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Recovery of Zooplankton Communities to Whole-Lake Disturbance

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Recovery of Zooplankton Communities to Whole-Lake Disturbance

by

Brian Newton McGann

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Environmental Science and Management

Thesis Committee:
Angela Strecker, Chair
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Abstract

Community assembly following disturbance is a key process in determining the composition and function of the future community. However, replicated studies of community assembly at whole ecosystem scales are rare. Here, I describe a series of whole-lake experiments in which the recovery of zooplankton communities is tracked following an ecosystem-scale disturbance. Fourteen lakes in eastern Washington were chosen: seven lakes were treated with rotenone, while the remaining seven were reference. Each lake was monitored up to six months before and one to two years after the rotenone treatments. Zooplankton tows were taken monthly, at a shallow, intermediate, and deep site in each lake, and were later enumerated and identified. A depth profile of environmental variables was taken at the deepest site. Community responses following disturbance were assessed using coarse metrics of abundance and diversity, community composition measures, and the relative importance of species traits was assessed by grouping taxa into functional groups. Communities were considered recovered if there was no significant difference between treatment and reference in zooplankton community metrics of abundance, diversity, and composition.

There was a steep decline in the abundance and diversity of the zooplankton community post-treatment. In many of the lakes, cyclopoid copepods, the group with a unique dormancy strategy, were the first group to recover, remained dominant for a few months, and may have exhibited priority effects advantages. Calanoid copepods were the slowest group to recover, perhaps due to their slow rate of development. There were varying recovery times and patterns between lakes, potentially based upon geographic

location and severity of the winter season. These findings suggest that dormancy strategies, rate of development, and abiotic conditions following disturbance may be important in helping to understand recovery processes. Results of this study may give insight to disturbance ecology and the relative importance abiotic versus biotic characteristics that structure post-impacted communities.

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Chapter One

Background

Fires, flash floods, deforestation, and volcanic eruptions are examples of disturbances that can have drastic consequences, often causing major effects to natural communities. Over time, disturbance events shape ecosystems and landscapes as communities become adapted to cope with these natural fluctuations (Dayton 1971, Pearsons and Lamberti 1992, Gunderson 2000). A moderate level of disturbance can lead to higher diversity, as disturbance opens up niches for species to fill (Hobbs and Huenneke 1992). However, repeated stressors over a period of time may cause legacy effects, in which a community becomes dominated by disturbance-tolerant species and is pushed to a new equilibrium (Walsh et al. 2005). It is vital to understand how ecosystems are shaped by and respond to disturbances, especially for resource managers, who need the ability to predict recovery processes following disturbance in order to adjust their management strategies (Holling and Meffe 1996). Although disturbance is a widely studied phenomenon in ecology, the question remains as to what factors cause communities to exhibit varying responses to disturbance (Fraterrigo and Rusak 2008). However, disturbance ecology is a difficult field to study due to the stochastic nature of these events occurring across the landscape.

Due to the unpredictability of natural disturbances, anthropogenic disturbances offer a unique opportunity to study ecosystem responses to potentially novel stressors. As the world continues to become greatly impacted by human disturbance and alteration, it becomes ever more important to understand recovery processes in the context of

anthropogenic stressors. In many cases human activities are disturbances that communities have historically not been exposed to. These novel disturbances can transform ecosystems (Brasher 2003). In many cases these systems are not just subject to one anthropogenic disturbance, but rather many disturbances, both natural and anthropogenic, whose interactions influence and determine ecosystem response (Uriate et al. 2009). Following extensive periods of anthropogenic disturbance, communities may exhibit characteristics that prohibit normal secondary succession patterns from occurring (Aide et al. 1995). For example, Zimmerman et al. (1995) found that land use histories affected species composition and therefore the abundance of pioneer species following disturbance. Understanding responses to disturbance in altered communities is an essential and underexplored phenomenon.

Community assembly occurs in the aftermath of extreme disturbances. If the disturbance is extreme enough to kill the entire community, then recovery is dependent upon organisms that can remain viable (e.g., through dormancy) and those that can disperse back into the recovered area (Arnott and Yan 2002, Brock et al. 2003, Howeth and Leibold 2010, Gray and Arnott 2011). The assembly of the community following extreme disturbances is dependent upon the diversity of organisms migrating into the area, the connectivity between source and sink populations, the productivity of the system, and the level of disturbance (Chase 2003). Early recovering species may show priority effects advantages in which the first species to colonize or emerge retains advantages in the long term and may deter the recovery of other species (HilleRisLambers et al. 2012, Louette and De Meester 2007, Tucker and Fukami 2014).

These early recovering species may be those that are most resistant (i.e., the ability of an organism to withstand a disturbance unaffected) (Grimm and Fisher 1989). Early recovering species may also be pioneers, those that have high growth rates and are able to take advantage of open niches following disturbance (Rozendaal et al. 2017). Low levels of disturbance following a major disturbance allow for the coexistence of species and may prevent competitive exclusion by inhibiting priority effects (Tucker and Fukami 2014). However, recovery to disturbance is an intricate process involving more than just community assembly.

Community assembly is usually followed by community succession where the community switches from being dominated by fast-growing species to slower growing species that are more efficient at resource allocation (Koch 1974, Tilman 1990). Once the abiotic characteristics of the habitat recover, recovery accelerates, but there is not a simple straight line to recovery as successional, or developing, communities can evolve in steps (Keller et al. 2002, Dupuis et al. 2015). These steps of recovery may include dominance by resilient members at first, and changes brought about by the composition and development of the predator community (Keller et al. 2002, Dupuis et al. 2015). Resilience, i.e., the ability of an community to return back to a steady equilibrium following disturbance, can be affected by anthropogenic stressors and can be measured by the adaptive capacity of a community to transform to a new equilibria (Gunderson 2000). Secondary succession following disturbance is dynamic as diversity can peak before communities reach equilibrium, which may take decades (Schoonmaker and McKee 1988). Long-term studies offer unique perspectives on secondary successional

processes because they can be used to determine baseline conditions prior to impact and also to document patterns that develop slowly after impact (Peterson et al. 2003, Turner et al. 2003). Clearly it is important to understand long-term secondary successional processes in communities, but these processes are dependent upon the community composition of species rebounding from the disturbance.

Disturbance to ecosystems is not uniform as some species are more affected than others due to their morphological, physiological, and behavioral characteristics or traits (Walker 1991, Brown et al. 1999, Stephens and Finney 2002, Russell et al. 2009). The interplay between colonization and competitive abilities of species, and the ability of successional niche species to sustain their early dominance into later recovery shapes communities and sustains diversity (Pacala and Rees 1998, Uriarte et al. 2012). The relative importance of traits in affecting competitive interactions in the developing community is still unclear. To truly understand the development of a community following disturbance it is necessary to understand what characteristics of a species help to drive its recovery trajectory. Differential rates of recovery between species can be attributed to a number of characteristics and interactions. The life history strategy of species is essential in determining the colonization and population growth potential following disturbance, as taxa differ in fecundity, life span, production of resistant propagules, intrinsic growth rate, and minimum population densities needed for establishment (Allan 1976, Cáceres 1998, Arnott and Yan 2002, Olden et al. 2006). Once communities are established, the competitive interactions among species are dependent upon resource limitation, resource partitioning, environmental fluctuations,

and predation, which may affect exploitative competition (DeMott 1989). An in-depth analysis is needed for disturbance ecology studies, as in many cases recovering communities may not exhibit differences in abundance, richness, or diversity, but instead may exhibit differences in community composition and functional diversity (Zimmerman et al. 1995, Willig et al. 1996). However, these recovery processes are usually slow developing and must be studied in the right context or system to adequately understand processes.

Lakes are an ideal setting with which to study the process of recovery from disturbance, and the zooplankton living within them are particularly useful study organisms. Lakes have clear boundaries (Post et al. 2007) and undergo a vast array of environmental disturbances, such as acidification, drought, fires, agriculture, and fisheries management, either directly or through interactions with their watersheds. Zooplankton are ideal study organisms due to their small size, short life span, ease of collection, and sensitivity to environmental conditions (Spitze 1995, Hanazato 2001). Zooplankton are known to disperse overland through natural and human vectors, but the relative importance and quantity of overland dispersal is poorly understood (Sorensen and Sterner 1992, Johnson et al. 2001, Cáceres and Soluk 2002, Havel and Shurin 2004, Figuerola et al. 2005, Gray and Arnott 2011). Recovery to disturbance is an ecosystem-wide phenomenon, so a comprehensive study must include community aspects, which are often not represented in small-scale experiments and can be better understood in ecosystem-scale, whole-lake manipulation experiments (Schindler 1998).

Few disturbances are as extreme and as short-lived as rotenone treatments to remove fish communities from lakes. Rotenone, a piscicide, has been used in fisheries management since the early 1930s (Krumholtz 1950). From a fisheries perspective, trout lakes function at the highest when managed as a monoculture in which other fish species do not compete with trout for food resources (Barrow and Peters 2001). The presence of other fish species may reduce the size and catch rate of trout, as there is increased competition for food resources and altered trophic-level dynamics (Holmen et al. 2003, Zimmerman and Vondracek 2006, Browne and Rasmussen 2009). When these lakes become unproductive, from a trout-management perspective, they may be treated with rotenone, a chemical highly toxic to both invertebrate and vertebrate animals, to remove the competing, non-game fish species (Bradbury 1986). Following rotenone treatment, trout lakes are frequently restocked with fingerling rainbow trout in the spring, with the assumption that lakes are safe and productive for trout growth (Rowe 2001). However, trout fingerling growth and survival is dependent upon the composition and abundance of the zooplankton community in the lake (Beauchamp 1990, Tabor et al. 1996). Despite the potential for impacts on non-target organisms, the effects of rotenone on non-target organisms, like zooplankton, are not fully understood.

Though the effects of rotenone on zooplankton have been studied, there is no clear understanding of differential rates of recovery to the piscicide (Vinson et al. 2010). Zooplankton are known to be extremely susceptible to rotenone, with high mortality rates at low doses (Dalu et al. 2015). A review by Vinson et al. (2010) found that zooplankton community abundance recovers usually within three months, but diversity and

community composition take up to and more than year to recover. However, prior studies addressing the recovery of invertebrates to rotenone differed in the definition of recovery, relied upon small sample sizes, and had little replication (Vinson et al. 2010). Prior studies have shown that the taxonomic group that first recovers differs among studies, with some studies showing copepods responding first and other studies showing small cladocerans recovering first (Kiser et al. 1963, Anderson 1970, Melaas et al. 2001, Peterson et al. 2011, Dalu et al. 2015). The recovery of zooplankton is greatly affected by the alteration of the fish community, as the extermination of zooplanktivorous fish alters the predation pressure (Duggan et al. 2015). There still remains the need for a well-designed experiment to determine the effects of rotenone on zooplankton and the ensuing recovery process.

In this study I aim to accomplish a number of goals with regards to recovery from a major anthropogenic disturbance. My objective is to look at community assembly in zooplankton communities in response to rotenone treatment and compare them to baseline natural changes using a Before-After-Control-Impact (BACI) experiment, a well-known study design used in testing for environmental impacts (Underwood 1991, 1993; McDonald et al. 2000). Here I define recovery as no significant difference between treatment and reference communities in metrics of zooplankton abundance, diversity, and community composition, as well as abundances of major taxa. Categorizing major taxa into functional groups will help to understand if there are common species traits that can give insight into recovery trajectories (Table 1.1). I will compare recovery trajectory from a major anthropogenic disturbance to other

intermediate disturbances or stressors, such as fish stocking in lakes. I will then use these results to help inform fisheries management to ensure stocking strategies following rotenone treatment align with zooplankton recovery patterns.

I hypothesize that the important mechanisms affecting the dynamics of recovery will be: 1) dormancy strategies, 2) predator compositional changes, and 3) competitive interactions (Figure 1.1), which leads to some testable predictions. Although dispersal of viable diapaused zooplankton from nearby lakes may be a factor in community assembly following disturbance, these rates are thought to be low and potentially unimportant relative to within lake emerging populations (Bohonak, and Jenkins 2003, Gray and Arnott 2011). First, I hypothesize that for a zooplankton community to recover from a disturbance via emergence from the sediment, it must contain species that lay diapausing eggs, or survive in encysted juvenile stages that can undergo a period of resistant dormancy before emerging when conditions become favorable (Cáceres 1998, Arnott and Yan 2002). I predict that more productive lakes with warmer climates will recover faster, as zooplankton need warmer temperatures to emerge from dormancy, and those emerged zooplankton will have higher food availability (Arnott and Yan 2002, Vadeboncoeur et al. 2003). Further, I predict that the first group of zooplankton to rebound following the disturbance will be cyclopoid copepods, as they undergo dormancy in encysted juvenile stages and thus will have a developmental advantage over species that need to wait for the right conditions to emerge from diapause, such as calanoid copepods and cladocerans (Nalepa 1985). Secondly, I predict that predatory community shifts, i.e. fish stocking, will be a key determinant in the rate of recovery of zooplankton communities, as this acts

as a stressor to the community. I predict that the ‘priority effects’ advantage of cyclopoids will be short lived, as disturbance is known to allow the coexistence of multiple species and prevent competitive exclusion (Tucker and Fukami 2014). In this circumstance, fish stocking may serve to be a disturbance mechanism that allows for coexistence of multiple species. Thirdly, I hypothesize that later successional patterns will be dependent upon group traits such as resource allocation efficiency, developmental time, and reproduction strategies. These mechanisms will affect recovery processes, resulting in varying recovery times between lakes and between zooplankton taxa.

Tables

Table 1.1: Major zooplankton functional groups used in this study. Grazing efficiency, dispersal ability, and development time are based on rates relative among the groups

Trait/ Strategy	Cladocera	Cyclopoida	Calanoida	Source
Reproduction type	Asexual/Sexual	Sexual	Sexual	Thorp and Covich 2009
Dormant stage	Resting eggs	Encysted juvenile	Resting eggs	Thorp and Covich 2009
Grazing efficiency	High	Low	Medium	Barnett and Beisner 2013
Feeding type	Filtration	Raptorial	Stationary suspension	Barnett and Beisner 2013
Development time	Fast	Medium	Slow	Allan 1976

Figures

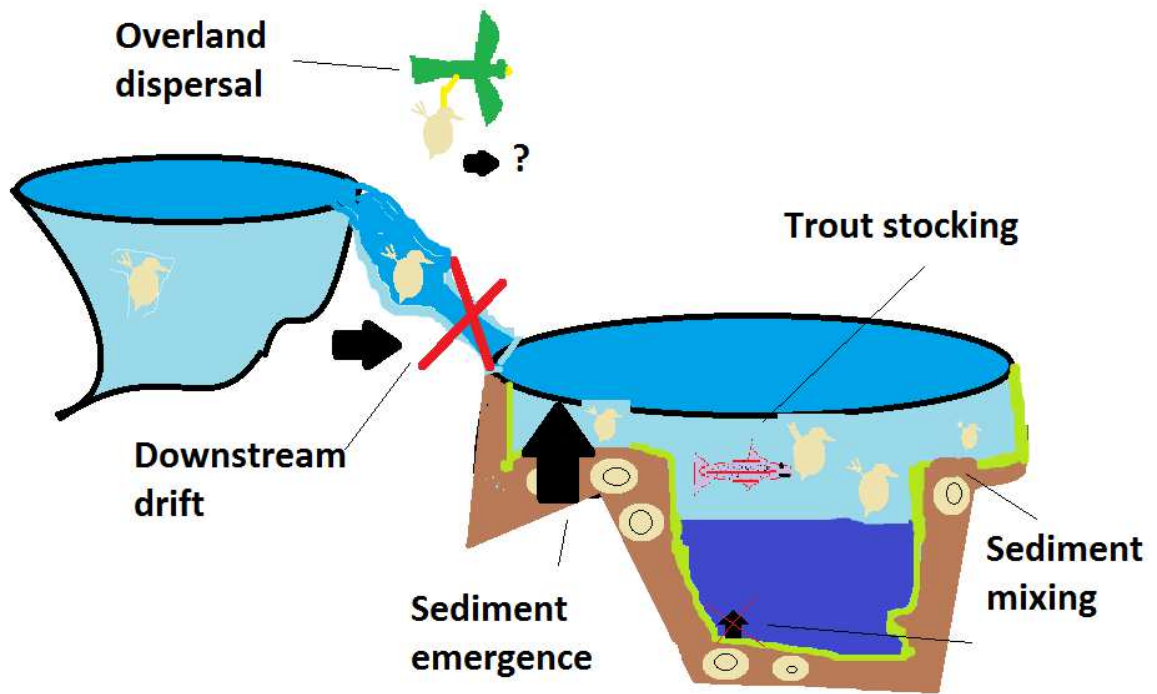


Figure 1.1: Conceptual model of zooplankton recovery to disturbance

Chapter Two

Introduction

Disturbances are a key factor that shapes landscapes, and the responses of species following disturbances determine community composition. The intensity and return interval of disturbances shapes community diversity, and can drive community characteristics as they become adapted to these events (Dayton 1971, Hobbs and Huenneke 1992, Pearsons and Lamberti 1992, Gunderson 2000). However, anthropogenic disturbances have become prevalent across the landscape and pose new threats that communities are not adapted to. For instance, anthropogenic disturbances can shift communities to new equilibria (Aide et al. 1995, Brasher 2003). The factors that influence community responses to disturbance are still uncertain, but remain a vital concern for resource managers whose understanding of recovery processes helps to dictate their management strategies (Holling and Meffe 1996, Fraterrigo and Rusak 2008).

Recovery to disturbance is a dynamic process that evolves as time passes. Immediately following severe disturbances, community assembly occurs, which is dependent on immigration and emergence from dormancy, and can be affected by the severity of the disturbance and system characteristics (Brock et al. 2003, Chase 2003, Ferrenberg et al. 2013, Myers et al. 2015). The first species that appear following disturbance tend to be those that are resistant to the disturbance, as well as species that are quick to develop, and may show priority effects advantages where their early

colonization leads to short-term dominance of the community (Grimm and Fisher 1989, HilleRisLambers et al. 2012, Louette and De Meester 2007, Tucker and Fukami 2014, Rozendall et al. 2017). Additional stressors on the community, such as predator introductions, may reduce the importance of priority effects and lead to secondary succession, where the community evolves to consist of slower developing species (Koch 1974, DeMott 1989, Tilman 1990, Keller et al. 2002, Dupuis et al. 2015). Secondary succession is dependent upon species interactions in the developing community, which are affected by resource levels, abiotic conditions, predation, and species traits (Vieira et al. 2016, Uriarte et al. 2012). For example, Del Moral and Chang (2015) found that soil infertility, level of disturbance, and the domination of a nitrogen-fixing species affected plant succession of communities impacted by the Mount St. Helens eruption. However, the relative importance of the factors that drive interactions in the developing community are still unclear.

Prior studies on community recovery from disturbance have limitations. One of the major issues is that the disturbance is unplanned, thus there are rarely pre-impact samples to determine baseline conditions prior to impact. Research at long-term research sites has documented slow developing successional processes from unplanned disturbances, but in many cases these studies lacked replication and appropriate reference systems (Peterson et al. 2003, Turner et al. 2003). Another difficulty with studies of recovery from disturbance is the emphasis on specific target effects in a community, i.e. the creation of tree gaps by large tree mortality acts to maintain tree diversity (Hubbell et al. 1999). Schindler (1998) highlighted the need to study disturbances on a larger scale,

as small scale experiments may not accurately assess larger scale processes, upon which lake management decisions depend. Additionally many studies rely on coarse structural attributes, such as abundance, richness or diversity, which may miss certain recovery patterns. For instance, species could respond differently to disturbances, but as a result of compensatory dynamics, coarse structural attributes may miss this pattern (Klug et al. 2000). Relative species abundance changes are provided in studies using community compositional analysis, which may find differences in recovering community composition, when no effect is detected using coarse attributes (Zimmerman et al. 1995, Tilman 1996, Willig et al. 1996). Ideally, recovery from disturbance is studied from replicated, whole-ecosystem scale disturbances that examine both short- and longer-term responses following the impact (Siedl et al. 2014, Schaffer et al. 2017).

Lakes are a model system for studying disturbance recovery because of their defined boundaries (Post et al. 2007). Zooplankton are especially useful subjects due to their small size, short life span, ease of collection, and sensitivity to environmental perturbations (Spitze 1995, Hanazato 2001). Previously, whole lake manipulations have resulted in clear ecological responses, such as eutrophication following the addition of phosphorous treatments (Schindler 1974). Rotenone, a pesticide used to manage fish populations, is an example of severe, short-lived disturbance, due to its high toxicity and its ability to rapidly breakdown to non-toxic forms (Finlayson et al. 2014, Dalu et al. 2015). Although rotenone is used to target nuisance fish populations, it can have severe effects on non-target organisms, including crustacean zooplankton (Melaas et al. 2001). Previous studies reviewed by Vinson et al. (2010) on the recovery of zooplankton

communities to rotenone have been equivocal, varying in the time to recovery and taxon-specific sensitivity. However, these results were largely based upon short-term, unreplicated studies with no agreed upon definition of recovery, e.g., Duggan et al. (2015) based their findings on an unreplicated study, and limited sampling frequency in Melaas et al. (2001) did not account for seasonal fluctuation in their analysis.

In this study, I aimed to determine what abiotic and biotic factors influence the recovery of zooplankton communities to rotenone treatment. These objectives were attained by assessing the recovery of rotenone-treated lakes to non-treated lakes by sampling before and after impact, using a Before-After-Control-Impact (BACI) design (Underwood 1991, 1993; McDonald et al. 2000). BACI studies are an excellent way to assess changes in a community in response to a disturbance, as the effect of treatment on the impacted sites is compared to baseline changes in the reference sites using before and after sampling. Here, I define recovery as no significant differences in zooplankton community structure, functional trait groups, and composition when compared to reference lakes (Xiang et al. 2014).

I hypothesize that there will be three major mechanisms structuring recovery: 1) dormancy strategies, 2) predator alterations, 3) competitive interactions. First, I hypothesize that warmer, more productive lakes will recover the fastest as they will have the most successful emergence from diapaused eggs and higher phytoplankton resources for zooplankton dispersed into the lake. Emergence from diapause and dispersal from surrounding lakes are likely the two major mechanisms of zooplankton recovery (Cáceres 1998, Arnott and Yan 2002, Vadeboncoeur et al. 2003, Dalu et al. 2015). Further I

predict that the first functional group to recover will be the cyclopoid copepods, as they undergo dormancy in a more advanced stage compared to calanoid copepods and cladocerans, and may have priority effects advantages (Nalepa 1985). Secondly, I predict that the stocking of the lakes with trout following treatment will result in a disturbance that reduces the early colonizer advantages and allows for coexistence of major functional groups (Tucker and Fukami 2014). Thirdly, I predict that in the spring, succession will switch from faster developing species, to those that are better at resource allocation, as there will be more food available to support a broad range of functional groups (Koch 1974, Tilman 1990). Dormancy strategies, predator alterations, and competitive interactions will result in variation in recovery patterns between lakes, which will also be influenced by abiotic conditions and community composition prior to the treatment.

Methods

Study sites and design

In order to test my hypotheses, the recovery of zooplankton was monitored via a Before-After-Control-Impact (BACI) experiment. In my study, the impacts on seven rotenone lakes were compared to seven reference lakes. Rotenone was applied to lakes in the fall of either 2014 or 2015. All of the lakes in my study are located in eastern Washington in three distinctive ecoregions: (1) the Columbia Plateau, includes Amber, Badger, Dry Falls, Lower Hampton, Rat, Upper Hampton, and Widgeon lakes; (2) the Okanogan, , includes Big Twin and Lost lakes; and (3) the Canadian Rocky Mountain

region, , includes Bayley, Browns, Cedar, McDowell, and No Name lakes (Figure 2.1). The Columbia Plateau ecoregion is a semiarid heterogeneous landscape with a mix of channeled scabland and coulee areas, thick glacial deposited soils, sagebrush vegetation, and is highly impacted by large irrigation agriculture, including the vast Columbia Basin Project. The Okanogan and Canadian Rocky Mountain regions are mountainous landscapes of wide valleys with a more diverse geological foundation ranging from sedimentary, volcanic, metamorphic rock to unconsolidated deposits. The climate of these regions consists of hot, dry summers, to frigid, snowy winters with more snowfall increasing as one moves east. The lower elevations in the Okanogan and Canadian Rocky Mountain ecoregion are dominated by shrub-steppe grassland, where the ridges and hills contain a variety of conifer forests. The northeastern part of the state is largely partitioned into national forests, tribal territories and national wildlife refuges with some small-scale agriculture in the low valleys.

Rotenone and reference lakes were chosen purposely to be as similar as possible. The study lakes are relatively small (4.5 – 88 ha), low elevation (305 – 1300m), shallow to moderate depth (6 – 30m), and mostly mesotrophic (total phosphorus (TP) from 8 – 33 $\mu\text{g/L}$) (Table 2.1). There were no significant differences between reference and rotenone lakes for each of these variables, except for total nitrogen, which was significantly higher in reference lakes using a Welch's *t*-test, which assumes unequal variances between groups (Table 2.1). These lakes are hydrologically disconnected to other large waterbodies. Both reference and rotenone lakes were stocked every year with fingerling trout by Washington Department of Fish and Wildlife.

Sampling methodology

Lakes were sampled monthly by B. McGann (summer) and fisheries biologists of Washington Department of Fish and Wildlife (fall through spring) from June 2014 to September 2016 (Table 2.2). Winter sampling was inconsistent due to ice conditions and accessibility. Rotenone lakes were sampled more intensively in the weeks before and after rotenone exposure, when possible. Each lake was sampled at three sites for zooplankton: a shallow site, a middle site (intermediate between the deep and shallow sites), and the deepest spot in the lake, determined by a bathymetric map. This sampling methodology allowed me to assess the full diversity of zooplankton in the lake, including littoral taxa (Walseng et al. 2006). The shallow site was at least 4-m deep to account for the length of the net. The same locations were sampled at each visit to the lake, which was confirmed by the use of a portable GPS unit. At each location a sample of zooplankton was taken using a vertical plankton tow, using a net with a mesh size of 80 μm and a diameter of 30 cm. Zooplankton samples were preserved at a final concentration of 70% ethanol for later enumeration and identification.

At the deep site in each lake, physical and chemical characteristics were measured at each sampling visit using various meters (Appendix A1). Generally, the same meter was consistently used on each lake; however, six data points were removed when district biologists suspected irregularities in meter output. Temperature, pH, conductivity, and dissolved oxygen were recorded at 1-m intervals. Also, a Secchi disk reading, used for water clarity, was taken at each deep site. In July of each sampling year, an integrated water sample of the epilimnion was taken using a 2.5-cm diameter tube sampler for

purposes of nutrient analysis. These unfiltered water samples were frozen immediately until analysis. Samples were analyzed with a Shimadzu UV-1800 Spectrophotometer (Shimadzu, Kyoto, Japan) at the Cooperative Chemical Analytical Laboratory following CCAL 33A.3 for total nitrogen (Cooperative Chemical Analytical Laboratory 2013) and CCAL 35B.2 for total phosphorus (Cooperative Chemical Analytical Laboratory 2010).

Zooplankton enumeration and identification

Morphologically-based identification of the zooplankton community was conducted through the use of a Leica M165C microscope and IC80HD camera (Leica Microsystems Inc., Buffalo Grove, IL). In order to reduce the high number of samples to enumerate, composite samples were made of each lake by volume-weighting the deep, middle, and shallow sites. A Folsom plankton splitter (Wildco Wildlife Supply Company, Yulee, FL) was used to subsample until the sample was dilute enough to count a reasonable number of individuals. The enumeration procedure followed Strecker and Arnott (2005), which included counting at least 50 adult individuals of each species, 25 juveniles of each order, until reaching 250 individuals per sample. This protocol is designed to search more of the sample for rare species. Adult individuals were identified to species level when possible, and copepod juveniles were identified to order or subclass using taxonomic keys (Thorp and Covich 2009, Haney et al. 2013).

Statistical analysis

Metrics of community structure were calculated for each sample, including Shannon-Wiener diversity, total density for all crustacean zooplankton, and total density

for each of the three major functional groups (calanoids, cyclopoids, cladocerans) in these lakes. It was necessary to categorize taxa within these groups because many species were only found in a fraction of lakes. Additionally these taxonomic divisions also generally represent differences in function, such as feeding type, mode of reproduction, dormancy strategies, and relative development speeds (Appendix B1, B2). These metrics were averaged monthly to compare baseline trends in the reference lakes to trends in the rotenone lakes.

I tested for differences in water quality parameters (specific conductance, Secchi depth, dissolved oxygen, pH) and zooplankton structural metrics (total density, diversity, functional group abundance) using linear mixed effects models (LME). LME models are common to BACI experiments with repeated measures data testing the effects of disturbance (Underwood 1991). LME models are a valid alternative method for repeated measures ANOVA, because they can account for non-normality, time-series dependence, and can potentially model covariance (McDonald et al. 2000). LME models estimate linear parameters, taking into consideration both fixed effects (e.g., disturbance) and random effects (e.g., sites) using a maximum likelihood iterative approach (Lewis 1998).

Lakes that were treated with rotenone in 2014 and 2015 were analyzed in separate models (hereafter referred to as 2014 rotenone and 2015 rotenone), in order to account for the differences in treatment years. Two LME models were run for each metric of 2014 rotenone lakes: year one and year two following treatment. The 2014 rotenone year one model contrasted the four rotenone lakes with the seven reference lakes from June 2014 to September 2015; whereas the year two model again used pre-impact data from

June to September 2014 contrasted with post-impact data from September 2015 to September 2016. A single LME model was used for 2015 rotenone lakes, contrasting reference and rotenone lakes from May 2015 to August 2016. Additionally, pre-existing differences between reference and rotenone lakes before any treatment was applied were tested with LME models for both 2014 rotenone and 2015 rotenone lakes, contrasting metrics from June to September of each respective treatment year.

My model parameters consisted of the fixed effects: 1) treatment (i.e., reference vs. rotenone); 2) period (before vs. after, where after is separated into year one and year two post-impact for 2014 rotenone lakes); and 3) the interactive effect of period and treatment (the BACI effect of concern) (Bro et al. 2004). The random effects in my model included random intercept of month, lake, and month*lake interaction. Significant fixed effects were tested using a likelihood ratio test comparing the full model to a null model (i.e., a model similar to the full model but without the fixed effect of interest). Assumptions to linear mixed effects models include linearity of observed data, absence of collinearity, homoscedasticity normal distribution of residuals, absence of influential data points, and independence (which is accounted for in my model through the inclusion of all non-independent random effects) (Zuur et al. 2009). These assumptions were tested visually through q-q plots, residual plots, and histograms of residuals. Models with overly influential data points were re-analyzed without the outliers to ensure model assumptions were met. The models were fitted using the restricted maximum likelihood method, which selects the best model, incorporating both mean and covariance. Models

were simplified using criterion-based procedures in which predictors are chosen based on lowest values for Akaike Information Criterion (Gurka 2006).

In order to best understand patterns in community composition data, I used Non-Metric Multidimensional Scaling (NMDS) of the species composition of all fourteen lakes. NMDS is a common method for analyzing community changes to a stressor (Shafi et al. 2013). The purpose of NMDS is to represent objects in a reduced number of dimensions to visualize patterns of similarity or dissimilarity among the objects being grouped. NMDS starts with an initial random configuration of the data and organizes the data into axes by reducing the difference between ordinated and actual distance between sites (Clarke 1993). I used Bray-Curtis distance, as this is a common method to quantify the differences between two communities using species relative abundance (Faith et al. 1987). Species abundances were square-root transformed to adjust for potential skewed effects from overly abundant species. One time point (McDowell Lake, 11/6/2015) was removed because there were no live zooplankton. I included only those species present in >1 lake and >5% of samples in order to reduce the influence of rare taxa (Cao et al. 2001). Juveniles were excluded, as well as *Leptodora kindtii*, which may not have been accurately sampled with daytime tows, and all time points and lakes were run simultaneously to compare results across the entire study. Increased variation in community composition of rotenone lakes before and after treatment compared to reference lakes before and after treatment was tested using a beta dispersion test, which tests for homogeneity among multivariate dispersions between groups (Anderson 2006).

Because there was a significant difference in group dispersion, PERMANOVA test could not be used (Anderson and Walsh 2013).

Differences in recovery patterns between lakes were assessed by analyzing individual lakes trends in the 2014 rotenone and the 2015 rotenone lakes. The effects of fish predation alteration to the lake communities were assessed by comparing spring stocking times of trout fry to community dynamics in the first year after rotenone treatment, using relative abundance of the major functional groups in the lakes.

All models were fitted in R version 3.1.2 (R Development Core Team 2014) using functions in the lme4 (Bates et al. 2015), nlme (Pinheiro et al. 2014), vegan (Oksanen et al. 2007), and MASS (Venables and Ripley 2002) packages.

Results

Changes in water quality

Reference and rotenone lakes did not display any changes in water quality parameters following treatment (Figure 2.2, Appendix C1). Secchi depth, surface pH, surface dissolved oxygen, and specific conductance did not show any significant interaction effects, indicating that there was no effect of the treatment on these water quality variables (Table 2.3, Figure 2.2). However, there was a significant BACI interactive effect for Secchi depth for the first year after treatment in 2015 rotenone lakes. This difference in Secchi depths is thought to be an effect of sample size rather than biological significance, as two out of the three rotenone lakes showed mean Secchi depths differences of <0.3 m following treatment, with the one exception of Badger Lake,

which had a difference of 2.9 m before and after treatment (Figure 2a). This may have been a result of sampling during different seasons, as Badger was sampled in the winter months following treatment, but in late summer before treatment.

Effects of rotenone on community structure of zooplankton

Mean monthly zooplankton abundances in 2014 rotenone lakes showed a steep drop off immediately following treatment when compared to relatively stable reference lake abundances (Figure 2.3a). The total abundances for rotenone lakes then showed a rapid increase to pre-treatment levels by February of the following year (~4 months after treatment), which exceeded pre-treatment levels for 2-3 months, and then remained steady for the remainder of the study duration (Figure 2.3a). There was a significant interaction effect between period and treatment for 2014 rotenone lakes year one (Table 2.4), indicating that the treatment had a significant negative effect on zooplankton abundances. This effect was no longer significant in the second year following treatment for the 2014 rotenone lakes (Table 2.4), indicating that recovery had occurred. The same trend was apparent for total abundances of 2015 rotenone lakes, which showed a drastic decrease in abundances following treatment and then a return to pre-treatment levels by May of the following year (~7 months after treatment); however, there was no significant interaction. The lack of significance was due to the removal of overly influential post-treatment samples in the rotenone lakes, which when included resulted in a significant effect, but violated an assumption of the LME (Table 2.4).

Shannon-Weiner diversity showed a sudden decrease following treatment in 2014 rotenone lakes, and a slight increase in diversity by April of the following year (~6 months after treatment), after which it displayed increased variation (Figure 2.3b). There was a significant interactive effect for the Shannon-Weiner diversity for the 2014 rotenone lakes in both year one and year two post impact indicating that diversity still had not recovered to pre-impact levels two years after treatment (Table 2.4). Shannon-Weiner diversity showed a steep decline following treatment in 2015 rotenone lakes and a slight increase in diversity levels by June of the following year (~8 months after treatment) (Figure 2.3b). There was also a significant interaction for diversity of the 2015 rotenone lakes, indicating that rotenone reduced diversity in the year following rotenone treatment and that recovery did not occur (Table 2.4).

When data were analyzed using the major zooplankton functional groups, patterns emerged in the rates of response to rotenone treatment. Calanoid abundance declined steeply following rotenone treatment and were the slowest functional group to recover, not reaching pre-treatment abundances for the duration of the study (Figure 2.4a). There was a significant BACI interaction for calanoid abundance in the 2014 rotenone lakes in both year one and year two, as well as 2015 rotenone lakes, suggesting that treatment with rotenone had a negative impact across all treatment lakes, with little recovery even two years after treatment (Table 2.5). Cladoceran abundance showed intermediate recovery times following the disturbance, returning to pre-treatment abundances by April or May of the following year (6 - 7 months after treatment) (Figure 2.4b). There was a significant interactive effect for year one for the 2014 rotenone lakes, and a marginally

significant interaction for 2015 rotenone lakes, but no interaction for year two of the 2014 rotenone lakes (Table 2.5), suggesting that there was recovery for cladoceran abundances in year two for 2014 rotenone lakes. Cyclopoid abundances were the fastest to recover in both 2014 rotenone and 2015 rotenone lakes following impact, with rapid returns to pre-treatment levels in only a couple of months, between February and April of the following year (4-6 months after treatment) (Figure 2.4c). There was a significant interactive effect for cyclopoid copepods in year one of 2014 rotenone and 2015 rotenone lakes, but no interaction for year two of the 2014 rotenone lakes (Table 2.5), which suggests that cyclopoid recovered to previous abundances by year two after treatment.

Community composition

Analysis of community composition showed increasing variability in treatment lakes following impact when compared to relatively stable community composition in reference lakes before and after impact (Figure 2.5a-d). This change in community variability between treatment and reference lakes after rotenone treatment was significant using the beta dispersion test ($df= 3, 226; F=32.546; p<0.001$). The stress value of the NMDS was 0.20, which is borderline as values of <0.1 are good interpretations without risk of misleading results, and values > 0.2 should be interpreted with caution; however this is expected due to the unique circumstance of ordinating drastically different post-treatment communities containing only one or two species in low abundances, in conjunction with healthy reference communities (Clarke 1993). To be conservative, I will emphasize broad spatial patterns rather than specific directional shifts based on this stress value. The increased variability post-treatment can be attributed to changes in the

abundance of cyclopoid (e.g., *Diacyclops thomasi*, *Acanthocyclops robustus*, *Mesocyclops edax*) and calanoid (e.g., *Leptodiaptomus novamexicanus*, *Skistodiaptomus oregonensis*) copepods, as well as the littoral cladoceran *Chydorus* spp. (Figure 2.5e).

Individual lake recovery trajectories in community composition showed varying degrees of community dissimilarity following disturbance, but a return to pre-treatment community composition by around June of the year following disturbance was typical (~8 months after treatment) (Figure 2.6).

Differences in recovery between lakes

Lake recovery was dynamic among individual lakes, but two general trends were noticed. Three of the 2014 rotenone lakes that were located in close proximity (Lower Hampton, Upper Hampton, Widgeon) show similar trends: fast recovery by cyclopoid copepods within four to five months following treatment, followed by recovery of cladocerans, and very slow, if any, recovery by calanoid copepods (Figure 2.1, 2.7a, b, d). The same is true of one 2015 rotenone lake, Badger, which shows the same rapid increase of cyclopoids, followed by cladocerans, with calanoids recovering faster (Figure 2.8a). A different trend is apparent in two other rotenone lakes located farther north and in distinct ecoregions (i.e., McDowell, No Name), in which cladocerans recover quickest by around June of the following year (~8 months after treatment), with no short-term domination by cyclopoid copepods (Figure 2.1, 2.7b, 2.8b). No clear trend is noted for Rat Lake due to limited sampling efforts (Figure 2.8c, Table 2.2). Following fish stocking in each of the rotenone lakes, there seems to be common responses. Abundance

increased in the first year following rotenone treatment, but seem to level off or decrease following fish stocking (Figure 2.7, 2.8).

Discussion

In this study I looked at the recovery of zooplankton communities in seven lakes that were treated with rotenone and compared those findings to baseline changes in seven reference lakes. Species traits, including dormancy strategy and rate of development, were key determinants to describing the recovery process, as I found that functional groups recovered at varying rates. There were also differences to recovery patterns between lakes, as two patterns emerged in the recovery process. These two recovery patterns differed in both which group first responded and time to total abundance recovery and could be divided up based upon geographic location and abiotic characteristics. I found that zooplankton abundances recovered quickly to pre-treatment densities, but recovery of diversity and community composition took longer. Using different metrics to analyze recovery trajectories can lead to various interpretations of a “recovered” community, and analyzing multiple community metrics can be helpful in describing recovery patterns. These findings can give insight into the major drivers of recovery to disturbance and may help guide management of these lakes following rotenone treatment.

Species traits were useful to understand different recovery processes between major groups in my study. The major zooplankton functional groups in this study differ in a number of traits including dormancy strategy, reproduction type, feeding, resource

allocation efficiency, and development speed. Dormancy strategies are a key determinant of early community assembly processes following disturbance, as both the intensity and timing of a disturbance can create dynamic emergence responses among taxa following disturbances (Russell et al. 2015). Cyclopoid copepods, the fastest group to rebound in this study, diapause through a juvenile copepodid stage, potentially allowing them to emerge at an advanced stage of development (Figure 2.4c). Cyclopoids also acquire resources raptorially, giving them the ability to take advantage of altered resources following disturbance (Barnett and Beisner 2013). The ability to take advantage of resources altered by disturbance can be a vital trait to understanding recovery trajectory, as those species taking advantage of altered conditions immediately following disturbance may temporarily dominate (Duah-Gyamfi et al. 2014). This was consistent with findings from similar studies showing rapid recovery by cyclopoids in a system where the species composition and abundance of phytoplankton is briefly affected by rotenone (Anderson 1970, Beal and Anderson 1993). In my study, following a short-term domination by early recovering species, later successional processes appeared to take hold. Cladocerans showed rapid population increases once spring emergence initiated (Figure 2.4b). Cladoceran traits, such as fast growth rates, asexual reproduction, and efficiency in resource allocation, may be integral to their rapid population growth following disturbance (Haddad et al. 2008). The rapid recovery to pesticide exposure by communities is dependent upon the persistence of the toxic chemical in the waterbody (Hua and Relyea 2014), which in the case of rotenone is only a matter of weeks before converting to a non-toxic form (Vasquez et al. 2012). This short persistence of toxicity

and efficiency in growth rates likely allowed the cladocerans to rebound in the spring months. Calanoids were the slowest group to recover in all of the treated lakes, with abundances not reaching pre-treatment levels in many of the rotenone lakes for the duration of the study (Figure 2.4a). Calanoids are thought to recover slowly due to emergence from diapaused eggs, slow development time, mate encounter rates at low densities, and a narrow range of edible food sizes (Barnett and Beisner 2013). The slow recovery to disturbance for calanoids has been depicted before in a similar study (e.g. Melass et al. 2001). Traits, like dormancy and development time, may be key indicators of the likelihood and speed of recovery of different taxa.

There were two distinct trends in recovery to rotenone application among the various lakes studied. Lakes located in the southern part of the study area responded similarly to the rotenone treatment, i.e., rapid recovery and short-term domination by cyclopoids, followed by recovery of cladocerans. By contrast, two lakes in the northern half of the study area responded differently, i.e., no short-term domination of cyclopoids, but rather a rapid recovery of cladocerans in the spring months. One major distinction between these sets of lakes is the ecoregion that they are located in. The southern lakes are located in the Columbia Plateau ecoregion, and have sagebrush-dominated catchments and higher average winter temperatures (Bailey 1998). The two northern lakes have more mountainous forested catchments and a much lower average winter temperature, leading to conditions with higher snowfall and longer ice durations (Bailey 1998). Although research has indicated that there is significant algal production under ice cover, this primary productivity is dominated by large surface attached diatoms that

are not a suitable food source for pelagic consumers (Hampton et al. 2015). Extensive ice cover in the two northern treatment lakes may inhibit early recovery in the winter months, and prevent any group from establishing priority effects. The differences in patterns between lakes may be further exaggerated by the emergence rates of major groups from diapause, as cladoceran emergence is more affected by temperature than is the emergence of copepods (Jones and Gilbert 2016). The abiotic characteristics of the environment are a key driver in understanding differential recovery rates between sites, and the recovery of zooplankton communities to rotenone is dependent upon these characteristics. These distinctions in recovery observed in this study may help to explain the variation in recovery process seen in previous studies and further emphasize the need to consider the abiotic habitat characteristics when analyzing recovery from disturbance.

The findings of my study further emphasize the need to analyze multiple metrics of community structure to ensure that communities are recovered. The rotenone lakes in this study recovered to pre-treatment abundances within a few months following disturbance. However, this recovery of community abundance did not concur with recovery of community composition or diversity, which occurred much later. This was in part due to compensatory dynamics where early recovering species reached high abundances, but the full community still had not reached pre-treatment absolute abundances. Using the results from this study, it can be seen that the metrics chosen for analysis are vital in determining recovery time. Recent studies have demonstrated the need to assess recovery trajectories using a variety of metrics, including multivariate composition data, to ensure that assessments of recovered communities are accurate

(Johns et al. 2014, Goosem et al. 2016). Utilizing both univariate and multivariate metrics in analysis of recovering communities can be a more robust style of analysis, and may help to avoid inadequate evaluations of ecological processes.

Although the results of my study are encouraging for the field of disturbance ecology, there are several limitations that need be considered. One of the most significant limitations is the inconsistency in sampling frequency and timing across all of the study sites. Due to ice conditions in the winter, as well as inaccessibility due to a forest fire, some lakes were sampled more intensely than others following the disturbance, especially in the winter months. Reference lakes were particularly under-sampled compared to rotenone lakes. I do not believe this to be a factor that would influence results because an effect of rotenone treatment was seen in all treatment lakes regardless of the sampling schedule. The lack of reference samples in the months immediately following disturbance may have affected the interpretation of a recovered community, but a difference in communities would still be likely due to a small but present over-wintering community in these lakes (Grosbois et al. 2017). Another factor is that all lakes were not sampled for water quality parameters using the same meter. This was accounted for by eliminating any data points in which the meter was malfunctioning, and is further alleviated by studies showing no significant prolonged alteration of water chemistry as a direct result of the rotenone treatment (Anderson 1970, Melass et al. 2001). The last limitation to consider is possible alterations to the phytoplankton and rotifer community as a direct result of rotenone application, which were not assessed in my study. These factors have been studied before by Duggan et al.

(2015), which indicated a short term shift in phytoplankton composition, and fluctuating rotifer abundances following rotenone treatment, but no long-term effects, indicating that food resource changes would likely not significantly alter the zooplankton community in the following years. The degree of replication and the sampling schedule containing both before and after treatment samples leads us to believe that the strength of our study design gives solid foundation to our results.

The recovery of communities to whole-ecosystem scale disturbances is a dynamic process dependent on both biotic and abiotic characteristics. Species traits are an important aspect to the recovery processes, as both dormancy strategies and development time prove to be important characteristics for resource managers to consider when understanding recovering communities (Fraterrigo and Rusak 2008). Abiotic habitat characteristics in the aftermath of disturbance can also greatly affect the recovering communities, and may inhibit emergence from dormancy, which is a significant process to measure when assessing community recovery (Myers et al. 2015). Understanding the duration of priority effect domination can be essential in recovery but may be dependent upon the abiotic conditions of the site and additional management actions following disturbance (Tucker and Fukami 2014, Duggan et al. 2015). Considering the functional groups present in the pre-treatment community, as well as predicting abiotic conditions in the habitat, may alter management decisions to ensure resource needs can be met in the recovered community.

Tables

Table 2.1: Summary of lake historical, physical, and chemical metrics, with means and standard deviations (SD) for reference and rotenone lakes and results of Welch's two sample *t*-tests. Variables represent averages prior to rotenone treatments. years post= years since last rotenone treatment, Z_{\max} = maximum depth, TP = total phosphorus, TN = total nitrogen, pH= surface pH, cond= water column specific conductance

Lake	years post	area (ha)	Z_{\max} (m)	mean depth (m)	elevation (m)	TP ($\mu\text{g/L}$)	TN ($\mu\text{g/L}$)	pH	cond ($\mu\text{S/cm}$)
Reference									
Browns	59	35.6	7	-	1165	3	170	7.07	24
Bayley	Never	6.8	6	-	800	17	570	7.67	127
Cedar	21	19.8	7	-	730	12	760	7.96	364
Amber	30	36.8	10	-	740	12	750	7.93	293
Dry Falls	62	35.6	8	-	415	21	1200	9.47	975
Big Twin	35	26.3	17	-	615	17	1590	8.42	286
Lost	43	18.2	10	-	1300	5	470	8.81	163
<i>Mean</i>	<i>42</i>	<i>25.6</i>	<i>9.3</i>		<i>825</i>	<i>12</i>	<i>790</i>	<i>8.19</i>	<i>319</i>
<i>reference</i>	\pm	\pm	\pm		\pm	\pm	\pm	\pm	\pm
<i>(\pm SD)</i>	<i>15</i>	<i>10.5</i>	<i>3.7</i>		<i>310</i>	<i>6</i>	<i>440</i>	<i>0.73</i>	<i>288</i>
2014 Rotenone									
McDowell	11	27.9	7	3.05	785	6	330	7.24	74
Upper Hampton	13	20.6	18	3.75	310	20	520	8.83	300
Lower Hampton	13	7.7	12	7.19	305	51	640	8.91	391
Widgeon	13	4.5	12	4.33	320	7	380	8.52	327
2015 Rotenone									
No Name	68	7.3	7	4.57	955	17	370	7.60	171
Badger	15	88.2	30	14.17	740	7	380	7.90	175
Rat	12	28.7	20	21.64	570	15	490	7.86	244
<i>Mean</i>	<i>21</i>	<i>26.4</i>	<i>15.1</i>	<i>8.39</i>	<i>570</i>	<i>16</i>	<i>440</i>	<i>8.12</i>	<i>240</i>
<i>rotenone</i>	\pm	\pm	\pm	\pm	\pm	\pm	\pm	\pm	\pm
<i>(\pm SD)</i>	<i>19</i>	<i>26.9</i>	<i>8.2</i>	<i>6.45</i>	<i>265</i>	<i>16</i>	<i>110</i>	<i>0.64</i>	<i>108</i>
df	11	12	12		12	12	12	12	12
<i>t</i>	2.03	-0.07	-1.72		1.65	-0.55	1.87	0.18	0.63
<i>p</i>	0.067	0.946	0.122		0.124	0.595	0.107	0.864	0.547

Table 2.2: Sampling schedule for the first half of the study, where numbers indicate the number of trips per month in each lake.

Month	<u>2014</u>						<u>2015</u>						
	6	7	8	9	10	11	12	1	2	3	4	5	6
Reference													
Amber	1	1	1	1	1	1			1	1		1	1
Bayley	1	1	1	1	1					1	1	1	1
Big Twin		1	1	1	1	1			1		1	1	1
Browns	1	1	1	1	1						1	1	1
Cedar	1	1	1	1	1					1	1	1	1
Dry Falls		1	1	1	1				1	1	1	1	1
Lost		1	1	1	1	1					1	1	1
<i>sub-total</i>	<i>4</i>	<i>7</i>	<i>7</i>	<i>7</i>	<i>7</i>	<i>3</i>			<i>3</i>	<i>4</i>	<i>6</i>	<i>7</i>	<i>7</i>
2014 Rotenone													
Lower Hampton		1	1	1	3	1	1	1	1	1	1	1	1
McDowell	1	1	1	1	3	2				1	1	1	1
Upper Hampton		1	1	1	3	1	1		1	1	1	1	1
Widgeon		1	1	1	3				1	1	1	1	1
<i>sub-total</i>	<i>1</i>	<i>4</i>	<i>4</i>	<i>4</i>	<i>12</i>	<i>4</i>	<i>2</i>	<i>1</i>	<i>3</i>	<i>4</i>	<i>4</i>	<i>4</i>	<i>4</i>
2015 Rotenone													
Badger												1	1
No Name		1											1
Rat													1
<i>sub-total</i>		<i>1</i>										<i>1</i>	<i>3</i>
total	5	12	11	11	19	7	2	1	6	8	10	12	14

Table 2.3: Sampling schedule for the second half of the study, where numbers indicate the number of trips per month in each lake.

Month	<u>2015</u>					<u>2016</u>								Total	
	7	8	9	10	11	1	2	3	4	5	6	7	8		9
Reference															
Amber	1	1		1			1	1	1		1	1	1		19
Bayley	1	1	1	1				1	1	1	1	1	1		19
Big Twin	1	1	1		1					1		1	1		16
Browns	1									1	1	1	1		13
Cedar	1	1	1	1				1	1	1	1	1	1		19
Dry Falls	1	1	1	1	1					1		1	1	1	18
Lost	1	1	1									1	1		13
<i>sub-total</i>	<i>7</i>	<i>6</i>	<i>5</i>	<i>4</i>	<i>2</i>		<i>1</i>	<i>3</i>	<i>3</i>	<i>5</i>	<i>4</i>	<i>7</i>	<i>7</i>	<i>1</i>	117
2014															
Rotenone															
Lower	1	1	1	1	1	1				1		1		1	23
McDowell	1	1	1	1						1		1	1		20
Upper	1	1	1	1	1	1				1		1		1	22
Widgeon	1	1	1	1	1							1		1	18
<i>sub-total</i>	<i>4</i>	<i>4</i>	<i>4</i>	<i>4</i>	<i>3</i>	<i>2</i>				<i>3</i>		<i>4</i>	<i>1</i>	<i>3</i>	83
2015															
Rotenone															
Badger	1	1	1	1		1	1	1	1		1	1	1		13
No Name	1	1	1	1				1		1	1	1	1		11
Rat	1	1	1							1		1	1		7
<i>sub-total</i>	<i>3</i>	<i>3</i>	<i>3</i>	<i>2</i>		<i>1</i>	<i>1</i>	<i>2</i>	<i>1</i>	<i>2</i>	<i>2</i>	<i>3</i>	<i>3</i>		31
total	1	1	1	10	5	3	2	5	4	1	6	1	1	4	231

Table 2.4: Results of the linear mixed effects models for the water quality variables specific conductance and pH. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC). * $p < 0.05$

Response	Rotenone Group	Period	Effect	χ^2, ICC	<i>p</i>- value
Specific conductance	2014	Year One	Treatment	0.153	0.696
			Period	6.307	0.012*
			Treatment:Period	0.549	0.459
			Lake	0.930	
	2014	Year Two	Treatment	0.097	0.755
			Period	1.431	0.232
			Treatment:Period	0.041	0.840
			Lake	0.944	
	2015	Year One	Treatment	0.683	0.409
			Period	0.443	0.506
			Treatment:Period	0.245	0.620
			Lake	0.910	
pH	2014	Year One	Treatment	0.182	0.670
			Period	0.890	0.345
			Treatment:Period	0.050	0.824
			Lake	0.356	
	2014	Year Two	Treatment	0.474	0.491
			Period	0.656	0.418
			Treatment:Period	0.052	0.820
			Lake	0.410	
	2015	Year One	Treatment	0.413	0.521
			Period	1.731	0.188
			Treatment:Period	1.475	0.225
			Lake	0.388	

Table 2.5: Results of the linear mixed effects models for the water quality variables dissolved oxygen and Secchi depth. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC).
* $p < 0.05$

Response	Rotenone Group	Period	Effect	χ^2, ICC	<i>p</i>- value
Dissolved oxygen	2014	Year One	Treatment	2.674	0.102
			Period	7.004	0.008*
			Treatment:Period	1.659	0.198
			Lake	0.010	
	2014	Year Two	Treatment	6.531	0.011*
			Period	0.044	0.996
			Treatment:Period	0.590	0.443
			Lake	0.051	
	2015	Year One	Treatment	3.795	0.051
			Period	1.701	0.192
			Treatment:Period	2.618	0.106
			Lake	0.081	
Secchi	2014	Year One	Treatment	1.163	0.281
			Period	3.824	0.051
			Treatment:Period	1.568	0.211
			Lake	0.166	
	2014	Year Two	Treatment	1.834	0.176
			Period	2.240	0.135
			Treatment:Period	1.855	0.173
			Lake	0.344	
	2015	Year One	Treatment	0.713	0.399
			Period	0.621	0.431
			Treatment:Period	4.786	0.029*
			Lake	0.500	

Table 2.6: Results of the linear mixed effects models for zooplankton metrics. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC). * $p < 0.05$

Response	Rotenone Group	Period	Effect	χ^2, ICC	<i>p</i>-value
Abundance	2014	Before	Treatment	4.313	0.038*
			Lake	0.213	
	2014	Year One	Treatment	0.006	0.940
			Period	11.44	<0.001*
			Treatment:Period	12.26	<0.001*
			Lake	0.186	
	2014	Year Two	Treatment	3.959	0.047*
			Period	18.30	<0.001*
			Treatment:Period	0.417	0.5182
	2015	Before	Treatment	0.653	0.419
			Lake	0.462	
	2015	Year One	Treatment	2.431	0.119
			Period	5.371	0.020*
			Treatment:Period	0.234	0.628
			Lake	0.074	
Shannon-Weiner Diversity	2014	Before	Treatment	1.451	0.228
			Lake	0.157	
	2014	Year One	Treatment	2.298	0.130
			Period	1.869	0.172
			Treatment:Period	14.20	<0.001*
			Lake	0.223	
	2014	Year Two	Treatment	0.025	0.874
			Period	0.445	0.505
			Treatment:Period	6.360	0.012*
	2015	Before	Treatment	4.734	0.030*
			Lake	0.417	
	2015	Year One	Treatment	0.175	0.676
			Period	5.541	0.019*
			Treatment:Period	24.36	<0.001*
			Lake	0.291	

Table 2.7: Results of the linear mixed effects models for the calanoid functional group. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC). * $p < 0.05$

Response	Rotenone Group	Year	Fixed Effect	χ^2, ICC	<i>p</i>-value
Calanoid abundance	2014	Before	Treatment	0.017	0.898
			Lake	0.528	
	2014	Year One	Treatment	16.08	<0.001*
			Period	23.42	<0.001*
			Treatment:Period	34.96	<0.001*
			Lake	0.131	
	2014	Year Two	Treatment	2.258	0.133
			Period	8.537	0.003*
			Treatment:Period	5.787	0.016*
			Lake	0.296	
	2015	Before	Treatment	3.595	0.058
			Lake	0.455	
	2015	Year One	Treatment	8.253	0.004*
			Period	7.346	0.007*
Treatment:Period			15.32	<0.001*	
Lake			0.386		

Table 2.8: Results of the linear mixed effects models for the cladoceran functional group. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC). * $p < 0.05$

Response	Rotenone Group	Year	Fixed Effect	χ^2 , ICC	p-value
Cladoceran abundance	2014	Before	Treatment	0.027	0.869
			Lake	0.000	
	2014	Year One	Treatment	9.200	0.002*
			Period	11.09	<0.001*
			Treatment:Period	17.20	<0.001*
			Lake	0.022	
	2014	Year Two	Treatment	0.465	0.495
			Period	14.11	<0.001*
			Treatment:Period	0.653	0.419
			Lake	0.025	
	2015	Before	Treatment	0.592	0.442
			Lake	0.480	
	2015	Year One	Treatment	2.632	0.105
			Period	7.026	0.008*
Treatment:Period			3.478	0.062	
Lake			0.177		

Table 2.9: Results of the linear mixed effects models for the cyclopid functional group. Fixed effects (Treatment, Period, and Treatment:Period interactive effect) were significance tested with ANOVA (χ^2), whereas random effect (Lake) consistency are reported with intraclass correlation values (ICC). * $p < 0.05$

Response	Rotenone Group	Year	Fixed Effect	χ^2 , ICC	p-value
Cyclopid abundance	2014	Before	Treatment	3.605	0.058
			Lake	0.640	
	2014	Year One	Treatment	1.583	0.208
			Period	11.36	<0.001*
			Treatment:Period	6.971	0.008*
			Lake	0.596	
	2014	Year Two	Treatment	2.735	0.098
			Period	4.448	0.035*
			Treatment:Period	2.043	0.153
	2015	Before	Lake	0.602	
			Treatment	2.031	0.154
	2015	Year One	Lake	0.538	
			Treatment	0.424	0.515
	2015	Year One	Period	1.238	0.266
Treatment:Period			4.208	0.040*	
Lake			0.483		

Figures

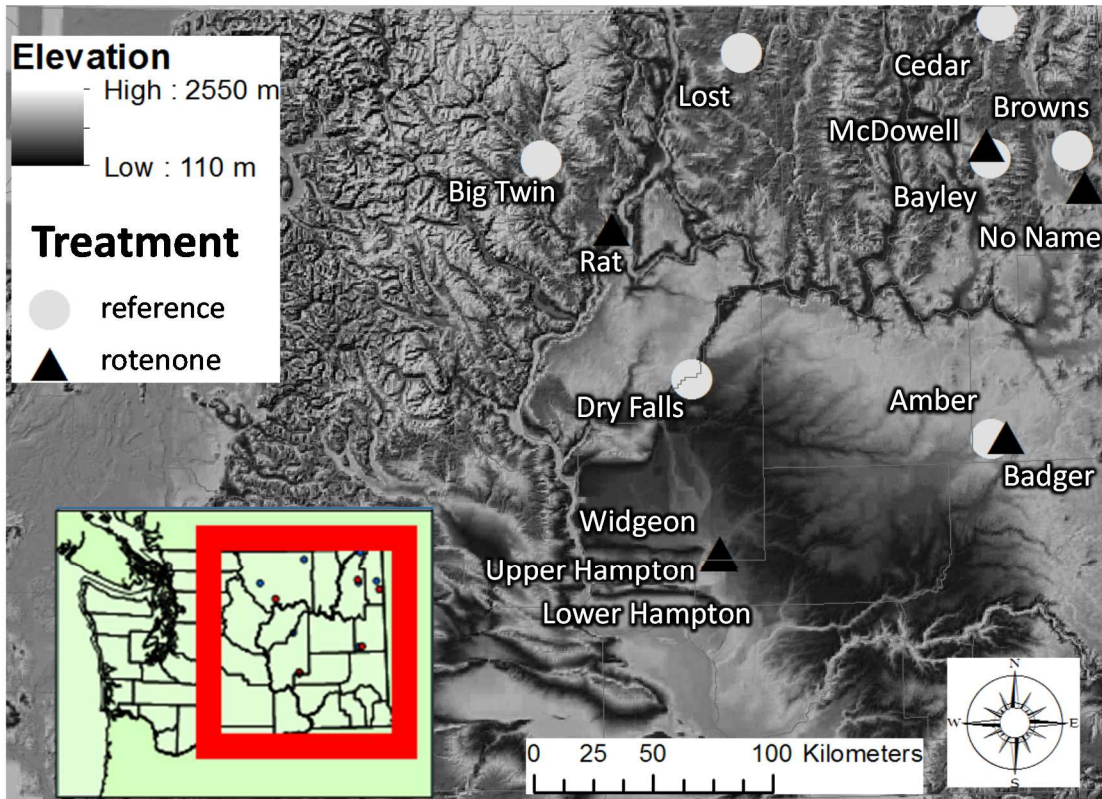


Figure 2.1: Map of study lakes in eastern Washington based on elevation gradient. Inset shows relative position in the state of Washington.

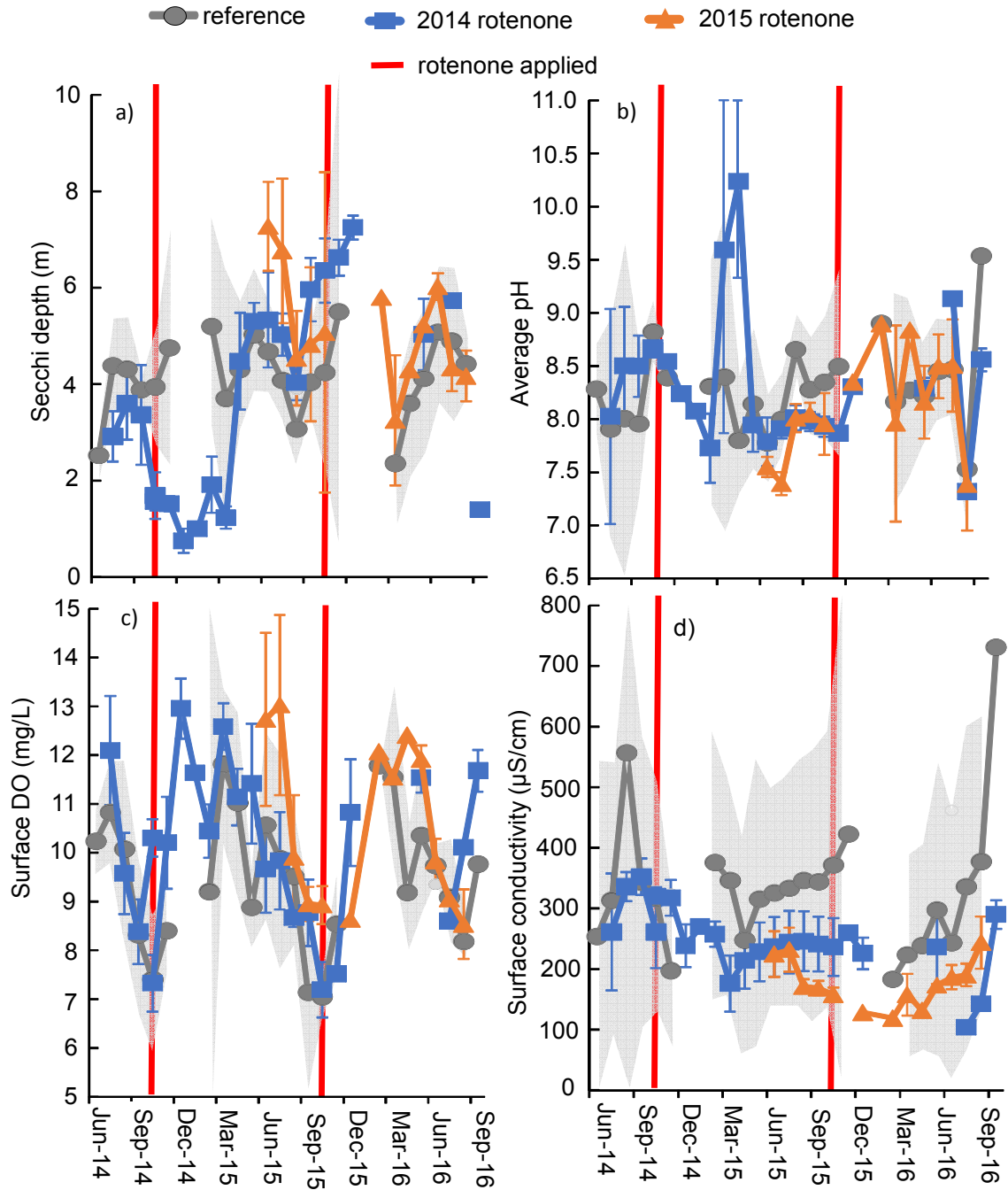


Figure 2.2: Monthly averaged a) Secchi depth (m), b) pH, c) surface dissolved oxygen (DO) concentration (mg/L), and d) specific conductance ($\mu\text{S}/\text{cm}$) for 2014 rotenone, 2015 rotenone, and reference lakes. Gray bars represent 95% confidence intervals for reference lakes, error bars for rotenone lakes represent ± 1 standard error, and red lines indicate date of treatment.

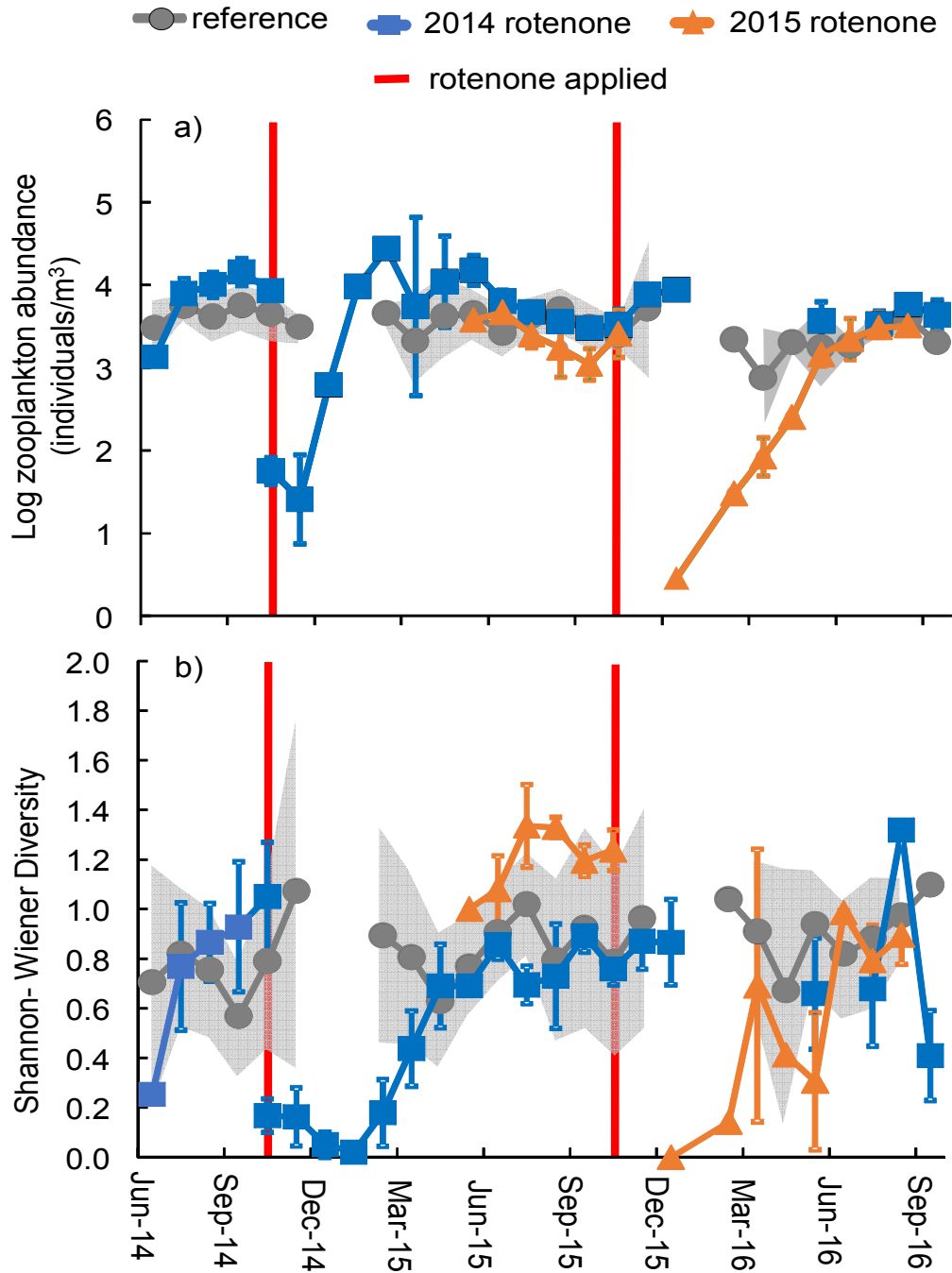


Figure 2.3: Monthly averaged a) log zooplankton abundances (individuals/m³) and b) Shannon-Wiener diversity for 2014 rotenone, 2015 rotenone, and reference lakes. Gray bars represent 95% confidence intervals for reference lakes, error bars for rotenone lakes represent ± 1 standard error, and red lines indicate date of treatment. See Table 2 for sample sizes.

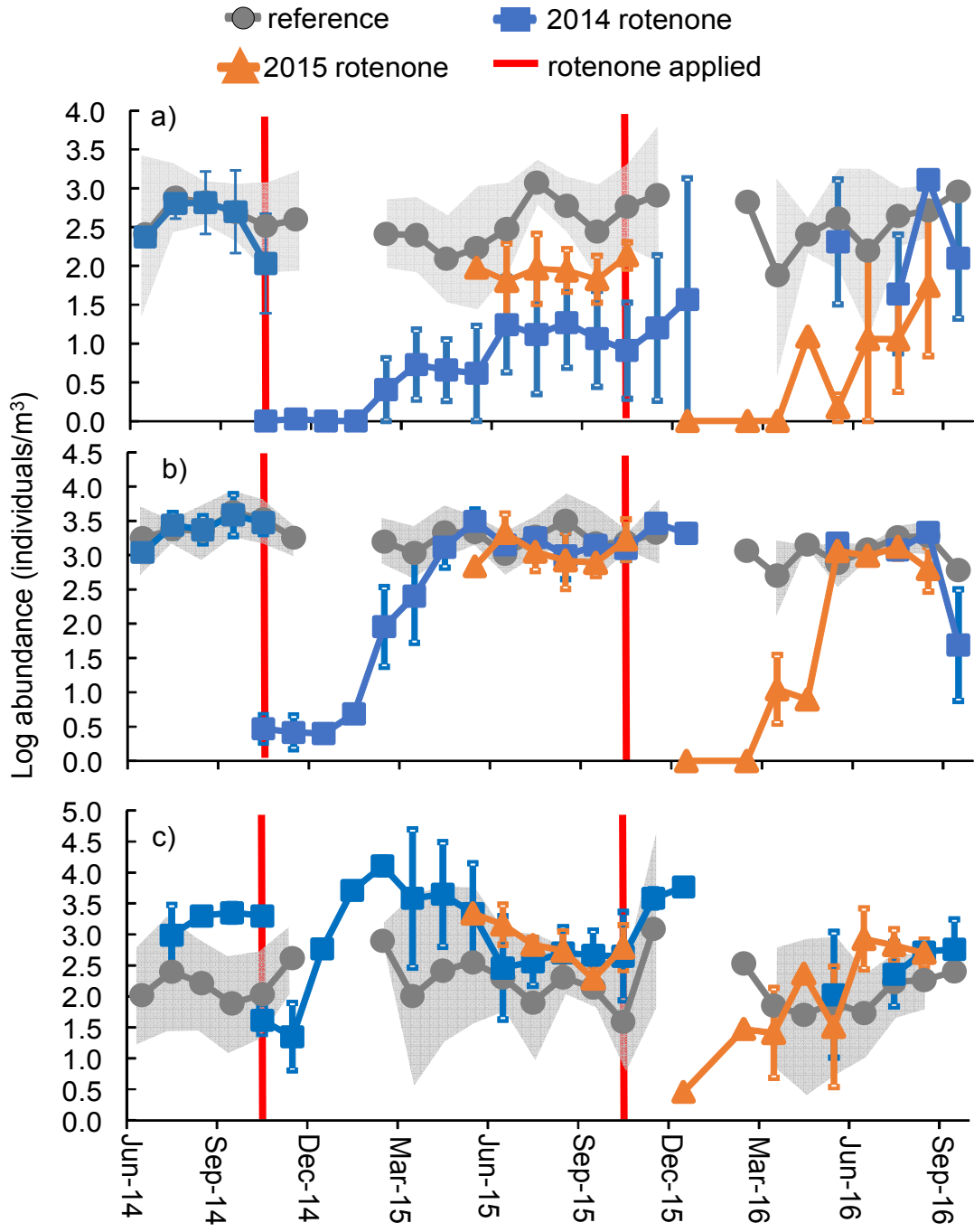


Figure 2.4: Monthly averaged log a) calanoid abundance, b) cladoceran abundance, and c) cyclopoid abundance (individuals/m³) for 2014 rotenone, 2015 rotenone, and reference lakes. Gray bars represent 95% confidence intervals for reference lakes, error bars for rotenone lakes represent ± 1 standard error, red lines indicate date of treatment for 2014 and 2015 rotenone lakes

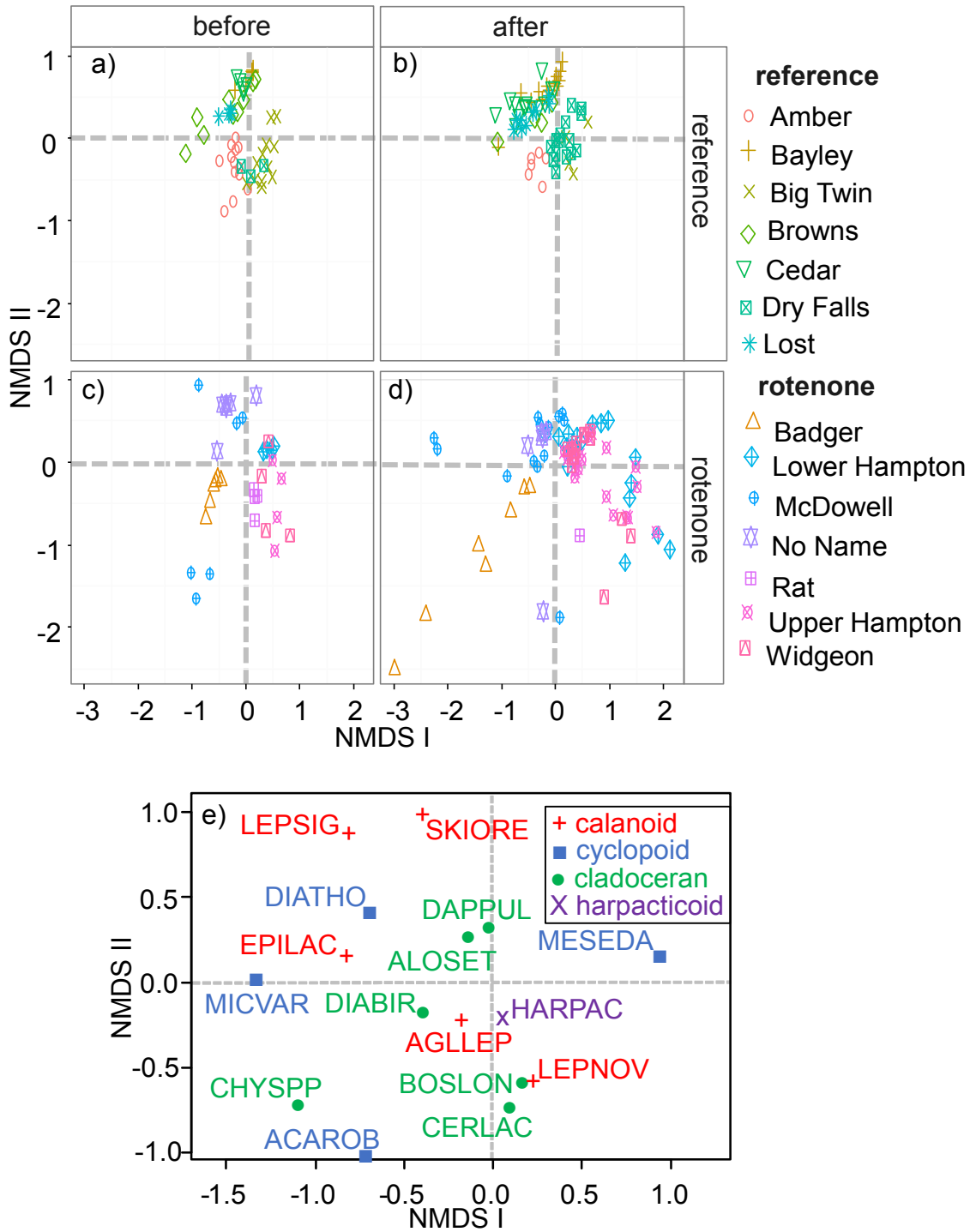


Figure 2.5: NMDS ordination of zooplankton communities contrasting reference lakes a) before and b) after, with rotenone lakes c) before, and d) after. e) Species scores for common taxa contributing to the ordination plot, with different symbols for major groups.

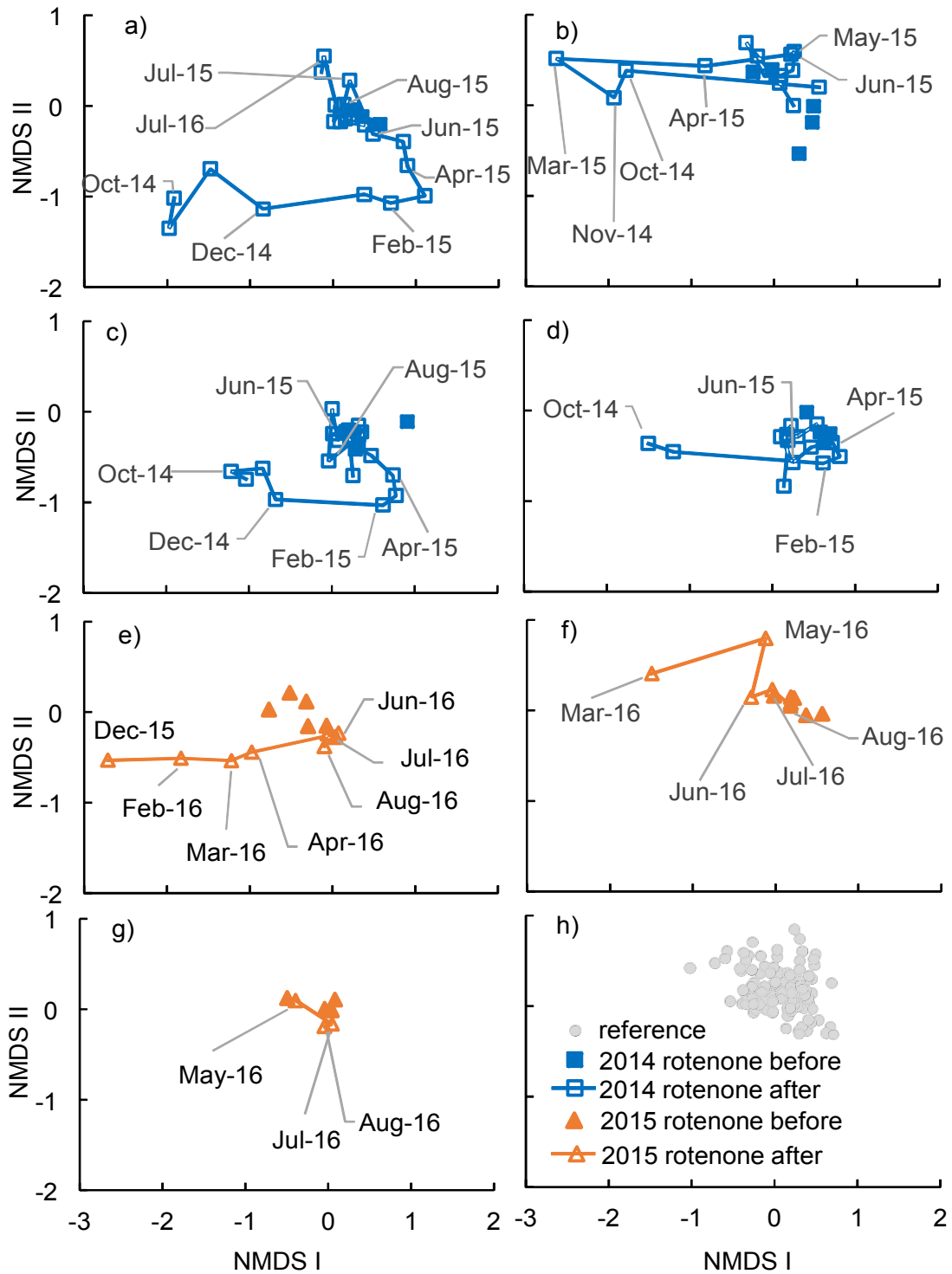


Figure 2.6: Recovery trajectories for all treatment lakes and entire set of reference points from NMDS: a) Lower Hampton, b) McDowell, c) Upper Hampton, d) Widgeon, e) Badger, f) No Name, g) Rat, and h) all reference lakes throughout the study (2014-2016).

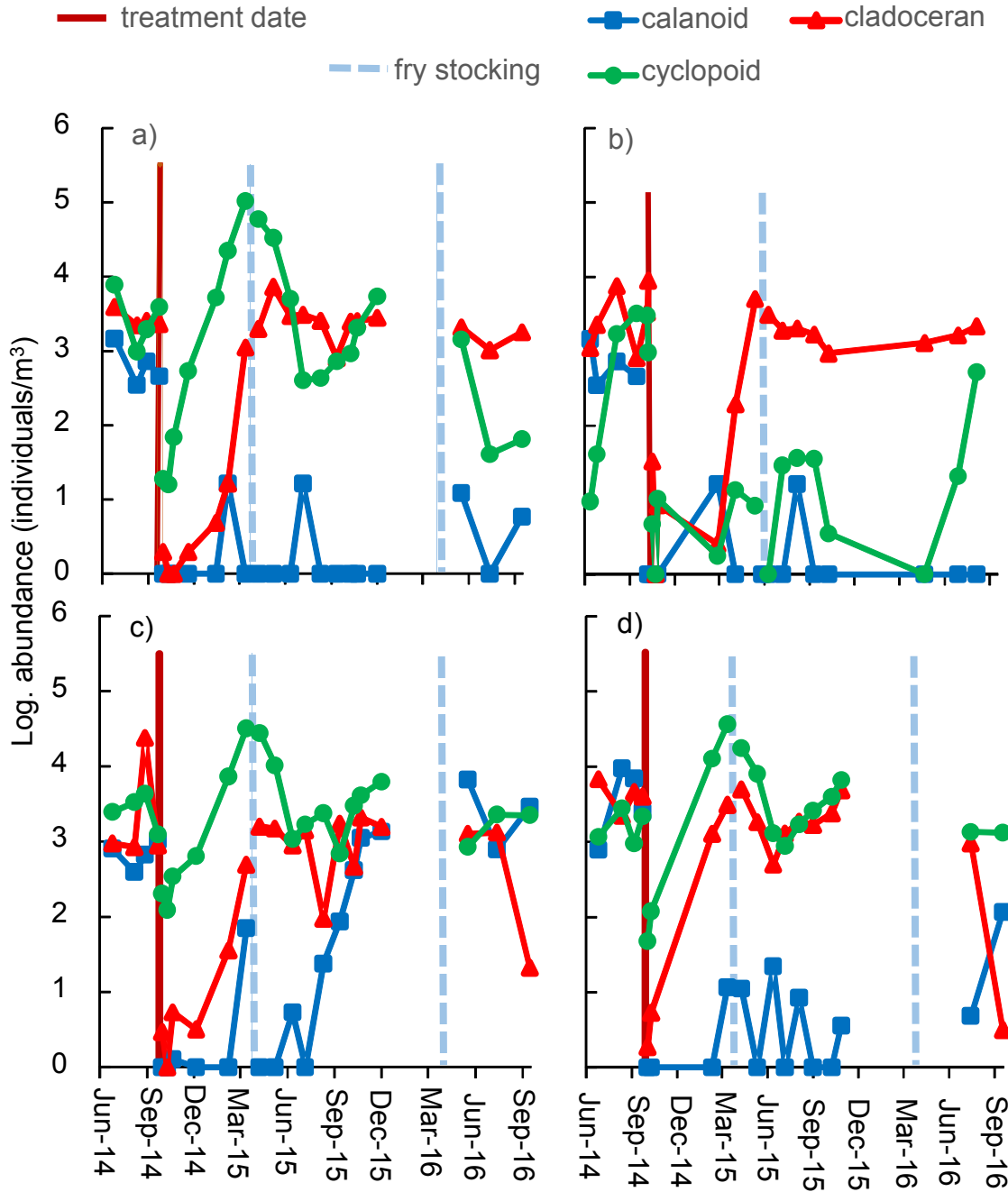


Figure 2.7: Log functional group abundances (individuals/m³) of the four 2014 rotenone lakes: a) Lower Hampton, b) McDowell, c) Upper Hampton, and d) Widgeon. Vertical lines denote dates of treatment and fish stocking.

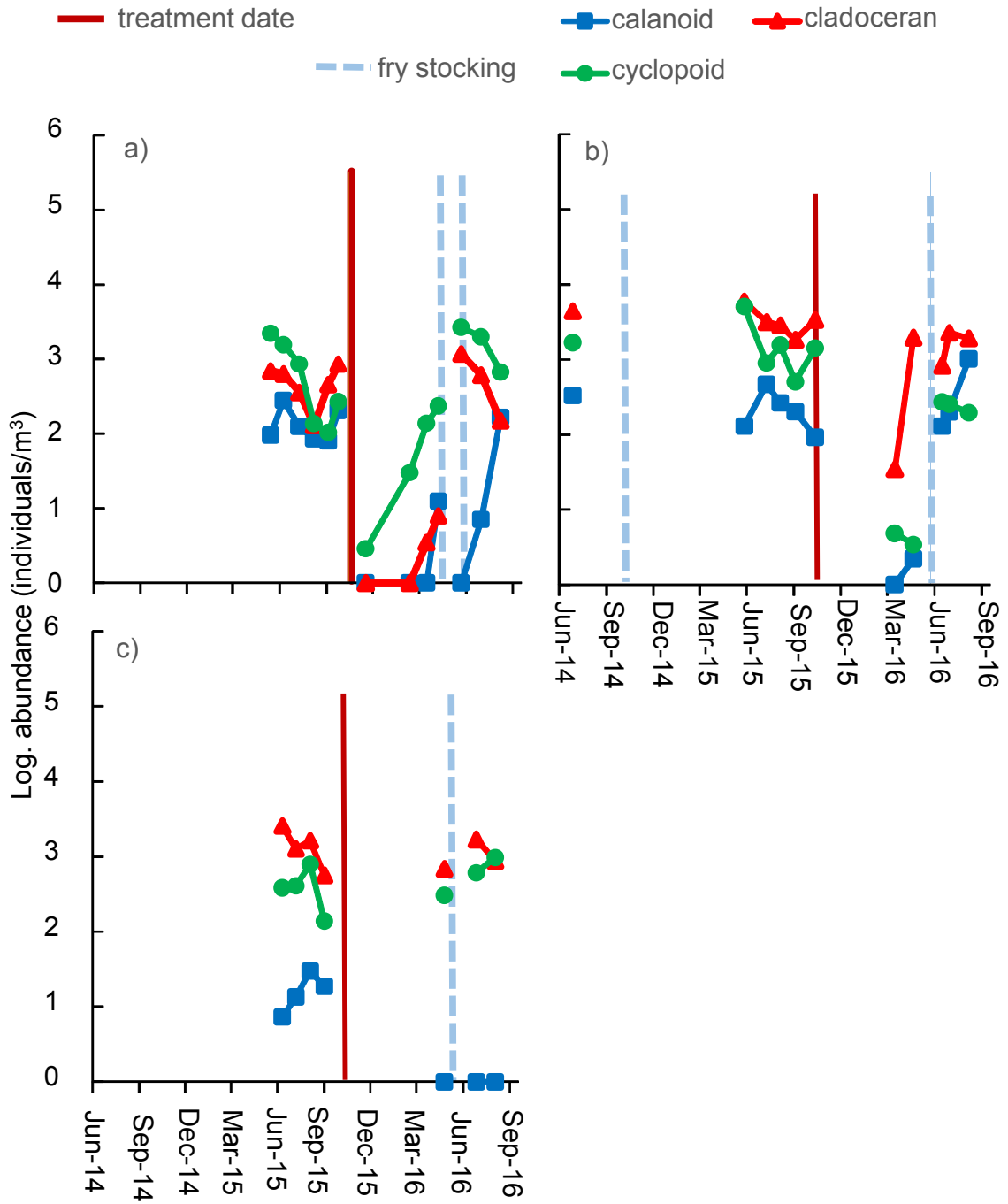


Figure 2.8: Log functional group abundances (individuals/m³) of the three 2015 rotenone lakes: a) Badger, b) No Name, and c) Rat. Vertical lines denote dates of treatment and fish stocking

Chapter Three

Conclusions and Future Work

Recovery from disturbance was studied by analyzing the recovery pattern of zooplankton communities following an intense short-lived whole lake anthropogenic disturbance. Understanding the species traits that lead to faster recovery rates following disturbance was a major goal of this study. I found that dormancy strategies, rate of development, and selectivity in resource selection may all be vital traits leading to fast recovery. As important as understanding the functional diversity of the recovering community is in predicting recovery patterns, there are also underlying abiotic drivers that may lead to variations in recovery between sites treated with similar disturbances. I found that differences in the climatic conditions of the disturbed area can lead to differences in recovery patterns and rates. The ability of lower trophic level consumers to emerge or colonize into the area following disturbance is related to their ability to survive and reproduce given the climatic conditions. Therefore, the timing of the disturbance may be a key factor as the disparity in the severity of winter conditions in this study may have led to variations in recovery. This research also highlighted the need to focus analysis on more detailed measures of community composition rather than coarse structural attributes. By analyzing community composition results in a community composition framework insights can be drawn about recovery that might be missed otherwise. The importance of abiotic and biotic drivers to the recovery process of zooplankton communities in lakes treated with rotenone may be useful in helping to guide future management of these resources.

The understanding of lake recovery patterns to rotenone application is vital for resource managers. Following treatment with rotenone, government agencies need to understand when a lake is safe for restocking with fish, and if those fish will have adequate food resources to grow and develop. Rotenone persistency in the lake is monitored with fish bioassays, which help to determine when the toxic form of rotenone has degraded to low enough levels for fish to survive; however, the toxicity of the lake is not the only concern for resource managers (Hisata 2002). Resource managers also must be able to predict when the lake's zooplankton community has recovered enough to support the growth of trout fry, which are a major diet resource of these trout. The growth of the trout in these lakes helps to maintain a productive fishery at a much lower cost than stocking with catchable size trout. In the year following rotenone treatment, managers usually wait until later in the spring to restock with fry, assuming that the zooplankton community has yet to recover fully (Hisata 2002). I believe this practice should continue, as lakes in this study recovered abundances early in the spring; however, these abundances were largely composed of smaller cyclopoid species, which are less desirable for young trout. Trout lake managers also need to consider the geographic location that their recovering lake is located in. Previously, stocking practices have been based upon lake temperatures in which lakes with more severe winters are stocked later in the year (Bruce Bolding, pers. comm.). I think this tradition should continue as lakes located in the northern half of this study first showed rebounding populations later in the spring season. The first major stocking of fry in the spring following treatment was hypothesized to have an effect on diversity; however, no effect was determined in this

study. Further research might highlight any effects the stocking of fry has on the recovery process, and give better insight into the altered dynamics in the zooplankton community.

The investigation into the recovery of zooplankton from disturbance has led to questions that may lead to future work on this topic. One of the primary reasons for studying the recovery of zooplankton communities to rotenone treatment was to determine when the recovered community would have rebounded enough to support the growth of trout fingerlings. The recovering zooplankton community can be assessed as adequate food sources for growing trout fry if measurements are made of each species following treatment, to understand if the effect of treatment had on the body size of zooplankton. Another aspect that may give insight into the rehabilitation of trout fisheries would be to analyze the growth rates of trout fry in a similar study design, to see if and when the effect of treatment enhances trout growth. Another avenue of further research would be to assess if rotenone has a legacy effect on the treated lake communities. Many lakes are treated multiple times with rotenone to restore fisheries (in my study 6 out of the 7 reference lakes had at one point been treated with this piscicide), and some are treated at frequent intervals, around 8-10 years. This repetitive exposure to rotenone may induce changes that are not seen in short duration studies, but may be analyzed through a paleo-limnological lens. Sediment cores were taken in July 2016 of all the lakes in the study, with the idea that diapaused eggs may give insight into how these lakes may have been altered through time. There are many avenues of research that this study has opened up for exploration.

The results of this study may also assist with assessment of other altered communities. Many agricultural pests are treated with pesticides to reduce the effect of invasive or nuisance species on yield loss; however, these practices may be ineffective if native populations are to remain unharmed (Davidson and Rieske 2016). Understanding which statistical approach to utilize in analysis and which species traits to consider in the recovery process may help to understand the extent of this pesticide use on native creatures. This study may also give insight into unintended consequences of management efforts. My findings can also be extrapolated for work on ecosystems that are less resilient, and have longer recovery times. Fuel extraction in fire-prone regions has recently become an area of emphasis as fire regimes continue to change, but the question remains as to where to concentrate these efforts (Regos et al. 2016). By understanding what causes ecosystems to recover differently to disturbance, and what characteristics to consider when predicted ecosystem response may help to prioritize action plans, to enhance both production and resistance of our resources. The results of this study may guide management strategies and help to better predict ecosystem response to disturbance.

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Appendices

Appendix A.1: Table summarizing water meters used for each visit to lake in the first half of the study: 1= YSI ProPlus (PSU), 2= YSI Pro-DSS (Spokane County), 3= Unknown post rehab meter used, 4=WDFW District 1 Hydrolab, 5= YSI 6820 V2 (Grant County)

Month	<u>2014</u>		8	9	10	11	12	<u>2015</u>					
	6	7						1	2	3	4	5	6
Reference													
Amber		1	1	1	2			2	2		2	1	
Bayley	4	1		1	4					4	4	4	
Big Twin		5		5	5	5		5		5		1	
Browns		1	1	4	4						4	4	
Cedar	4	1		1	4					4	4	4	
Dry Falls		5	5	5	5			5	5	5	5	5	
Lost		5	5	5	5	5					5	1	
2014 Rotenone													
Lower Hampton		5	5	5	5,5,5	5	5	5	5		5	5	
McDowell		1	1		4,3,3	4				4	4	4	
Upper Hampton		5	5/5	5	5,5,5	5	5		5	5	5	5	
Widgeon			5	5	5,5,5			5	5	5	5	5	
2015 Rotenone													
Badger												1	
No Name												4	
Rat												1	

Appendix A.2: Table summarizing water meters used for each visit to lake in the second half of the study: 1= YSI ProPlus (PSU), 2= YSI Pro-DSS (Spokane County), 3= Unknown post rehab meter used, 4=WDFW District 1 Hydrolab, 5= YSI 6820 V2 (Grant County)

Month	2015					2016								
	7	8	9	10	11	12	2	3	4	5	6	7	8	9
Reference														
Amber	2	2		2			2	2	2		2	1	1	
Bayley	4	4	4	4				4	4	4		4	1	
Big Twin	1	1	5		5					5			1	
Browns	4									4	4	4	1	
Cedar	4	4	4	4				4	4	4	4	4	1	
Dry Falls	5	5	5	5	5					5		5	5	5
Lost	1	1	5										1	
2014 Rotenone														
Lower Hampton	5	5	5	5		5				5				5
McDowell	4	4	4	4						4		4	1	
Upper Hampton	5	5	5	5	5	5				5				5
Widgeon	5	5	5	5	5									5
2015 Rotenone														
Badger	2	2	2	2		2	2	2	2		2	1	1	
No Name	4	4	4	4					4	4	4	4	1	
Rat	1	1	5							5		1	1	

Appendix B.1: Table classifying copepod species found in this study

Order	Family	Species	Feeding
Cyclopoida	Cyclopidae	<i>Acanthocyclops robustus</i>	Raptorial
		<i>Diacyclops thomasi</i>	Raptorial
		<i>Microcyclops varicans</i>	Raptorial
		<i>Mesocyclops edax</i>	Raptorial
		<i>Tropocyclops prasinus</i>	Raptorial
Calanoida	Diaptomidae	<i>Aglaodiaptomus leptopus</i>	Suspension
		<i>Leptodiaptomus novamexicanus</i>	Suspension
		<i>Leptodiaptomus signicauda</i>	Suspension
		<i>Skistodiaptomus oregonensis</i>	Suspension
	Temoridae	<i>Epischura lacustris</i>	Current cruiser

Appendix B.2: Table classifying branchiopod species found in this study

Order	Family	Species	Habitat	Feeding
Cladocera				
	Chydoridae			
		<i>Alona setulosa</i>	Littoral	Filtration
		<i>Camptocercus</i> spp.	Littoral	Filtration
		<i>Chydorus sphaericus</i>	Littoral	Filtration
		<i>Kurzia media</i>	Littoral	Filtration
		<i>Leydigia</i> spp.	Littoral	Filtration
		<i>Oxyurella brevicaudis</i>	Littoral	Filtration
	Macrothricidae			
		<i>Macrothrix laticornis</i>	Pelagic	Filtration
	Moinidae			
		<i>Moina macrocopa</i>	Pelagic	Filtration
	Polyphemidae			
		<i>Polyphemus pediculus</i>	Pelagic	Raptorial
	Bosminidae			
		<i>Bosmina longirostris</i>	Pelagic	Filtration
	Daphnidae			
		<i>Ceriodaphnia lacustris</i>	Pelagic	Filtration
		<i>Daphnia ambigua</i>	Pelagic	Filtration
		<i>Daphnia mendotae</i>	Pelagic	Filtration
		<i>Daphnia pulex</i>	Pelagic	Filtration
		<i>Simocephalus serrulatus</i>	Pelagic	Filtration
	Sididae			
		<i>Diaphanosoma birgei</i>	Littoral	Filtration
		<i>Latona glacialis</i>	Littoral	Filtration
	Holopedidae			
		<i>Holopedium gibberum</i>	Pelagic	Filtration
	Leptodoridae			
		<i>Leptodora kindtii</i>	Pelagic	Raptorial

Appendix C.1: Nutrient concentrations for reference and rotenone lakes.

Lake/Type	Total Phosphorus ($\mu\text{g/L}$)				Total Nitrogen ($\mu\text{g/L}$)			
	2014	2015	2016	Average	2014	2015	2016	Average
<i>Reference</i>								
Browns	3	14	6	8	170	300	280	250
Bayley	17	63	20	33	570	770	710	683
Cedar	12	12	11	12	760	670	870	767
Amber	12	21	11	15	750	830	820	800
Dry Falls	21	26	26	24	1200	1250	1200	1217
Big Twin	17	16	18	17	1590	1220	1190	1333
Lost	5	8	8	7	470	560	650	560
<i>2014</i>								
<i>Rotenone</i>								
McDowell	6	17	11	11	330	430	650	470
Upper Hampton	20	27	19	22	520	550	550	540
Lower Hampton	51	35	25	37	640	760	650	683
Widgeon	7	29	23	20	380	530	670	527
<i>2015</i>								
<i>Rotenone</i>								
No Name	7	17	13	12	270	370	440	360
Badger	n/a	7	9	8	n/a	380	650	515
Rat	n/a	15	18	17	n/a	490	630	560