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Effects Of Local And Regional Processes On The Structure Of Notonecta Metacommunities

Mitra Asgari
Wayne State University, fb7457@wayne.edu

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EFFECTS OF LOCAL AND REGIONAL PROCESSES ON THE STRUCTURE OF *NOTONECTA* METACOMMUNITIES

by

MITRA ASGARI

DISSERTATION

Submitted to the Graduate School

of Wayne State University,

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Approved By:

Advisor Date

DEDICATION

To Jamil and Shoja, the cornerstone of my life.

ACKNOWLEDGMENTS

I still remember the day I received the admission letter to join the Biology Ph.D. program at Wayne State University. My joy and happiness were indescribable. This journey has brought so many valuable moments to my life and helped me grow to be a better version of myself. Now that I am getting close to finishing this chapter of my life, I want to take this opportunity to express my deepest appreciation to so many wonderful people who have made the past six years of my life memorable.

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I also want to thank the wonderful people who I met at W. K. Kellogg Biological Station, Patrick Hanly, Gary Mittelbach, and Steve Hamilton, for their kind support and guidance. This research was not possible without the funding provided by my advisor's

NSF grant and his generosity in letting me to use his Subaru Forester, during the field seasons.

In the end, I want to express my deepest gratitude to my parents who have been the constant source of hope, strength, and inspiration in my life as well as my little brother, whose wittiness has always cheered me up. And lastly, I want to thank Tejeshwar Rao, a precious friend I found here who made my days brighter with his kind heart and his constant support of my dreams.

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CHAPTER 1 INTRODUCTION

Background

Biodiversity has been studied at molecular, cellular, individual, population, community, and ecosystem levels. Studies of biodiversity at the community level involve the maintenance and distribution of species in time and space considering interactions that organisms have with one another and their environment. The community is defined as a system of populations linked to one other by strong interactions in the habitat they occupy while having weaker interactions with other populations outside their ecosystem (Lampert and Sommer 2007). Studying the species distribution patterns and the processes which drive such patterns is a central goal of community ecology (Logue et al. 2011). The increasing risk of species extinction and habitat destruction during the past few decades has greatly motivated community ecologists to understand the drivers of species coexistence, diversity and distribution patterns. Such an understanding can provide essential information for management, conservation, and the restoration of natural habitats and the species occupying them (Brown et al., 2011; Siqueira et al., 2012a; Heino, 2013a).

Historically, drivers of community structure have been studied within small, ecologically homogenous spaces, commonly called patches or local sites (Clements 1936; Ricklefs 1987). These local processes are mainly categorized into two groups: abiotic conditions and biotic interactions. Abiotic factors such as chemical, physical and geomorphological properties of local sites can affect colonization and establishment of species at the local scale by acting on species' physiological requirements and tolerances. Along with the site conditions, biotic interactions such as predation, competition and facilitation could further influence the outcome of community structure within each site as well. Early in the development of ecological theory, ecologists acknowledged that local sites are open to the migration of individuals and such movements could influence the structure of communities as well. Early explorations of such spatial processes were performed by plant ecologists (e.g. Greig-Smith 1952) and later presented in classic studies such as island biogeography theory (MacArthur and Wilson 1967). These early developments evolved into modern metapopulation theory (Hanski and Gilpin 1991) and metacommunity theory (Leibold et al. 2004). Metapopulations and metacommunities are a group of suitable local sites which are surrounded by unsuitable landscape and are connected by movement of individuals of one (Andrewartha and Birch 1954) or several species occupying them (Wilson 1992; Leibold et al. 2004). Metapopulation and metacommunity perspectives consider the role of regional processes in addition to local factors. These include the effects of dispersal rate, range and capability of organisms, the size of the pool they migrate from, and invasion history (Hebert 1974; Palmer et al. 1996).

In many systems, research findings suggest the joint effect of local and regional processes in shaping community structure (Burke and Grime, 1996; Tilman 1997; Shurin 2000; Shurin et al. 2000). Thus, recent studies have focused more on measuring the relative importance of local and regional processes on community structure. Recent investigations have also begun to consider the role of dispersal mode, habitat choice and spatial scale which were less explored in earlier studies (Cottenie 2005).

Aquatic habitats provide great oppurtunities to study the dynamics and organisation of metacommunities (Brown et al., 2011; Heino, 2011; Lindström &

Langenheder, 2012). Among aquatic habitats, ponds are shallow freshwater bodies with diverse origins and global distributions. Ponds provide suitable habitats for a diverse group of aquatic and semi-aquatic organisms. Often a large number of ponds with different characteristics are found in a regional area, and they are surrounded by terrestrial landscapes which are inhospitable for survival, growth, and reproduction of the aquatic organism. Thus, they often approximate the patch-like structure of many metapopulation and metacommunity models, making them ideal testing grounds for theoretical predictions.

A considerable amount of research has examined the contribution of local and regional processes on community organization of pond dwelling organisms (Shurin et al. 2000; Briers and Warren 2000; Mouquet and Lorea 2003; Noonberg and Abrams, 2005; Jeffries 2005; McCauley 2007). However, the number of studies which have considered the effects of dispersal behavior and spatial scale is limited (but see De Bie et al. 2012; Henry and Cumming 2016). Also, most studies have used snapshot approaches, ignoring temporal variation in metacommunity patterns and processes (but see Henry and Cumming 2016). In fishless ponds, aquatic insects are commonly top predators and can alter the structure of lower trophic levels such as zooplankton communities. However, we are not aware of any prior studies of the mutual importance of local and regional processes on metacommunity organization of such macroinvertebrates or how such processes vary through time.

In order to address the research gaps presented above, we selected *Notonecta* species (Hemiptera: Notonectidae) which are common macroinvertebrates found in fish and fishless ponds in North America. They are aquatic insects that spend their entire life cycle in water and are considered size-selective pond predators. They are also capable of flight and dispersal distances up to 1.6 km (Briers and Warren 2000). These characteristics make them ideal organisms for examining metacommunity processes and predator-prey relationships. In the following chapters we use a pond surveys, mesocosm experiments and pond experiments to investigate the distribution patterns and the processes affecting community structure of *Notonecta* species. In addition to examining the causes of variation in Notonecta community structure, we also explored the consequences of variation in the predatory effects of *Notonecta* on zooplankton communities.

Research outline

In the second chapter, we present the results of a field experimental in which we tested the interactive effects of the invertebrate predator, *Notonecta undulata*, and productivity on zooplankton community diversity. While several studies have examined the interactive effects of herbivory and productivity on primary producer diversity, experimental studies of such effects in predator-prey systems are rare. Furthermore, most prior studies have utilized consumer presence/absence to test consumer effects on prey diversity; experimental manipulations using gradients of consumer density are rare. We used an aquatic field mesocosm experiment in which initial density of the predator and productivity were manipulated to test their interactive effects on diversity of seven zooplankton species that were common in surrounding ponds. We used open systems to allow for natural dispersal and behaviorally-mediated numerical responses by the flight-capable predator. Our results showed that effects of predators on zooplankton diversity depended on productivity level. At low, prey species richness declined while at high productivity it showed a unimodal relationship with increasing the predator density. Our findings are generally consistent with model predictions in which predators can facilitate prey coexistence and diversity at intermediate levels of productivity and predation intensity. Our work also shows that the functional form of the relationship between prey diversity and predation intensity can be complex and highly dependent on environmental context.

In the third chapter, we address how temporal variation (seasonality) impacts the relative effects of local and regional processes on metacommunity organization of *Notonecta* species. We present the results of a two-year study of seasonal variation in *Notonecta* metacommunity structure in fishless ponds in southern Michigan. We used variation partitioning (Borcard et al., 1992; Borcard and Legendre 1994) to investigate the relative contribution of environmental and spatial processes to notonectid metacommunity structure and compared results across sampling dates within years to test if the relative contribution of these processes changed over the growing season. Our results showed that a combination of environmental, spatial and spatially structured environmental components contributed to notonectid community structure. Effects also varied seasonally and inter-annually. In the first year of the study, a large amount of community variation was explained by these components with the ratio of environmental to spatial components increasing through the growing season - indicative of the increasing importance of environmental filters and species sorting. In contrast, overall less variation was explained by both spatial and environmental components in the second year of the study. Furthermore, the spatial component played the largest role in explaining variation over the growing season. Compositional variation was generally observed at small to intermediate spatial scales, with community dissimilarity exhibiting negative spatial autocorrelation. Our results confirm the importance of both spatial and environmental processes in the organization of metacommunities. Our work also highlights the importance of considering temporal variation at intra- to inter-annual scales in order to gain a more comprehensive understanding of variation in metacommunity structure.

In the last chapter, we present results of an in situ, introduction experiment in which we investigated the effects of local environmental conditions versus dispersal limitation on the heterogenous distribution of *Notonecta* species in fishless ponds. We selected six ponds that differed naturally in their occupancy by the two most common *Notonecta* species and using in situ mesocosms, adults and juveniles of the two species were introduced to the ponds and performance and adult emigration were assessed. Our results provide some support for the importance of local environmental control of *N. irrorata*'s distribution. They also suggest that dispersal limitation, rather than local environmental factors, may be responsible for the absence of *N. undulata* from one pond.

CHAPTER 2 INTERACTIVE EFFECTS OF PRODUCTIVITY AND PREDATION ON ZOOPLANKTON DIVERSITY

A version of this work has been published:

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Introduction

What determines patterns of species coexistence and diversity in local communities remains an enduring question in community ecology (Hutchinson 1959, Chesson 2000, Tilman 2004, HilleRisLambers, et al. 2012). Despite its long history, this basic question remains far from resolved. Among the local abiotic processes, productivity has long been viewed as a potentially important driver of diversity (Tilman 1982, Tilman and Pacala 1993, Waide, et al. 1999). However, the strength and form of the relationship between diversity and productivity remains controversial with positive, negative and unimodal patterns evident in the literature (Mittelbach, et al. 2001, Chase and Leibold 2002, Gillman and Wright 2006, Pärtel, et al. 2007, Adler, et al. 2011, Fraser, et al. 2015). Variation in the relationship between productivity and diversity has been linked to various local and regional processes, such as disturbance (Kondoh 2001; Scholes et al. 2005), predation (Holt et al. 1994; Leibold 1996; Worm et al. 2002), and spatial scale (Chase and Leibold 2002). For example, at larger regional spatial scales, the relationship between productivity and diversity has been found to be generally positive while at smaller spatial scales (local sites) a hump shape relationship is commonly reported (Mittelbach et al. 2001; Gillman and Wright 2006; Partel et al. 2007). What drives variation in productivity-diversity relationships has important implications for understanding future impacts on biodiversity as many systems face increasing threats from anthropogenic nutrient pollution, a driver of productivity.

Besides productivity, predation is another local factor that has been found to influence prey diversity as well (Paine 1966; Lubchenco 1978; Sih et al. 1985; Olff and Ritchie 1998; Proulx and Mazumder 1998). Depending on whether more prey species are excluded or facilitated as a result of consumer presence, consumers can either increase or decrease diversity of prey trophic levels (Paine and Vadas 1969, Pacala and Crawley 1992, Leibold 1996, Proulx and Mazumder 1998, Hillebrand, et al. 2007). Coexistence of prey species with different competitive abilities can be achieved if inferior resource competitors are also less susceptible to predation (Vance 1978, Holt, et al. 1994, Leibold 1996). When such trade-offs are present, predators can indirectly facilitate defended prey species by selectively removing less defended, superior resource competitors – the well-known keystone predator effect (e.g., Brooks and Dodson 1965, Paine 1966, Holt, et al. 1994, Leibold 1996, Steiner 2003a). Many studies suggest the necessity of understanding the interactive effects of consumers and productivity on species coexistence and prey diversity (Holt, et al. 1994, Leibold 1996). The effects of predators on prey communities can, in theory, vary with productivity (Vance 1978, Armstrong 1979, Leibold 1989, Holt, et al. 1994, Leibold 1996). Positive effects of predators on prey diversity and evenness are predicted to be maximized at intermediate levels of productivity and/or predator density (Vance 1978, Holt, et al. 1994, Leibold 1996). Hence, predator effects on prey communities are predicted to be highly context dependent: enhancing diversity and evenness from low to intermediate levels of productivity (or low to intermediate predation pressures) and reducing diversity and evenness of prey at high levels of productivity (or high levels of predation pressure) (Leibold 1996). While prior studies have provided support for keystone predation (e.g., Brooks and Dodson 1965, Blaustein 1998, Steiner 2003a), few have experimentally examined the interaction between predation and productivity on prey community diversity (though see Proulx, et al. 1996, Bohannan and Lenski 2000, Kneitel and Miller 2002, Jiang and Morin 2005, Jiang and Adams Krumins 2006). Moreover, most of this prior research has only considered plant and microbial community diversity.

A common assumption of many models of predator-prey interactions is that predators can respond numerically (via reproduction) to changing prey abundance and composition (e.g., Vance 1978, Holt, et al. 1994, Leibold 1996). In many natural systems, predators are often larger than their prey and generally have longer generation times. For mobile predators that can respond behaviorally to changing prey abundance and composition, behavioral responses such as immigration or emigration to local patches may be a more important factor influencing local predator abundance and predation effects at short time scales. Hence, experimental studies that maintain fixed densities of otherwise mobile predators could under- or over-estimate predator effects on prey communities. How prey diversity responds to gradients of predation intensity is not clear from existing models. However, it is conceivable that increasing predation pressure from low to intermediate levels may strengthen predator-mediated coexistence of competing prey, promoting diversity. Conversely, high levels of predation may strengthen selection for defended prey taxa, reducing diversity at the high end of predation gradients. Hence, prey diversity may exhibit a unimodal relationship with predator density. Furthermore, facilitative effects of predators are more likely to emerge when productivity levels are high enough to meet the resource needs of less competitive but more defended prey taxa. Thus, unimodal relationships are more likely at intermediate to high levels of productivity. At low productivity levels, we predict monotonic declines in prey diversity with increasing predator abundance due to the increasing probability of prey population extinctions.

Few studies have used gradients of predator densities to examine the functional form of the relationship between predation intensity and prey diversity (e.g., Diehl 1992, Eitam and Blaustein 2010); even rarer are studies that have combined gradients of predators with manipulations of productivity (though see Kneitel and Miller 2002). Here we present the results of a field mesocosm experiment in which we tested the interactive effects of the size- selective invertebrate predator, *Notonecta undulata*, and productivity on zooplankton community diversity. We used two productivity levels achieved through nutrient manipulations and a range of initial predator densities but maintained communities open to predator emigration and immigration. Nutrient levels in our low and high productivity treatments were comparable to low and intermediate to high levels found within natural ponds in the study area, respectively (Leibold 1999, Steiner 2004). Thus, we predicted that predators would have the capacity to enhance prey diversity in the high productivity treatment, generating a unimodal relationship between prey diversity and predator density, but would have a weak or negative effect on diversity at low productivity. We also predicted that Notonecta would emigrate from the tanks and that emigration would be higher in the low productivity treatment due to potential food limitation.

Materials and Methods

Study species

The predator used in our experiment was the backswimmer, *Notonecta undulata* (Notonectidae) which is a flight-capable aquatic insect and wide-spread in shallow freshwater bodies throughout North and Central America (Chordas III, et al. 2005). We have observed that this species is the most abundant and widespread backswimmer in fishless ponds in southern Michigan. Members of this genus are size-selective zooplanktivores and have the capacity to alter the size structure and composition of their zooplankton prey communities (e.g., Scott and Murdoch 1983, Blaustein 1998). We used a zooplankton community composed of seven cladoceran species that were known to compete for shared algal resources (e.g., Lynch 1978, Tillmann and Lampert 1984, Gliwicz 1990), represented a range of body sizes (0.2-3mm maximum length), and were common in ponds in the study area (Steiner 2004). These species, ordered from largest to smallest, included: *Daphnia pulex*, *Ceriodaphnia reticulata*, *Scapholeberis mucronata*, *Diaphanosoma brachyurum Chydorus sphaericus*, *Pleuroxus denticulatus Bosmina longirostris* (hereafter referred to by genus). Prior work has shown that *Notonecta* feed selectively on larger prey, feeding disproportionately on large-bodied *Daphnia* species (Scott and Murdoch 1983), and that competitive ability among cladocera is positively related to body size (Gliwicz 1990; though see Lynch 1978, Steiner 2003b). Thus, our experimental taxa were expected to meet general model assumptions in which large-bodied *Daphnia pulex* was both the best competitor for algal resources and most susceptible to predation.

Experimental design

The experiment was performed during the summer of 2014 at the W. K. Kellogg Biological Station (KBS) Pond Lab Facility (Hickory Corners, Michigan). Experimental ponds consisted of cylindrical plastic cattle tanks filled with 300 L of well water. We used a fully factorial experimental design with 2 levels of productivity (in the form of nutrient additions) crossed with six initial notonectid densities (0, 1, 2, 3, 6, or 12 *N. undulata* adults per tank). Initial predator densities were chosen to span the range we have observed in natural ponds in the region and reported in the literature (Briers and Warren 2000, Shurin 2001, Steiner and Roy 2003, Hall, et al. 2004). All treatments were replicated 3 times for a total of 36 tanks. Low and high productivity treatments corresponded to total phosphorus levels of 23.3 and 293.3 µg P/L, achieved through additions of K_2HPO_4. Total phosphorus levels in ponds in the region range between 11 and 556 µg/L (Leibold 1999, Steiner 2004) with a mean value of 130 µg/L for ponds in the KBS area. Thus, phosphorus levels in our low and high productivity treatments corresponded to low and intermediate to high levels of phosphorus relative to natural systems. $NaNO_3$ was also added to maintain a fixed N: P molar ratio of 33:1 and phosphorus limitation across the productivity treatments. Phytoplankton was collected from 12 fishless ponds around KBS (15 L total), mixed and filtered through 30-µm mesh to remove zooplankton. This mixture was re-distributed evenly among tanks. Zooplankton species were collected from local ponds, maintained in laboratory culture and then introduced to the tanks at an initial density of 43 individuals per species. Adult *N. undulata* were collected from local ponds and maintained in 1000 L tanks until the start of the experiment. Zooplankton populations were allowed to grow for two weeks within the experimental tanks at which time *N. undulata*, were introduced at their target densities. We refer to this as day 0 of the experiment (2 July). All tanks were left uncovered to allow natural emigration and immigration of notonectids and zooplankton passive dispersal from surrounding ponds. As notonectids require a substrate to disperse from water bodies, a floating plastic plate (5x10cm) was left in each tank. Four adult snails (*Helisoma* sp.) were added to each tank to graze periphyton growth and recycle nutrients.

Sampling

Tanks were sampled for zooplankton and algal biomass weekly, up to day 84, the final day of the experiment (this duration was long enough to observe multiple generations of the prey species and one *Notonecta* reproductive event). To sample zooplankton, tanks were first gently mixed with a PVC pipe, then two 10-liter water samples were collected from the water column using a plastic bucket. Water samples were filtered through 80-µm mesh to isolate zooplankton and samples were preserved in acid Lugol's solution for later enumeration using a stereomicroscope. To measure algal abundance, an additional 500-ml water sample was collected from each tank using a PVC tube sampler and later filtered onto glass fiber filters for analysis of chlorophyll *a* following ethanol extraction. We analyzed two size fractions of algae: total chlorophyll *a* and chlorophyll *a* of algae filtered through a 30-µm mesh as a measure of small, edible algae (sensu Steiner 2003a). The relative abundance of grazer-resistant (>30 µm) chlorophyll *a* for each sample was calculated as the difference between the total and <30 µm chlorophyll fractions divided by total chlorophyll *a*. After each sampling, removed water was replaced with fresh medium at target nutrient levels. Thus, the experimental system was maintained as a semi-continuous culture. We monitored for and removed dead notonectids from the tanks every 2-3 days and exhaustively sampled live notonectids at the end of the experiment using a d-net.

Statistical methods

All analyses were performed in R version 3.0 (R Development Core Team 2011) with the exception of repeated measures ANOVAs which were performed using SYSTAT Version 13.0 (Systat Software, Inc., San Jose, CA, USA). To minimize the effects of transient zooplankton responses to notonectids, we analyzed data beginning on day 28 of the experiment (four weeks after introduction of predators). To examine notonectid effects on zooplankton community diversity, we used counts of notonectids at the end of the experiment (realized abundance). Maximum realized notonectid abundance varied between low and high productivity treatments with low productivity tanks ranging between 0 and 7 individuals and high productivity tanks ranging between 0 and 11. Analyses in which we restricted low and high productivity treatments to a comparable range of predator densities (tanks with 7 or less notonectids) produced similar results to those using the full range of predator densities. Thus, we present results from the latter. Although rotifers and copepods were not intentionally introduced to tanks, we observed these taxa in our samples which either invaded through passive dispersal or accidental introduction with our phytoplankton inoculation. Copepods were classified as either cyclopoid or calanoid and included with cladoceran species in analyses of zooplankton diversity. While this level of taxonomic resolution is crude, an examination of a random subset of samples revealed that calanoids were represented by a single species, *Aglaodiaptomus leptopus,* and cyclopoids by two species *Acanthocyclops robustus* and *Eucyclops serrulatus* (Patrick L. Hudson, U.S. Geological Survey, Great Lakes Science

Center, pers. comm.). Thus, identification of copepods at a higher taxonomic resolution would likely not affect our results to a great extent. Rotifers were not included in our analyses.

Zooplankton diversity was quantified using species richness (based on species presence/absence) and species evenness using Pielou’s index. To account for potential effects of limited sampling effort, we also quantified species diversity using the inverse Simpson’s index which puts greater weight on abundant species. Effects of productivity and realized notonectid abundance on diversity and evenness responses through time were analyzed using univariate repeated measures ANOVA (rm-ANOVA). In cases where time interactions with treatment effects were not detected, we analyzed responses averaged over time (between subjects effects) using GLM with Gaussian errors and a log link. Because we predicted zooplankton diversity would respond non-linearly to predator density, linear and quadratic effects of notonectid density were included in the analyses as well as the interactions between productivity and the linear and quadratic predictors. In cases where significant interactions between productivity and notonectid abundance were present, we tested the effects of notonectid abundance (both linear and quadratic effects) on diversity for the low and high productivity treatments separately using GLM with Gaussian errors. Model selection for the GLM analyses were performed using AIC and the step function in R. Assumptions of normality for the GLM analyses were met using Lilliefor’s test, Shapiro-Wilk’s test and visual inspection of plots of residuals.

Effects of productivity and notonectid realized abundance on zooplankton composition over time were analyzed using repeated measures PERMANOVA based on Bray-Curtis distances of square root transformed species relative abundances. To examine the effects of productivity and notonectid realized abundance on time-averaged zooplankton composition (between subjects effects), we performed principal coordinates analyses of the Bray Curtis distance matrix (of all sample dates) and used the centroid for each experimental tank as a measure of composition integrated over time. Centroids were based on the first five coordinate axes as these accounted for the majority of variation based on eigenvalues. Centroid coordinates were then analyzed using MANOVA testing for the effects of productivity and notonectid realized abundance and their interaction. In 12 out of 36 tanks we observed invasion by one or two adult individuals of aquatic beetle (Hydrophilidae or Dytiscidae) or the notonectid, *Notonecta irrorata*. Inclusion of these potential predators in our statistical analyses of zooplankton responses had no effects on our results and have been removed.

We analyzed $\log_{10}$ transformed total chlorophyll *a* and the relative abundance of grazer-resistant (>30-µm) chlorophyll *a* using separate univariate repeated measures ANOVAs, testing for the effects of productivity and notonectid realized abundance. In cases where time interactions with treatment effects were not detected, we analyzed responses averaged over time (between subjects effects) using GLM with Gaussian errors. Assumptions of normality for the GLM analyses were met using Lilliefor’s test, Shapiro-Wilk’s test and visual inspection of plots of residuals.

Results

We observed emigration, immigration and reproduction within the notonectid populations over the course of the experiment. Because offspring had matured to the adult stage by the end of the experiment, we could not separate the effects of immigration, emigration and reproduction on realized notonectid abundances at the end of the experiment. However, when comparing realized abundances to initial abundances (removing mortality), twenty out of 30 tanks showed net reductions in abundance, indicative of emigration (Fig. 1). Despite this, a gradient of abundances was maintained at both low and high productivity (Appendix A, Fig. 1). Realized abundances at the end of the experiment were positively related to initial abundance ($F_{1,35} = 5.61$, $p=0.02$, GLM quasi-Poisson errors), but no effects of productivity or an interaction were detected ($p>0.25$, GLM quasi-Poisson errors).

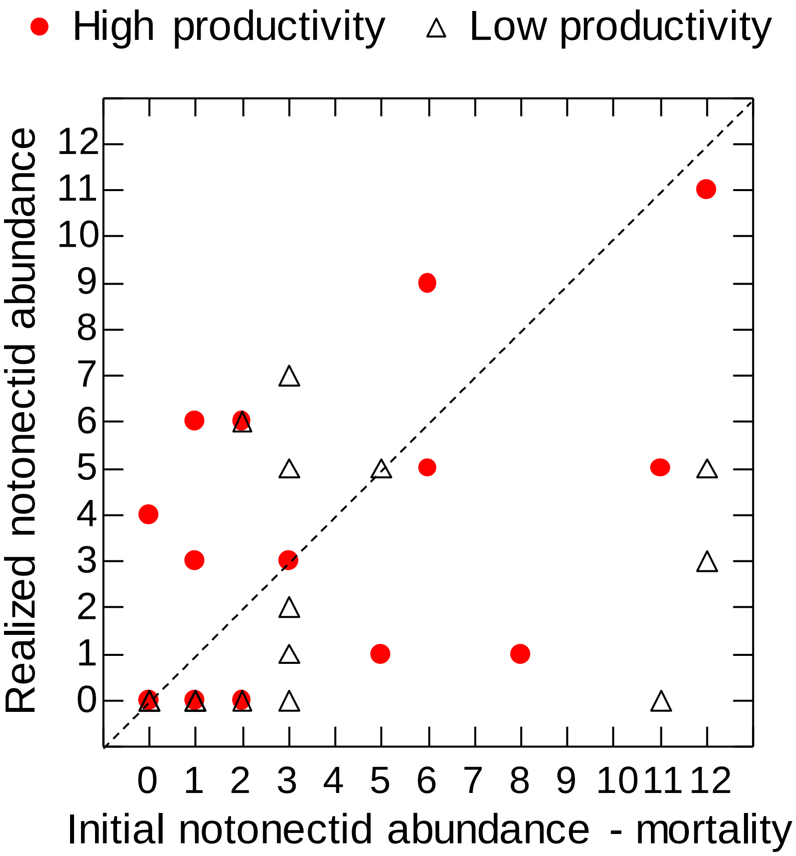


Figure 1. The relationship between realized notonectid abundance and initial notonectid abundance minus mortality (the total number of dead adult notonectids observed in the tanks over the course of the experiment); results are shown for both high and low productivity treatments. Values below the dashed 1:1 line are evidence of emigration (reduction in abundance in excess of mortality).

Repeated measures ANOVA revealed a significant time effect on zooplankton species richness ($F_{3,90}$= 4.59, $p<0.01$), but no effect of time on inverse Simpson diversity ($F_{3,90}$= 2.26, $p=0.09$) or species evenness ($p=0.32$). No time by treatment interactions were detected for all three measures of diversity (all $p>0.30$). When analyzing time-averaged diversity in the absence of predators, nutrient enrichment reduced zooplankton diversity measured as either species richness (Fig. 2A; $p<0.001$, productivity effect, ANOVA), inverse Simpson diversity (Fig. 2B; $p=0.01$, productivity effect, ANOVA) or evenness (Fig. 2C; $p=0.02$, productivity effect, ANOVA). Effects of notonectid abundance on diversity varied with productivity level; interactions between productivity and the quadratic effect of notonectid density were retained for species richness ($F_{1,30}$= 5.12, p= 0.03, GLM), inverse Simpson diversity ($F_{1,30}$= 5.37, $p=0.03$, GLM) and species evenness ($F_{1,30}$= 4.47, $p=0.04$, GLM). Analyzing productivity treatments separately, species richness declined with increasing notonectid abundance at low productivity (Fig. 2A; model $R^2=0.22$, $p=0.032$, GLM); the quadratic term was not retained in the model ($p>0.20$). At high productivity, a unimodal relationship emerged; a significant negative quadratic effect of notonectid abundance on richness was detected (Fig. 2A; $p=0.01$, GLM; model $R^2=0.26$, $p=0.04$, GLM). Inverse Simpson diversity showed no strong relationship, linear or quadratic, with notonectid abundance at low productivity (Fig. 2B; all $p>0.08$, GLM). Consistent with results for species richness, a significant negative quadratic term was detected for inverse Simpson diversity ($p=0.05$, GLM) at high productivity, suggesting that diversity first increased then declined with predator abundance in this treatment (Fig. 2B). However, the overall model was not significant ($R^2=0.13$, $p=0.14$). Evenness showed similar responses; no effects of notonectid abundance were detected at low productivity (Fig. 2C; all p>0.14, GLM). At high productivity, a significant negative quadratic term was detected (p=0.05, GLM) suggesting a hump-shaped relationship with predator abundance (Fig. 2C). However, the overall model was not significant (R^2=0.14, p=0.13).

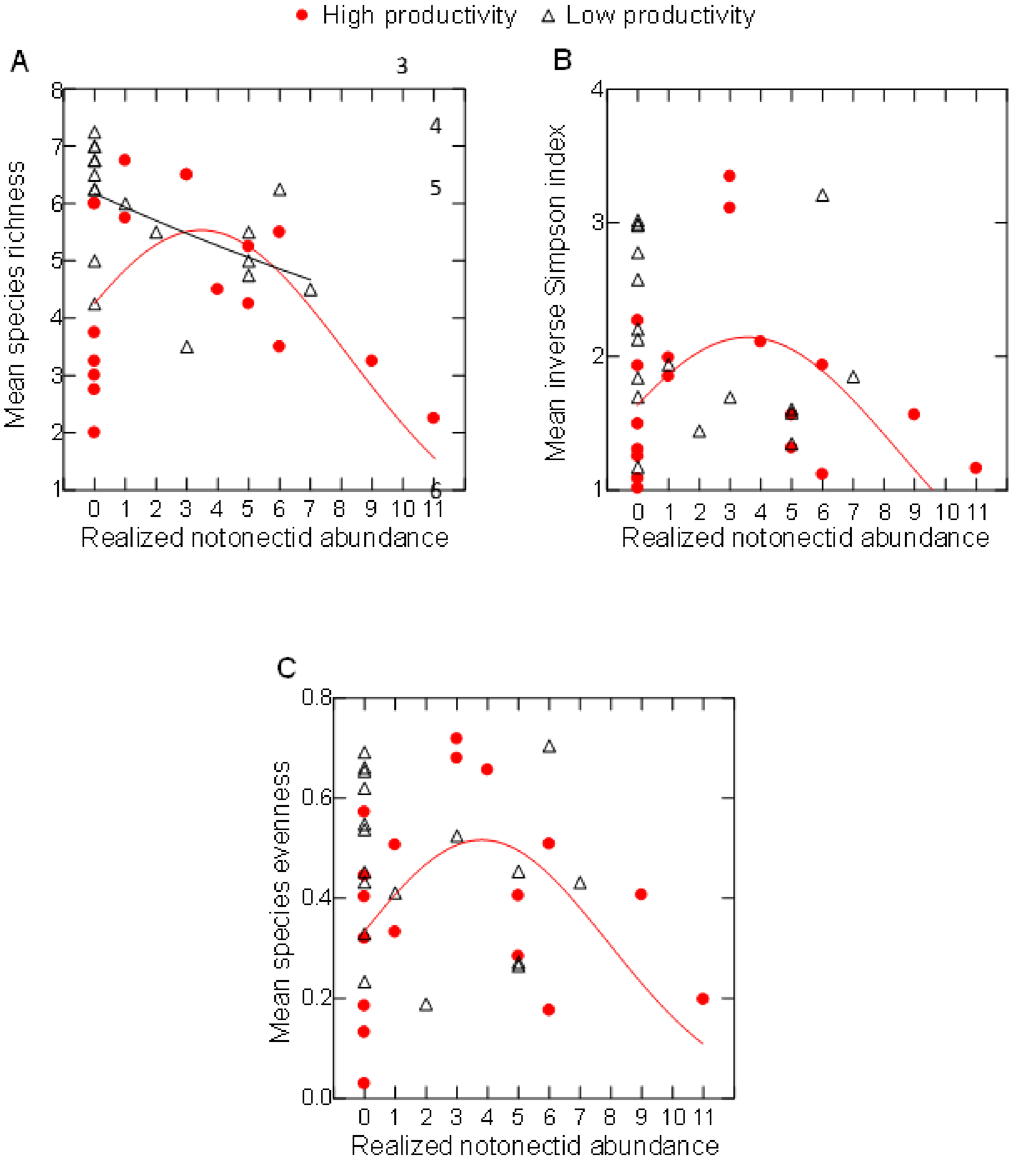


Figure 2. The effects of realized notonectid abundance and productivity (low versus high) on time-averaged zooplankton diversity measured as (A) species richness, (B) inverse Simpson diversity and (C) species evenness (Pielou's index). Lines are model fits from separate GLM analyses of the low and high productivity treatments (black and red lines, respectively).

Repeated measures PERMANOVA of zooplankton composition revealed a significant effect of time ($p<0.001$) but no interactions between time and treatments (all $p>0.60$, PERMANOVA). When looking across all dates (between subjects effects), composition was affected by notonectid realized abundance ($p=0.02$, Pillai's trace=0.36, $F_{5,32}=2.70$, MANOVA) and productivity ($p<0.001$, Pillai's trace=0.60, $F_{5,32}=8.28$, MANOVA) but not by their interaction ($p=0.26$, MANOVA). Figure 3 displays time-averaged relative abundances of zooplankton taxa in relation to productivity (Fig. 3A) and realized notonectid abundance (Fig. 3B). The relationship between zooplankton abundances and notonectid abundance separated by productivity treatment can be found in Figure 2 (Appendix A). In general, low productivity treatments were dominated by calanoid copepods followed by *Bosmina*. This shifted to dominance by cyclopoid copepods at high productivity (Fig. 3A). When averaging across productivity treatments, zooplankton composition transitioned from relatively even communities in the absence of notonectids to dominance by *Bosmina* at low to intermediate notonectid abundances (Fig. 3B). Communities appeared to become more even at intermediate predator abundances, transitioning to dominance by calanoid and cyclopoid copepods at the highest predator abundances (Fig. 3B).

Repeated measures ANOVAs revealed a significant effect of time on $\log_{10}$ total chlorophyll *a* ($F_{3,96}= 3.32$, $p<0.023$) but no effect of time on the relative chlorophyll *a* concentration of grazer resistant (>30 µm) algae ($p=0.53$). There were no time x treatment interactions for either response variable (all $p>0.2$). When analyzing time-averaged measures, total chlorophyll *a* was on average higher in the high productivity treatment relative to low productivity ($F_{1,32}= 35.42$, $p<0.001$, GLM; Appendix A, Figure 3). We detected no effect or interaction of notonectid abundance on time-averaged total chlorophyll *a* (p>0.16, GLM; Figure 3). There were no effects of productivity, notonectid abundance or an interaction on time-averaged relative abundance of the >30-µm size fraction of chlorophyll *a* (all p>0.50, GLM; Appendix A, Figure 4).

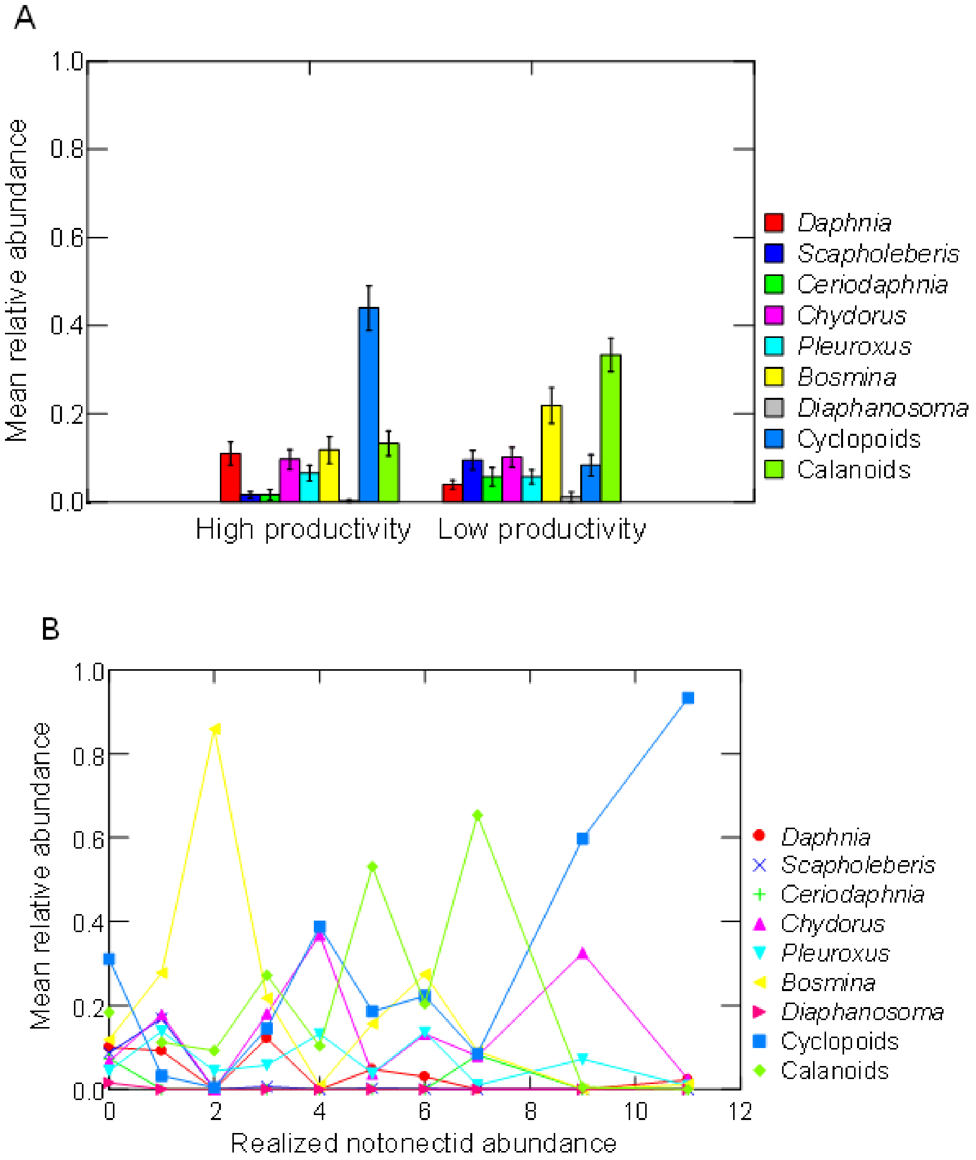


Figure 3. Time-averaged relative abundances of zooplankton taxa in relation to productivity and realized notonectid abundance. (A) Mean relative abundances (+/- S.E.) in the high and low productivity treatments, averaging across notonectid abundances. (B) Mean relative abundances in relation to realized notonectid abundance, averaging across productivity treatments.

Discussion

Over the course of the experiment, we observed emigration, immigration and reproduction within the notonectid populations. However, we could not separate the effects of immigration, emigration and reproduction on realized notonectid abundances since offspring had matured to the adult stage by the end of the experiment. Nevertheless, by observing the reduction in realized abundances to initial abundances (removing mortality) we can conclude that emigration occurred. Realized abundances at the end of the experiment were positively related to initial abundance, but no effects of productivity or an interaction were detected.

Our results demonstrate that the effects of predators on prey composition and diversity depend on the interaction between productivity and predation intensity. In the absence of predators, nutrient enrichment reduced zooplankton diversity measured as either species richness, inverse Simpson diversity or evenness. How predators modified prey diversity depended on productivity level. Low to intermediate levels of predation intensity promoted species richness in the high productivity treatment, resulting in levels comparable to the unenriched state in the absence of predators (Fig. 2). This effect was reversed at higher notonectid densities resulting in declines in prey species richness. In contrast to effects at high productivity, predators showed no tendency to promote diversity at low productivity; species richness instead declined with increasing predator abundance. Phosphorus levels in our low and high productivity treatments were chosen to represent levels close to low and intermediate to high levels found in natural ponds in the region, respectively. Thus, our findings are consistent with general model predictions in which predators facilitate prey coexistence and diversity at intermediate levels of productivity. Despite this, it is important to point out that this prediction was not strongly supported when measuring diversity as either species evenness or inverse Simpson diversity. While both measures tended to exhibit a unimodal relationship with predator abundance at high productivity (significant negative quadratic terms were retained for both models), overall model R^2 values were low and p values were not significant.

Several species accounted for observed zooplankton diversity responses. When predators were absent, a greater number of zooplankton species were present and had comparable relative abundances at low productivity compared to high productivity where cyclopoid copepods dominated. This taxon experienced reductions with increasing predation pressure at high productivity - a response that was accompanied by an increase in the incidence and relative abundance of several other zooplankton species, enhancing diversity (Appendix A, Fig. 2). One potential concern is that the cyclopoid species observed in our experiment are omnivores and may act as both competitors and predators of zooplankton. Indeed, zooplankton species richness (not counting cyclopoid copepods) on average showed a significant negative relationship with cyclopoid density (Appendix A, Fig. 5). However, analysis of residuals from this relationship revealed notonectid and productivity effects that were similar to those presented above; a significant unimodal relationship with predator abundance was still evident at high productivity (Appendix A, Fig. 6). Thus, variation in cyclopoid copepod densities cannot fully account for observed effects of notonectids on prey species richness.

While our results supported some general model predictions, they also showed interesting deviations from model expectations. Many models of predator effects on diversity assume a trade-off among prey in competitive ability and susceptibility to predation – i.e., stronger resource competitors are more susceptible to predation (Holt, et al. 1994, Leibold 1996). Consequently, prey diversity is predicted to be low in the absence of predators, regardless of productivity level (Holt, et al. 1994, Leibold 1996). We did not observe this; diversity tended to be highest in the absence of predators in the low productivity treatment. A possible explanation was the presence of a diverse phytoplankton assemblage and resource partitioning among zooplankton species which may have facilitated coexistence in the absence of predators. While we did not observe significant treatment effects on the size structure of algae in our experiment (i.e. the relative abundance of grazer-resistant algae), this measure of resource quality was admittedly crude and could not account for compositional differences that may have existed among treatments. Productivity and predation intensity were also predicted to interactively affect zooplankton community composition, shifting dominance from highly competitive but predator-susceptible prey (i.e., large-bodied *Daphnia pulex*) to less competitive but less susceptible species (e.g. small-bodied cladocera) in the high productivity treatment. We found some support for this prediction. At high productivity, *Daphnia pulex* had the highest relative abundance among cladocera in the absence of predators (Appendix A, Fig. 2 A, B). Increasing predator abundance in this treatment was associated with an increase in the relative abundance of small-bodied cladodera and a decline in *D. pulex*. This is consistent with a trade-off between competitive ability and susceptibility to predation among these species. While shifts in cladoceran composition contributed to patterns of diversity, as noted above, cyclopoid copepods were also a significant component of the zooplankton community in our experiment. Interestingly, cyclopoids dominated at both the low and high ends of the predation gradient under high productivity (Appendix A, Fig. 2 A, B) – a pattern that does not fit general model predictions.

Our work complements prior studies which have shown that consumers can have positive or negative effects on local species diversity depending on productivity level (Proulx and Mazumder 1998, Bohannan and Lenski 2000, Worm, et al. 2002, Jiang and Morin 2005, Jiang and Adams Krumins 2006, Hillebrand, et al. 2007). Several of these have shown that consumers can promote the diversity of their resource communities at high levels of productivity by preventing the dominance of a few taxa while at low productivity levels consumers may decrease biodiversity (Proulx and Mazumder 1998, Jiang and Adams Krumins 2006, Hillebrand, et al. 2007). While aspects of these studies mirror our findings, most have focused on plant-herbivore interactions (Proulx, et al. 1996, Proulx and Mazumder 1998, Bakker, et al. 2006, Hillebrand, et al. 2007). Studies of the interactive role of predation and productivity on prey diversity are limited (though see (Kneitel and Miller 2002). More importantly, few have empirically examined the functional form of the relationship between prey diversity and predator abundance (e.g., Diehl 1992, Eitam and Blaustein 2010) or how such relationships are altered by productivity (Kneitel and Miller 2002). For systems composed of consumers with longer generation times relative to their resources, resource diversity responses at short times scales may occur in response to relatively fixed predator densities. For such communities, comprehending variation in species diversity in both space and time may depend vitally on illuminating the form of the relationship between diversity and predation intensity. Our work shows that such responses can be complex and highly context dependent.

CHAPTER 3 METACOMMUNITY STRUCTURE OF *NOTONECTA* SPECIES IN FISHLESS PONDS

Introduction

Community Structure and Metacommunity Theory

Understanding the processes influencing the spatial and temporal distribution of species is a main focus of ecological studies. Community structure is affected by local and regional processes. Local processes affect population persistence and abundance of species through biotic interactions and abiotic environmental conditions within relatively small spatial domains - (hereafter called local sites or patches) (Shurin 2000). Regional processes, such as species dispersal among patches and colonization/extinction dynamics, can also affect the dynamics and structure of local populations and communities (Mac Arthur and Wilson 1967; Gilpin and Hanski 1991, Leibold et al. 2004).

Metacommunity theory (Leibold et al., 2004) considers the interplay of both local and regional processes as drivers of species distributions among isolated patches. In an early review and synthesis, Leibold et al. (2004) identified four general models that may explain the structure and dynamics of natural metacommunities: the neutral, patch-dynamic, mass effects and species sorting models. The neutral model assumes that local patches are homogenous and species are functionally identical. Community structure is affected by random speciation, extinction, and migration (Hubbell, 2001) rather than by differential species' responses to environmental variation. The patch-dynamic model assumes that local sites are homogenous and colonization-extinction events drive metacommunity structure. The maintenance of species diversity in these models is commonly dependent on colonization-competition trade-offs among species (Hastings 1980; Tilman 1982). The species-sorting model assumes that all species have equal dispersal ability and access to all patches. Thus, dispersal limitation is not a restricting factor, and community structure is determined by local processes such as biotic interactions and species' tolerances to abiotic environmental conditions (Chase & Leibold 2003). Finally, mass effects models incorporate spatial heterogeneity in environmental conditions as well as variation among species in competitive ability. Dispersal in such models can alter local competitive interactions via source-sink effects with ultimate effects on local diversity being highly dependent on the rate of species movement (strong mass effects emerge at intermediate to high rates of dispersal).

Recent Directions in Metacommunity Studies

A considerable amount of the research has been performed to distinguish the role of the four metacommunity perspectives in different systems (Van der Gucht et al. 2007; McCauley et al. 2008; Leibold and Loeuille 2015). Findings from several studies show that community structure is often affected by more than a single process, and thus the models are not mutually exclusive (Cottenie 2005; Gravel et al. 2006; Logue et al. 2011). Consequently, recent publications have advocated revision of the terminology used by Leibold et al. 2004 to better integrate the metacommunity paradigms and encompass more of the complexities inherent in natural systems (Logue et al. 2011; Winegardner et al. 2012). For instance, dispersal rate is a key factor joining three of the metacommunity models: lack of dispersal for some species in the patch-dynamic model, a sufficient but low rate of dispersal for species in the species-sorting model, and a high rate of dispersal in mass effects model (Winegardner et al. 2012; Heino et al. 2015). Thus, variation among taxa in dispersal capacity or behavior (e.g. habitat choice) can strongly alter the model mechanisms at play and resultant predictions (Resetarits 2005; Heino et al. 2015). For example, several studies have shown that active dispersal reduces dispersal limitation of taxa and promotes species sorting when compared to taxa with passive dispersal modes (Maloney & Munguia, 2011; Soininen et al., 2011; De Bie et al., 2012; Heino 2013; though see Heino et al., 2012; Landeiro et al., 2012; Schulz et al., 2012; Grönroos et al., 2013).

Related to dispersal capacity is the role of spatial scale. Although the four metacommunity paradigms consider environmental conditions of patches (e.g., homogenous vs. heterogenous conditions), only one (the neutral model) makes explicit predictions with regards to spatial scale. Implicit in many metacommunity models is that all patches have an equal probability of immigration/emigration and the relative location of patches in space is not considered. Thus, these models assume that all sites are evenly distributed in the landscape and have the same degree of connectivity among patches. In natural systems, scale can potentially alter this assumption and predicted dynamics. For example, survey studies show that distributions of patches in landscapes are generally irregular and connectivity among patches varies (Hanski & Ovaskainen 2000; Ovaskainen et al. 2002; Spiesman and Cumming 2008). Increasing the spatial scale of a study may also increase the degree of environmental heterogeneity observed among patches (e.g., Nekola and White 1999) as well as the heterogeneity of landscape features surrounding local patches, reducing connectivity and enhancing isolation.

Integrating spatial scale into existing metacommunity models may provide a better understanding of the processes affecting spatial variation in community composition. As mentioned, neutral theory predicts that compositional dissimilarity among communities increases with increasing spatial scale. However, in the absence of the neutral processes, a similar pattern may conceivably emerge for the remaining three models. Mass effects models predict high compositional similarity among patches when dispersal rates are high (Mouquet and Loreau 2003; Kneitel and Miller 2003). Thus, at small spatial scales, where all sites are in close proximity to each other, we expect little variation in community composition due to high connectivity among sites (sensu Mouquet and Loreau 2003; Ng et al. 2009). Mass effects models predict that reduced dispersal rates reduce mass effects and enhance compositional dissimilarity via underlying spatial heterogeneity and species sorting (Mouquet and Loreau 2002 and 2003). Thus, variation in community structure may increase with increasing spatial scale due to decreasing connectivity and increasing dispersal limitation. In the absence of mass effects, the species sorting model predicts potentially high levels of compositional dissimilarity even at small spatial scales depending on the degree of environmental heterogeneity among patches. However, dissimilarity may increase with increasing scale due to reduced connectivity, increasing dispersal limitation and increasing stochastic variation in dispersal history. In the patch dynamic model, compositional variation among patches is a product of colonization-extinction events, with competition-colonization trade-offs commonly assumed among species. In these models, some degree of compositional variation may be expected even at small spatial scales. However, increasing scale may increase the potential inclusion of patches of low connectivity, favoring species with greater dispersal capacity. Thus, compositional dissimilarity may increase with increasing focal scale.

Temporal Variability in Metacommunity Organizations

While metacommunity studies in the last decade have attempted to disentangle spatial and environmental processes, these have largely used a snapshot approach, examining spatial variation in community structure at a single time point (e.g., McCauley et al., 2008; Heino & Mykr, 2008, De Bie et al. 2012). However, the conditions of most natural communities exhibit some degree of temporal variation (e.g., Barnes 1983; Bengtsson et al., 1997) that may lead to changes in community structure over time (Bloch et al. 2007, Azeria and Kolasa 2008). The effect of time can be especially pronounced in temperate regions where seasonal variation exists. Seasonality can influence abiotic factors such as solar radiation, water availability and temperature, as well as biotic processes such as dispersal behavior (Bonte et al., 2008; Dingle 2009), foraging activity (Fleming and Heithaus 1986; Norman 1994), population dynamics and the strength of species interactions (Garcia & Cabrera-Reves 2008). Only a handful of metacommunity studies have considered temporal variation; these have shown that the relative importance of spatial and environmental processes can vary with time (Heino & Mykr, 2008; Erös et al., 2012a; Langenheder et al. 2012; Fernandes et al., 2014; Henry and Cumming 2016). Thus, considering temporal variation, especially in seasonal systems, may be vital for attaining a comprehensive understanding of the relative importance of spatial and environmental processes in the organization of metacommunities.

To address how temporal variation (seasonality) impacts the relative effects of spatial and environmental processes on metacommunities, we performed a two-year study of seasonal variation in metacommunity structure in fishless ponds in southern Michigan. Ponds are excellent model systems for metacommunity studies (e.g., Jeffries 1994; Briers and Warren 2000; McCauley et al. 2006; Heino 2011), having defined boundaries, considerable spatiotemporal variation in biotic/abiotic conditions (Jeffries 1988; Chase 2007) and organisms that differ greatly in tempo and mode of dispersal. We focused on the community structure of *Notonecta* species (Hemiptera: Notonectidae) which are flight-capable insects and common predatory macroinvertebrates in fishless ponds. We addressed the following questions: (1) What are the relative effects of environmental and spatial factors on notonectid community structure? (2) Which environmental variables and spatial scales are responsible for such variation? (3) Is the relative importance of environmental and spatial processes on species distributions affected by temporal variation? (4) Are observed patterns consistent with predictions of general metacommunity models? We used variation partitioning (Borcard et al., 1992; Borcard and Legendre 1994) to investigate the relative contribution of environmental and spatial processes to notonectid metacommunity structure (questions 1-2) and compared results across sampling dates within years to test if the relative contribution of these processes changed over the growing season (question 3). We predicted that the contribution of environmental and spatial components to notonectid community structure would change over the growing season. Notonectids are known to exhibit mass dispersal events in the mid spring and early fall (Walton 1935; Fernando 1959; McCauley et al., 2009). Thus, we predicted that mass effects would be strongest during these periods, reducing the significance of environmental components. We further predicted that environmental effects would increase within the growing season once species colonized ponds, due to direct and indirect effects of the environment on growth, reproduction, survival and emigration. We used variation partitioning to address question 4 (Cottenie 2005). For landscapes such as ours in which heterogeneity in environmental conditions is known to exist, significant pure environmental components (PE) are consistent with species-sorting and suggest that neutral processes are not occurring. Significant pure spatial components in the absence of environmental effects is consistent with patch-dynamic models or neutral theory. If both pure environmental and pure spatial components are significant then a combination of species-sorting, patch-dynamic and/or mass effects may jointly drive metacommunity organization.

Our results showed that a combination of environmental, spatial and spatially structured environmental components contributed to notonectid community structure. Effects also varied seasonally and inter-annually. In the first year of the study, a large amount of community variation was explained by these components with the ratio of environmental to spatial components increasing through the growing season - indicative of the increasing importance of environmental filters and species sorting. In contrast, overall less variation was explained by both spatial and environmental components in the second year of the study. Furthermore, the spatial component played the largest role in explaining variation over the growing season. In contrast to our general predictions, variation in community structure did not emerge consistently at large spatial scales. Rather, compositional variation was generally observed at small to intermediate spatial scales, with community dissimilarity exhibiting negative spatial autocorrelation. Our results confirm the importance of both spatial and environmental processes in the organization of metacommunities. Our work also highlights the importance of considering temporal variation at intra- to inter-annual scales in order to gain a more comprehensive understanding of variation in metacommunity structure.

Materials and Methods

Species of interest

We focused on *Notonecta* species (Notonectidae: Hemiptera), which are common, widespread macroinvertebrates of lentic waters across North America (e.g., Clark 1928; Blaustein 1998; Briers and Warren 2000; Chordas et al. 2005). These insects have an incomplete life cycle with five larval stages (instars I-V), with wing development and flight capability occurring in the adult stage. These size-selective aquatic predators spend their juvenile stage in a single aquatic habitat. Adult stages are considered strong active dispersers (Briers and Warren 2000; McCauley et al. 2009) that can fly up to 1.6. km between the aquatic habitats during mass dispersal events (Briers and Warren 2000).

Study area and sampling sites

The study sites were fishless ponds located within the Michigan State University, Kellogg Biological Station (KBS), Lux Arbor Reserve, (Hickory Corners, Michigan, USA. Only fishless ponds located within the 5.65 km2 reserve were selected for this study; ponds that lacked notonectids were excluded (Fig 1). Fish are known to exert a strong influence on notonectid abundance and composition (Bennet and Streams 1986). Thus, we chose to focus on systems that lacked this strong top-down effect. We sampled 11 ponds in 2014 and 12 ponds in 2015. To cover the reported 1.6 km dispersal range of notonectid adults (Briers and Warren 2000), we attempted to sample any water body found within a 2 km radius of each pond. The exceptions were two ponds within the 2 km radius of a single pond (Lux 3 Fig 1), that were located on private lands and could not be sampled. The average, minimum, and maximum distance between the fishless ponds were 900 m, 69 m, and 2.22 km, respectively.

All selected ponds were natural and contained water year-round during our study period and in several years prior to our study (Stephen K. Hamilton, Michigan State University, pers. comm). The landcover around the ponds included deciduous forests and grassland (Fig1). The ponds were variable in terms of water chemistry, size, area, depth, canopy cover, and invertebrate biodiversity (Table 1 A, B, Appendix B). The climate of the study area is temperate with well-defined seasons. January and July are the coldest and warmest months of the year with average of -8 and 28 degrees C˚, respectively.

Figure 1. Map of the study area, showing the locations of the selected fishless ponds (white circles) in Lux Reserve Arbor, Michigan, USA.

Sampling and data collection

Ponds were sampled monthly from May to September in two consecutive years (2014 and 2015) for water chemistry, macroinvertebrate community composition and zooplankton community composition. To sample macroinvertebrates and zooplankton, multiple transects were placed randomly perpendicular to the pond edge (from edge to the center, up to 1m depth). The number of transects used at each pond differed depending on pond area.

Macroinvertebrates, including *Notonecta* species, were sampled using a D-net with 30 x 50 cm dimensions and mesh size of 1 mm. Samples were collected along multiple transects at equal intervals. The number of net sweeps varied between 10 to 20 sweeps for each pond depending on pond area. In the first year of the survey all the collected macroinvertebrates were preserved in 70% ethanol for laboratory identifications but in the second-year, collected specimens were identified at field and were returned to the ponds after identification and enumeration.

Zooplankton were sampled by collecting water along multiple transects at equal intervals using a 2-liter pitcher and filtered through an 80-µm sieve. The total volume sampled varied between 10 to 40 liters for each pond depending on pond area and depth. Zooplankton samples were preserved in 10% acid Lugol’s solution for later identification to the genus level and enumeration.

For each sampling date, water temperature, pH, dissolved oxygen, and conductivity were measured using a portable handheld YSI meter. Measurements were recorded at 10 cm depth at equal intervals along each transect. The values were averaged for each pond for statistical analyses. During each sampling date, 500 ml of pond water was collected along the transect, kept on ice and in the dark for later analyses of total phosphorus (TP) as a measure of pond productivity and chlorophyll *a* (Chl *a*) as a measure algal biomass. To measure chlorophyll-a, algae were concentrated by filtering 50 ml of collected water onto Whatman GF/B filters then analyzed using narrow band fluorometry following ethanol extraction (Welschmeyer 1994). To measure TP, 50 ml of sample water was frozen for later analysis using the ammonium molybdate method and persulfate digestion (Wetzel and Likens 1991).

Spatial structure and spatial predictors

To produce spatial variables for the selected ponds, we used distance-based Moran's Eigenvector Maps, dbMEMs (also called dbMEM spatial eigenfunctions). The dbMEM eigenfunctions were formerly called principle coordinates of neighborhood matrices (PCNM, Borcard and Legendre 2002; Borcard et al. 2004). MEMs are orthogonal spatial variables (eigenvectors) which represent complex spatial structures at various spatial scales (Peres-Neto and Legendre 2010). Calculation of these variables are based on truncated geographic distance matrix among sampling sites. The dbMEMs process produces n-1 MEMs, which are different representations of how sampling sites are spatially related. The first MEM represents the broadest configuration in community data, while the last MEM represents the finest scale of arrangement.

The MEM eigenvalues are proportional to Moran's I coefficient of spatial correlation and can have positive or negative values (Dray et al. 2006; Legendre and Legendre 2012). A MEM with high positive eigenvalue has positive autocorrelation which means closer sites have a more similar community composition. On the other hand, a MEM with a high negative value shows negative autocorrelation and represents the situation where sites closer to each other are less similar. In ecological studies, features with positive spatial correlations represent contagious events which are common in nature such as mortality, growth, reproduction, and migration (Legendre and Legendre 2012). On the other hand, significant negative correlations could be related to local factors such as some biotic interactions (e.g., territorial behaviors, competition between species, or effects of localized specialist predators and pathogens) (Borcard et al. 2011).

Statistical Analysis

We used variation partitioning (Borcard et al. 1992; Borcard and Legendre 1994) to study how pure environmental (PE), pure spatial (PS), and spatially structured environmental (SSE) elements were related to variation in notonectid community composition. We focus here on the composition of adult notonectids because of their dispersal capability (results for juveniles can be found in Table 4, Appendix B). Variation partitioning reveals the shared and unique contributions of environmental and spatial variables to total variation in community composition. This test uses the adjusted R-squared values from redundancy analysis (RDA) of abundance data (Legendre and Gallagher 2001). We focused analyses on two notonectid species, *Notonecta undulata* and *Notonecta irrorata*, which numerically dominated communities across ponds (inclusion of rare notonectid species did not alter our general results or conclusions). Variation partitioning was performed for each sampling date separately (sensu Erös et al. 2012; Fernandes et al. 2013; Henry and Cumming 2016) as well as abundances averaged over sampling dates within each survey year. Distance-based redundancy analysis (dbRDA) based on Bray-Curtis dissimilarity of species abundance with Monte Carlo permutation tests (n = 999) was used to test the significance of unique fractions of environmental and spatial models. A small value (0.000008) was added to all density values before dbRDA performed (Legendre and Legendre 1998) to solve the problem of zero samples in using dbRDA. This constant was one tenth of the lowest notonectid density recorded from the surveyed ponds. The result of variation partitioning from different dates was compared to see if the relative contribution of the components varied with time.

Environmental predictors in our analyses included macroinvertebrate community composition (minus *Notonecta*), zooplankton community composition, total zooplankton biomass, pH and log-transformed TP, Chl *a*, conductivity, and dissolved oxygen concentration. Macroinvertebrate and zooplankton community composition were quantified using two separate Principal Coordinates Analyses (PCoA, Gower, 1966) based on Bray-Curtis dissimilarity of relative abundances of taxa. The first two axes produced by each PCoA, which captured greater than 50% of the variation in the input data, were included as predictors in the environmental matrix. Total zooplankton biomass (dry weight) was calculated by multiplying density of each taxon by a taxon-specific biomass conversion constant and then summing across taxa for each pond.

Since our study sites showed an irregular distribution in geographic space, a data-driven approach was performed for each sampling date before dbMEM analyses (sensu Dray et al. 2006). This approach allowed selection of the best combination of the connectivity matrix (CM) and spatial-weighting matrix (SWM) based on AIC for construction of MEMs. Also, trend surface analysis (Gittins 1968) was performed using a RDA model with pond coordinates as an explanatory variable and the notonectid community matrix as a response. This process detects any linear relationship between our community data and coordinates. Since MEMs analysis is ineffective in the presence of such linear trends, data was detrended for all sampling dates and the detrended residual was used in the forward selection of MEMs instead of the original data (Borcard et al. 2004). After calculation of MEMs and defining their spatial scales, the spatial correlation of MEMs based on Moran's index of spatial autocorrelation (Moran 1948; Cliff and Ord 1973) was calculated for each sample date. Grouping MEMs to represent spatial structure at certain spatial scales, is an arbitrary process and depend on the significant variables retained by selection process (Spiesman and Cumming 2008). The MEMs generally were grouped to form three regional scale categories: broad (MEM1-MEM3), intermediate (MEM4-MEM8), and fine (MEM9-MEM11). Since our ponds showed an irregular distribution, it is not possible to equate a specific distance to the spatial scale of each MEM (Spiesman and Cumming 2008). However, the first MEM, which represents the broadest spatial scale, corresponds to the whole study area (5.65 km2) while the last retained MEM represents the fine spatial scale and is related to the distance between adjacent ponds.

To determine significance of environmental predictors in our final models, we performed forward selection based on Monte Carlo permutation tests (n= 999) (Blanchet et al. 2008). For spatial variables, forward selection could not be performed as the models became saturated once all the MEMs were included. Consequently, MEMs were divided into positive and negative correlation groups and selection was performed for each group separately (sensu Blanchet et al. 2008). Variables were retained at $\alpha=0.1$ or the stated adjusted R-square (whichever came first) and then used to form positive and negative spatial models for variation partitioning (Peres-Neto and Legendre 2010). To examine the relative contribution of environmental and MEM variables to the environmental and spatial elements of variation partitioning, the adjusted R-squared value of these variables given by forward selection and dbRDA biplots were used.

We also examined the relationship between time-averaged abundances of *N. undulata* and *N. irrorata* and the distance to the closest source population, distance to the largest source population, and the average distance among the source populations, for each year separately using Pearson correlations. The source population was defined as ponds which were colonized by the same species within the same year (McCauley et al. 2009).

All analyses were performed using R version 3.0 (< www.r-project.org >). The spatial predictors were produced using functions within the adespatial, ade4, adegraphics (Dray et al. 2016), spdep, and maptools (Bivand et al. 2017) packages. Forward selection was performed using the packfor package (Dray et al. 2013). Principal coordinates analyses, distance-based redundancy analysis (dbRDA) and variance partitioning were carried out using the vegan package (Oksanen et al. 2013).

Results

Spatial and temporal distribution of Notonecta species

In both years, the ponds were occupied mainly by *Notonecta undulata* and/or *Notonecta irrorata.* A third species, *Notonecta insulata* had a very low abundance (1 or 2 individuals) and was found in two ponds in two of the sampling dates. Thus, only the first two species were included in further analyses. Between these species, *N. undulata* was more abundant and wide-spread (being found in 10 out of 11 ponds in the first year and 10 out of 12 ponds in the second year) compared to *N. irrorata* which was found in 7 out of 11 focal ponds in the first year and in 7 out of 12 ponds in the second year (Table 3, Appendix B). Although the number of ponds occupied by both species remained relatively constant between the two growing seasons, the identity of ponds occupied by *N. irrorata* showed more inter-annual variation than *N. undulata* (Fig 1 and 2, Appendix B).

Spatial weighting matrices and MEMs

The results of the data-driven analysis showed that a combination of distance criterion (dnn) of the connectivity network and binary weighting function contributed to the best model for all sampling dates. Then the component of the best model (i.e., the model with the lowest AIC) was used to create to create ten MEMs for 11 ponds in 2014 and 11 MEMs for 12 ponds in 2015, for each sampling date separately. Moran's index of spatial autocorrelation analyses, revealed positive spatial autocorrelations for MEM1, MEM2, and MEM3 and negative spatial autocorrelations for the remaining MEMs. Thus, we divided MEMs into positive and negative sub-models and ran forward selection for each separately. All of the significant MEMs retained across sample dates showed negative spatial autocorrelation and represented the intermediate to fine spatial scales (Table 1).

Variation partitioning

Forward selection was performed for all sampling dates (from June to September) in both years (Table 1), but variation partitioning could not be performed for June, August and September 2015 since no environmental variables were retained by forward selection (Fig 2, Table 1). Notonectid community structure was influenced by both environmental and spatial variables for most sample dates (Fig 2, Table 1 and 2). The components in total explained 25.2% to 97.1% (average of 67.7%) of the variance in notonectid community composition (Fig 2, Table 2). The Pure Environmental (PE) component had a highly variable contribution and explained zero (June, August and September 2015) to 63.9% (July 2014) of the total variance in community composition (average of 18.72%) (Fig 2, Table 2). The contribution of the Pure Spatial (PS) component fluctuated between 0.8% (August 2014) and 46.6% (September 2015) (average of 26.31%) and was significant ($p < 0.1$) for all sampling periods except for July 2014. Finally, the Spatially Structured Environmental (SSE) fraction (i.e., joint effects of spatial and environmental variables) varied between zero (July 2014, June, August, and September 2015) and 58% (June 2014), (average of 18.67%). Forward selection was performed for all sampling dates (from June to September) in both years using juveniles' response of the two species. However, variation partitioning could not be performed for any of the sampling dates since both environmental or spatial variables were not retained by forward selection for any of the dates (Table 4, Appendix B). When empty samples (i.e. samples where neither species was detected) were removed and no constant was added to the zero values, less variation was explained by the components using variation partitioning. However, in the first year, variation in the notonectid community was related more to PE and SSE and in the second year this variation was explained more by PS and SSE (Fig 3 and Table 5, Appendix B). When relative abundance of notonectid species was used as response variables in variation partitioning analyses, PS and SSE showed a more dominant role in explaining the variation in notonectid community composition (Figure 4 and Table 6, Appendix B).

Table 1. List of environmental and spatial (MEMs) variables retained by forward selection. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl *a*= Chlorophyll *a*, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2. None: indicates that no variable was retained by forward selection. NA: not applicable.

Sampling date/variables	**Environmental variables**	**Spatial variables (MEMs)**	**Spatial scale of MEMs**	**Autocorrelation of MEMs**
June 2014	Cond, Temp, DO, biomass, zoop2	MEM10	fine	negative
July 2014	Cond, zoop2, zoop1	MEM10	fine	negative
August 2014	DO, Chl *a*, biomass	MEM10	fine	negative
September 2014	Temp	MEM4, MEM10	intermediate, fine	negative
June 2014	None	MEM4, MEM11	intermediate, fine	negative
July 2015	Cond, DO, pH, zoop1	MEM11, MEM10, MEM9, MEM7	intermediate, fine	negative
August 2015	None	MEM11, MEM7, MEM9	intermediate, fine	negative
September 2015	None	MEM11, MEM6, MEM9, MEM5	intermediate, fine	negative

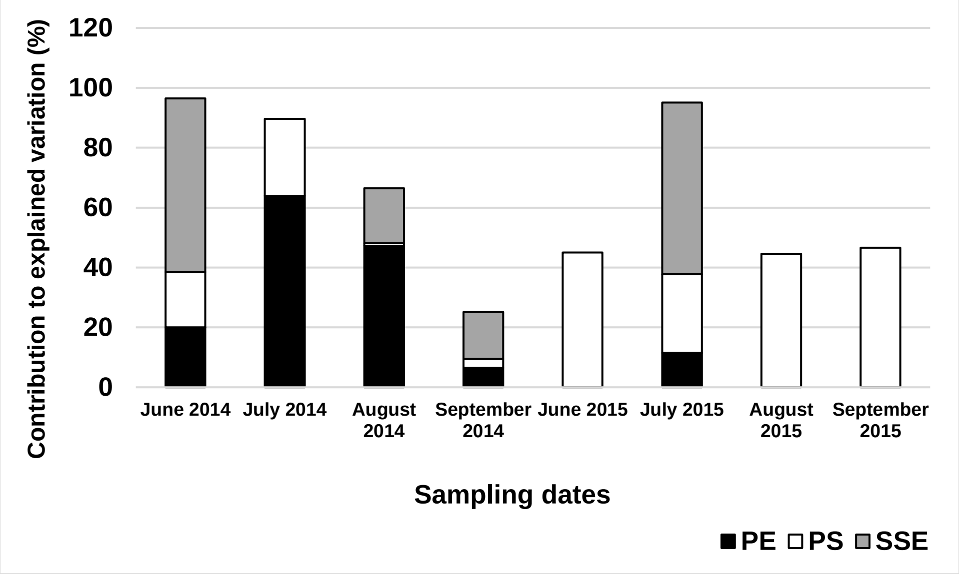


Figure 2. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), and spatially structured environmental (SSE) components to notonectid community structure for different sampling dates.

Table 2. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), spatially structured environmental (SSE) components, total (S+E) and unexplained variation (Residual), to notonectid community structure for all sampling dates.

	June 2014	***July 2014***	***August 2014***	***September 2014***	***June 2015***	***July 2015***	***August 2015***	***September 2015***
PE ***F***	20 64.29*	63.9 -112^{NS}	47.3 3.58*	6.5 3.9.	0	11.5 22.7**	0	0
PS ***F***	18.5 12.15*	25.7 -90^{NS}	0.8 0.23.	3 1.6.	45 3.36.	26.3 12.6**	44.6 2.5*	46.6 3.6*
SSE	58	0	18.4	15.7	0	57.3	0	0
Total ***F***	97.1 44.74*	89.6 -106.8^{NS}	66.5 2.74.	25.2 2.4^{NS}	45 3.36.	95 17.6**	44.6 2.5*	46.6 3.6*
Unexplained variation		14	33.5	74.6	55	42	55.4	53.4
Variables selected	MEM10 Cond Temp DO biomass zoop2	MEM10 Cond zoop2 zoop1	MEM10 DO Chl *a*, biomass	MEM4 MEM10 Temp	MEM4 MEM11	MEM11 MEM10 MEM9 MEM7 Cond DO pH zoop1	MEM1 MEM7 MEM9	MEM11 MEM6 MEM9 MEM5

*Notes: Percentage of variation explained (Fractions of adjusted explained variation (R2 Adj)), by the pure environmental component (PE), pure spatial component (PS), and spatially structured environmental (SSE) components and total variation explained (E+S) for each date are shown here. The significance of a fraction, after excluding other effects, is shown beside the fraction value. The empty cell represents the component which had a small negative value. Significance p values are '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1. NS, non-significant fraction. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl a= Chlorophyll a, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2.*

Drivers of notonectid metacommunity structure

Several environmental variables, both biotic and abiotic, contributed to the environmental component; adjusted R2 values ranged from 10.8 to 38% (Fig 3 A, Table 1, Appendix B). In June 2014, *N. undulata* abundance was positively correlated with temperature and dissolved oxygen and was negatively correlated with conductivity. Abundance of *N. irrorata* had an opposite relationship with these pond variables. Abundance of *N. undulata* showed a negative correlation and abundance *N. irrorata* showed a positive correlation with zooplankton total biomass and zooplankton PCoA axes 1 which is mainly driven by relative abundance of *Daphnia pulex* itself. In July 2014, abundance of *N. undulata* was negatively related to water conductivity and was positively related to zooplankton PCoA axes 1 and 2 which were driven by relative abundance of *D. pulex* and negatively related to the relative abundance of cyclopoids. However, abundance of *N. irrorata* was positively related to water conductivity and negatively related to zooplankton PCoA axes 1 and 2. Thus, the abundance of *N. irrorata* was positively related to relative abundance of cyclopoids, and negatively related to *D. pulex* relative abundance. In August 2014, *N. undulata* abundance was positively correlated with dissolved oxygen and negatively related to pond chlorophyll *a* and total zooplankton biomass. Abundance of *N. irrorata* showed the opposite correlation with these environmental variables. In September 2014, abundance of *N. undulata* was positively and *N. irrorata* was negatively correlated with water temperature. In June, August, and September 2015 no significant environmental variables were detected. However, in July 2015, abundance of *N. undulata* was positively correlated with dissolved oxygen and pH and was negatively correlated with water conductivity and zooplankton PCoA axes 1 which is driven by relative abundance of D.

pulex. *N. irrorata* abundance showed an opposite correlation with these variables (Fig 3 A, Fig 4).

The contribution of spatial variables (MEMs) to the spatial component ranged from 8 to 49.3% (Fig 3 B, Table 1, Appendix B). Like the environmental variables, the identity and contribution of spatial variables (MEMs) varied among sampling dates. In June, July, and August 2014, MEM10 was positively correlated with abundance of *N. undulata* and negatively correlated with abundance of *N. irrorata*. In September 2014, abundance of *N. undulata* was positively correlated with MEM10 and was negatively correlated with MEM4 while abundance of *N. irrorata* showed opposite correlation with these spatial variables. In June 2015, abundance of *N. undulata* was positively correlated with MEM11 and was negatively correlated with MEM4 while abundance of *N. irrorata* showed opposite correlation with these spatial variables. In July 2015, abundance of *N. undulata* was positively correlated with MEM7, MEM9, MEM10, and MEM11, and *N. irrorata* abundance was positively correlated with MEM7 and MEM10 and negatively correlated with MEM9 and MEM11. In August 2015, *N. undulata* was positively correlated with MEM7, MEM9, and MEM11 while abundance of *N. irrorata* was positively correlated with MEM7 and negatively correlated with MEM9 and MEM11. In September 2015, *N. undulata* abundance showed a positive relationship with MEM9 and MEM 11 and negative relationship with MEM 5 and MEM6 while *N. irrorata* showed the opposite correlation with the spatial variables (Fig 3 B, Fig 4).

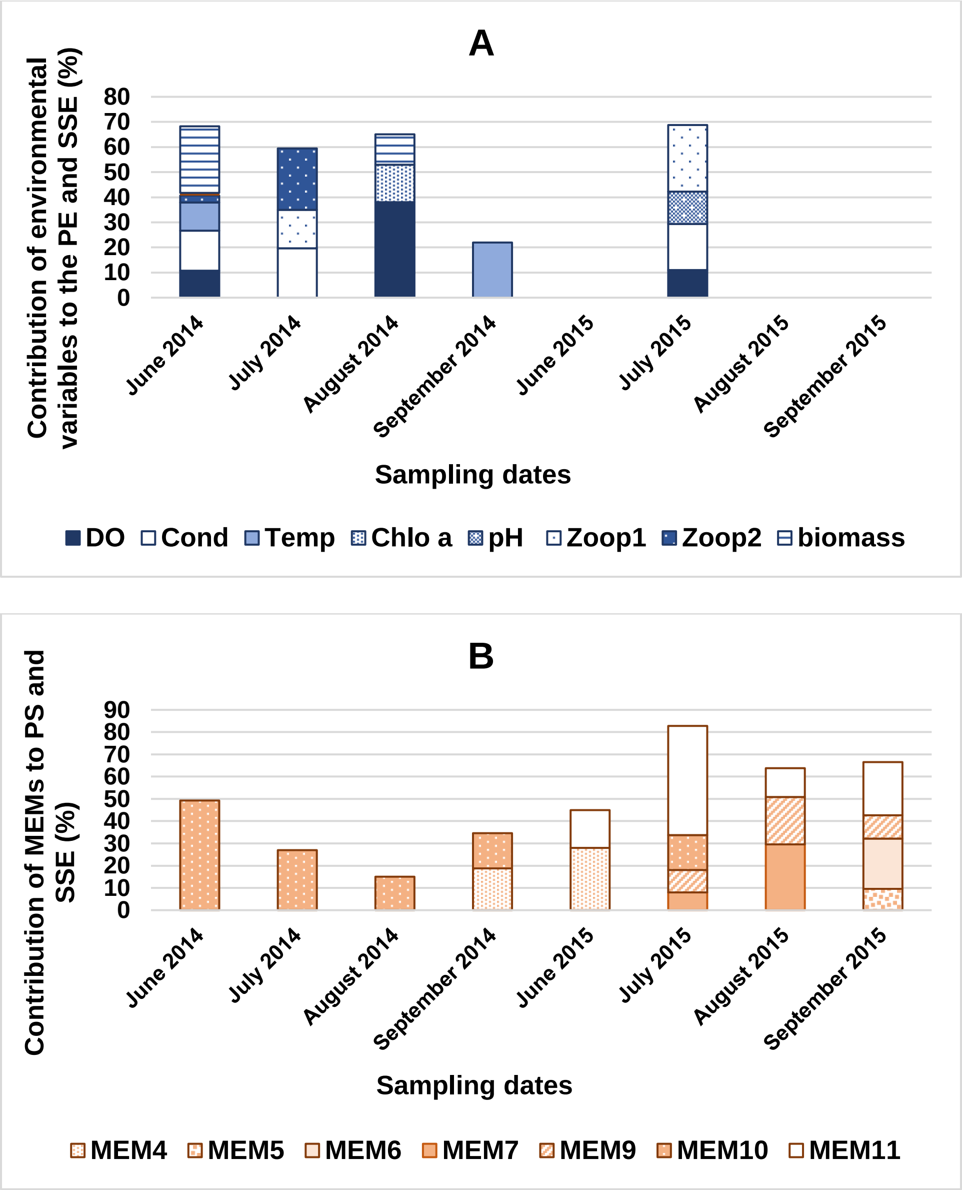
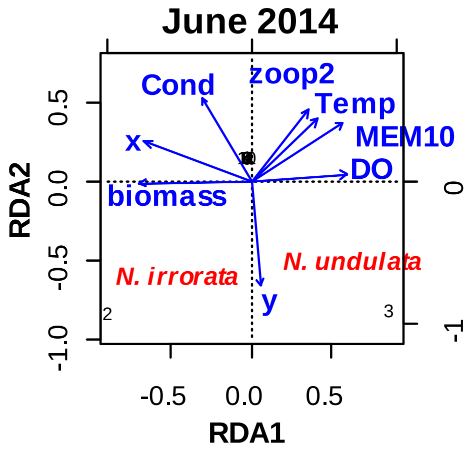
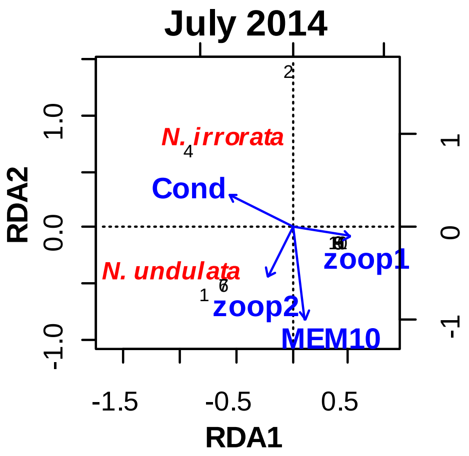
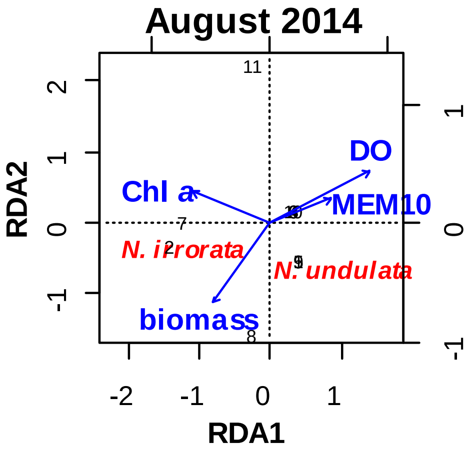
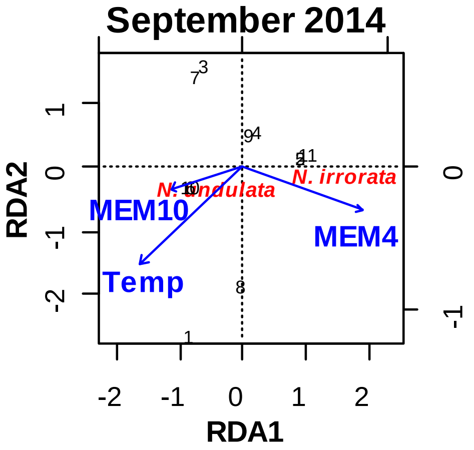


Figure 3. The contribution to adjusted R^2 by each environmental (A) and spatial (B) variable to PE, PS, and SSE components. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl *a*= Chlorophyll a, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2. MEM4-MEM7 represent intermediate and MEM9-MEM11 represent the fine spatial scale.


June 2014
Cond
zoop2
Temp
MEM10
x
DO
biomass
N. irrorata
N. undulata
y
2
3
RDA2
RDA1
-1.0
-0.5
0.0
0.5
-0.5
0.0
0.5
0
-1


July 2014
2
N. irrorata
4
Cond
N. undulata
zoop1
1
6
zoop2
MEM10
RDA2
RDA1
-1.0
0.0
1.0
-1.5
-0.5
0.5
1
0
-1


August 2014
11
DO
Chl a
MEM10
7
N. irrorata
2
N. undulata
9
biomass
8
RDA2
RDA1
-1
0
1
2
-2
-1
0
1
1
0
-1


September 2014
7
3
9
4
11
N. irrorata
N. undulata
MEM10
MEM4
Temp
8
1
RDA2
RDA1
-2
-1
0
1
-2
-1
0
1
2
0
-1

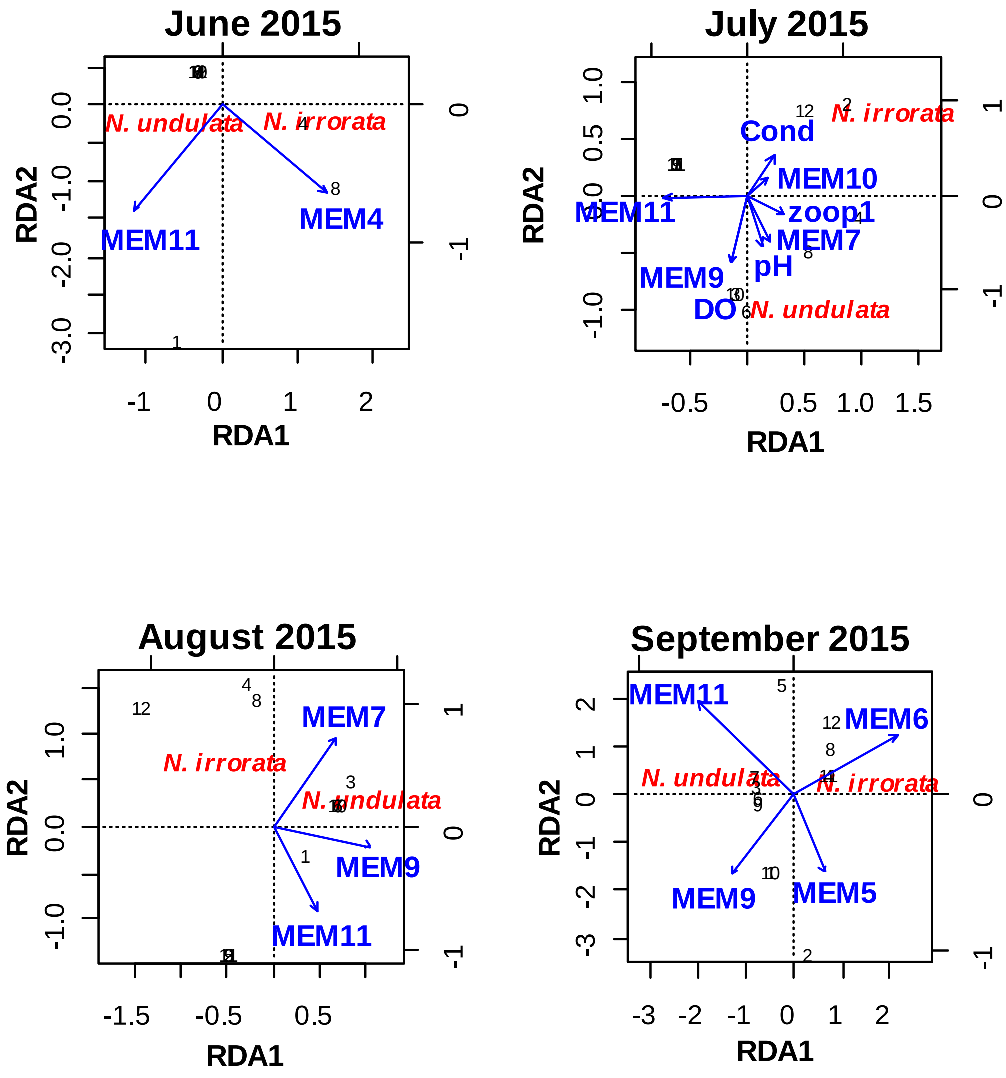


Figure 4. Canonical ordination (dbRDA) of notonectid abundance and environmental and spatial variables for different sampling dates. Response variables (shown by red text), were square root transformed abundance of *N. undulata* and *N. irrorata*. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl a= Chlorophyll a, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2. Spatial explanatory spatial variables were MEM4, MEM5, MEM6, MEM7, MEM9, MEM10, and MEM11. Shown are correlations between variables and each dbRDA axis.

Analyses of time-averaged notonectid composition showed 51.9% of variation was explained by environmental (24.8%), and spatially structured environmental processes (27.1%) in 2014. In 2015, 78.9% of variation in notonectid community was explained by spatial (45.3%), environmental (1.4%), and the spatially structured environmental processes (32.2%) (Fig 5, Table 3). In the first growing season, water temperature, pond chlorophyll *a*, and zooplankton PCoA axis 1 and in the second growing season, water temperature and dissolved oxygen were significant environmental variables. In the first year, abundance of *N. undulata* correlated positively with temperature and correlated negatively with chlorophyll a and relative abundance of *D. pulex* while *N. irrorata* abundance showed an opposite correlation with these pond variables. In the second year, abundance of *N. undulata* correlated positively with temperature and dissolved oxygen while abundance of *N. irrorata* was negatively correlated with these variables. In the first year, only MEM10 was significant (Table 3), with *N. undulata* exhibiting a positive correlation with MEM10 and *N. irrorata* showing a negative correlation with MEM10. In 2015, MEM5, MEM6, MEM7, MEM9 and MEM11 were significant (Table 3) with *N. undulata* showing positive correlations with MEM7, 9 and 11 and a negative correlation with MEM4, 5, 6. *N. irrorata* showed a positive correlation with MEM4, 5, 6 and negative correlation with MEM7, 9, and 11 in 2015.

Table 3. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), spatially structured environmental (SSE) components, total (S+E) and unexplained variation (Residual), to notonectid community structure averaged over the sampling dates for each growing season. The response variable was square root transformed abundance of notonectid species.

	2014	**2015**
PE	24.8	1.4
F	3.9.	19.36**
PS	0	45.3
F	0.31	5.84*
SSE	27.1	32.2
Total	51.9	78.9
F	3.06.	9.22*
Unexplained variation	53.4	21
Variables selected	MEM10 Temp Zoop1 Chl *a*	MEM4 MEM5 MEM6 MEM7 MEM9 MEM11 Temp DO

*Notes: Percentage of variation explained (Fractions of adjusted explained variation (R2 Adj)), by the pure environmental component (PE), pure spatial component (PS), and spatially structured environmental components (SSE) and total variation explained (E+S) for each date are shown here. The significance of a fraction, after excluding other effects, is shown beside the fraction value. DO= dissolved oxygen, Temp= Temperature, Chl a= Chlorophyll a, zoop1= zooplankton PCoA axis 1. Significance p values are '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1. NS, non-significant fraction.*

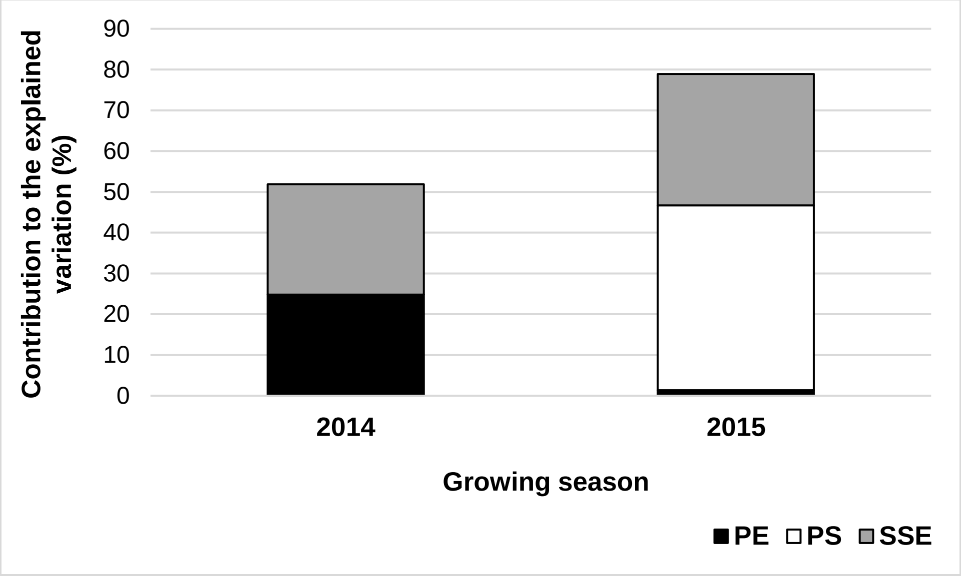


Figure 5. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), and spatially structured environmental (SSE) components to notonectid community structure averaged over the sampling dates for the first and second growing season.

When we examined the relationship between abundance of each notonectid species and pond isolation indices, a significant positive correlation was found between the distance to the largest source population and density of *N. undulata* in the first year (r=0.7, p=0.04, Pearson correlation) and the second year (r=0.6, p=0.05, Pearson correlation). Abundance of *N. irrorata* showed a positive significant correlation with the distance to the largest source population in the first year (r=0.8, p=0.01, Pearson correlation) and no relationship in the second year (r=0.58, p=0.1, Pearson correlation) (Fig 6). No significant correlations were found between abundance of each species and average distance among source ponds or distance to the closest source pond (Fig 5 Appendix B, r<0.4, p>0.1, Pearson correlation).

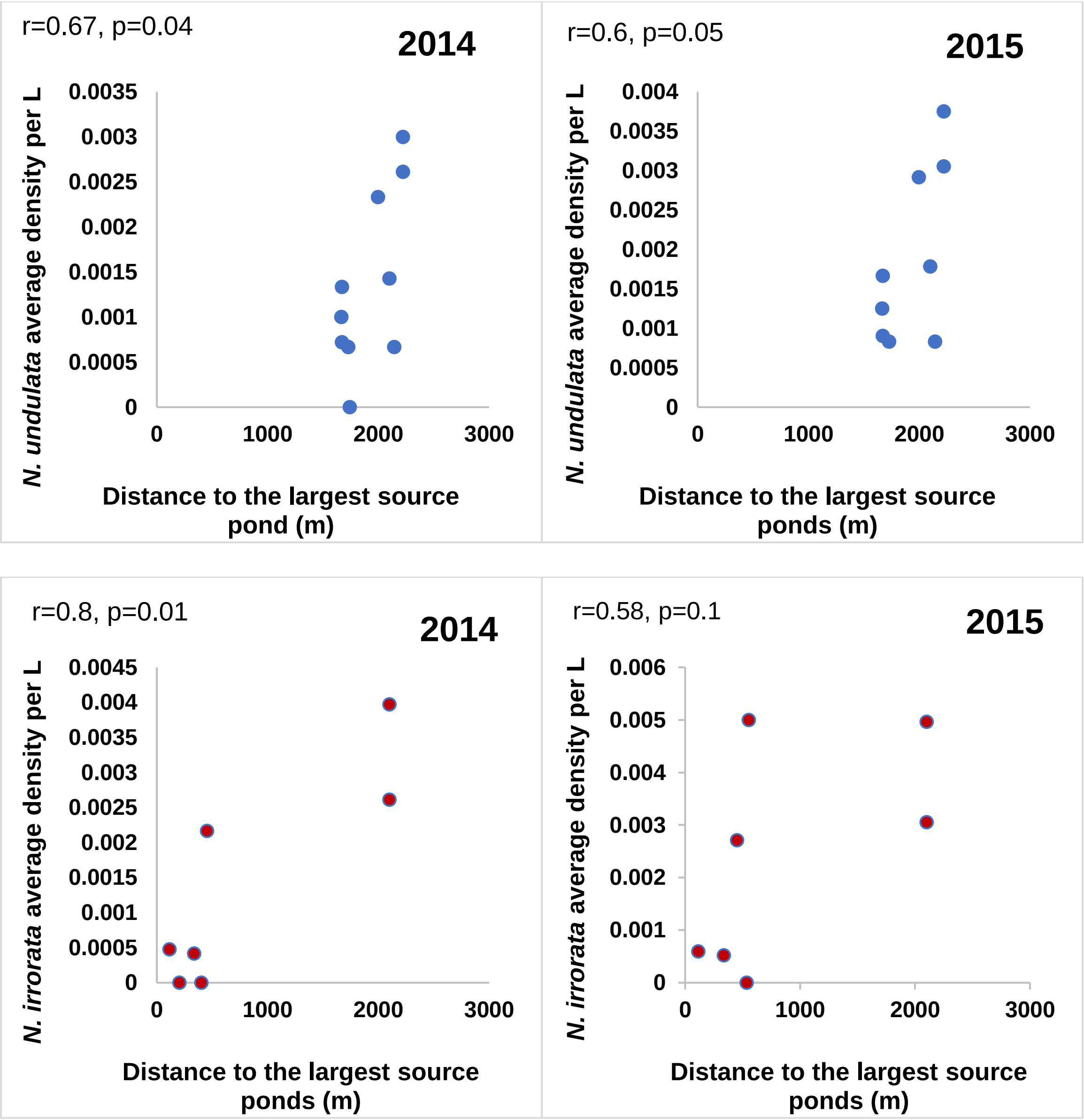


Figure 6. Relationship between the time-averaged abundance of adult notonectid species and distance to the largest source population for the first study year (2014) and second year (2015).

Discussion

Variation partitioning

We used variation partitioning to study the processes affecting the structure of notonectid communities. Our results show that pure environmental (PE), pure spatial (PS), and spatially structured environmental (SSE) components all contribute to spatiotemporal variation in notonectid communities among fishless ponds. The PS fraction is the pure spatial component which may be related to dispersal processes or dispersal limitation (De Bie 2012; Fernandes et al. 2013). The PE component signifies the effects of pond environmental variables that are not spatially structured. The last component, SSE, is the effect of spatially structured environmental variables in which spatial and environmental effects cannot be separated due to spatial covariation between the two. SSE may arise if increasing spatial scale encompasses greater variation in environmental conditions and is thus not inconsistent with species sorting if found significant. The presence of significant pure environmental effects and spatially structured environmental effects in our study supports the role of species-sorting and indicates that the organization of our notonectid communities is not dependent on neutral processes. However, environmental factors alone could not fully account for variation among communities; the presence of pure spatial effects also indicates that dispersal processes and/or dispersal limitation plays a role in structuring notonectid assemblages.

While we found significant contributions of both environmental and spatial components, there was considerable temporal variation in the magnitude and relative importance of these effects both within and between years. We predicted that spatial effects would dominate early in the growing season when notonectids are known to exhibit mass dispersal, and environmental effects would increase in importance later in the season. Results from the first year of our study somewhat supported our general predictions. In the beginning of the growing season (June), the spatially structured environmental component was dominant. In July and August, the contribution of environmental component was dominant. In September, an overall low amount of variation was explained which was mainly related to SSE. In the second year, a clear temporal trend of increasing environmental effects was not observed. In June, July, and August a low total amount of variation in notonectid community variation was explained by the pure spatial component while PE and SSE had minor contributions only in one month (July). The lack of strong environment effects in year two of our study is unknown; means and ranges of environmental variables did not differ greatly between years except for dissolve oxygen (Table 1 A, B and 2 Appendix B). This result highlights the importance of obtaining time-series and accounting for temporal variation when attempting to elucidate the drivers of community structure.

Drivers of spatial and environmental components

Multiple environmental and spatial variables contributed to the PS, PE, and SSE components while the indentity of these variables differed among the sampling dates. A varying combination of abiotic and biotic variables contributed to variation in notonectid community structure during the two growing seasons. During the first growing season, a trend was observed in the relative importance of abiotic and biotic environmental variables. Late season patterns were associated with pond abiotic variables (temperature) while a combination of abiotic and biotic factors (prey composition) were detected mid-season. In the second year, community composition was weakly associated with environmental predictors. When present, a combination of pond abiotic (dissolved oxygen, conductivity, pH) and biotic variables were related to notonectid composition.

In the first growing season, spatial components were driven by variables representing fine (MEM10) and/or intermediate (MEM4) spatial scales. Moreover, fine spatial processes were more influential in the beginning and mid growing season (June, July, August) while intermediate-scale spatial variables became more important later in the season (September). Similarly, during the second growing season, spatial processes representing the fine (MEM9, MEM10, MEM11) and/or intermediate (MEM4, MEM5, MEM6, MEM7) spatial scales were associated with variation in notonectid composition. The absence of compositional variation at broad spatial scales was not consistent with our general predictions; we predicted increasing compositional dissimilarity with increasing scale due to the effects of dispersal limitation, stochastic dispersal history and reduced connectivity. It is possible that our study did not encompass an adequate spatial area for such effects to emerge. However, the maximum distance between our ponds (2.2 km) exceeded the known maximum dispersal distance of notonectids (1.6 km; Briers and Warren) and the mean distance between our ponds (900 m) exceeded distances at which most notonectid dispersal events occur (400-600 m; McCauley et al. 2009).

Although patterns of community variation were not detected at large spatial scales, fine to intermediate scale variation was prevalent. The presence of compositional variation at small spatial scales (e.g. among neighboring ponds) is consistent with some metacommunity model predictions (e.g. patch-dynamic and species sorting processes) and further suggests that strong mass effects were not occurring in our system. However, the fine and intermediate spatial variables detected in our analyses showed negative spatial autocorrelation. Hence, ponds that were closer to each other were more dissimilar in community composition when compared to ponds that were further apart. This pattern is not predicted by any of the general metacommunity models described above. Such patterns are generally thought to result from antagonistic biotic interactions such as competition, territorial behaviors or the presence of predators and pathogens (Hamilton and May 1977; Perrin & Mazalov 1999; Binckley & Resetarits 2005; Resetarits & Binckley 2009). They may also result from dispersal behaviors and active habitat selection to avoid low quality habitats - a process that has been observed in aquatic invertebrate taxa (Binckley and Resetarits 2005; Blaustein et al. 2005, McCauley et al. 2009). There are few studies of notonectid dispersal behavior and habitat choice. An experimental study of *N. irrorata* dispersal and colonization found a unimodal pattern of colonization versus distance to nearest source pond (i.e., a hump-shaped dispersal kernel), with the highest levels of colonization occurring at intermediate distances of 400-500m (McCauley et al. 2009). Thus, notonectids actively avoided neighboring habitats in favor of more distant ones - a possible adaptation by adults to avoid inbreeding, intraspecific competition or interspecific interactions (Cooper 1983; Giller 1986). Such behaviors may explain the presence of negative spatial autocorrelations in our study and the emergence of structural variation at small spatial scales.

Conclusions

Our findings complement previous studies (e.g., Cottenie 2005; Capers et al. 2009; Erös et al. 2012; Henry and Cumming 2016; Vanschoenwinkel et al. 2010; Fernandes et al. 2013) by showing that a combination of environmental and spatial processes influence the structure of metacommunities. Thus, inclusion of both spatial and environmental variables is necessary for understanding the factors affecting community organization. Moreover, our results confirm the presence of seasonal and inter-annual variation in the relative contribution of environmental and spatial processes on metacommunities. Only a handful of studies have used variation partitioning to examine temporal variation in the relative importance of environmental and spatial processes on communities (Erös et al.

2012; Fernandes et al. 2013; Padial et al. 2014; Henry and Cumming 2016). These, along with ours, make clear the importance of examining time-series to obtain a more comprehensive understanding of the processes affecting community structure. Depending on the month or year on which one focused, very different pictures of spatial-environmental effects would have emerged in our study system had one used a snapshot approach.

Finally, our work makes clear that dispersal processes, including dispersal behavior, may be vital for comprehending the structure of metacommunities. Many of the spatial patterns we observed were not easily explained by general metacommunity models - most notably the significance of small-scale spatial variation combined with negative spatial autocorrelation in community composition. While further work is required to elucidate the drivers of these patterns in our system, they are consistent with known notonectid dispersal behavior and dispersal kernels. Hence, our work joins a growing body of studies (e.g. Resetarits 2005; Vonesh et al. 2009; Resetarits and Silberbush 2016) that suggests that dispersal behavior and habitat selection may be vital ingredients for understanding community assembly and spatial variation in community structure.

CHAPTER 4 PROCESSES DRIVING THE DISTRIBUTION OF *NOTONECTA* SPECIES AMONG FISHLESS PONDS: AN EXPERIMENTAL TEST OF LOCAL VERSUS REGIONAL EFFECTS

Introduction

Understanding the processes that influence the distribution of species is a central focus of community ecology. Historically, ecology, as a discipline, has focused on the role of local (within site) processes such as biotic interactions and abiotic environmental conditions within relatively small spatial domains. With the development of metapopulation (Hanski and Gilpin 1997, Hanski 1999) and metacommunity ecology (Leibold et al. 2004, Holyoak et al. 2005b), increasing emphasis has been placed on regional (between site) processes, including the role of dispersal and dispersal limitation (Mouquet and Loreau 2003; Ricklefs 2004; Thompson and Townsend 2006). Several studies have revealed mutual effects of local and regional processes on species distributions (Cottenie and Meester 2004; Cottenie 2005; Heino et al. 2015). However, direct experimental tests of spatial processes, such as dispersal limitation, are surprisingly rare.

In theory, dispersal rate can influence the strength and outcome of local environmental processes, including biotic interactions. For example, when of sufficient magnitude and in the absence of dispersal limitation, dispersal can facilitate species-sorting, in which local community composition is a product of local processes (Van der Gucht et al. 2007; Vanschoenwinkel 2008). Historically, abiotic conditions and species interactions have been considered to be important elements of local drivers of community assembly (Andrewartha and birch 1954; Ricklefts 1987; Hunter and Price 1992). However, a growing body of research highlights the importance of habitat choice (i.e. behavioral responses to local habitat quality) as a driver of assembly and metacommunity structure (Resetarits and Wilbur 1989; Resetarits 2005; Pollard et al. 2017). When dispersal rates are extremely high, "mass effects" may result, reducing the influence of local conditions and altering the outcome of species interactions (Holt 1985b; Danielson 1991; Souffreau et al. 2014). Thus, regional (spatial) processes can become the dominant factor determining community composition. On the other hand, a lack of adequate amounts of dispersal can result in dispersal limitation for some taxa, increasing the relative importance of regional effects. When combined with stochastic population extinction, dispersal limitation may increase compositional variation among local communities. It is also conceivable that dispersal limitation may increase the prevalence of stochastic variation in colonization history among patches, potentially increasing compositional variation among patches via priority effects (Hebert 1974; Palmer et al. 1996).

A considerable number of observational studies have addressed the relative contribution of local and regional processes to community structure (Chase 2003; Cottenie et al. 2003; Cottenie 2005; Jeffries 2005; Beisner et al. 2006; Vanormelingen et al. 2008; McCauley et al. 2008; De Bie et al. 2012; Padial et al. 2014). Most of these have shown that both local and regional processes impact communities (Chase 2003; Cottenie and Meester 2004; McCauley et al. 2008). However, few studies have utilized experimental species introductions in natural habitats to directly test whether dispersal limitation influences local community assembly. This approach has been used to examine the relative importance of local and regional factors on community structure of several taxa including grassland plants (Tilman 1997), and zooplankton (Shurin 2000; Cottenie and Meester 2004). Some of these studies found a mutual effect of local and regional processes on community structure (Tilman 1997; Cottenie and Meester 2004), while Shurin (2000) found an insignificant role of dispersal limitation compared to biotic interactions on community organization of zooplankton (Shurin 2000).

Here, we present results of an in situ, introduction experiment in which we investigated the effects of local environmental conditions versus dispersal limitation on the distribution of *Notonecta* species in fishless ponds. *Notonecta*, or backswimming bugs, are flying aquatic insects, capable of active dispersal among water bodies. Our prior surveys of fishless ponds in southern Michigan showed that systems are primarily dominated by two competing species, *Notonecta undulata* and *Notonecta irrorata*, but distributions and patterns of co-occurrence of these species are highly heterogeneous. While some ponds contain only one of the two species, others contain both. What drives this variation is unknown. To test whether dispersal limitation or pond environmental conditions explain the absence of notonectid species from some systems, we selected six ponds that differed naturally in their occupancy (three ponds with only *N. undulata*, two with only *N.irrorata*, and one occupied by both species). Using in situ mesocosms, adults and juveniles of the two species were introduced to the ponds and performance and adult emigration were assessed. If dispersal limitation is the primary driver of notonectid species occurrence, we expect to see adults and juveniles of a given species perform well when introduced to ponds in which they are naturally absent compared to ponds in which they are present. Alternatively, if pond environmental conditions determine species composition, we expect adults and juveniles of a given species to show reduced performance in ponds in which they are naturally absent compared to ponds in which they are naturally present. We also predict that adult emigration rates will be higher in ponds in which they are naturally absent compared to ponds in which they are present.

Materials and Methods

Study species

Notonecta species (Notonectidae: Hemiptera) are common, widespread macroinvertebrates in lentic waters across North America (e.g., Clark 1928; Blaustein 1998; Chordas et al. 2005). These planktivorous insects have an incomplete life cycle with five juvenile stages (instar I-V) spent in a single waterbody and a flight capable adult stage in which dispersal among systems may occur. Our study focused on two species, *Notonecta undulata* and *Notonecta irrorata*, as our prior surveys showed that these two species numerically dominate fishless ponds in our study area.

Study sites

The study sites were fishless ponds located within the Michigan State University, Kellogg Biological Station (KBS), Lux Arbor Reserve, (Hickory Corners, Michigan, USA) (Fig1). Our prior surveys found that *N. undulata* and *N. irrorata* have heterogeneous distributions among ponds within the study area; some ponds are occupied by one of the two species while in other ponds both species co-occur. We selected six fishless ponds (Lux 1, Lux 2, Lux 3, Lux 10, Lux 12, Lux 16) that varied in their relative abundances of the two notonectid species (Fig 2). Lux 1, Lux 3 and Lux 10 were occupied only by *N. undulata*, Lux 2 with *N. irrorata*, and Lux 12 and Lux 16 with both species (Fig 2). The selected ponds were variable in terms of water chemistry, size, area, depth, canopy cover, and biodiversity. All selected ponds were permanent and contained water year-round.

Figure 1. Map of the study area, the location of the fishless ponds surveyed (circle) and fishless ponds selected for this experiment (filled circle) in Lux Reserve Arbor, Michigan, USA.

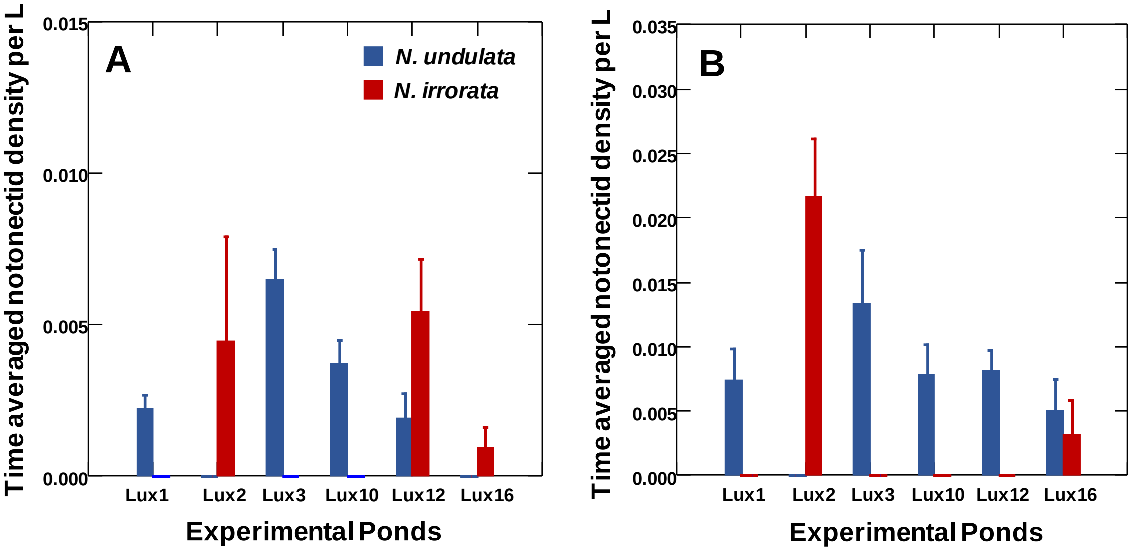


Figure 2. The density of *N. undulata* and *N. irrorata* (adults and juveniles) across the experimental ponds during (A) the 2015 growing season and (B) the 2016 growing season (the year of the experiment). Values are averaged across months (mean±SE).

Experimental set up

We performed four in situ mesocosm experiments during the summer of 2016: an adult growth experiment, an adult survival experiment, an adult dispersal experiment (to examine short-term emigration responses) and a juvenile growth/survival experiment. Each treatment was replicated four times. For the adult experiments, enclosures consisted of open-top, 60-L plastic containers. The sides of the enclosures had four 10x10 cm openings covered with nylon mesh (5-mm mesh size) to allow exchange of water with the surrounding pond environment. This mesh size is small enough to keep the introduced notonectid individuals within the enclosures and large enough to allow prey such as zooplankton and small macroinvertebrates to enter. For the adult growth and survival experiments, enclosure tops were covered with fiberglass mesh (1-mm mesh size) to prevent immigration/emigration of notonectids. Enclosures were left uncovered for the adult dispersal experiment. For the juvenile experiment, enclosures consisted of 4-L plastic containers with their tops covered by 1-mm mesh. Enclosures for all experiments were anchored to the pond bottom and suspended in the water column using floats to keep their tops above the water surface. Prior to the start of the experiments, adult and juvenile *N. undulata* and *N. irrorata* were collected from surrounding fishless ponds and maintained in outdoor 1000-L mesocosms at the KBS pond lab facility. Cultures were maintained at low densities, and fed non-limiting concentrations of pond zooplankton supplemented with lab-reared *Daphnia pulex*. For all the experiments, responses of *N. undulata* and *N. irrorata* were assessed in monoculture, simultaneously in each study pond. For the adult growth, survival and dispersal experiments, we introduced six adults of either *N. undulata* or *N. irrorata* to every enclosure. For the juvenile growth/survival experiment, each enclosure received two size-matched, third instar juveniles of the same species (average length 4.5 mm for *N. undualta* and 5 mm for *N. irrorata*). The results of prior surveys showed that mean natural adult densities were 0.001 per L for *N. undulata* (range: 0.0008 – 0.008 per L) and 0.0009 per L for adult *N. irrorata* (range: 0.0008 – 0.01 per L). Mean natural densities of juveniles were 0.0008 per L for *N. undulata* (range: 0.0008 – 0.007 per L) and 0.0006 per L for *N. irrorata* (range: 0.0008 – 0.005 per L). Thus, experimental densities created conditions with elevated adult and juvenile intraspecific competition.

The adult survival experiment started on July 5th and ended after one week (July 13th). The adult dispersal experiment started on July 5th and was terminated after three days (July 8th). For the dispersal experiment, each adult was color-coded on their hemelytra (forewings) using waterproof markers before being introduced to account for potential movement of individuals among the open enclosures. The adult growth experiment started on July 15th and ended after ten days (July 25th). For the growth experiment, all adults were weighed on the first day of the experiment before being introduced to the enclosures. The juvenile growth experiment was started on June 7th and ended on July 14th (37 days). Since all juveniles from our stock cultures were in the third larval stage and roughly the same size, 10 individuals of each species were randomly selected, and their length measured prior to the start of the experiment for calculation of average initial length. To promote turnover of water and food, enclosures for all of the experiments were raised and immersed in the water column every other day. Enclosures for the juvenile experiment had a smaller mesh size (to retain juveniles in the containers) that may have excluded some zooplankton prey. To counter this, we supplemented each enclosure with zooplankton collected from the study pond in a volume equal to the enclosure volumes. Enclosures were inspected for dead individuals every other day for the adult experiments and once weekly for the juvenile experiment. Dead individuals were removed when found and preserved in 70% ethanol.

Pond abiotic and biotic variables

On July 20th, pond abiotic and biotic variables were measured to examine the relationship between notonectid experimental responses and pond environmental conditions. Macroinvertebrates including *Notonecta* species were sampled at equal intervals along a randomly-placed transect from pond edge to the center using a 30 x 50 cm D-net with 1 mm mesh size. All collected macroinvertebrates were returned to their source pond after identification and enumeration in the field.

Zooplankton were sampled by collecting pond water using a 2-liter pitcher and filtering it through an 80-µm sieve. The total volume sampled varied between 10 to 40 liters for each pond depending on the area and depth of the water body. The samples were collected at equal intervals along multiple transects. Zooplankton samples were preserved in 10% acid Lugol's solution for laboratory identification (to the genus level) and enumeration. Total zooplankton biomass was calculated by multiplying the density of each taxon by a taxon-specific biomass conversion constant (which is average dry weight for that taxon) and then summing across all taxa for each pond.

Water temperature, pH, dissolved oxygen, and conductivity were measured using a portable YSI meter. Measurements were recorded at equal intervals of each transect by holding the probe 10 cm below the water surface and averaged for statistical analyses. In mid-June, these measures were also performed within the experimental enclosures to monitor for differences between ambient and enclosure environments. A 500-ml water sample was also collected from the center of each pond to measure total phosphorus (TP) and chlorophyll *a*, as correlates of pond productivity. To measure chlorophyll a, 50 ml of the collected water was filtered onto Whatman GF/B filters, extracted in 95% ethanol and measured using narrow band fluorometry (Welschmeyer 1994). To quantify TP, 50 ml of the collected water was frozen for later analysis using the ammonium molybdate method and persulfate digestion (Wetzel and Likens 1991).

Statistical Analyses

Primary response variables of interest were correlates of habitat suitability (survival, growth and emigration). For the adult survival experiment, we measured survivorship as the number of individuals found alive at the end of the experiment. For the adult growth experiment, we quantified somatic growth rate of every individual alive at the end of the experiment within each enclosure as growth rate = (ln (final weight of each individual/average initial weight of all individuals)/10 days). Growth rates were then averaged across individuals to obtain a single rate per enclosure. From the adult dispersal experiment, we measured emigration by subtracting the number of individuals found at the end of the experiment from the initial number (minus mortality). Inspection of the color marks on the hemelytra showed no evidence of adult movement between enclosures of the dispersal experiment. Notonectid mortality in the dispersal experiment was low, and one to two individuals were found dead in only six enclosures. For the juvenile growth/survival experiment, we observed high rates of mortality by the end of the experiment. We measured survivorship as persistence (the maximum number of days that juveniles survived within each enclosure). We also measured somatic growth rate of every juvenile at the time of death or the end of instar V within each enclosure as growth rate = (ln (final length of each individual/average initial length of individuals)/37 days). Growth rates were then averaged across individuals to obtain a single rate per enclosure. Individuals that died within the first week were not included in the analyses.

We tested the effects of pond identity, species identity and their interaction on survival and dispersal of adults using GLM with Poisson errors or quasi Poisson errors in cases where overdispersion was detected (Crawley 2005). Four enclosures for the adult survival experiment were damaged and not included in the following analyses. To examine the effects of pond identity, species identity and their interactive effect on adult growth rates, we used GLM with Gaussian errors. Because adult mortality was observed in some enclosures, we included the number alive at the end of the experiment as a continuous covariate in our models. All replicates from Lux 12 and some replicates from other ponds were damaged in the adult growth experiment and not included in the following analyses. The effects of pond, species identity and their interaction on juvenile persistence (number of days) and growth rate were tested using GLM with Gaussian errors. Assumptions of normality and homogeneity of errors for the GLM with Gaussian errors analyses were tested using Shapiro – Wilk 's test, Levene's test and visual inspection of plots of residuals. Non-parametric Kruskal-Wallis tests were used and compared to the parametric tests whenever assumptions of normality were violated. Since some replicates were lost, we used type III sums of squares due to unequal replication.

To gain insight into potential environmental drivers of our experimental responses, we explored relationships between notonectid response variables and pond abiotic and biotic conditions at the time of the experiment using partial least squares regression (PLSR) (Carrascal et al. 2009). Notonectid response variables were averaged across replicates for the analyses and analyzed for each species separately. Predictor variables included pH, temperature, dissolved oxygen, conductivity, TP, chlorophyll *a*, and zooplankton total biomass, which were all log-transformed to improve normality and reduce heteroscedasticity except for pH. To reduce the number of zooplankton and macroinvertebrate taxa included in the environmental matrix, two separate principal coordinates analyses (PCoA, Gower, 1966) were performed using Bray-Curtis dissimilarity based on the relative abundances of taxa (results can be found in Table 1, Appendix C). The first two axes produced by each PCoA, which captured greater than 50% of the variation in the input data, were included as predictors. We used Pearson and Spearman correlation to examine the relationship between experimental responses and natural pond densities of the two notonectid species at the time of the experiment. All analyses were performed in R ver. 3.0 (< www.r-project.org >).

RESULT

Adult Experiments

We found no significant differences in pond abiotic conditions (pH, oxygen, temperature, and conductivity) when comparing measures inside the experimental enclosures and in the surrounding pond environment (Fig. 1, Appendix C). Survival of notonectid adults was fairly high (mean = 85% for both species, Fig 3A) and comparable for the two species. We found no significant effects of pond identity (X^2 (5, N = 36) = 0.8, p >0.1, GLM Poisson errors), species identity (X^2 (1, N = 35) = 0.89, p >0.1, GLM Poisson errors) or their interaction (X^2 (5, N = 30) = 1.07, p >0.1, GLM Poisson errors), on adult survivorship (Fig 3 A and B).

Emigration of adults was low (average 11% for *N. undulata* and 9% *N. irrorata*) and comparable between the two species. *N. undulata* showed dispersal from enclosures located in all experimental ponds except for Lux 10. *N. irrorata* dispersed from all ponds except for Lux 2. There was a significant effect of pond identity on dispersal ($F_{5,42}$=2.8, p=0.03, GLM quasi Poisson errors). However, there was no significant effect of species identity ($F_{1,41}$=0.5, p=0.47, GLM quasi Poisson errors) and no interactive effect ($F_{5,36}$=1.08, p=0.38, GLM quasi Poisson errors) on notonectid dispersal (Fig 3 C and D).

Across experimental ponds, *N. undulata* had a higher average adult growth rate (0.019±0.017, mean±SD) compared to *N. irrorata* (0.005±0.009); there was a significant effect of species identity on growth ($F_{1,31}$=7.9, p=0.008, GLM Gaussian errors). We found no significant effects of pond identity ($F_{4,13}$=0.007, p>0.1, GLM Gaussian errors), number alive at the end of the experiment ($F_{1,13}$=0.012, p>0.1, GLM Gaussian errors) or interactive effect (p>0.5, GLM Gaussian errors), on adult growth. However, assumptions of normality were violated, regardless of data transformation. When using non-parametric tests, there was no effect of pond on growth rates of adult *N. undulata* (H (4) = 3.18, p=0.5, Kruskal Wallis) and a weak effect on *N. irrorata* (H (4)= 9.19, p=0.06, Kruskal Wallis) (Fig 3 E and F).

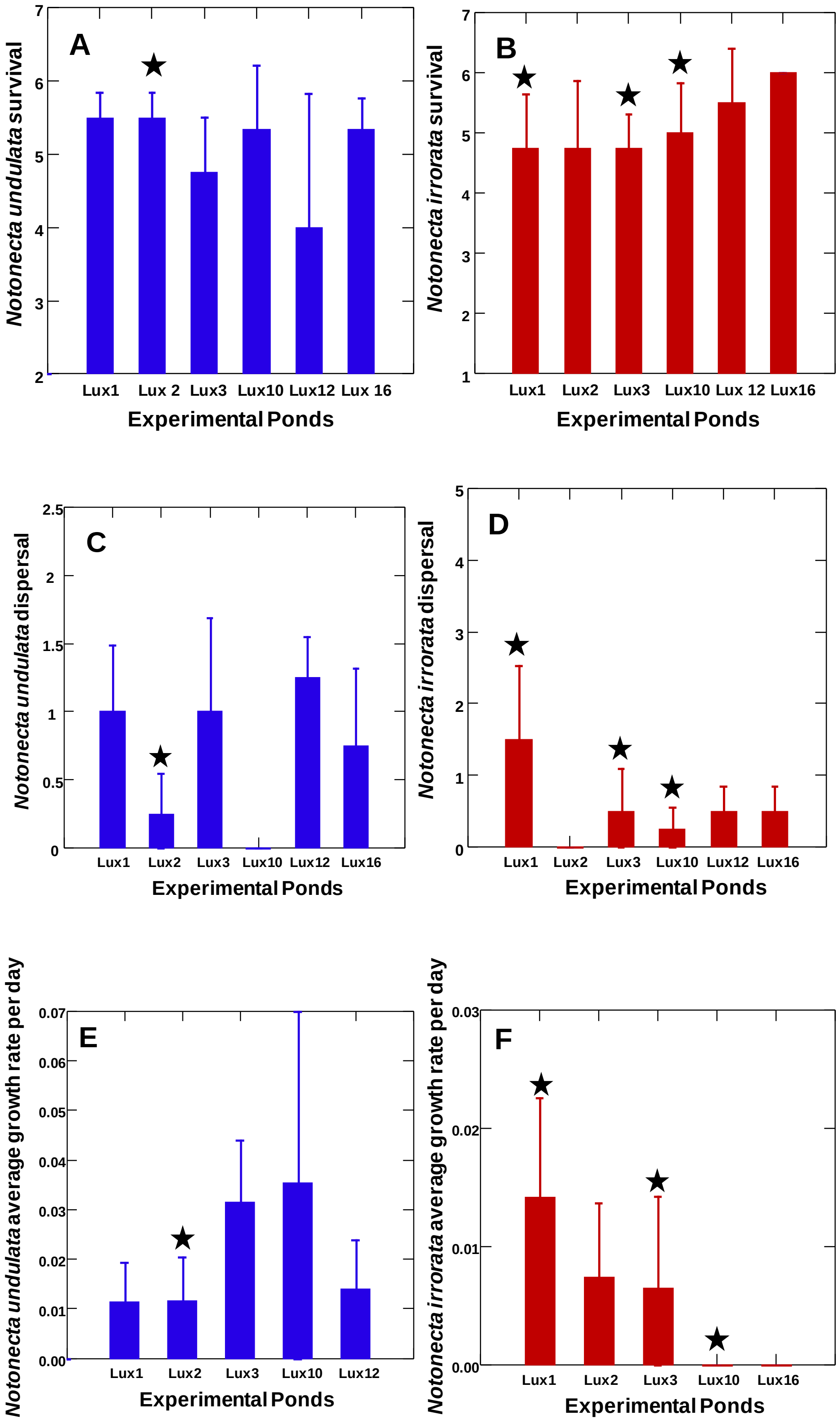


Figure 3. Results of the adult notonectid experiments showing survival (A and B), dispersal (C and D), and growth rate (E and F) responses of *Notonecta undulata* (blue

bars) and *Notonecta irrorata* (red bars) among the experimental ponds. Stars denote ponds in which the focal species was naturally absent. Values are means (±SE).

Juvenile Experiment

There was a weak effect of species identity on juveniles' growth rate ($F_{1,35}$=3.73, p=0.06, GLM Gaussian errors). We found no significant effects of pond identity ($F_{5,31}$=2.08, p=0.1, GLM Gaussian errors), or interactive effects ($F_{4,26}$=1.67, p>0.1, GLM Gaussian errors) on juvenile growth. However, assumptions of normality were violated, regardless of data transformation. No significant differences among ponds were present when analyzing average growth of *N. undulata* (H (5) = 6.53, p=0.2, Kruskal-Wallis test) and a weak effect when analyzing *N. irrorata* (H (4) = 8.6, p=0.07, Kruskal Wallis) (Fig 4 A and B).

A significant interactive effect of pond identity and species identity was found ($F_{5,32}$=2.89, p=0.028, GLM Gaussian errors) on juvenile persistence. However, assumptions of normality were violated, regardless of data transformation. Juvenile persistence did not differ between species (W = 207.5, p=0.8, Mann-Whitney test) and did not differ among ponds for *N. undulata* (H (5) = 9.01, p=0.1, Kruskal Wallis) (Fig 5 B). However, a significant difference among ponds was found when analyzing *N. irrorata* juvenile persistence (H (5) = 16.88, p=0.004, Kruskal Wallis). Persistence of *N. irrorata's* juveniles was significantly higher in Lux 2 and Lux 16 compare to the other experimental ponds (p<0.001, pairwise comparison of means by Tukey HSD test)

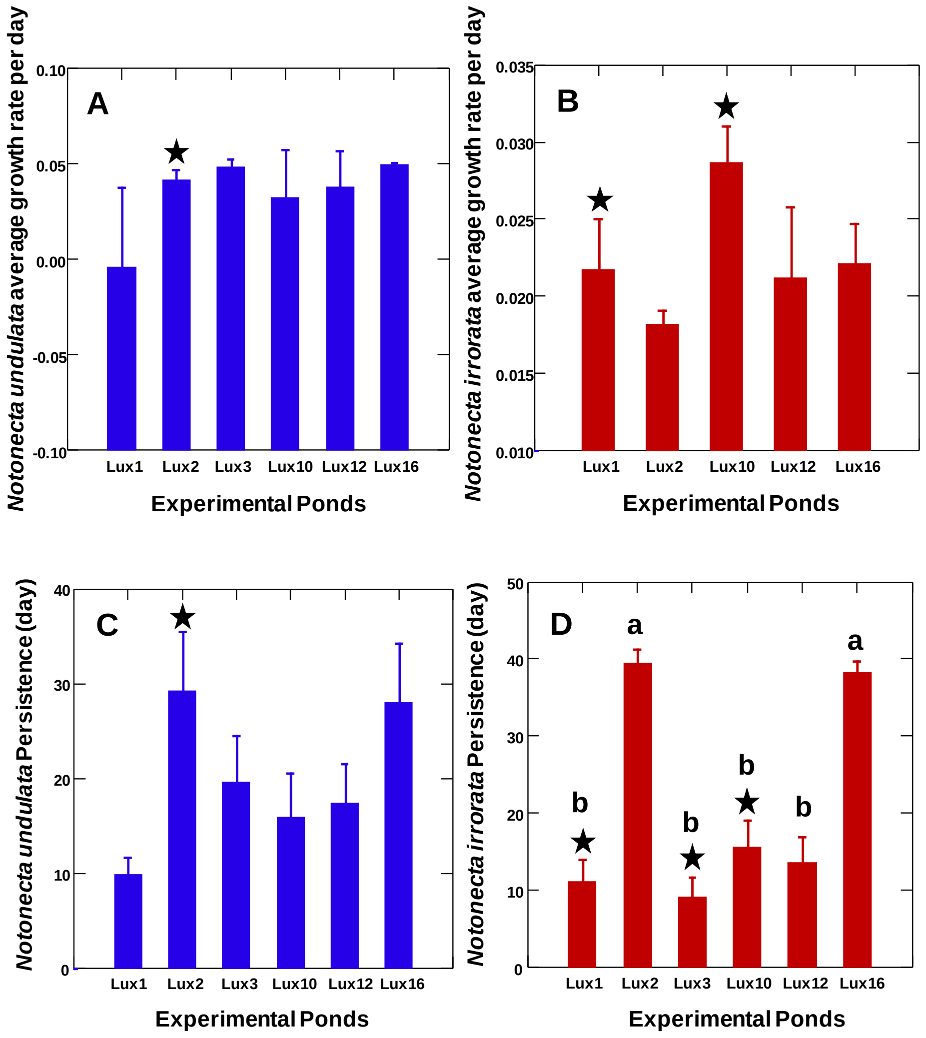


Figure 4. Results of the juvenile notonectid experiments. Shown are growth rate (A and B) and persistence time (C and D) of *Notonecta undulata* (left, blue bars) and *Notonecta irrorata* (right, red bars) among the experimental ponds. Stars denote ponds in which the focal species was naturally absent. Letters indicate which ponds were statistically different from each other ($p<0.05$). Shown are means (±SE).

The relationship between experimental responses and natural notonectid densities

We found no relationships between natural pond notonectid densities and experimental responses (survival, dispersal or growth rate) of either *N. undulata* or *N. irrorata* adults (Fig 5A, B, C, D, E, F; all $p>0.10$, Spearman correlation). When analyzing juvenile responses, we did not find any correlation between natural pond notonectid densities and growth for either species (Fig 6 A, B; all $p>0.10$, Spearman correlation) or persistence for *N. undulata* (Fig 6 C; p>0.10, Spearman correlation). However, there was a positive significant correlation between pond notonectid densities and persistence of *N. irrorata* juveniles (Fig 6 D; r_S=0.84, p=0.03. Spearman correlation).

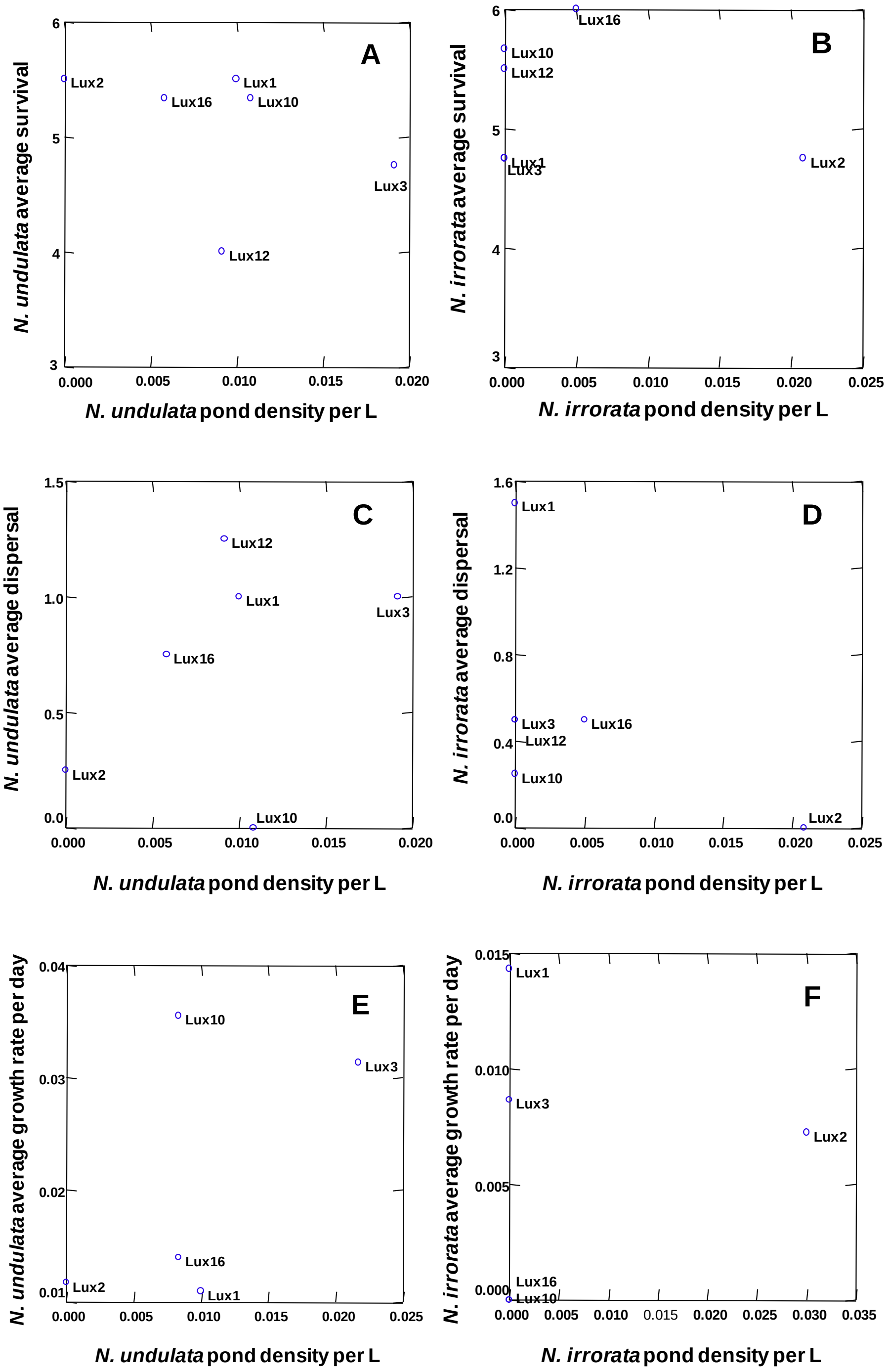


Figure 5. The relationship between experimental responses of adult *N. undulata* and *N. irrorata* (averaged across replicates) and natural density of the notonectid species within

the experimental ponds. Responses shown are adult survival (A, B), dispersal (C, D) and growth rate (E, F).

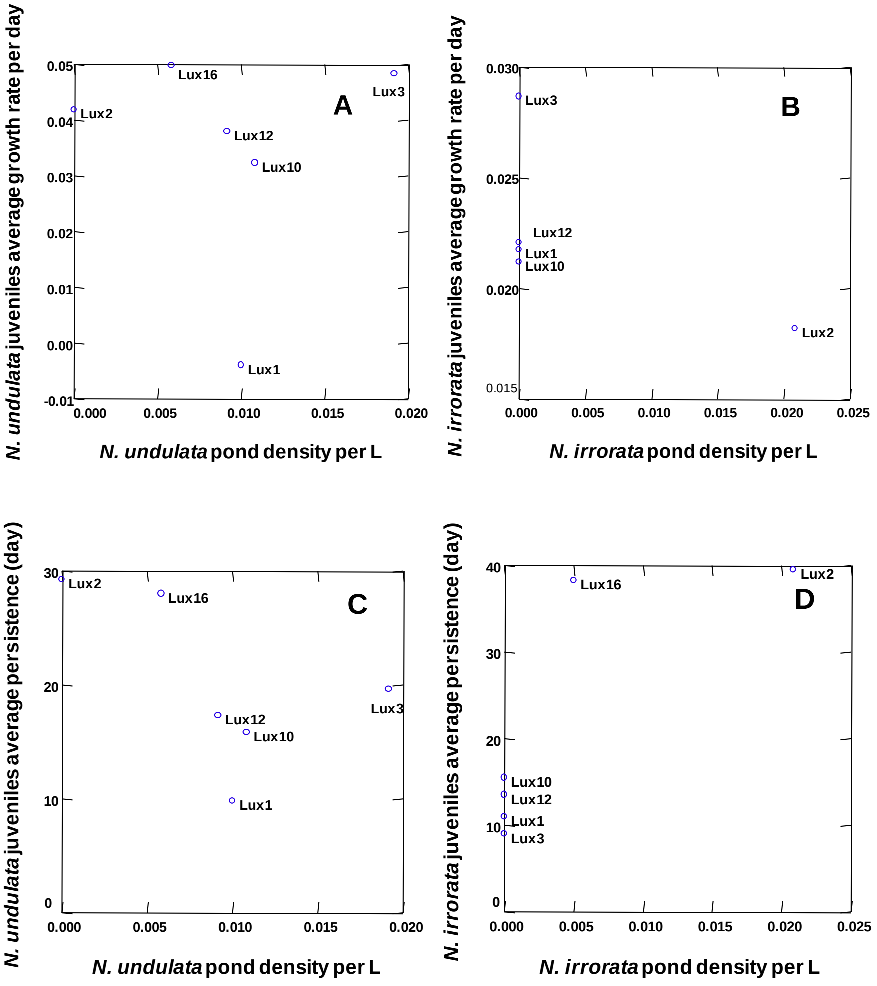


Figure 6. The relationship between experimental responses of juvenile *N. undulata* and *N. irrorata* (averaged across replicates) and natural density of the notonectid species within the experimental ponds. Responses shown are juvenile growth (A, B) and persistence (C, D).

The relationship between adult and juvenile responses and pond environmental conditions

We present results only for the first component of the partial least squares regression (PLSR) analyses, which accounted for 35.6% to 96% of the variation in our response variables. When analyzing adult survival, the first component accounted for 40.49% of the variation in *N. undulata* adult survival (Table1). However, the correlation between *N. undulata* survival and component 1 was not statistically significant (Fig. 7A; r=0.63, P=0.6, Pearson correlation). PLSR component 1 explained 64.87% of the variance in *N. irrorata* survival and was most strongly associated with increasing pond productivity (chlorophyll *a*) and zooplankton total biomass (Table 1). The relationship between *N. irrorata* survival and the first component of the PLSR is shown in Figure 7B (r=0.8, p=0.05, Pearson correlation).

Table 1. Results of the partial least squares regression analysis (PLSR) of *N. undulata* and *N. irrorata* survival (response variables) using eleven environmental predictor variables. Loading COMP1: loadings of each variable in the first PLSR component. R^2: the proportion of the variance in the response variable accounted for by component 1 of the PLSR. DO: log dissolved oxygen, Cond: log conductivity, Temp: log temperature, TP: log total phosphorus, Chlo *a*: log chlorophyll *a*, pH: pH, zoop total biomass: log zooplankton total biomass, zoop1: zooplankton PCoA axis 1, zoop2: zooplankton PCoA axis 2, macro2: macroinvertebrate PCoA axis2.

Survival	***N. undulata***	***N. irrorata***
Predictor	**Loading COMP1**	**Loading COMP1**
DO	0.296	-0.346
Temp	-0.02	-0.004
pH	-0.135	0.208
TP	-0.832	0.936
Chlo a	-1.06	1.203
Cond	-0.43	1.064
Zoop total biomass	-1.83	2
Zoop1	-0.811	1.055
Zoop2	0.619	-0.77
Macro1	-0.745	0.69
Macro2	-1.118	1.14
R^2	40.49	64.87

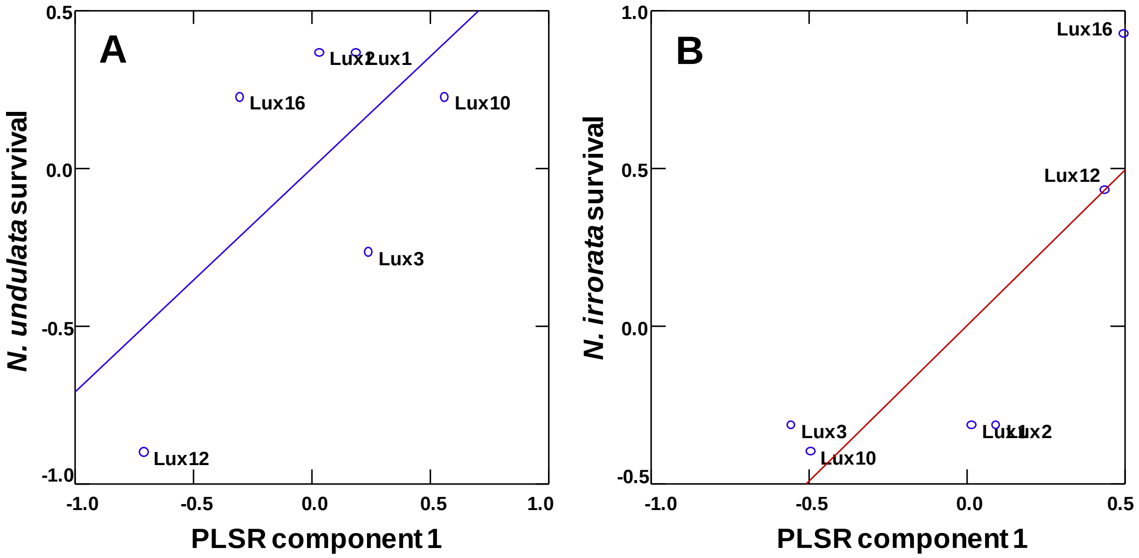


Figure 7. Results of partial least squares regression (PLSR) analyses examining the relationship between mean responses from the in situ pond experiments and environmental variables. Shown are relationships between PLSR component 1 and mean survival of *N. undulata* (A) and *N. irrorata* (B) adults in each experimental pond (note that response variables have been scaled). Component loadings can be found in Table 1.

PLSR analysis of mean dispersal showed that the first PLSR component explained 48.97% of the variance in *N. undulata* dispersal (Table 2). However, the relationship between *N. undulata* dispersal and the first component axis was not significant (Fig. 8A; r= 0.7, p=0.1, Pearson Correlation). In contrast, *N. irrorata* dispersal was significantly correlated with the first component of the PLSR (Fig. 8B; r= 0.8, p=0.02, Pearson Correlation). Component 1 accounted for 76.15% of the variance in *N. irrorata* dispersal and was mainly associated with increasing pond productivity, zooplankton total biomass and relative abundance of cyclopoids (which was negatively associated with zooplankton PCoA axis 2) (Table 2).

Table 2. Results of the partial least squares regression analysis (PLSR) of *N. undulata* and *N. irrorata* dispersal (response variables) using eleven environmental predictor variables. Loading COMP1: loadings of each variable in the first PLSR component. R2: the proportion of the variance in the response variable accounted for by component 1 of the PLSR. DO: log dissolved oxygen, Cond: log conductivity, Temp: log temperature, TP: log total phosphorus, Chlo a: log chlorophyll a, pH: pH, zoop total biomass: log zooplankton total biomass, zoop1: zooplankton PCoA axis 1, zoop2: zooplankton PCoA axis 2, macro2: macroinvertebrate PCoA axis2.

Dispersal	***N. undulata***	***N. irrorata***
Predictor	**Loading COMP1**	**Loading COMP1**
DO	-0.295	0.024
Temp	-0.007	0.01
pH	0.182	0.11
TP	0.809	0.348
Chlo a	1.2	0.868
Conductivity	0.541	0.25
Zoop total biomass	2.098	1.082
Zoop1	0.397	-0.427
Zoop2	-1.175	-1.021
Macro1	0.645	-0.337
Macro2	0.794	0.474
R^2	48.97	76.15

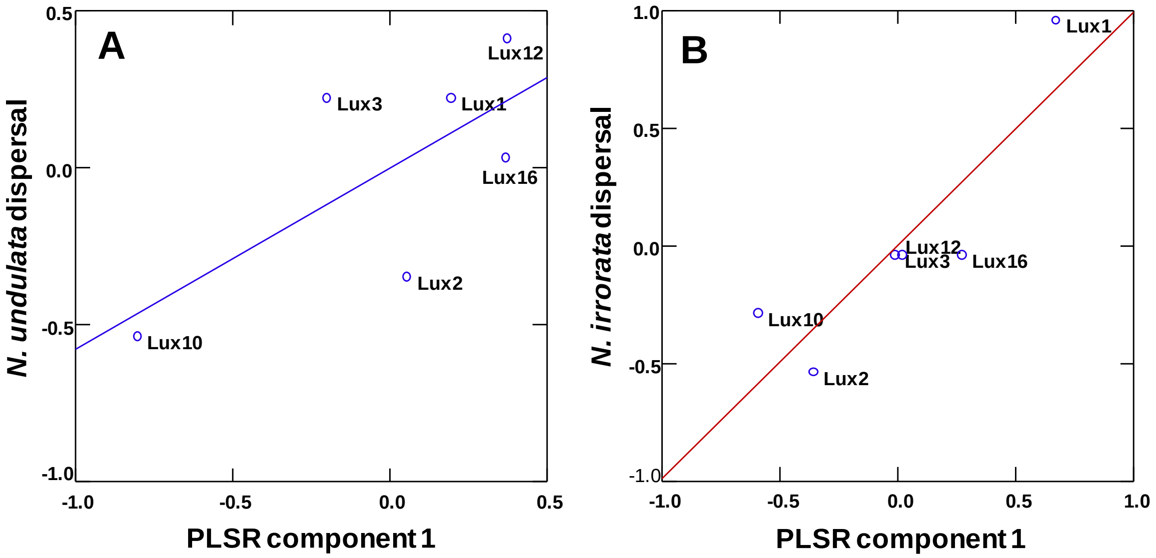


Figure 8. Results of partial least squares regression (PLSR) analyses examining the relationship between mean responses from the in situ pond experiments and environmental variables. Shown are relationships between PLSR component 1 and mean dispersal of *N. undulata* (A) and *N. irrorata* (B) adults in each experimental pond (note that response variables have been scaled). Component loadings can be found in Table 2.

PLSR component 1 explained 94.63% of the variance in *N. undulata* average adult growth rate (Table 3) and was significantly correlated with the response variable (Fig. 9A; r=0.97, p=0.005, Pearson Correlation). Component 1 was mainly associated with decreasing pond productivity, conductivity, zooplankton total biomass, and relative abundance of cyclopoids (which was negatively associated with zooplankton PCoA axis 2). When analyzing *N. irrorata* adult growth rates, the first PLSR component was significantly correlated with the response variable (Fig. 9B; r=0.89, p=0.04, Pearson Correlation) and accounted for 79.35% of the variation in the response. Component 1 was mainly associated with increasing zooplankton total biomass and relative abundance of cyclopoids (zooplankton PCoA axis 2).

Table 3. Results of the partial least squares regression analysis (PLSR) of *N. undulata* and *N. irrorata* growth (response variables) using eleven environmental predictor variables. Loading COMP1: loadings of each variable in the first PLSR component. R2: the proportion of the variance in the response variable accounted for by component 1 of the PLSR. DO: log dissolved oxygen, Cond: log conductivity, Temp: log temperature, TP: log total phosphorus, Chlo a: log chlorophyll a, pH: pH, zoop total biomass: log zooplankton total biomass, zoop1: zooplankton PCoA axis 1, zoop2: zooplankton PCoA axis 2, macro2: macroinvertebrate PCoA axis2.

Growth rate	***N. undulata***	***N. irrorata***
Predictor	**Loading COMP1**	**Loading COMP1**
DO	0.365	-0.03
Temp	0.055	-0.02
pH	-0.24	0.28
TP	-0.755	0.025
Chlo a	-1	0.22
Conductivity	-1.09	-0.26
Zoop total biomass	-1.97	1.21
Zoop1	-0.69	-0.71
Zoop2	1.10	-1.04
Macro1	-0.79	0.62
Macro2	-0.46	-0.51
R^2	94.63	79.35

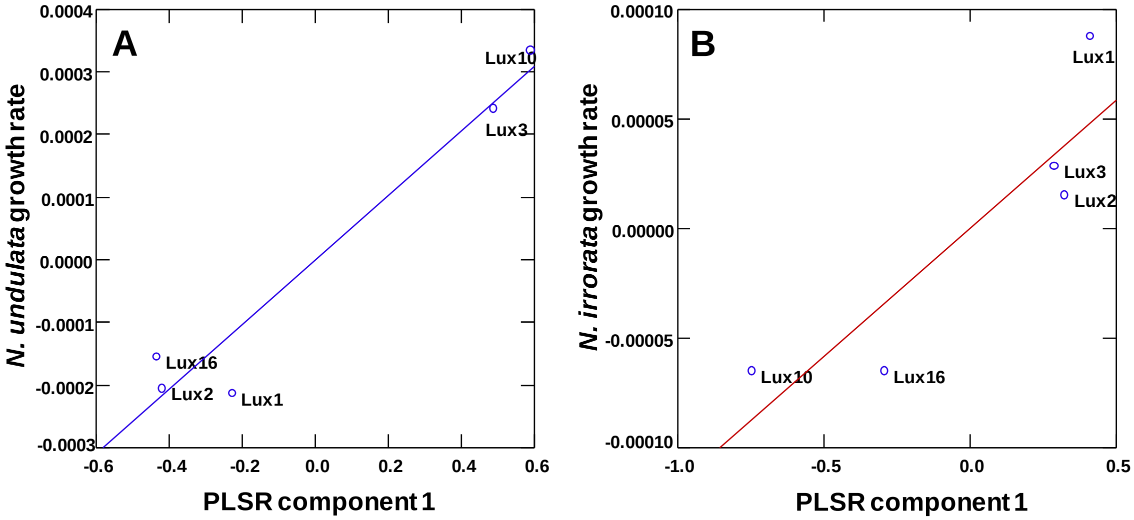


Figure 9. Results of partial least squares regression (PLSR) analyses examining the relationship between mean responses from the in situ pond experiments and environmental variables. Shown are relationships between PLSR component 1 and mean growth of *N. undulata* (A) and *N. irrorata* (B) adults in each experimental pond (note that response variables have been scaled). Component loadings can be found in Table 3.

When analyzing juvenile responses, the first PLSR component explained 74.01% of the variance in *N. undulata* juvenile growth rate and was associated with decreasing pH, zooplankton total biomass and relative abundance of chaoborids (increasing zooplankton PCoA axis 1) (Table 4). The first component also showed a significant correlation with *N. undulata* average juvenile growth rate (Fig. 10A; r=0.8, p=0.03, Pearson correlation). The first PLSR component accounted for 49.57% of the variance in *N. irrorata* juvenile average growth rate but was not significantly correlated with the response variable (Fig. 10B; r=0.7, p=0.1, Pearson correlation).

When analyzing juvenile persistence, results of the PLSR analysis showed that 35.58% of the variance in *N. undulata* persistence was explained by the first component (Table 4). However, the correlation between *N. undulata* persistence and the first component was not significant (Figure 10C; r=0.5, p=0.2, Pearson correlation). Similarly, PLSR component 1 explained 42.97% of variation in *N. irrorata* persistence (Table 4) but was not significantly correlated with the response variable (Fig. 10D; r=0.6, p=0.1, Pearson correlation).

Table 4. Results of the partial least squares regression analysis (PLSR) of *N. undulata* and *N. irrorata* juvenile growth rate and persistence (response variables) using nine environmental predictor variables. Loading COMP 1: loadings of each variable in the first PLSR component. R2: the proportion of the variance in the response variable accounted for by component 1 of the PLSR. DO: log dissolved oxygen, Cond: log conductivity, Temp: log temperature, TP: log total phosphorus, Chlo a: log chlorophyll a, pH: pH, zoop total biomass: log zooplankton total biomass, zoop1: zooplankton PCoA axis 1, zoop2: zooplankton PCoA axis 2.

Juvenile	***N. undulata***		***N. irrorata***	
	Growth	**Persistence**	**Growth**	**Persistence**
Predictor	**Loading COMP1**	**Loading COMP1**	**Loading COMP1**	**Loading COMP**
DO	-0.057	-0.39	-0.384	-0.39
Temp	-0.005	-0.043	-0.028	-0.035
pH	-0.56	-0.042	0.141	0.135
TP	0.009	0.88	0.834	0.855
Chlo a	-0.022	1.17	1.02	1.075
Conductivity	-0.085	0.39	0.316	0.355
Zooplankton total biomass	-0.79	0.52	0.97	0.89
Zoop1	0.46	-0.84	-1.05	-1.03
Zoop2	-0.32	0.42	0.087	0.23
R^2	74.01	35.58	49.57	42.97

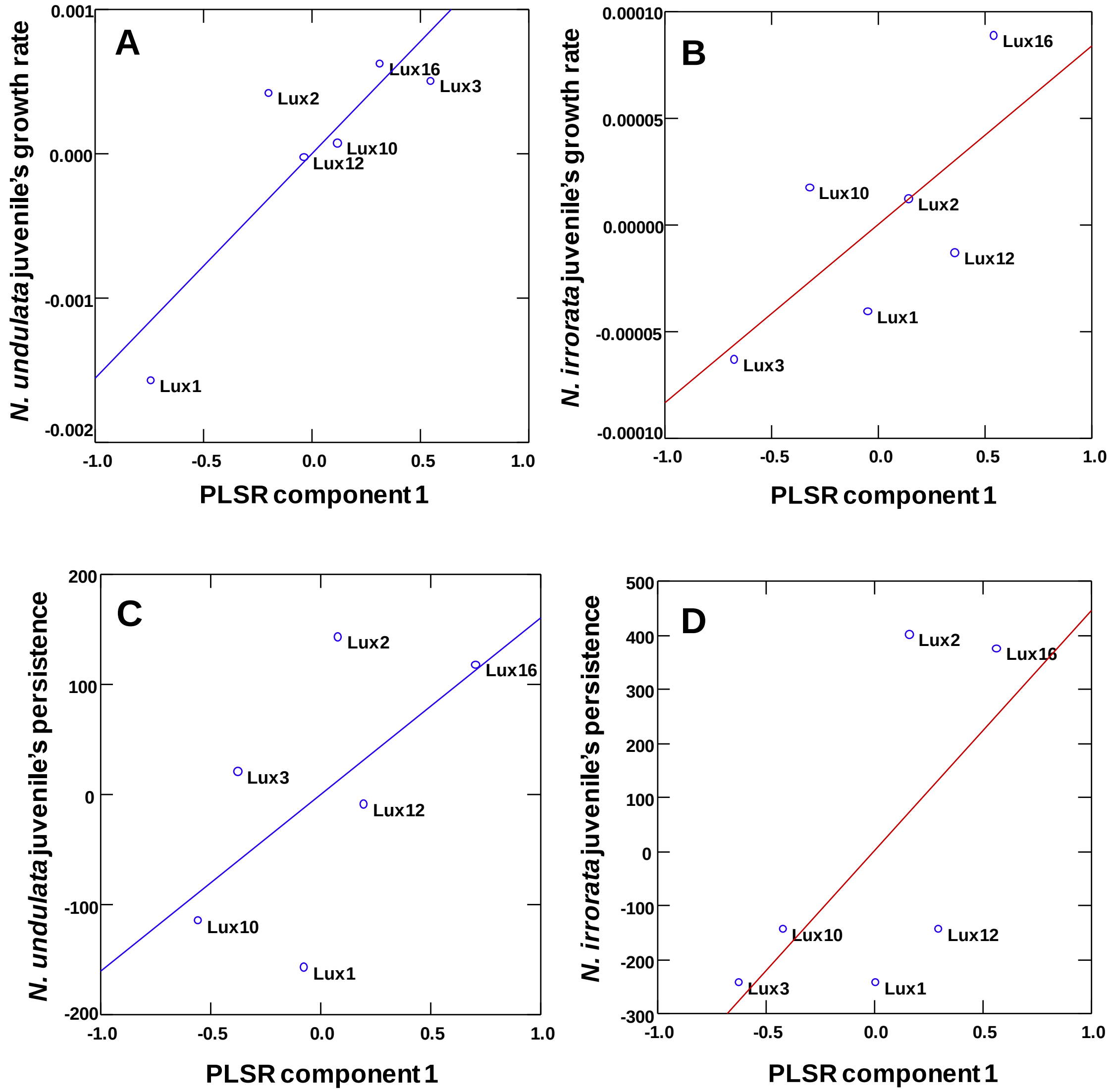


Figure 10. Results of partial least squares regression (PLSR) analyses examining the relationship between mean responses from the in situ pond experiments and environmental variables. Shown are relationships between PLSR component 1 and mean growth and persistence of *N. undulata* (A, C) and *N. irrorata* (B, D) adults in each experimental pond (note that response variables have been scaled). Component loadings can be found in Table 4.

DISCUSSION

We found limited evidence that local environmental factors determine presence/absence of notonectid species in our study ponds. When examining adult responses, we found no evidence of differential responses between *N. undulata* and *N. irrorata* and no significant differences in survival or somatic growth rate among the experimental ponds. Moreover, neither species displayed higher levels of emigration from ponds in which they were naturally absent compared to ponds in which they were present. We also found no relationships between adult survival, growth and dispersal and natural notonectid densities within the experimental ponds. Like adult responses, we found no difference in juvenile growth rates between species or among the experimental ponds. However, persistence of *N. irrorata* juveniles was significantly different across the experimental ponds. *N. irrorata* showed higher persistence in ponds Lux 2 and Lux 16 in which it naturally occurred compared to Lux1, Lux3, and Lux 10 in which it was absent. In contrast, *N. undulata* juvenile performance did not correspond to its natural presence/absence in the experimental ponds. Thus, our results provide some support for the importance of local environmental control of *N. irrorata's* distribution. They also suggest that dispersal limitation, rather than local environmental factors, may be responsible for the absence of *N. undulata* from Lux 2.

Although our experimental measures of performance were not overall good predictors of natural abundances, partial least squares regressions revealed several environmental correlates of the experimental response variables. *N. irrorata* adult survival, dispersal and growth rate were all positively correlated with measures of pond productivity (chlorophyll a and/or total zooplankton biomass) and increasing relative abundance of cyclopoid copepods (in the case of dispersal and adult growth). Among our experimental ponds, Lux 2 and Lux 16 showed the highest level of productivity (Total Phosphorus level 320 and 170 μ g l^{-1}, respectively); these two ponds are semi-forested waterbodies which are covered with a layer of duckweed vegetation in mid growing season. Zooplankton total biomass was generally high in all ponds except for Lux 3 and

Lux 10. The absence of *N. irrorata* from these two ponds, could be related to the low amount of zooplankton total biomass which could be driven by the low level of productivity in these sites.

Partial least squares regressions also revealed significant correlations between environmental predictors and *N. undulata* adult growth rate and juvenile growth rate. Interestingly, *N. undulata* adult and juvenile responses tended to run counter to *N. irrorata* responses, showing higher growth rates in ponds with lower productivity(chlorophyll a and/or zooplankton total biomass). Adults growth rates were also positively associated with decreasing relative abundance of cyclopoid copepods. The opposing responses between the *N. irrorata* and *N. undulata* is consistent with niche differentiation between the species. However, we can only speculate on the reason for *N. undulata's* reduced performance with increasing productivity. High productivity ponds tended to be associated with increasing relative abundance of cyclopoid copepods which was associated with increased growth rates of *N. irrorata* adults and reduced growth rates of *N. undulata* adults. Thus, variation in resource composition and different feeding preferences between the species may account for our results. Another possbility is that high productivity boosts growth of floating vegetation such as duckweed as was observed in Lux 2 and Lux 16 (ponds in which *N. undulata* had low abundance or was absent naturally). As a result, pond temperature tends to be lower in these ponds (average 16°C) compared to the other ponds during the growing season (average 20°C). Although not confirmed by our study (we found no strong temperature effects in the PLSR analyses), previous research has shown that *N. undulata* prefer warmer waterbodies which have rooted vegetation (Clark 1928; Streams and Newfield 1972).

As with any experimental study, there are limitations and caveats with regards to the present experiment. First, our study included only one pond in which *N. undulata* was naturally absent which limited the interpretation of the processes involved and weakened contrasts between pond types. Second, the high density of notonectids introduced to the adult and juvenile enclosures (relative to natural densities) could have imposed strong intraspecific resource competition. This may have reduced species performance in some ponds obscuring the contrast between ponds in which notonectid species were present versus absent. Third, several enclosures were lost during each experiment which led to reduced statistical power. Fourth, we did not observe reproduction in our enclosures, and thus we could not quantify this important component of fitness. It is possible that inclusion of reproduction could have resulted in stronger contrasts in performance among ponds and between species. Fifth, while we attempted to quantify emigration, we could not address oviposition behavior. Habitat selection for oviposition sites is known to be an important factor influencing species presence/absence and metacommunity structure (Resetarits & Wilbur 1989; Resetarits 2005). The capacity for notonectids to exhibit such behaviors is unknown. Lastly, each of the experiments was only performed one time during the growing season, thus ignoring potential temporal variation in environmental conditions. Our previous survey studies of fishless ponds in the region indicate that the importance of environmental factors in the structure of notonectid assemblages can vary greatly over the growing season and even between years.

The findings from our study contribute to our limited understanding of the relative importance of local and regional processes in the structure of natural communities. There are few studies which have used experimental introductions such as ours to address dispersal limitation. These have focused on a variety of aquatic and terrestrial taxa including zooplankton, bacteria, plants, amphipods, and barnacles (Tilman 1997; Dick et al. 1997; Roughgarden et al. 1988; Shurin 2000; Cottenie and Meester 2004). While some of these studies found a joint effect of local and regional processes on community structure (Tilman 1997; Cottenie and Meester 2004), others found a minor role of dispersal limitation compared to biotic interactions (Shurin 2000). Most of these studies concluded that the relative contribution of local and regional processes to species distributions is connected to the motility and dispersal ability of their study organisms. Distributions of organisms which can easily move between local sites through active or passive dispersal (e.g., zooplankton and bacteria) were more strongly affected by environmental filtering than dispersal limitation (Shurin 2000; Van der Gucht et al. 2007; Jones and McMahon 2009).

Despite the limitations discussed above, the current study provides valuable information on the relative importance of local and regional processes affecting the distribution of a group of dispersal-capable organims. In this study we included both adult and juvenile responses of species to provide a more inclusive picture of the processes affecting community organization. However, our work leaves many questions unanswered. Future studies would do well to include a broader range of study sites as well as multiple experiments performed at different times of the years. Furthermore, consideration of other response variables such as oviposition behavior and reproduction would provide a more comprehensive understanding of processes structuring notonectid communities.

APPENDIX A

Figure 1. The relationship between realized and initial notonectid abundances in high and low productivity treatments. Shown is the model fit from the GLM analysis (the relationship is for both low and high productivity treatments combined). See Results for model statistics.

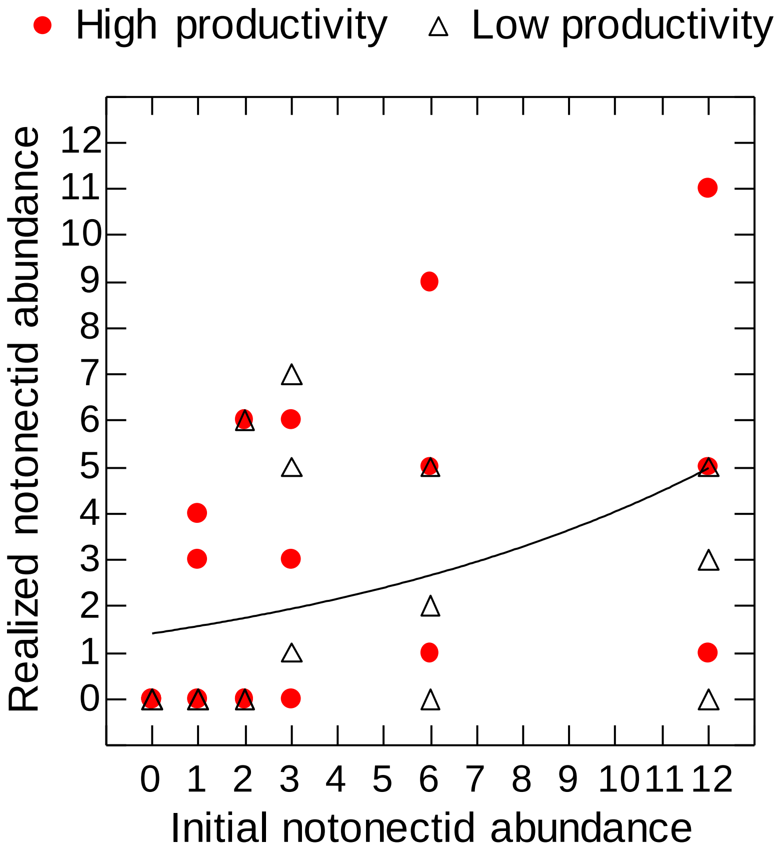
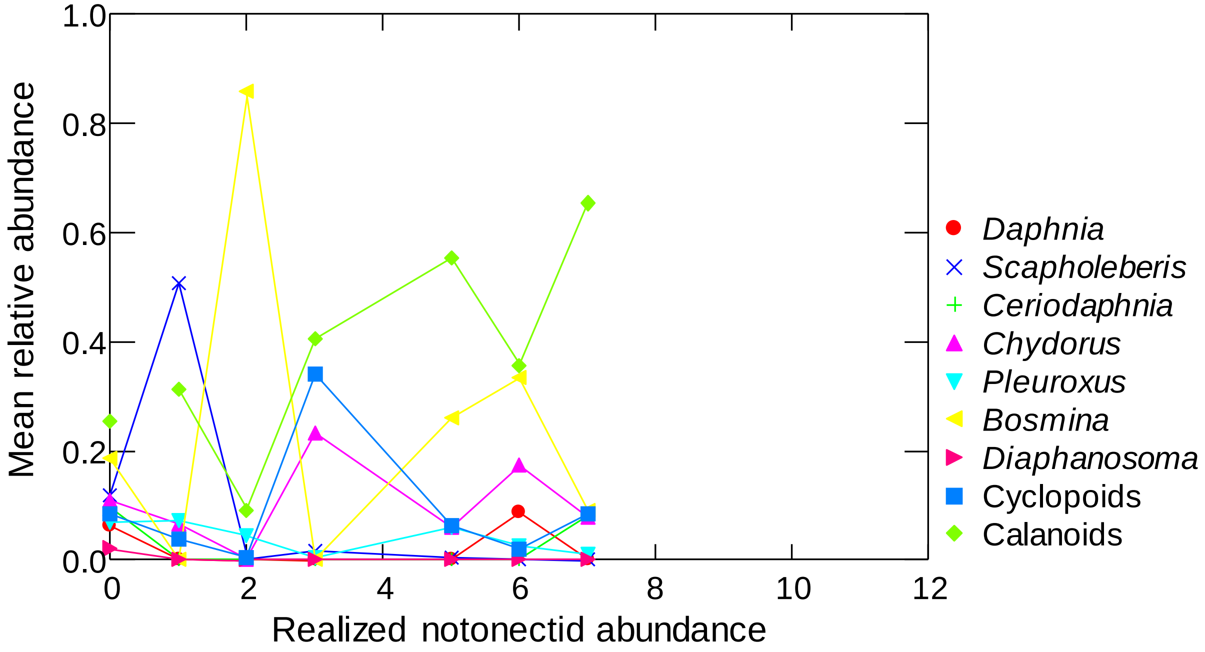


Figure 2. The relationship between time-averaged relative abundances of zooplankton taxa and realized notonectid abundance for (A) low productivity and (B) high productivity treatments.

A. Low productivity



B. High productivity

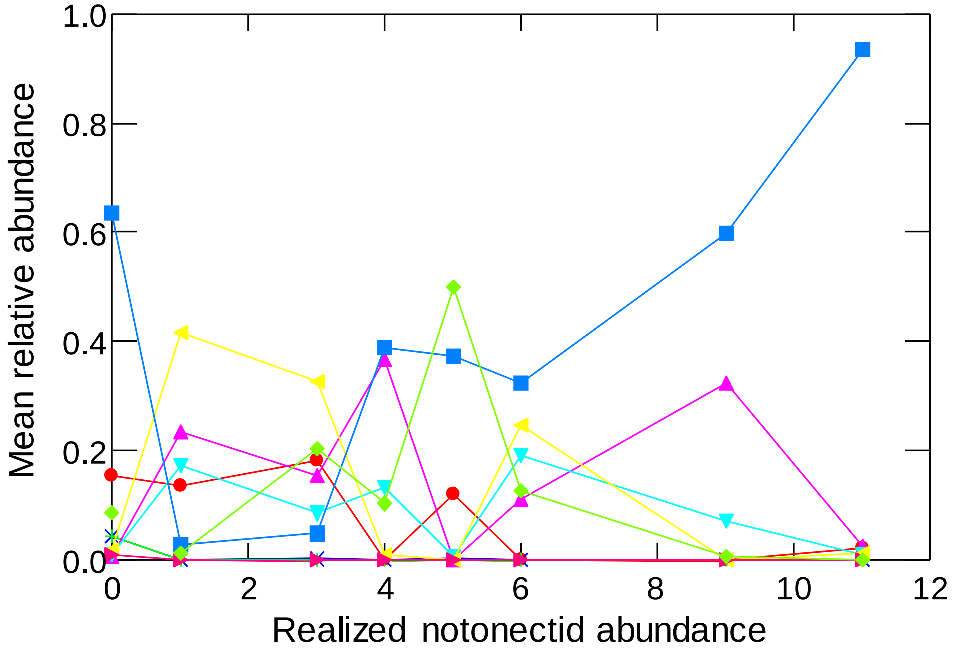


Figure 3. The relationship between time-averaged log10 total chlorophyll a (µg/L) and realized notonectid abundance in the high and low productivity treatments. Shown are model fits from separate linear regressions for the low productivity (black line) and high productivity (red line) treatments.

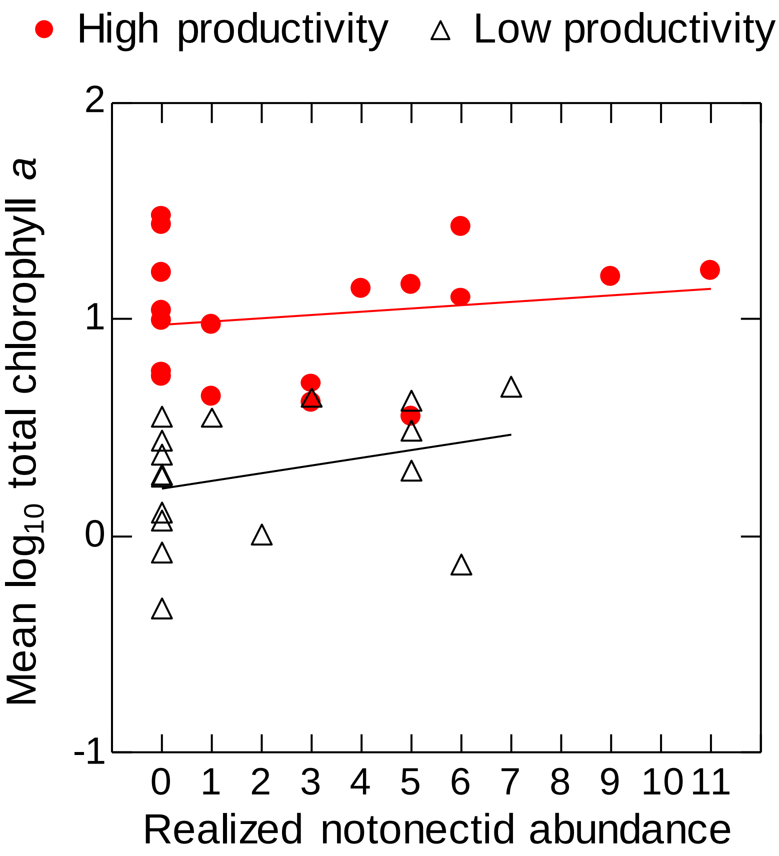


Figure 4. The relationship between time- averaged relative concentration of grazer-resistant (>30-µm) chlorophyll a and realized notonectid abundance in the high and low productivity treatments. Shown are model fits from separate linear regressions for the low productivity (black line) and high productivity (red line) treatments.

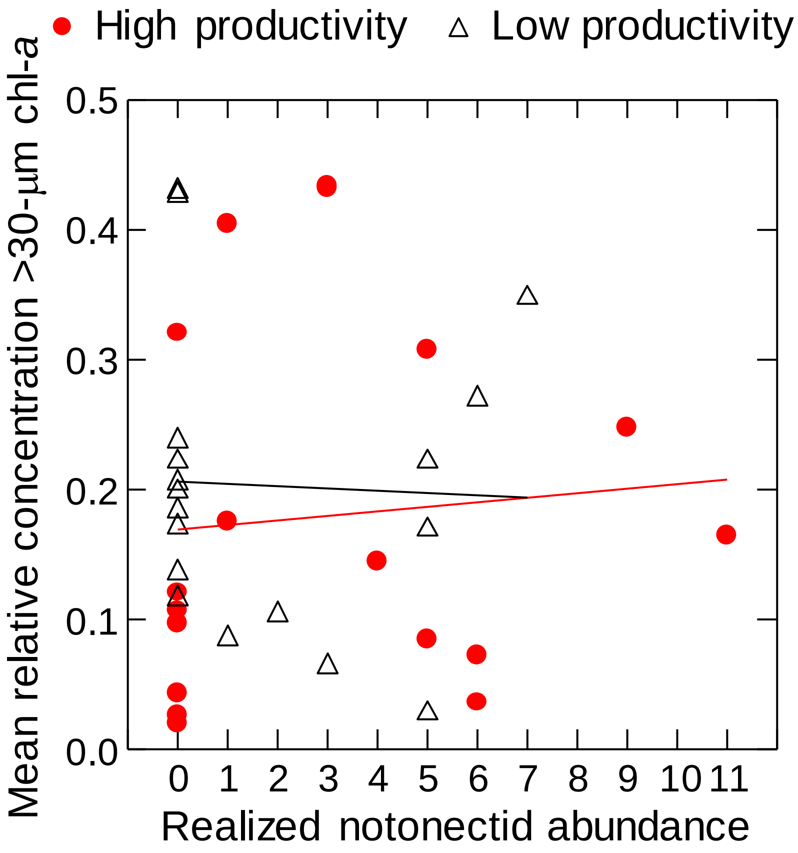


Figure 5. The relationship between time-averaged zooplankton species richness (excluding cyclopoid copepods) and time-averaged log10 cyclopoid density in high and low productivity treatments. Mean $\log_{10}$ cyclopoid density had a significant negative effect on mean species richness ($F_{1,30} = 5.95$, $p = 0.02$, GLM Gaussian errors) but no effect of productivity and no interaction between cyclopoid density and productivity were present ($p > 0.70$, GLM Gaussian errors). Shown is the model fit for a reduced model containing only mean $\log_{10}$ cyclopoid density as a predictor.

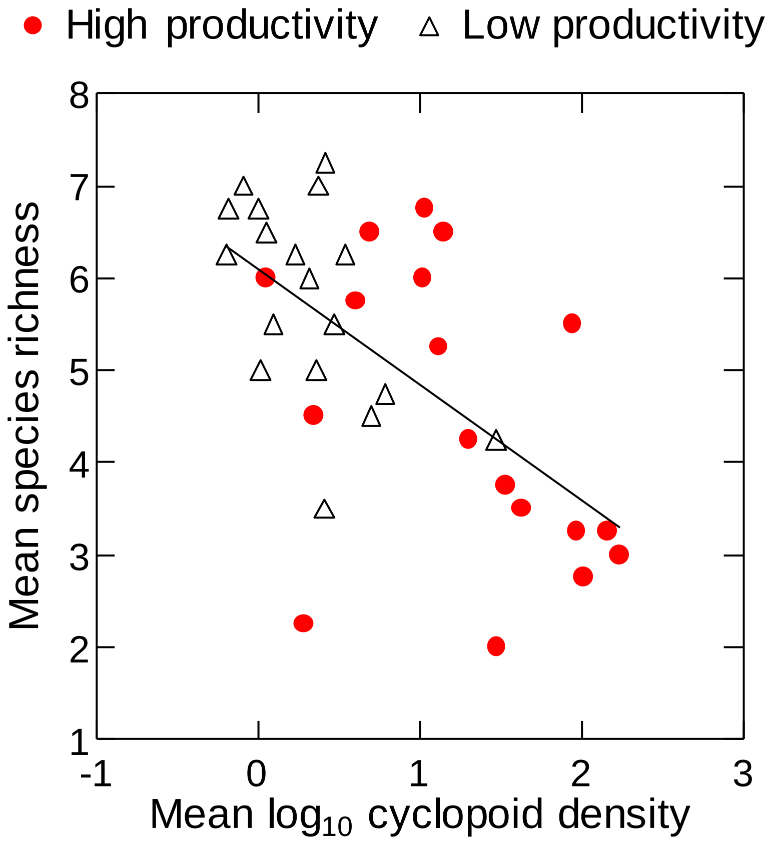
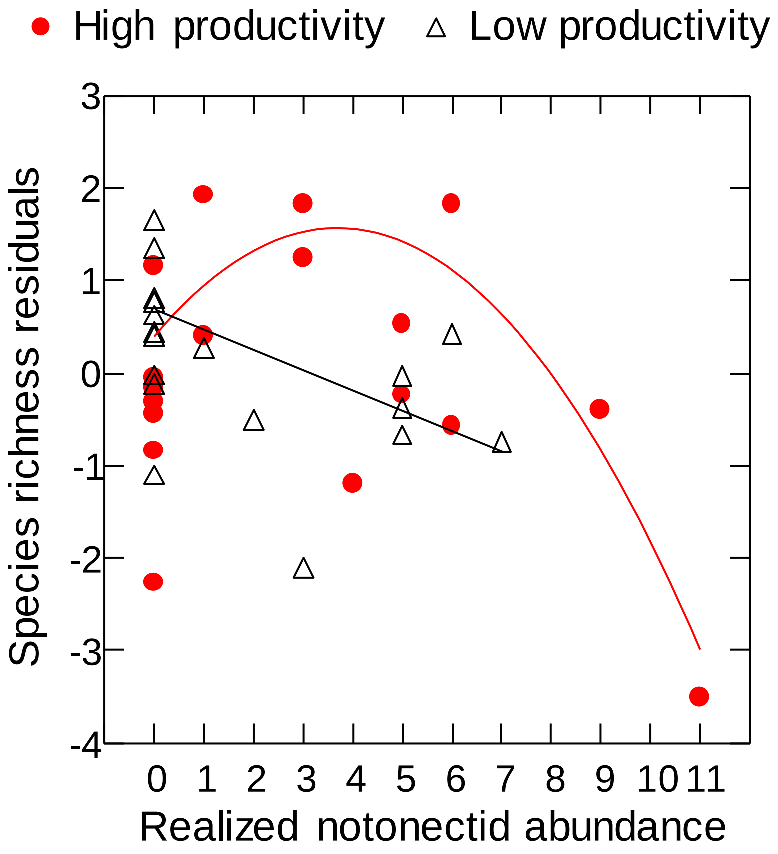


Figure 6. The relationship between zooplankton species richness residuals and realized notonectid abundance at different levels of productivity. Residuals were obtained from the linear regression between time-averaged zooplankton species richness (excluding cyclopoids) and time-averaged $\log_{10}$ cyclopoid density as the predictor (as in Fig. 5, Appendix 1). Effects of realized notonectid abundance and productivity on residual species richness were analyzed using GLM with Gaussian errors (including linear and quadratic effects of notonectids). This analysis produced a significant interaction between productivity and the quadratic effect of notonectid abundance (F1,30 = 5.83, p = 0.02). Analyzing low and high productivity treatments separately, a weak negative effect of notonectid abundance on residual species richness was detected at low productivity (p= 0.07, R2= 0.15, linear regression). At high productivity, a significant negative quadratic effect of notonectid abundance was present (p< 0.01, model p= 0.01, R 2 = 0.36, linear regression). Shown are model fits from the separate linear regressions for the low productivity (black line) and high productivity (red line) treatments.



APPENDIX B

Table 1. Summary of abiotic environmental variables sampled for each fishless pond during the (A) 2014 growing season and (B) 2015 growing season. Values are mean(+/-SD), maximum and minimum across all sampling dates.

A. First growing season-2014

	Temperature			pH			Oxygen			Conductivity			TP		
Pond/variable	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**
Lux 1	21.8±2.3	19.8	24.7	7.5±0.4	6.8	8.3	4.5±1.3	2.6	6	37.4±9.4	24	53	0.09±0.02	0.04	0.13
Lux 2	16.6±2.2	13.5	18.1	7.9±0.5	7.2	8.4	1.9±0.6	1.2	2.7	58.4±5.3	51	59	0.32±0.03	0.28	0.36
Lux 3	20.5±1.9	17.7	23	8.5±1.07	6.8	9.7	7.5±3	3.1	11.5	9.3±2.2	6.4	11.9	0.07±0.02	0.04	0.11
Lux 8	19.5±2.2	16.4	22.5	8±0.4	7.5	8.6	4.8±1.1	3.8	6.6	246.6±33.6	198	284	0.04±0.01	0.03	0.08
Lux 9	21±2.3	17.9	24.1	8.2±0.4	7.4	8.6	6.2±1.5	4.3	7.7	29.5±2.1	27	32	0.06±0.02	0.04	0.09
Lux 10	21.5±2.2	18.8	23.8	8±0.4	7.3	8.4	6.7±1.3	5.2	8.7	39.2±9.3	33	58	0.03±0.01	0.01	0.06
Lux 11	18.9±2.3	16.1	22	7.7±0.3	7.2	8	3.3±1.3	1.9	5.7	69.4±11.2	51	83	0.24±0.11	0.12	0.39
Lux 12	20.4±2.6	16.3	23.9	7.8±0.8	6.3	8.6	4.7±2.1	1.7	7.9	19.8±3.5	16.2	26.6	0.09±0.05	0.04	0.18
Lux 13	20.5±2.4	17.6	23	7.7±0.3	7.2	8	4.9±1.4	3.2	6.8	60.6±7.6	48	69	0.04±0.005	0.03	0.04
Lux 14	19.8±2.3	16.3	22.8	7.6±0.6	6.7	8.3	4.3±1	3	5.9	25.5±3.5	22.3	30	0.10±0.06	0.03	0.2
Lux 16	17.9±2.4	14.3	20.6	7.9±0.4	7	8.4	2.9±2.2	1.5	4.4	32.4±2.2	31	36	0.17±0.03	0.12	0.22

B. Second growing season-2015

	Temperature			**pH**			**Oxygen**			**Conductivity**			**TP**		
Pond/variable	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**	**Mean±SD**	**Min**	**Max**
Lux 1	20.8±4.02	15.8	28	7.87±0.4	7.2	8.5	4.5±2.6	1.2	8.9	34.5±10.2	22.5	55.4	0.11±0.04	0.07	0.18
Lux 2	16.1±3.2	12.2	20.4	7.95±0.7	6.6	8.7	3.2±1.9	0.7	7.9	35.23±12.7	19.6	60	0.29±0.2	0.08	0.6
Lux 3	20.22±3.4	14.7	25.4	8.36±0.6	7.1	8.9	4.16±2.6	1	7.9	10.22±2.75	7	16	0.05±0.02	0.03	0.09
Lux 8	19.24±2.6	15.4	22.4	7.81±0.5	7.1	8.4	4.8±2.3	1.4	8.58	214.9±49	112	279	0.03±0.005	0.02	0.04
Lux 9	20.38±2.2	17.3	23.4	8.22±0.4	7.6	8.5	5.6±3.1	1.9	11	20.18±5.3	8.4	26	0.05±0.01	0.03	0.07
Lux 10	21.7±2.4	17.7	24.7	8.28±0.3	7.8	8.7	6.13±2.7	1.6	9.7	24.9±6.3	12	31	0.02±0.005	0.01	0.03
Lux 11	18.9±2.3	15.4	22.8	7.73±0.4	7.1	8.2	3.3±2.3	0.9	7.3	50±8.1	34	62	0.27±0.1	0.1	0.49
Lux 12	19.73±3.4	15.7	24.9	8.27±0.8	7.1	9.6	4.4±1.8	2.2	8	16.5±4.8	9.9	25.6	0.10±0.06	0.04	0.2
Lux 13	19.13±3.9	11.9	24.1	7.68±0.6	6.6	8.4	3.54±1.7	1.6	7.2	42±18.7	34	63	0.07±0.03	0.03	0.1
Lux 14	19.1±2.9	15.6	23.6	7.72±0.7	6.4	8.5	3.98±1.02	2.2	5	21.5±6.3	9.3	29	0.2±0.02	0.04	0.1
Lux 16	16.77±3.03	12.4	21.4	8.04±0.3	7.4	8.5	2.64±2.5	0.4	6.9	24.6±9.3	2.4	31	0.2±0.06	0.09	0.27
Corner	19.60±1.76	8.3	22.6	7.61±0.22	7.2	8.8	3.83±3.16	0.7	8.8	27.81±9.96	11	37	0.23±0.03	0.12	0.27

Notes: Temperature ((°C), Oxygen= dissolved oxygen(mgl^{-1}), Conductivity (µS), TP= Total Phosphorus (mgl^{-1}).

Table 2. The result of two sample t-tests comparing time-averaged density of *Notonecta* species and pond environmental variables between the two sampling years.

Variables	**df**	***t***	***p***
N. undulata	20	0.59	0.55
N. irrorata	20	0.4	0.69
Temperature	20	-0.98	0.38
pH	20	1.34	0.1
Dissolved oxygen	20	3.01	0.006
Conductivity	20	1.07	0.29
TP	20	0.05	0.95
Chlorophyll *a*	20	0.4	0.69

Table 3. Occupancy and population turnover (colonization and extinction) for the two species of *Notonecta* in surveyed ponds during the two growing seasons.

Growing season	**Number of surveyed ponds**	**Number of ponds occupied by**	
		N. undulata	***N. irrorata***
2014	11	10	7
2015	12	10	7

Figure 1. Density (per liter) of *N. undulata* (black) and *N. irrorata* (grey) populations (adult and juveniles) across surveyed ponds during 2014 growing season.

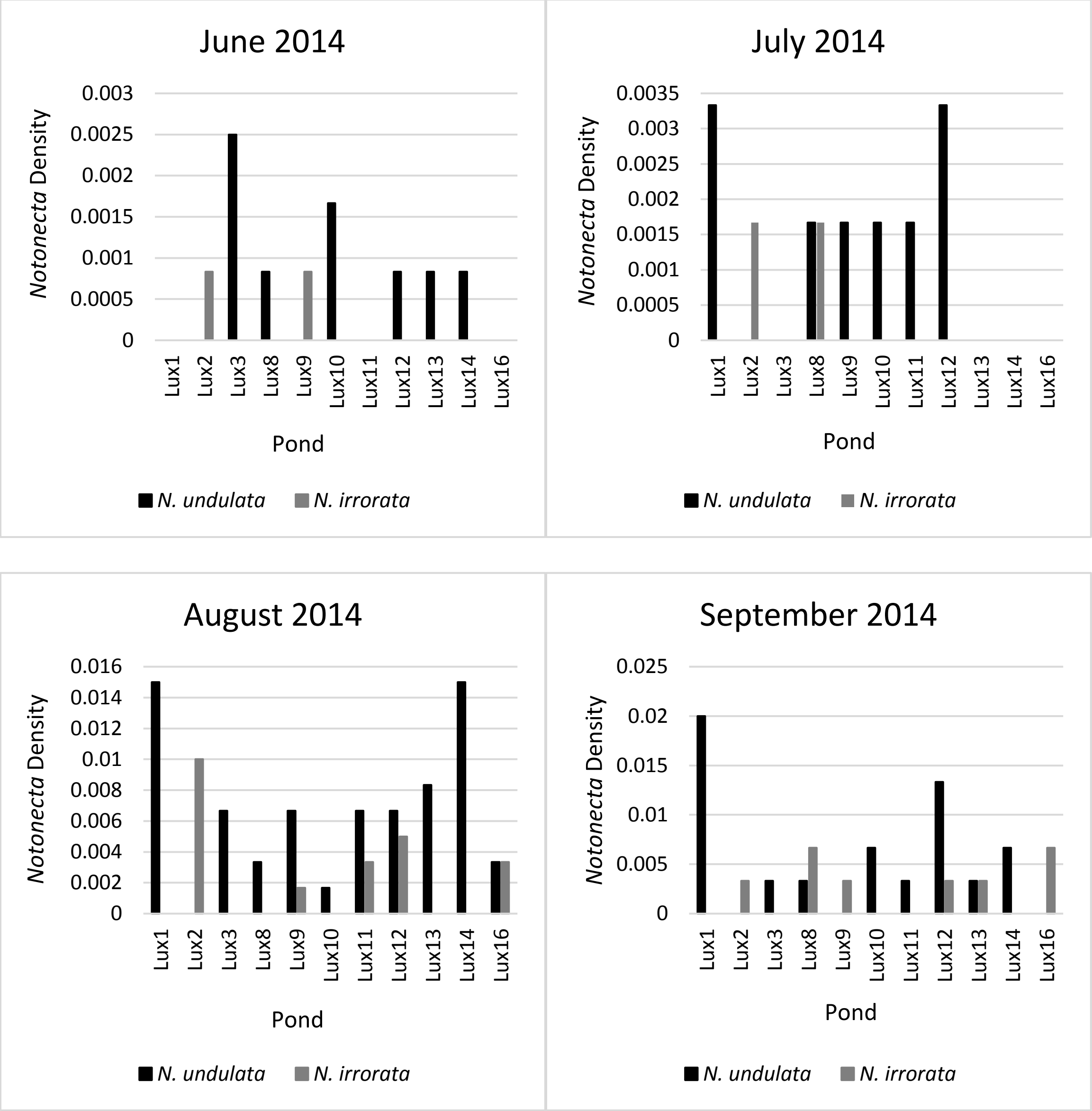


Figure 2. Density (per liter) of *N. undulata* (black) and *N. irrorata* (grey) populations (adult and juveniles) across the surveyed ponds during 2015 growing season.

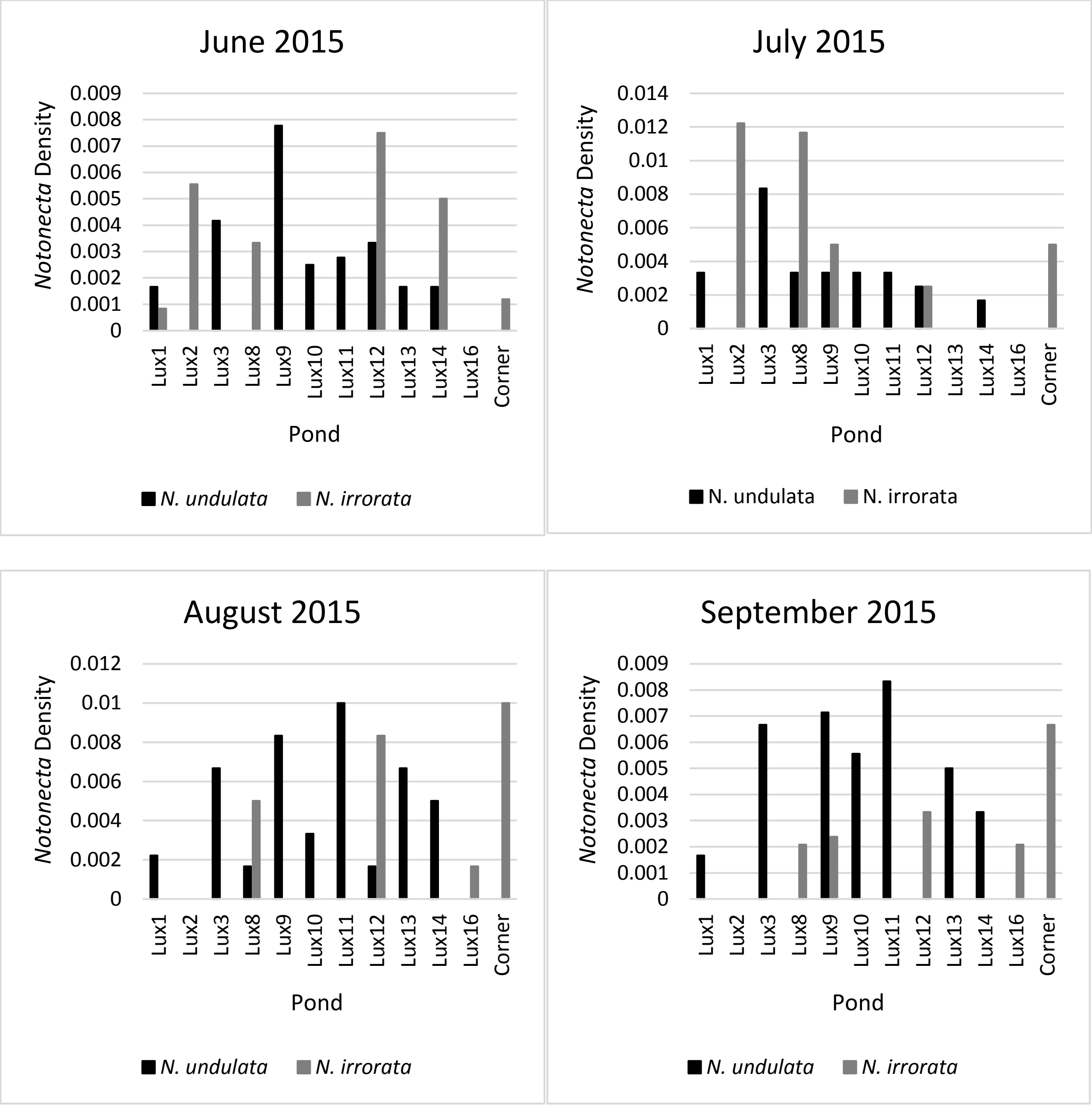


Table 3. The Contribution of variance (AdjR2) by each environmental and spatial variable to pure environmental (PE) and pure spatial (PS) component of variation partitioning.

Variable	June 2014	July 2014	August 2014	September 2014	June 2015	July 2015	August 2015	September 2015
DO	10.8.		38**			11.		
Temp	11.2*			22*				
pH						12.8*		
Cond	15.9.	19.7*				18.4.		
Chl a			15*					
biomass	26.6**		12*					
zoop1		15.3*				26.6*		
zoop2	2.8.	24.4*						
MEM4				18.8.	28.			
MEM5								9.6.
MEM6								22.5*
MEM7						8*	29.6.	
MEM9						10*	21.3.	10.5.
MEM10	49.3**	27**	15.	15.8.		15**		
MEM11					17.	49**	12.9.	24.

*Note: Significance p values are ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1. NS, non-significant fraction. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl a= Chlorophyll a, pH, biomass= Total zooplankton biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2.*

Table 4. List of environmental and spatial (MEMs) variables retained by forward selection when the response variable was square root transformed density of *Notonecta* juveniles, empty samples were removed, and a constant was added to the zero values. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl a= Chlorophyll a, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2. None: no significant variables returned by the selection process. NA: not applicable.

Sampling date/variables	MEMs	Spatial scale of MEMs	Autocorrelation of MEMs	Environmental variables
June 2014	None	NA	NA	TP
July 2014	None	NA	NA	None
August 2014	MEM5	intermediate	negative	None
September 2014	None	NA	NA	None
June 2015	MEM10, MEM4	fine, intermediate	negative	None
July 2015	MEM3, MEM8	large, intermediate	positive, negative	None
August 2015	MEM7	intermediate	negative	None
September 2015	None	NA	NA	None

Table 5. List of environmental and spatial (MEMs) variables retained by forward selection when the response variable was square root transformed density of notonectid species, empty samples were excluded and no constant was added to the zero values.DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl *a*= Chlorophyll *a*, pH, biomass= zooplankton total biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2. None: no significant variables returned by the selection process. NA: not applicable.

Sampling date/variables	**Environmental variables**	**Spatial variables (MEMs)**	**Spatial scale of MEMs**	**Autocorrelation of MEMs**
June 2014	None	None	NA	NA
July 2014	None	None	NA	NA
August 2014	DO, Chl *a*, biomass	MEM6, MEM9	intermediate, fine	negative
September 2014	Temp	MEM4, MEM10	intermediate, fine	negative
June 2014	None	None	NA	NA
July 2015	DO	MEM5, MEM6	fine	negative
August 2015	None	MEM5, MEM6, MEM7	intermediate, fine	negative
September 2015	None	MEM5	intermediate	negative

Figure 3. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), spatially structured environmental (SSE) components to notonectid community structure for different sampling dates. Response variable is the square root transformed density of notonectid species.

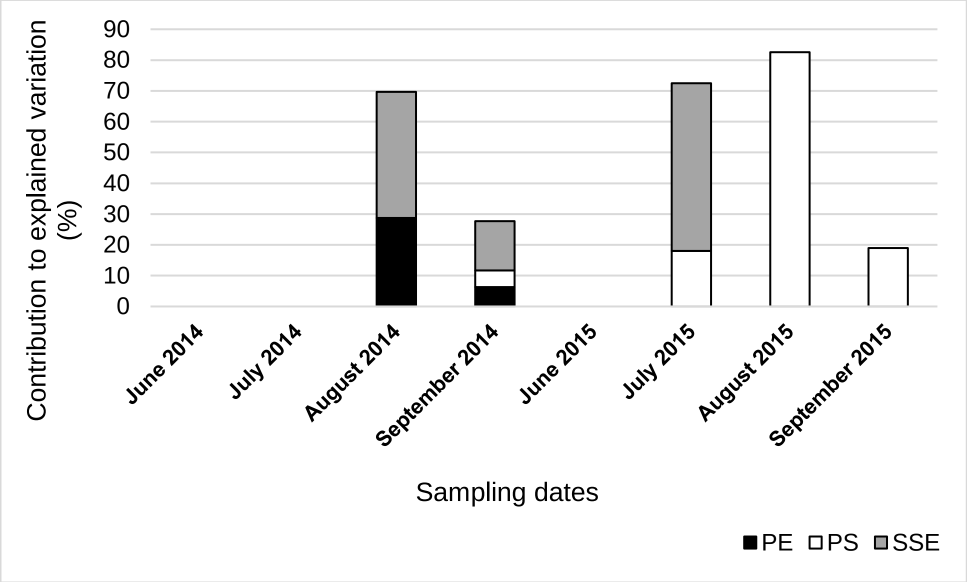


Table 6. List of environmental and spatial (MEMs) variables retained by forward selection. The response variable was the relative abundance (Hellinger transformed) of notonectid species, empty samples were excluded, and no constant was added to zero values. DO= dissolved oxygen, Temp= Temperature, Cond= conductivity, Chl a= Chlorophyll a, pH, biomass= Total zooplankton biomass, zoop1= zooplankton PCoA axis 1, zoop2= zooplankton PCoA axis 2, macro2= macroinvertebrate PCoA axis2. None: indicates that no variable was retained by forward selection. NA: not applicable.

Sampling date/variables	Environmental variables	Spatial variables (MEMs)	Spatial scale of MEMs	Autocorrelation of MEMs
June 2014	None	None	NA	NA
July 2014	None	MEM5	fine	negative
August 2014	DO, macro2, pH	MEM6	intermediate	negative
September 2014	Temp	MEM4, MEM5, MEM10	intermediate, fine	negative
June 2014	None	None	NA	NA
July 2015	Temp	MEM5	fine	negative
August 2015	None	MEM5, MEM6, MEM7	intermediate, fine	negative
September 2015	None	MEM5, MEM6, MEM8, MEM9, MEM10	Intermediate, fine	negative

Figure 4. The result of variation partitioning analyses showing the contribution of pure environmental (PE), pure spatial (PS), spatially structured environmental (SSE) components to notonectid community structure for different sampling dates. Response variable is the square root transformed density of notonectid species.

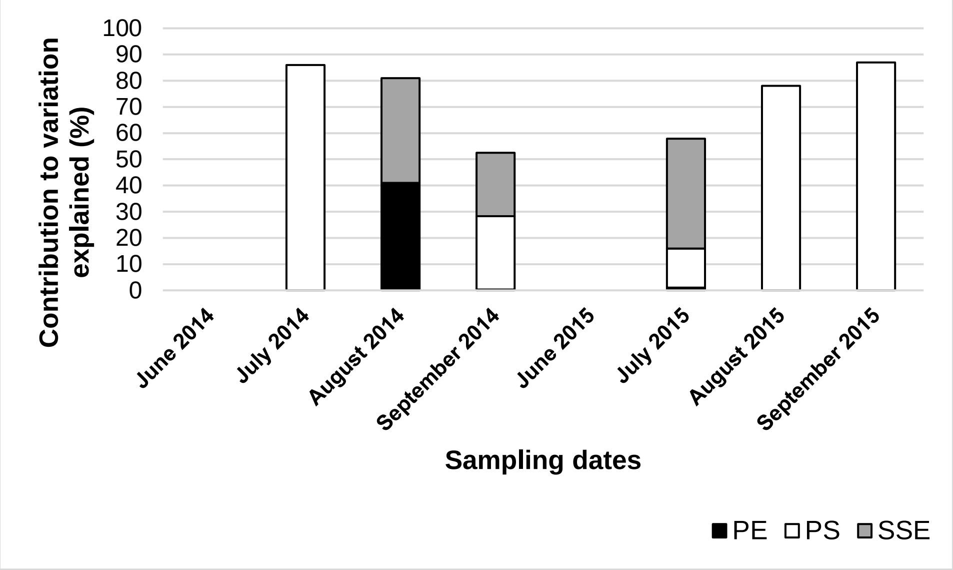
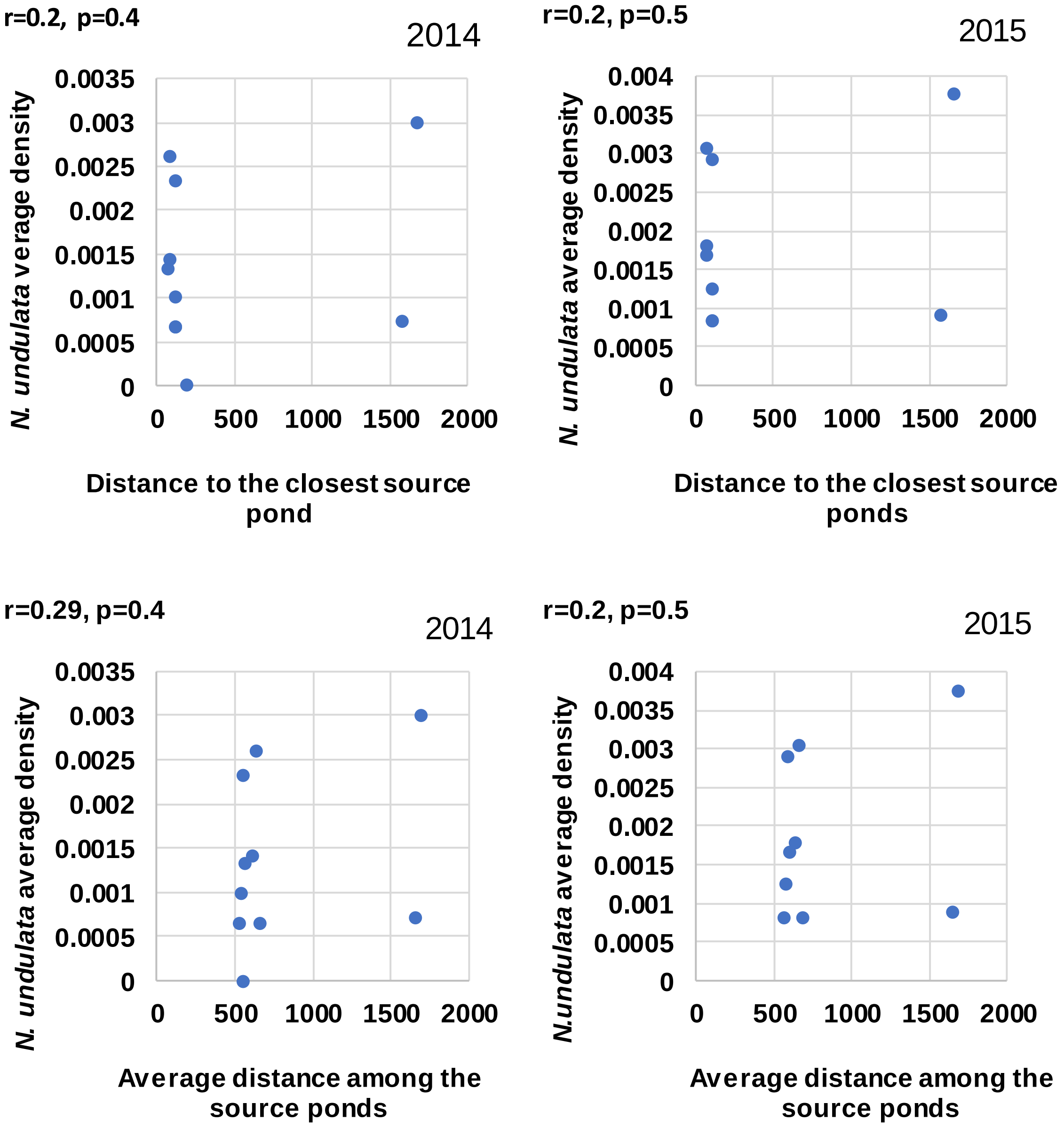
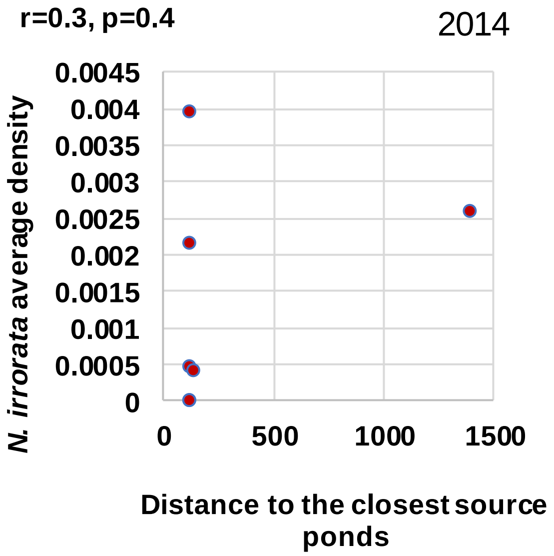
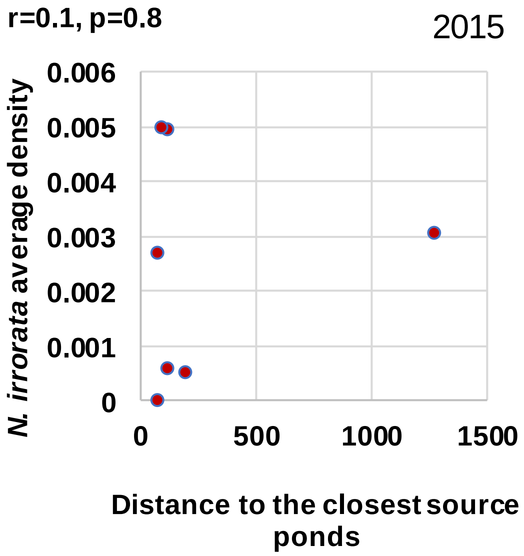
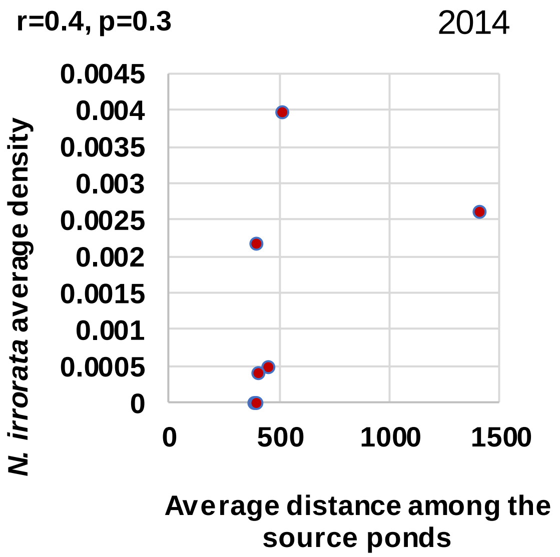


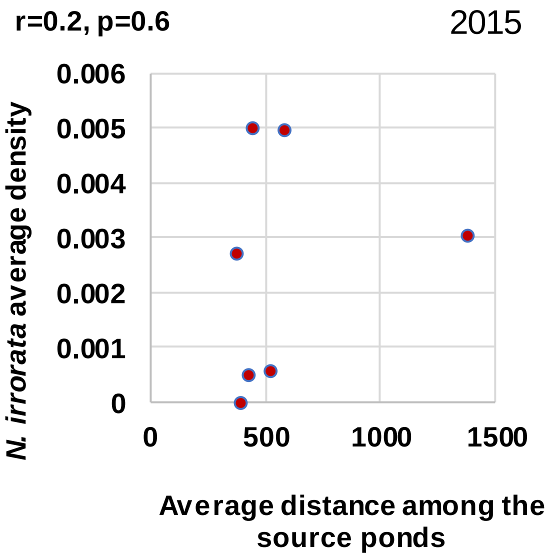
Figure 5. Relationship between the density (per liter) of adult notonectid species and pond connectivity measures. The X axis is distance to the closest source pond and average distance among the source ponds. The y axis is time-averaged abundance of *N. undulata* or *N. irrorata*, for first (2014) and second (2015) growing seasons. Distance values presented in the x axes are meters.




r=0.3, p=0.4
2014
N. irrorata average density
0.0045
0.004
0.0035
0.003
0.0025
0.002
0.0015
0.001
0.0005
0
0
500
1000
1500
Distance to the closest source ponds


r=0.1, p=0.8
2015
N. irrorata average density
0.006
0.005
0.004
0.003
0.002
0.001
0
0
500
1000
1500
Distance to the closest source ponds


r=0.4, p=0.3
2014
N. irrorata average density
0.0045
0.004
0.0035
0.003
0.0025
0.002
0.0015
0.001
0.0005
0
0
500
1000
1500
Average distance among the source ponds


r=0.2, p=0.6
2015
N. irrorata average density
0.006
0.005
0.004
0.003
0.002
0.001
0
0
500
1000
1500
Average distance among the source ponds

APPENDIX C

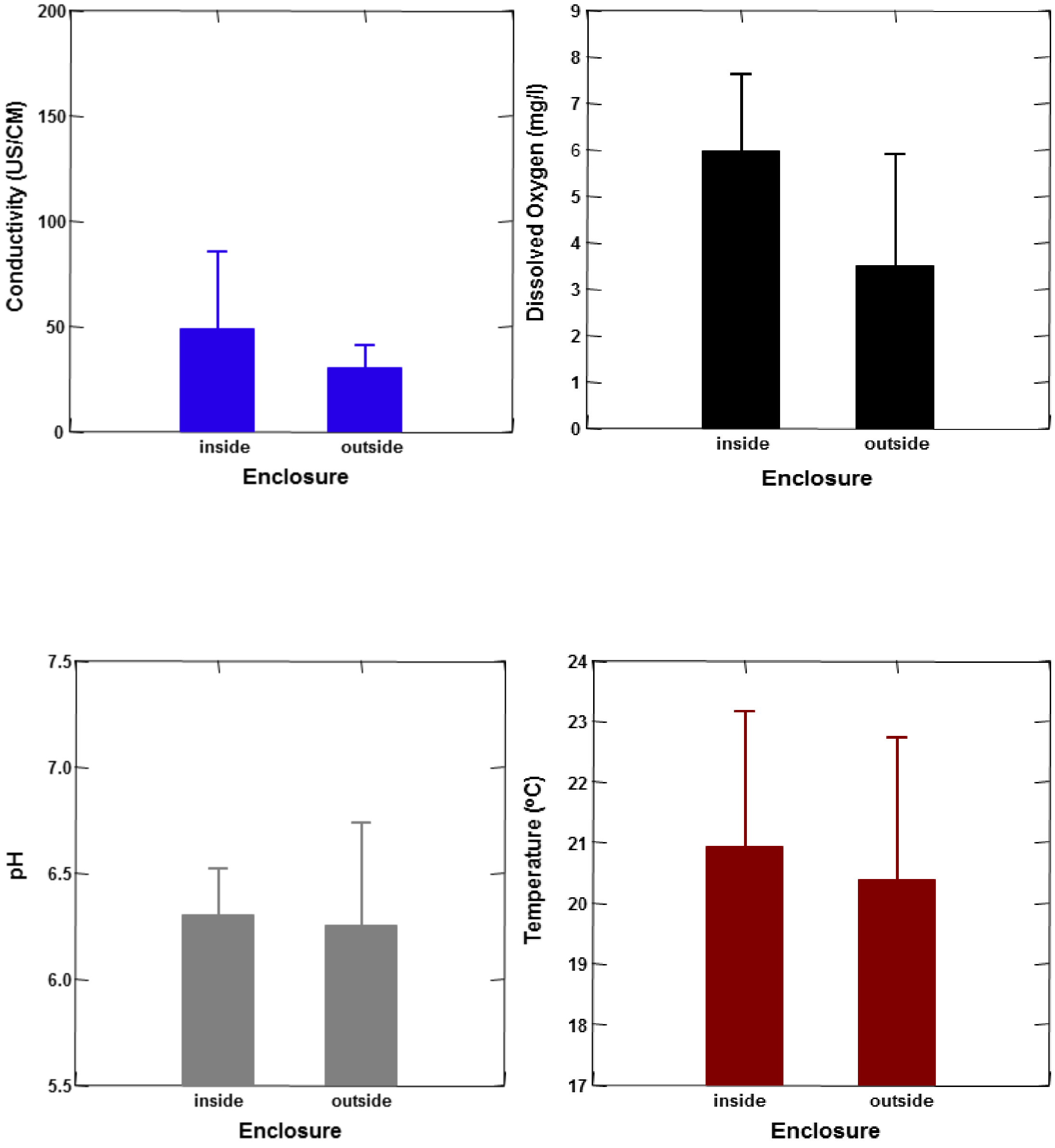
Table 1. The Principal Coordinate of Analysis (PCoA) axis 1 and 2 scores for pond zooplankton (A, C) and macroinvertebrates (B). Relative abundances of zooplankton and macroinvertebrates collected in mid-July were used for PCoA axes (A, B) used in the adult PLSR analyses. Relative abundances of zooplankton were averaged across June and July to calculate zooplankton PCoA axes (C) used for PLSR analyses of juvenile responses.

A. Zooplankton relative abundance		
	PCoA axis 1	**PCoA axis 2**
Daphnia	0.060057573	-0.11571529
Ceriodaphnia	0.003413213	-0.12748259
Scapholeberis	0.065892772	0.19012273
Pleuroxus	-0.118015502	-0.01770182
Chydorus	-0.108079551	-0.01724952
Simocephalus	-0.343394071	-0.05647418
Calanoids	-0.165262290	0.03571080
Cyclopoids	0.259406298	-0.47553264
Copopodites	0.543622057	-0.12209307
Rotifers	-0.010759765	0.60149447
Choaborus	-0.570868077	-0.26226345

B. Macroinvertebrates relative abundance		
	PCoA axis 1	**PCoA axis 2**
N. undulata	-0.1915671	0.48130997
N. irrorata	0.9180352	-0.15408953
dytiscid larvae	0.3125211	-0.12960783
corixid	-0.5332373	0.09086884
Buenoa	-0.3260041	-0.23252259

C. Zooplankton relative abundance		
	PCoA axis 1	**PCoA axis 2**
Daphnia	-0.02115226	0.104203119
Ceriodaphnia	-0.09765069	0.012350693
Scapholeberis	0.16986741	0.038912195
Diaphanosoma	0.01137730	-0.067621768
Alona	0.06271010	-0.004104616
Pleuroxus	0.07646663	0.009842993
Chydorus	0.11213775	0.029648231
Simocephalus	0.12432564	0.070275961
Calanoids	0.13953388	-0.118053639
Cyclopoids	-0.42212402	0.322279699
Copopodites	-0.39994274	-0.375733344
Rotifers	0.38478911	-0.102444902
Choaborus	0.28331991	0.216980546

Figure 1. Abiotic measures taken inside the experimental enclosures ("inside") and in the surrounding pond environment ("outside"). Values were averaged across enclosures and ponds (means, +/-S.E.). No significant differences were found when comparing inside versus outside (all p>0.1, t-test).



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ABSTRACT

EFFECTS OF LOCAL AND REGIONAL PROCESSES ON THE STRUCTURE OF NOTONECTA METACOMMUNITIES

by

MITRA ASGARI

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Advisor: Dr. Christopher F. Steiner

Major: Biological Sciences

Degree: Doctor of Philosophy

Understanding the processes influencing the spatial and temporal distribution of species is the main focus of ecological studies. Community structure and organization is affected by local and regional processes. Local processes affect population persistence and abundance of species through biotic interactions and abiotic environmental conditions within local sites. Regional processes, such as species dispersal among patches and colonization/extinction dynamics, can also affect the dynamics and structure of local populations and communities. Metacommunity theory considers the interplay of both local and regional processes as drivers of species distributions among isolated patches. Recent studies, suggest considering features such as habitat type, dispersal mode, and the spatial scale, along with examining time-series to obtain a more comprehensive understanding of the processes affecting community structure. To address how temporal variation impacts the relative effects of local and regional processes on metacommunity organization, we performed a two-year study of seasonal variation in *Notonecta* metacommunity structure in fishless ponds in southern Michigan. Our result showed that notonectid community composition was affected by

environmental, spatial, and spatially structured environmental processes. Notonectid metacommunity structure was affected by several ponds' environmental factors and fine to intermediate spatial scales. We also found significant seasonal changes in the relative contribution of environmental and spatial processes to notonectid community structure. Furthermore, with a series of pond in situ studies, we experimentally tested the effects of local conditions versus dispersal limitation on the heterogenous distribution of *Notonecta* species in fishless ponds using adult and juveniles' responses. Our results provide some support for the importance of local environmental control of *N. irrorata*'s distribution. They also suggest that dispersal limitation, rather than local environmental factors, may be responsible for the absence of *N. undulata* from Lux 2. The findings from our study contribute to our limited understanding of the relative importance of local and regional processes in the structure of natural communities. The outcome of our research confirms the inclusion of both spatial and environmental variables for understanding the factors affecting community organization. Moreover, our findings make clear the importance of examining time-series to obtain a more comprehensive understanding of the processes affecting community structure. Finally, our work makes clear that the inclusion of features such as spatial scale of the study and dispersal behavior, may be vital for comprehending the structure of metacommunities.

AUTOBIOGRAPHICAL STATEMENT

Mitra Asgari

EDUCATION:

2012-2018 Ph.D. in Biology, Wayne State University, Detroit, Michigan, USA
2006-2009 M.Sc. (Marine Biology), Shahid Beheshti University, Tehran, Iran
2002-2006 B.Sc. (Biology), Shahid Beheshti University, Tehran, Iran

PUBLICATIONS:

Asgari, M., & Steiner, C. F. (2017). Interactive effects of productivity and predation on zooplankton diversity. Oikos.

Amini-Yekta, F., Izadi, S., Asgari, M., Aghajan-Pour, F., & Shokri, M. R. (2017). Higher taxa as surrogates for species richness in intertidal habitats of Qeshm Island in the Persian Gulf. Marine Biodiversity, 1-8.

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AWARDS:

2015 T. Wayne and Kathryn Porter Graduate Fellowship, KBS
2015 Graduate Student Professional Travel Award, WSU
2015 Aquatic Ecology Committee Travel Award, Ecological Society of America
2016 GEOC Graduate Teaching Award, WSU
2016 N.I.H. Broadening Experiences in Scientific Training (BEST), WSU program teaching internship award
2017 Graduate Teaching Assistant Award, Department of Biological Sciences, WSU