.06E-02	3.63E-05		+			10	-20.323	68.2	7.87	0.006
48	1.547	+	-1.05E-02	-1.18E-04	+		1.55E-06		11	-19.681	70.8	10.43	0.002
56	1.399	+	-4.33E-03	-1.60E-04		+	1.55E-06		11	-20.259	71.9	11.58	0.001
32	1.908	+	-4.62E-02	4.34E-04	+	+			13	-16.472	72.9	12.58	0.001
1	0.4855								2	-34.523	73.4	13.01	0
3	0.6476		-4.00E-03						3	-33.747	74.2	13.8	0
5	0.5793			-3.87E-05					3	-33.985	74.6	14.27	0
7	0.7216		-1.06E-02	7.90E-05					4	-33.574	76.3	15.93	0
64	1.88	+	-4.00E-02	2.37E-04	+	+	1.55E-06		14	-16.395	77.6	17.23	0
39	0.6929		-4.33E-03	-1.18E-04			1.55E-06		5	-33.542	78.8	18.49	0
128	2.079	+	-8.31E-02	1.60E-03	+	+	-9.19E-06	+	17	-14.094	90	29.64	0

Table A5.10. Dredge table for edible chlorophyll a. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the linear (N) and quadratic (N²) nutrient column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
2	0.3828	+							5	-16.887	45.5	0.0	0.257
1	0.1199								2	-20.689	45.7	0.16	0.237
5	0.178			-2.40E-05					3	-20.278	47.2	1.68	0.111
6	0.4409	+		-2.40E-05					6	-16.388	47.3	1.78	0.105
3	0.1901		-1.74E-03						3	-20.401	47.5	1.93	0.098
4	0.4531	+	-1.74E-03						6	-16.538	47.6	2.08	0.091
7	0.1318		3.43E-03	-6.22E-05					4	-20.193	49.5	3.99	0.035
8	0.3947	+	3.43E-03	-6.22E-05					7	-16.285	50.1	4.53	0.027
39	0.04415		2.24E-02	-6.61E-04			4.72E-06		5	-19.593	51	5.41	0.017
40	0.3071	+	2.24E-02	-6.61E-04			4.72E-06		8	-15.553	51.8	6.21	0.011
22	0.443	+		-2.48E-05		+			9	-14.489	53	7.44	0.006
12	0.4786	+	-2.36E-03		+				9	-15.118	54.2	8.7	0.003
24	0.3968	+	3.43E-03	-6.31E-05		+			10	-14.375	56.3	10.8	0.001
16	0.4202	+	2.80E-03	-6.22E-05	+				10	-14.846	57.3	11.74	0.001
56	0.3091	+	2.24E-02	-6.62E-04		+	4.72E-06		11	-13.568	58.6	13.03	0
48	0.3326	+	2.18E-02	-6.61E-04	+		4.72E-06		11	-14.059	59.5	14.01	0
32	0.4977	+	-4.06E-03	2.04E-05	+	+			13	-13.801	67.6	22.06	0
64	0.4101	+	1.49E-02	-5.78E-04	+	+	4.72E-06		14	-12.971	70.7	25.2	0
128	0.5616	+	-1.79E-02	4.57E-04	+	+	-3.44E-06	+	17	-10.987	83.8	38.25	0

Appendix 6

Abundance, Richness, and Chlorophyll Dredge Tables from the First Week

Table A6.1. Dredge table for total zooplankton abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	7.144								2	-321.734	647.8	0.0	0.398
3	6.98		3.94E-03						3	-321.319	649.3	1.51	0.187
5	7.073			2.86E-05					3	-321.58	649.8	2.03	0.144
7	6.787		2.19E-02	-2.24E-04					4	-320.601	650.3	2.55	0.111
39	6.995		-2.72E-02	1.41E-03			-1.35E-05		5	-319.323	650.4	2.62	0.107
2	7.389	+							5	-320.745	653.3	5.46	0.026
4	7.217	+	4.09E-03						6	-320.283	655.1	7.32	0.01
6	7.313	+		2.97E-05					6	-320.573	655.7	7.9	0.008
8	7.025	+	2.25E-02	-2.30E-04					7	-319.492	656.5	8.69	0.005
40	7.231	+	-2.55E-02	1.37E-03			-1.32E-05		8	-318.2	657	9.25	0.004
12	7.212	+	4.20E-03		+				9	-319.838	663.7	15.88	0
22	7.295	+		3.74E-05		+			9	-320.23	664.5	16.67	0
16	7.003	+	2.41E-02	-2.48E-04	+				10	-318.902	665.4	17.6	0
24	6.984	+	2.44E-02	-2.44E-04		+			10	-318.941	665.5	17.68	0
48	7.22	+	-2.90E-02	1.53E-03	+		-1.47E-05		11	-317.262	666	18.16	0
56	7.205	+	-2.83E-02	1.52E-03		+	-1.45E-05		11	-317.33	666.1	18.3	0

32	7.085	+	1.61E-02	-1.47E-04	+	+		13	-318.656	677.3	29.52	0	
64	7.295	+	-3.67E-02	1.66E-03	+	+	-1.51E-05		14	-316.922	678.6	30.85	0
128	7.288	+	-3.51E-02	1.60E-03	+	+	-1.47E-05	+	17	-316.693	695.2	47.41	0

Table A6.2. Dredge table for cladoceran abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
39	0.856		-2.88E-02	7.91E-04			-5.74E-06		5	11.744	-11.7	0	0.564
1	0.6678								2	6.874	-9.4	2.3	0.179
3	0.6911		-5.76E-04						3	7	-7.3	4.39	0.063
40	0.9143	+	-2.88E-02	7.91E-04			-5.74E-06		8	13.889	-7.1	4.59	0.057
5	0.6721			-1.78E-06					3	6.883	-7.1	4.62	0.056
7	0.7493		-5.73E-03	6.21E-05					4	7.831	-6.5	5.2	0.042
2	0.726	+							5	8.536	-5.3	6.42	0.023
4	0.7494	+	-5.76E-04						6	8.672	-2.8	8.92	0.007
6	0.7304	+		-1.78E-06					6	8.545	-2.5	9.18	0.006
8	0.8076	+	-5.73E-03	6.21E-05					7	9.577	-1.7	10.07	0.004
48	0.9885	+	-3.06E-02	7.91E-04	+		-5.74E-06		11	14.568	2.3	14.02	0.001
56	0.9534	+	-2.88E-02	7.74E-04		+	-5.74E-06		11	14.321	2.8	14.51	0
12	0.8236	+	-2.41E-03		+				9	9.193	5.6	17.34	0
22	0.7695	+		-1.79E-05		+			9	8.875	6.2	17.97	0
16	0.8818	+	-7.56E-03	6.21E-05	+				10	10.123	7.3	19.06	0
24	0.8467	+	-5.73E-03	4.60E-05		+			10	9.925	7.7	19.46	0
64	1.042	+	-3.54E-02	8.48E-04	+	+	-5.74E-06		14	17.166	10.5	22.19	0
32	0.9355	+	-1.23E-02	1.19E-04	+	+			13	12.176	15.6	27.37	0
128	1.163	+	-6.17E-02	1.68E-03	+	+	-1.23E-05	+	17	22.23	17.4	29.08	0

Table A6.3. Dredge table for rotifer abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	7.14								2	-321.677	647.7	0.0	0.398
3	6.973		3.97E-03						3	-321.261	649.2	1.51	0.187
5	7.068			2.88E-05					3	-321.523	649.7	2.03	0.144
7	6.778		2.21E-02	-2.26E-04					4	-320.538	650.2	2.54	0.112
39	6.987		-2.70E-02	1.41E-03			-1.35E-05		5	-319.277	650.3	2.64	0.106
2	7.384	+							5	-320.7	653.2	5.49	0.026
4	7.211	+	4.12E-03						6	-320.238	655	7.34	0.01
6	7.308	+		2.99E-05					6	-320.529	655.6	7.93	0.008
8	7.017	+	2.27E-02	-2.32E-04					7	-319.443	656.4	8.71	0.005
40	7.223	+	-2.54E-02	1.37E-03			-1.32E-05		8	-318.166	657	9.3	0.004
12	7.204	+	4.28E-03		+				9	-319.793	663.6	15.91	0
22	7.289	+		3.80E-05		+			9	-320.184	664.4	16.69	0
16	6.992	+	2.44E-02	-2.50E-04	+				10	-318.853	665.3	17.61	0
24	6.974	+	2.46E-02	-2.46E-04		+			10	-318.889	665.4	17.69	0
48	7.211	+	-2.89E-02	1.54E-03	+		-1.47E-05		11	-317.226	665.9	18.2	0
56	7.196	+	-2.83E-02	1.52E-03		+	-1.46E-05		11	-317.292	666	18.33	0
32	7.073	+	1.65E-02	-1.51E-04	+	+			13	-318.614	677.2	29.55	0
64	7.285	+	-3.65E-02	1.66E-03	+	+	-1.52E-05		14	-316.893	678.6	30.91	0
128	7.276	+	-3.44E-02	1.59E-03	+	+	-1.46E-05	+	17	-316.661	695.1	47.46	0

Table A6.4. Dredge table for copepod abundance. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	0.4265								2	17.975	-31.6	0.0	0.406
3	0.3859		1.00E-03						3	18.647	-30.6	1.0	0.246
5	0.4021			1.01E-05					3	18.476	-30.3	1.34	0.208
7	0.3719		2.24E-03	-1.50E-05					4	18.731	-28.3	3.31	0.078
39	0.3504		6.89E-03	-1.61E-04			1.16E-06		5	18.981	-26.2	5.43	0.027
2	0.4165	+							5	18.534	-25.3	6.32	0.017
4	0.3758	+	1.00E-03						6	19.225	-23.9	7.72	0.009
6	0.3921	+		1.01E-05					6	19.05	-23.6	8.07	0.007
8	0.3618	+	2.24E-03	-1.50E-05					7	19.312	-21.1	10.5	0.002
40	0.3404	+	6.89E-03	-1.61E-04			1.16E-06		8	19.569	-18.5	13.13	0.001
12	0.4382	+	-5.37E-04		+				9	20.652	-17.3	14.32	0
22	0.4135	+		1.22E-06		+			9	19.592	-15.2	16.44	0
16	0.4242	+	7.04E-04	-1.50E-05	+				10	20.745	-13.9	17.72	0
24	0.3833	+	2.24E-03	-2.38E-05		+			10	19.862	-12.1	19.49	0
48	0.4028	+	5.35E-03	-1.61E-04	+		1.16E-06		11	21.021	-10.6	21.01	0
32	0.5286	+	-8.53E-03	9.64E-05	+	+			13	24.634	-9.3	22.36	0
56	0.3618	+	6.89E-03	-1.70E-04		+	1.16E-06		11	20.126	-8.8	22.8	0
64	0.5071	+	-3.89E-03	-5.01E-05	+	+	1.16E-06		14	24.969	-5.1	26.49	0
128	0.4722	+	3.67E-03	-2.89E-04	+	+	3.04E-06	+	17	25.46	10.9	42.53	0

Table A6.5. Dredge table for total zooplankton richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N: N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	1.193								2	48.525	-92.7	0.0	0.331
3	1.171		5.51E-04						3	49.463	-92.3	0.46	0.263
5	1.181			5.17E-06					3	49.135	-91.6	1.12	0.189
7	1.159		1.63E-03	-1.30E-05					4	49.763	-90.4	2.34	0.103
39	1.177		-2.39E-03	1.14E-04			-1.00E-06		5	50.661	-89.6	3.17	0.068
2	1.211	+							5	49.359	-87	5.77	0.018
4	1.189	+	5.51E-04						6	50.338	-86.1	6.59	0.012
6	1.198	+		5.17E-06					6	49.995	-85.4	7.28	0.009
8	1.176	+	1.63E-03	-1.30E-05					7	50.652	-83.8	8.92	0.004
40	1.195	+	-2.39E-03	1.14E-04			-1.00E-06		8	51.592	-82.5	10.19	0.002
12	1.164	+	1.16E-03		+				9	50.82	-77.6	15.08	0
22	1.181	+		1.22E-05		+			9	50.487	-77	15.75	0
24	1.159	+	1.63E-03	-5.94E-06		+			10	51.16	-74.7	17.99	0
16	1.152	+	2.24E-03	-1.30E-05	+				10	51.142	-74.7	18.03	0
56	1.178	+	-2.39E-03	1.21E-04		+	-1.00E-06		11	52.124	-72.8	19.9	0
48	1.17	+	-1.78E-03	1.14E-04	+		-1.00E-06		11	52.105	-72.8	19.94	0
32	1.155	+	1.96E-03	-9.65E-06	+	+			13	51.238	-62.5	30.25	0
64	1.173	+	-2.06E-03	1.17E-04	+	+	-1.00E-06		14	52.206	-59.6	33.11	0
128	1.181	+	-3.64E-03	1.67E-04	+	+	-1.39E-06	+	17	53.231	-44.6	48.08	0

Table A6.6. Dredge table for cladoceran richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	1.012								1	-63.478	129.1	0.0	0.304
5	0.8733			5.36E-05					2	-62.505	129.3	0.27	0.265
3	0.8279		4.35E-03						2	-62.661	129.6	0.59	0.227
7	0.917		-3.11E-03	8.74E-05					3	-62.475	131.6	2.56	0.085
2	1.099	+							4	-62.143	133.4	4.37	0.034
39	1.002		-2.15E-02	6.57E-04			-4.42E-06		4	-62.243	133.6	4.57	0.031
6	0.9603	+		5.36E-05					5	-61.17	134.1	5.04	0.024
4	0.9149	+	4.35E-03						5	-61.327	134.4	5.36	0.021
8	1.004	+	-3.11E-03	8.74E-05					6	-61.14	136.8	7.76	0.006
40	1.088	+	-2.15E-02	6.57E-04			-4.42E-06		7	-60.908	139.3	10.25	0.002
22	0.9628	+		5.27E-05		+			8	-60.917	142.5	13.42	0
12	0.9191	+	4.26E-03		+				8	-60.985	142.6	13.56	0
16	1.004	+	-2.89E-03	8.38E-05	+				9	-60.815	145.6	16.57	0
24	1.004	+	-2.91E-03	8.43E-05		+			9	-60.891	145.8	16.72	0
48	1.089	+	-2.13E-02	6.53E-04	+		-4.42E-06		10	-60.583	148.8	19.69	0
56	1.089	+	-2.16E-02	6.62E-04		+	-4.48E-06		10	-60.652	148.9	19.83	0
32	1.01	+	-3.35E-03	8.91E-05	+	+			12	-60.778	157.1	28.05	0
64	1.092	+	-2.14E-02	6.47E-04	+	+	-4.33E-06		13	-60.556	161.1	32.05	0
128	1.097	+	-2.24E-02	6.77E-04	+	+	-4.56E-06	+	16	-60.389	176.4	47.37	0

Table A6.7. Dredge table for rotifer richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	0.9385								2	47.976	-91.6	0.0	0.5
5	0.9437			-2.13E-06					3	48.075	-89.5	2.14	0.171
3	0.9407		-5.34E-05						3	47.984	-89.3	2.33	0.156
7	0.9214		1.65E-03	-2.05E-05					4	48.686	-88.2	3.4	0.091
39	0.9372		-1.76E-03	8.70E-05			-8.48E-07		5	49.292	-86.8	4.81	0.045
2	0.958	+							5	48.523	-85.3	6.34	0.021
6	0.9632	+		-2.13E-06					6	48.626	-82.7	8.92	0.006
4	0.9602	+	-5.34E-05						6	48.532	-82.5	9.11	0.005
8	0.9409	+	1.65E-03	-2.05E-05					7	49.253	-81	10.62	0.002
40	0.9567	+	-1.76E-03	8.70E-05			-8.48E-07		8	49.877	-79.1	12.52	0.001
12	0.9616	+	-8.74E-05		+				9	50.539	-77.1	14.55	0
22	0.9602	+		-9.08E-07		+			9	49.968	-75.9	15.69	0
16	0.9423	+	1.62E-03	-2.05E-05	+				10	51.338	-75.1	16.54	0
24	0.938	+	1.65E-03	-1.93E-05		+			10	50.64	-73.7	17.93	0
48	0.9581	+	-1.79E-03	8.70E-05	+		-8.48E-07		11	52.032	-72.6	18.99	0
56	0.9537	+	-1.76E-03	8.82E-05		+	-8.48E-07		11	51.309	-71.2	20.44	0
32	0.9624	+	-1.62E-04	8.97E-07	+	+			13	52.471	-64.9	26.68	0
64	0.9781	+	-3.57E-03	1.08E-04	+	+	-8.48E-07		14	53.206	-61.6	30.01	0
128	1.026	+	-1.39E-02	4.34E-04	+	+	-3.41E-06	+	17	56.761	-51.7	39.92	0

Table A6.8. Dredge table for copepod richness. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	0.7161								2	31.808	-59.3	0.0	0.469
3	0.6962		4.93E-04						3	32.129	-57.6	1.7	0.2
5	0.7057			4.32E-06					3	31.991	-57.3	1.98	0.175
7	0.6814		1.80E-03	-1.57E-05					4	32.313	-55.5	3.81	0.07
39	0.7084		-4.03E-03	1.68E-04			-1.45E-06		5	33.1	-54.4	4.86	0.041
2	0.7231	+							5	32.571	-53.4	5.91	0.024
4	0.7031	+	4.93E-04						6	32.905	-51.3	8.03	0.008
6	0.7126	+		4.32E-06					6	32.761	-51	8.32	0.007
8	0.6883	+	1.80E-03	-1.57E-05					7	33.096	-48.7	10.6	0.002
40	0.7153	+	-4.03E-03	1.68E-04			-1.45E-06		8	33.915	-47.2	12.11	0.001
12	0.6721	+	1.26E-03		+				9	34.952	-45.9	13.39	0.001
22	0.7015	+		8.90E-06		+			9	34.605	-45.2	14.08	0
16	0.6573	+	2.57E-03	-1.57E-05	+				10	35.164	-42.7	16.55	0
24	0.6772	+	1.80E-03	-1.12E-05		+			10	34.974	-42.4	16.93	0
48	0.6843	+	-3.27E-03	1.68E-04	+		-1.45E-06		11	36.075	-40.7	18.57	0
56	0.7042	+	-4.03E-03	1.73E-04		+	-1.45E-06		11	35.875	-40.3	18.97	0
32	0.6076	+	6.96E-03	-6.88E-05	+	+			13	36.847	-33.7	25.6	0
64	0.6345	+	1.13E-03	1.15E-04	+	+	-1.45E-06		14	37.839	-30.9	28.41	0
128	0.5669	+	1.58E-02	-3.47E-04	+	+	2.19E-06	+	17	42.322	-22.8	36.47	0

Table A6.9. Dredge table for total chlorophyll a. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of $\Delta < 2$. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	-0.01196								2	-0.414	5.2	0.0	0.48
3	-0.05709		1.11E-03						3	-0.086	6.8	1.69	0.207
5	-0.04017			1.17E-05					3	-0.148	7	1.81	0.194
7	-0.06685		1.98E-03	-1.04E-05					4	-0.07	9.3	4.13	0.061
2	0.05473	+							5	0.183	11.4	6.25	0.021
39	-0.09625		8.34E-03	-2.11E-04			1.58E-06		5	0.113	11.5	6.39	0.02
4	0.009597	+	1.11E-03						6	0.521	13.5	8.35	0.007
6	0.02651	+		1.17E-05					6	0.457	13.6	8.48	0.007
8	-0.000166	+	1.98E-03	-1.04E-05					7	0.537	16.4	11.27	0.002
40	-0.02956	+	8.34E-03	-2.11E-04			1.58E-06		8	0.726	19.2	14.04	0
22	0.04883	+		2.43E-06		+			9	1.295	21.4	16.26	0
12	0.03327	+	5.30E-04		+				9	0.868	22.3	17.11	0
24	0.02215	+	1.98E-03	-1.96E-05		+			10	1.378	24.8	19.68	0
16	0.0235	+	1.39E-03	-1.04E-05	+				10	0.885	25.8	20.67	0
56	-0.007244	+	8.34E-03	-2.20E-04		+	1.58E-06		11	1.575	28.3	23.13	0
48	-0.005893	+	7.76E-03	-2.11E-04	+		1.58E-06		11	1.076	29.3	24.12	0
32	-0.01029	+	4.38E-03	-4.65E-05	+	+			13	2.708	34.6	29.43	0
64	-0.03969	+	1.08E-02	-2.47E-04	+	+	1.58E-06		14	2.918	39	33.81	0
128	-0.06623	+	1.65E-02	-4.29E-04	+	+	3.01E-06	+	17	4.702	52.4	47.26	0

Table A6.10. Dredge table for edible chlorophyll a. Plus signs (+) indicate retention of the mussel (M) predictor variable and numbers below the nutrient (N) and nutrient² (N²) column headers indicate retention of these predictors. The minimum adequate model was chosen using criteria of delta < 2. Best model chosen is indicated in bold.

Model	Intercept	M	N	N ²	M:N	M:N ²	N:N ²	M:N:N ²	df	logLik	AICc	delta	weight
1	-0.1416								2	-6.242	16.8	0.0	0.538
3	-0.152		2.58E-04						3	-6.229	19.1	2.32	0.169
5	-0.1409			-2.79E-07					3	-6.242	19.1	2.34	0.167
7	-0.1915		3.75E-03	-4.21E-05					4	-6.034	21.2	4.4	0.06
2	-0.05524	+							5	-5.375	22.5	5.71	0.031
39	-0.2056		6.80E-03	-1.38E-04			7.59E-07		5	-6.003	23.8	6.96	0.017
4	-0.06568	+	2.58E-04						6	-5.361	25.3	8.46	0.008
6	-0.05457	+		-2.79E-07					6	-5.375	25.3	8.49	0.008
8	-0.1052	+	3.75E-03	-4.21E-05					7	-5.158	27.8	11.01	0.002
22	-0.08724	+		1.32E-05		+			9	-3.359	30.7	13.91	0.001
40	-0.1193	+	6.80E-03	-1.38E-04			7.59E-07		8	-5.126	30.9	14.09	0
12	-0.1118	+	1.40E-03		+				9	-4.356	32.7	15.9	0
24	-0.1379	+	3.75E-03	-2.87E-05		+			10	-3.12	33.8	17.02	0
16	-0.1513	+	4.89E-03	-4.21E-05	+				10	-4.142	35.9	19.06	0
56	-0.152	+	6.80E-03	-1.25E-04		+	7.59E-07		11	-3.084	37.6	20.79	0
48	-0.1654	+	7.94E-03	-1.38E-04	+		7.59E-07		11	-4.108	39.6	22.84	0
32	-0.1414	+	4.02E-03	-3.16E-05	+	+			13	-1.098	42.2	25.39	0
64	-0.1555	+	7.07E-03	-1.28E-04	+	+	7.59E-07		14	-1.058	46.9	30.11	0
128	-0.2095	+	1.87E-02	-4.96E-04	+	+	3.66E-06	+	17	0.726	60.4	43.56	0

Appendix 7

Zooplankton Abundance and Rotifer Richness

Table A7.1. Raw abundance counts (individuals/L) for all cladocerans and copepods from the first sampling week.

Nutrient (µg/L)	Density (mussels/L)	<i>Ceriodaphnia quadrangula</i>	<i>Daphnia pulex/pulicaria</i>	<i>Daphnia mendotae</i>	<i>Bosmina luederi/freyi</i>	<i>Scapholeberis kingi</i>	<i>Alona rectangular</i>	<i>Alona guttata</i>	<i>Chydorus sphaericus</i>	<i>Cyclopoid copepodid</i>	<i>Cyclopoid nauplii</i>	<i>Calanoid copepodid</i>	<i>Calanoid nauplii</i>	<i>Epischura lacustris</i>	<i>Eucyclops agilis</i>	<i>Diaptomous ashlandi</i>	<i>Cyclops scutifer</i>	<i>Diaptomous oregonensis</i>
0	0.0		13.9	6.5	0.9					4.6							2.8	
5	0.0		1.1	1.6						1.6	0.5	1.6			1.1			
15	0.0		1.6	2.1	0.4		0.4			3.3	2.5	2.1	0.4				1.6	0.8
25	0.0		1.5	0.7						0.7	1.5	0.7	0.7				1.1	
35	0.0		1.6	0.5						1.6	3.7	1.6					3.2	
45	0.0		2.1	0.4	0.4					0.4	1.2	2.1					0.8	
55	0.0	1.1	5.3	1.6						2.1	2.1	1.6	1.1					0.5
65	0.0		2.9		0.4		1.2			1.6	0.8	1.2	0.8				0.8	
75	0.0		2.5	1.2	1.2		0.4		0.4	1.6	3.3	0.8	1.2				2.9	
85	0.0			0.5	1.1	0.5				2.6	2.6	0.5					2.1	
0	0.25		4.2	2.1	0.5					1.6	0.5	1.1					1.1	
5	0.25		2.3	4.2					0.5	1.4	2.8	0.9				0.5	0.9	
15	0.25		1.1	0.5						13.2	1.6						1.6	

25	0.25		1.9	0.7	0.4			1.1	2.2	1.5	0.7			2.2	
35	0.25		0.5											1.1	
45	0.25		3.2	1.1				1.6	1.6	1.1				0.5	
55	0.25		0.8	2.5				1.6	1.2	2.5	1.6			2.1	0.4
65	0.25		3.7	0.5	0.9	0.5		3.2	2.3	0.5	1.4			0.9	0.5
75	0.25		2.8	1.4			1.4	2.3	2.3	1.4	0.9			1.9	
85	0.25		2.1	1.1				2.1	2.6	0.5				2.1	
0	0.5		2.5	0.8				3.3	3.3	1.6	0.4	0.4		2.1	
5	0.5		1.6	0.8				0.4	1.2	0.4	0.4			0.4	0.4
15	0.5		3.2	0.5				2.8	4.2	1.4	0.5			0.5	
25	0.5		2.1	2.1					2.6		1.6			3.7	
35	0.5		0.9					0.9	3.2	0.9				3.2	
45	0.5		1.1	2.1	0.5			2.6	1.1	1.1	0.5			1.1	0.5
55	0.5		1.1		0.5			2.6	2.6	1.6	0.5			0.5	
65	0.5		2.3	0.5	0.5			1.4	3.2	0.5	0.5			2.8	
75	0.5		1.4	2.3				2.8	1.9	1.4				1.4	
85	0.5		1.2	0.8			0.4		2.9	0.4				1.6	
0	1.0		2.3	1.4				0.9	2.3					0.9	
5	1.0		1.6	1.2	0.4			1.2	1.2					0.4	
15	1.0		1.1	2.2	0.4			1.5	2.2	0.7	0.7			1.5	
25	1.0	0.5	2.1	1.6				1.1	2.6					3.2	
35	1.0		1.1	1.6				2.1	2.6	0.5				1.6	
45	1.0	0.5	4.6	1.9				0.5	0.9	1.9	0.9			2.8	
55	1.0		3.7	1.2	0.8		1.2	2.1	1.2	1.2	0.8			4.1	
65	1.0		2.8	1.4	0.5	0.5	1.4	2.3	3.7					3.7	

75	1.0	0.7	0.3		0.3			0.7	0.3	0.3	2.0		1.3
85	1.0	1.6	0.8	0.8		1.2	0.4	0.8	2.5	0.8			2.1

Table A7.2. Raw abundance counts (individuals/L) for all rotifers from the first sampling week.

Nutrient (µg/L)	Density (mussels/L)	<i>Polyarthra remata</i>	<i>Keratella cochlearis</i>	<i>Synchaeta</i> spp.	<i>Kellicottia longispinia</i>	<i>Gastropus stylifer</i>	<i>Lecane inermis</i>	<i>Lecane tudicola</i>	<i>Polyarthra major</i>	<i>Lepadella patella</i>	<i>Lecane tenuiseta</i>	<i>Monostyla copeis</i>	<i>Pompholyx sulcata</i>	<i>Keratella quadrata</i>	<i>Keratella hiemalis</i>	<i>Trichocerca multicornis</i>	<i>Conochilus unicornis</i>	<i>Asplantha priodonta</i>	<i>Monstyla closteroerca</i>	<i>Keratella serrulata</i>	<i>Lecane mira</i>	<i>Trichocerca pusilla</i>
0	0.0	30.9	507.4	587.7	6.2	14.8	2.5	1.2									4.9					
5	0.0	1351.5	366.7	48.5	32.3	12.1	8.1			1.0	1.0	1.0					9.1					
15	0.0	141.3	106.3	19.0	12.7	1.6	7.9			1.6				1.6								
25	0.0	1058.7	1069.8	119.0	9.5	7.9	46.0			12.7		1.6		1.6			27.0					
35	0.0	1333.3	236.5	6.3	20.6		6.3															
45	0.0	1266.7	479.4	100.0	15.9	6.3	30.2			1.6							3.2					
55	0.0	1409.5	271.4	14.3	15.9	4.8	15.9					1.6					1.6					
65	0.0	163.9	236.1	1.4	5.6		9.7										1.4	1.4				
75	0.0	1630.2	2717.5	17.5	3.2	3.2	11.1			1.6		1.6										
85	0.0	258.7	96.8	34.9	11.1		27.0			1.6												
0	0.25	837.5	444.4	12.5	19.4	5.6	4.2															
5	0.25	219.0	112.7	4.8	7.9		3.2					1.6	1.6									
15	0.25	1078.9	1586.7	152.2	13.3	4.4	10.0			4.4				1.1		1.1	26.7					
25	0.25	190.5	172.5	20.1	7.9	2.6	7.4	0.5		1.6												
35	0.25	341.3	28.6	12.7		3.2	11.1															
45	0.25	580.0	191.1	94.4	12.2	6.7	20.0			1.1							10.0			1.1		
55	0.25	185.7	965.1	6.3	14.3	4.8	3.2			1.6							6.3					
65	0.25	974.6	1025.4	246.0	12.7	6.3	20.6			11.1							22.2		1.6	1.6		
75	0.25	1007.9	352.4	25.4	15.9	6.3	7.9														1.6	
85	0.25	268.3	69.8	3.2	3.2	4.8	1.6															

0	0.5	581.0	146.0	25.4	19.0	15.9	14.3												
5	0.5	107.4	139.5	9.9	19.8	1.2	1.2												
15	0.5	555.6	238.1	22.2	28.6	6.3	12.7											6.3	
25	0.5	113.8	96.3	14.3	4.8	2.1	4.8		1.6				0.5					2.6	
35	0.5	976.2	1009.5	158.7	9.5	4.8	19.0		4.8									6.3	3.2
45	0.5	1295.2	336.5	19.0	19.0	6.3	11.1				1.6						1.6		
55	0.5	271.4	173.0	15.9	7.9	3.2	14.3											3.2	
65	0.5	514.3	182.5	27.0	6.3	3.2	6.3		3.2									6.3	
75	0.5	1109.5	1282.5	155.6	7.9	4.8	17.5		9.5									3.2	
85	0.5	266.7	406.9	6.9	6.9	4.2	12.5		1.4								1.4		
0	1.0	475.0	433.3	54.2	9.7	13.9	23.6		2.8									2.8	
5	1.0	462.2	260.0	25.6	10.0	2.2	11.1	1.1			1.1	1.1						2.2	
15	1.0	617.3	424.7	24.7	14.8	7.4	6.2										2.5	13.6	
25	1.0	184.1	46.0		4.8		2.6		0.5	0.5									
35	1.0	1563.5	1249.2	147.6	12.7	11.1	28.6		1.6									9.5	
45	1.0	607.9	423.8	14.3	14.3	4.8	22.2		3.2										
55	1.0	1.6	482.5	579.4	9.5	14.3	4.8		1.6									7.9	1.6
65	1.0	790.5	592.1	142.9	12.7	7.9	25.4		6.3			1.6						1.6	3.2
75	1.0	971.4	838.1	150.8	14.3	6.3	19.0		11.1				1.6					3.2	1.6
85	1.0	62.5	109.7	13.9	23.6		2.8				1.4								

Table A7.3. Raw abundance counts (individuals/L) for all cladocerans from the final sampling week.

Nutrient (µg/L)	Density (mussels/L)	<i>Ceriodaphnia quadrangula</i>	<i>Daphnia pulex/pulicaria</i>	<i>Daphnia mendotae</i>	<i>Bosmina luederi/freyi</i>	<i>Scapholeberis kingi</i>	<i>Alona rectangularis</i>	<i>Alona guttata</i>	<i>Alona quadrangularis</i>	<i>Acroperus harpae</i>	<i>Kurzia latissima</i>	<i>Pleuroxus truncatus</i>	<i>Graptoleberis testudinaria</i>	<i>Camptocercus rectirostris</i>	<i>Pleuroxus denticulatus</i>	<i>Polypheumus pediculus</i>	<i>Chydorus sphaericus</i>	<i>Eurycercus lamellatus</i>
0	0.0	16.4	0.5		21.7	3.7		0.5										90.5
5	0.0		1.6		0.5	5.3	19.0	1.6				7.9		0.5	0.5			76.2
15	0.0						3.7		0.5	0.5					0.5			4.8
25	0.0				3.7	1.6	4.2	2.6	138.6			2.1			1.1			111.6
35	0.0	19.0			42.3		1.6		3.2			14.8						140.2
45	0.0	0.5			9.7	0.9	0.9	20.4				2.3		0.5	0.5			44.9
55	0.0		19.6			15.3									18.0	0.5		377.2
65	0.0	14.8	0.8		27.2	1.2	3.7				0.4	0.4				0.8		54.7
75	0.0		3.2		127.5	15.3	32.3								11.1	6.3		201.6
85	0.0		14.8			2.6	1.1									3.2		173.0
0	0.25		9.5		0.5	1.1	24.9		0.5			0.5		4.2	15.9			43.4
5	0.25	1.6	2.1			2.1	13.2					2.1		1.6	18.0			7.9
15	0.25				0.5	5.3	29.1	2.6										113.2
25	0.25	1.9	4.2	0.5	6.9	1.9	0.5					1.4				9.7		40.7
35	0.25	0.5			2.6	1.6	45.5	2.1	16.4				3.7		2.6			13.2
45	0.25		14.3		4.8	17.5	230.2	36.5	1.6			1.6	1.6					471.4
55	0.25		10.6			1.6	34.9		8.5	4.8			0.5	3.2	0.5			21.7

65	0.25	2.6		6.9	47.1	11.1	45.5		1.6			0.5			97.4
75	0.25		23.8		6.9	0.5	10.1		14.8	0.5			2.6		5.8
85	0.25		31.2		7.4	1.1	22.2		1.1		13.2		1.1		18.5
0	0.5		0.5	2.6		7.4	7.4	1.1					0.5	2.6	259.8
5	0.5		1.6			3.7	2.1	46.0	2.1					2.1	1.6
15	0.5				0.5	3.7	46.0	7.9		1.1			2.6		21.2
25	0.5		13.2			1.1	4.8	29.6					1.1		4.8 64.6
35	0.5		3.2			10.1	23.8	4.2	2.1						51.3
45	0.5		76.7			10.6	34.4		1.1					3.7	241.8
55	0.5		0.5			3.7	13.8		2.1			0.5	1.1		4.2
65	0.5	1.1				4.8	45.5	2.1	0.5	1.1			2.1	3.7	6.9
75	0.5		15.9			5.3		0.5							11.6 23.8
85	0.5		3.2		0.5	3.2	3.2	1.1	1.1			2.6			40.7
0	1.0		6.9		0.5	5.3	24.3	15.3						3.7	40.2 1.6
5	1.0		0.5		0.5	1.1	69.8	0.5	4.8				1.1	4.2	19.0 1.1
15	1.0					0.5	19.0							25.9	15.3
25	1.0		0.5			13.8	45.0	2.6						0.5	52.4
35	1.0		11.6		1.6	7.9	93.1	5.8					1.1	2.6	32.3
45	1.0		1.6		0.5	3.2	2.6								9.0
55	1.0						14.8		7.4		1.1				34.4
65	1.0		21.7		0.5	4.2	59.8						2.6	0.5	6.3 43.4
75	1.0				1.6	0.5	7.4	0.5	1.1					1.1	2.1 196.8
85	1.0					0.5	13.2	0.5	16.4			2.6		3.7	11.1

Table A7.4. Raw abundance counts (individuals/L) for all copepods from the final sampling week.

Nutrient ($\mu\text{g/L}$)	Density (mussels/L)	<i>Cyclopoid copepodid</i>	<i>Cyclopoid nauplii</i>	<i>Calanoid copepodid</i>	<i>Calanoid nauplii</i>	<i>Eucyclops agilis</i>	<i>Cyclops scutifer</i>	<i>Diaptomous oregonensis</i>	<i>Cyclops vernalis</i>	<i>Macrocyclus albidus</i>	<i>Mesocyclops edax</i>
0	0.0	10.1	20.1	0.5						3.2	
5	0.0	2.6	193.1	0.5	0.5					4.8	
15	0.0	0.5					0.5			0.5	
25	0.0	14.8	38.1				1.1		0.5	4.2	
35	0.0	45.0	68.8				0.5		3.2	2.1	
45	0.0	6.5	15.3				0.5	0.5		1.4	0.9
55	0.0	23.3	202.6	0.5					5.3	3.7	2.1
65	0.0	2.5	3.3						0.4	3.7	
75	0.0	2.1	6.3				2.6	1.6		7.9	0.5
85	0.0	147.1	20.6	15.9					6.9	7.4	0.5
0	0.25	3.2	13.8		1.1				0.5	1.6	
5	0.25	20.6	32.3	0.5			0.5		0.5	1.1	
15	0.25	29.1	21.7				1.1		2.6	2.1	
25	0.25	17.1	47.7				0.9			0.5	0.5
35	0.25	14.3	13.8						0.5	1.1	
45	0.25	171.4	866.7				1.6		3.2	9.5	
55	0.25	4.8	80.4						0.5	5.3	

65	0.25	68.8	113.8					0.5	2.1	0.5
75	0.25	1.1	3.7						1.6	
85	0.25	16.9	66.1				0.5		1.6	
0	0.5	119.0	49.7	0.5	2.6		0.5	2.6	6.3	
5	0.5	2.6	6.9						2.6	
15	0.5	11.6	12.7				0.5		1.6	
25	0.5	1.6	42.9				1.1		1.6	
35	0.5	12.7	225.4						3.7	
45	0.5	28.0	37.0				6.3		10.1	
55	0.5	5.3	7.4						1.1	
65	0.5	54.0	105.3						2.6	
75	0.5	40.2	39.7				0.5	3.7	3.7	0.5
85	0.5	35.4	96.8					0.5	1.1	
0	1.0	32.3	43.9	2.1	0.5	1.1	1.6		4.8	
5	1.0	9.0	16.4					0.5	2.1	
15	1.0	3.7	12.2						1.1	
25	1.0	34.4	47.1				0.5		3.2	
35	1.0	8.5	200.0				3.2		7.4	
45	1.0	1.6	9.5						1.6	
55	1.0	28.6	43.9						1.1	
65	1.0	6.9	14.8					0.5	9.0	
75	1.0	29.1	38.6				3.7	4.2	14.3	
85	1.0	8.5	36.5						1.1	

Table A7.5. Raw abundance counts (individuals/L) for all rotifers from the final sampling week.

Nutrient (µg/L)	Density (mussels/L)	<i>Polyartha remata</i>	<i>Keratella cochlearis</i>	<i>Gastropus stylifer</i>	<i>Lecane inermis</i>	<i>Lecane tudicola</i>	<i>Collotheca pelagica</i>	<i>Lepadella patella</i>	<i>Monostyla copeis</i>	<i>Pompholyx sulcata</i>	<i>Trichocerca multicornis</i>	<i>Conochilus unicornis</i>	<i>Trichocerca multicornis</i>	<i>Monstyla closteroerca</i>	<i>Keratella serrulata</i>	<i>Lecane mira</i>	<i>Trichocerca rattus</i>	<i>Trichocerca pusilla</i>	<i>Trichocerca lata</i>	<i>Mytilina ventralis</i>	<i>Trichocerca cylindrica</i>	<i>Monostyla stenroosi</i>	<i>Euchlanis parva</i>	<i>Euchlanis dilatata</i>
0	0.0		1.6											87.3	4.8		3.2	1.6						
5	0.0		9.5											3.2		44.4								
15	0.0		39.7	1.6					1.6						9.5						15.9			
25	0.0	7.9	238.1					22.2						27.0	3.2			4.8						
35	0.0	4.8	3052.4		1.6				1.6					1.6										
45	0.0		7.9						1.6			1.6		57.1							11.1			
55	0.0																	1.6						
65	0.0		17.5					1.6																
75	0.0		28.6											4.8		11.1								
85	0.0		1.6					1.6						7.9		3.2	1.6							
0	0.25													6.3		1.6		1.6						
5	0.25	4.8	6.3							1.6				4.8										
15	0.25		1.6			1.6	25.4						1.1	23.8	111.1		1.6	12.7						
25	0.25																							
35	0.25		49.2		1.6																			
45	0.25		1.4					6.3						28.6	1.6		9.5							
55	0.25		1.2					1.4						1.4										

65	0.25		1.6			1.2			3.7	2.5		1.2		1.2		1.2
75	0.25								0.5		0.5					
85	0.25								1.6							
0	0.5						14.3					71.4	14.3			
5	0.5		3.2													
15	0.5													17.5		
25	0.5		4.8						6.3							
35	0.5		1.6						7.9							39.7
45	0.5		3.2						7.9							
55	0.5					1.6			4.8					6.3		
65	0.5								1.6							
75	0.5					4.8					4.8					
85	0.5		14.3						14.3		30.2		3.2			
0	1.0		2.8						1.6	15.9						
5	1.0						1.4		2.8	1.4		1.4	5.6			
15	1.0			1.6				2.5					1.6			
25	1.0		1.6						4.8							
35	1.0		1.6			3.2			3.2							
45	1.0		1.4	1.4									1.6	6.3		
55	1.0		6.3						1.4				1.4			
65	1.0		9.5			3.2			1.6							
75	1.0		1.6					1.6	1.6		1.6					
85	1.0	62.5	109.7	2.8					1.6	1.6		1.6

Figure A7.1 Relationship between nutrient treatment and cladoceran abundance for all mussel treatment densities from the first week of the experiment. Best fit line is used to show the significant relationship between cladoceran abundance and the linear and quadratic nutrient terms ($P < 0.05$). Note log scale used on the y-axis.

Figure A7.2 Rotifer richness in each mussel treatment (n=10). Bottom and top edges of boxes represent the first and third quartiles respectively, with a dark, horizontal line as the median. Whiskers encompass data points that lie within 1.5 times the inner quartile range, data outside this range is shown as separate points. Different letters over boxes indicate mussel treatments with significantly different abundances ($P < 0.05$, Table A2.3).