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AQUATIC COMMUNITIES IN NORTHERN FOREST WETLANDS:

CHARACTERISTICS AND INFLUENCES OF TIMBER HARVEST

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ABSTRACT

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Using exploratory analysis, I assessed natural variation and responses to experimental timber harvest by aquatic invertebrate communities in 16 seasonally flooded wetlands in old-growth (70+ years since harvest) aspen stands in north central Minnesota. In the post-treatment year, I also assessed responses of algae and other wetland physical features to the experimental treatments.

Pre-treatment analysis of aquatic invertebrate communities revealed that wetland hydroperiod and organic carbon concentration influenced invertebrate distribution and abundance, although wetland spatial differences between clusters accounted for the greatest variation. Post-treatment analysis also indicated strong influence of hydroperiod, carbon concentration and spatial variation on invertebrate communities. Additionally, wetlands associated with clear-cut treatments had longer hydroperiods, increased primary productivity, and both positive and negative invertebrate responses. Algae exhibited no significant response to treatment or measured environmental variables.

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TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGMENTS iii

LIST OF TABLES ix

LIST OF FIGURES x

INTRODUCTION 1

OBJECTIVES 3

LITERATURE REVIEW 4

- Wetland background 4
- Organic matter in wetlands 8
- Algae in wetlands 12
- Invertebrates in seasonal wetlands 14

MATERIALS AND METHODS 17

- Study sites 17
- Invertebrate sampling 22
- Water quality parameters 26
- Algae sampling 27
  - Phytoplankton 27
  - Periphyton 28
- Wetland physical features 28
- Statistical analysis 29

RESULTS 33

Pre-treatment (2000) 35
Invertebrates 33
Post-treatment (2001) 42
Physical features 42
Invertebrates 51
Algae 75
DISCUSSION 83
Sources of natural variation in invertebrate communities 83
Wetland physical and community response to treatment 87
CONCLUSIONS 95
LITERATURE CITED 97

APPENDIX A

INVERTEBRATES 105

APPENDIX B

ENVIRONMENTAL VARIABLES 106

APPENDIX C

ALGAE 107

APPENDIX D

ANOVA RESULTS 108

LIST OF TABLES

Table Page

1. Results from multi-response permutation procedure (MRPP) assessing differences among invertebrate communities in a priori treatment wetlands (2000) 40

2. Results of RDA on invertebrate communities and significant environmental variables sampled on 15 May 2000 41

3. Results of RDA on invertebrate communities and significant environmental variables sampled on 13 May 2001 61

4. Results from multi-response permutation procedure (MRPP) to find the most similar sampling periods between year (highest P value).... 64

5. Results from multi-response permutation procedure (MRPP) assessing differences in invertebrate communities in treatment wetlands (2001) 67

6. Results of RDA on invertebrate communities and significant environmental variables sampled on 28 May 2001 72

7. Results of partial RDA on invertebrate communities and significant environmental variables sampled on 18 June 2001 75

LIST OF FIGURES

Figure Page

1. Maps showing location of study wetlands……………………………… … 19

2. Types of logging treatments imposed on the 16 study wetlands 21

3. Hydroperiod duration (initial days of inundation) of study wetlands in pre (grey) and post-treatment (black) years.......... 25

4. Annual changes in invertebrate taxon diversity for 2000 and 2001 in 16 seasonal forest wetlands 35

5. PCA relating temporal changes in invertebrate communities from seven wetlands common to the first four sampling periods from 2000.......... 37

6. PCA of invertebrate communities in 16 wetlands on 15 May 2000 showing taxa with r^2>0.20 for either axis. 39

7. Partial RDA of invertebrate communities in 16 wetlands from 15 May 2000 with cluster as covariable.......... 44

8. Histogram showing the partitioning of variance in the invertebrate communities by variables from 15 May 2000 46

9. PCA on invertebrate communities and joint plot with those environmental variables chosen as significant in partial RDA from 15 May 2000 48

10. Ice-out differences related to treatments in 16 study wetlands in 2001.......... 50

11. PCA showing the relationship between hydroperiod and the pre-treatment assignment on 16 study wetlands from 2000 53

12. PCA showing the relationship between hydroperiod, chlorophyll-a concentration and the post-treatment wetlands (17 May 2001) 55

13. Mean numbers of *Eubranchipus* in relation to treatment type.......... 58

14. RDA on invertebrate communities and significant environmental variables from 16 study wetlands (13 May 2001) 60

15. Percentages of variance explained in invertebrate communities by significant variables from 13 May 2001 based on variance partitioning in partial RDA.. 63

16. PCA from 28 May 2001 indicating no apparent differences in the invertebrate communities based on treatment 66

17. RDA on invertebrate communities and environmental variables in 16 wetlands sampled on 28 May 2001 69

18. PCA from 28 May 2001 on invertebrate communities and joint plot with those environmental variables found to be significantly correlated with changes in the invertebrate community with forward selection in RDA 71

19. Partial RDA on invertebrate communities and significant environmental variables from 18 June 2001 74

20. Histogram showing the partitioning of variance in the invertebrate communities by variables from 18 June 2001 77

21. PCA showing the relationship among hydroperiod, chlorophyl *a* concentration and the post-treatment wetlands (28 May 2001) 79

22. PCA jointplot from 18 June 2001 of algal communities in relation to treatments 82

INTRODUCTION

Wetlands have long been viewed as dismal, bug-infested areas of nuisance and unsightliness. Past management of wetlands included draining and filling to “tame” the land and reduce disease (Prince 1997). In 1764, the Virginia Assembly created the Dismal Swamp Company to drain 40,000 acres of the Great Dismal Swamp for timber harvest and possible agricultural use (Niering 1997). Even in relatively recent time, this view persists. In the early portion of the 20th century, thousands of acres of prairie potholes were drained in Minnesota, North and South Dakota, and Iowa for farming.

In the past century, wetlands increasingly have been recognized for the important ecological role they play in the landscape, and as a result, preservation and restoration have become popular. As evidence of these changing views, 100,000 acres of the Great Dismal Swamp were donated to the Nature Conservancy in 1970 for preservation, and over 10,000 prairie potholes in Minnesota alone have been restored (Niering 1997). Identification of wetland ecosystems has been one of the most important aspects of wetland preservation. Currently, the extent of wetlands in the 48 contiguous states is assessed as mandated by the Emergency Wetlands Resources Act of 1986 (Dahl 2000), which has stimulated recent preservation and restoration of many wetland ecosystems.

Changing perceptions of wetlands are directly related to the knowledge we have gained about wetland ecology and function in landscapes. Wetlands are among the most productive ecosystems, surpassed only by Hawaiian sugarcane fields, due to wetlands’ great ability to store solar radiation as chemical energy

(Niering 1997). Wetlands are increasingly valued on the global scale for their roles in recharging groundwater, reducing the overland flow of water, filtering pollutants, carbon storage, and maintaining a diversity of animal species both within and beyond wetland boundaries (Niering 1997, Mitsch and Gosselink 1993, Oertli 1993).

In recent years, there also has been increasing awareness of the importance of small (<2 ha) seasonal wetlands (Biggs et al. 1991, terminology via Stewart and Kantrud 1971). Because of their small size (<0.4 ha), many small forest wetlands are not identified by the National Wetland Inventory (NWI) and, thus, are not protected by regulations. An absence of regulations, combined with incomplete knowledge of characteristics and function of seasonal wetlands, increases the importance of the remaining wetlands and underscores the need for understanding how to preserve them.

Seasonal forest wetlands typically range in size from a few square meters to over a hectare, although most are under 0.4 ha (Higgins and Merritt 1999). Over 1.2 million hectares of these temporary habitats exist in northern Minnesota (Trettin et al. 1997); this amount is only a fraction of what once dotted the landscape. Minnesota has lost 45% of an estimated 2,279,473 hectares of forest wetlands present prior to European settlement (Trettin et al. 1997). In the United States, total wetland area lost is estimated to be over 2 million hectares (Johnston 1994). Unregulated clear-cut logging may threaten the ecological integrity of many remaining seasonal forest wetlands. Specific knowledge of wetland function is needed in order to formulate best management practices (BMPs) for tree harvest adjacent to forest wetlands.

OBJECTIVES

The purpose of my study was to identify the natural variation in invertebrate communities of seasonal forest wetlands in old-growth aspen stands and to assess short-term effects of three types of experimental upland tree removal. A secondary goal of my study was to assess responses of the algal community to tree removal and follow any resultant fluctuations in the herbivorous invertebrates. My study was part of a collaborative effort with the U.S. Forest Service, the Minnesota Department of Natural Resources, the Natural Resources Research Institute, North Dakota State University, the University of Minnesota, the Cass County Forestry Department, and Potlatch Paper Company.

The main interests of the collaborators focused on ecological impacts of logging adjacent to seasonal wetlands in old-growth (70+ years since harvest) aspen stands. The goal of the extensive study was to provide empirical data that will contribute to ecologically based management guidelines for timber harvest adjacent to forest wetlands. As stated previously, my role in the study was to characterize invertebrate communities present in the undisturbed sites to identify factors that contribute to natural fluctuations in community composition and to assess potential changes in response to harvest. Other specialists are assessing wetland use by amphibians, birds, plants, and fungi as they are affected by the experimental timber harvest.

LITERATURE REVIEW

Wetland background

Wetlands are areas where water is the primary factor controlling the environment and the associated plant and animal life. Wetlands occur where the water table is at or near the surface of the land, or where the land is covered by shallow water that may be up to six feet deep (Niering 1997). Verry (1997) states that two conditions are necessary for wetland formation: suitable physiography and available water at the earth's surface. He also states that the source of water determines the wetland type. Five major wetland systems are recognized: marine, estuarine, lacustrine, riverine, and palustrine (Cowardin et al. 1979). Marine and estuarine systems describe coastal, salt-water wetlands, whereas the other three categories represent freshwater systems. Lacustrine wetlands are associated with lakes; riverine wetlands are found along rivers and streams; and palustrine wetlands represent those wetlands that are often referred to as marshes, swamps, and bogs.

The seasonal forest wetlands in north-central Minnesota are palustrine wetlands that exist in small depressions that may be continuous with the water table or "perched" above it. These depressions were formed following retreat of the glaciers of the last ice age 10,000 to 12,000 years ago. The water source for the wetlands is typically surface run-off from the surrounding watershed, but occasionally, the seasonal wetlands receive groundwater discharge and exhibit extended hydroperiods. Due to their perched nature and small size, seasonal wetlands typically dry during the summer and throughout winter months. The extent of this drying is directly related to the area and depth of the depression (Higgins and Merritt 1999). The resulting wet-dry cycle is primarily responsible for configuring resident animal communities and ecosystem characteristics in these wetlands (Schneider 1999). Hydrologic conditions affect many abiotic factors, such as nutrient availability and soil anaerobiosis, which can also influence the composition of wetland flora and fauna (Mitsch and Gosselink 1993, Schneider 1999).

Researchers have divided these temporary/seasonal wetlands into two categories, vernal and autumnal, depending on timing and duration of inundation (Higgins and Merritt 1999; Wiggins et al. 1980). Vernal pools flood only in the spring and are typically dry during the later part of the summer, fall, and winter. Autumnal pools are characterized by reflooding in the late summer and fall, and are inundated throughout winter and early spring. The presence of water during the autumn and winter influences faunal composition (Wiggins et al. 1980, Batzer and Sion 1999), but size and duration of a wetland during the vernal phase probably has the greatest impact on the resident invertebrate community (Higgins and Merritt 1999). It should be noted that the terms “vernal” and “autumnal” are not uniformly applied across regions. Timing and duration of flooding in these wetlands are highly variable and are dependent on regional precipitation.

Johnston (1994) suggested that cumulative adverse impacts to remaining wetlands might reduce their capacity to mitigate flooding and loading of suspended solids. Such cumulative impacts usually result from agricultural and silvicultural practices in the upland surrounding the wetlands. Such impacts, over time, may be direct or indirect, and may become cumulative (Johnston 1994). Indirect influences may originate some distance from an affected wetland, such as the release of pollutants into a river upstream from the wetland. A direct impact occurs when there is an immediate disturbance to the wetland basin, such as farming, or, in the case of forest wetlands, clear-cut logging. Documented impact results have been used to develop guidelines for protection of remaining wetlands. In a case in Louisiana (1985), the EPA vetoed a proposal that would have altered 1200 hectares of bottomland hardwood, stating (Johnston 1994, p. 51):

> In the last 80 years, over 800,000 acres of land in Louisiana have been lost. Recent losses of forested wetlands in the State are on the order of 87,200 acres annually. These losses affect not only biological, water quality, recreational, and flood protection benefits but also economic values of the wetlands because of the significance to Louisiana's coastal fishery.

In northern forest wetlands, silvicultural activities are a major direct disturbance. Tree removal increases the amount of light striking the wetland, enhances water table fluctuations (Verry 1986, Dube and Plamondon 1995), and promotes sedimentation through increased erosion. France (1997) describes how erosion increased in forest lakes, resulting from loss of protective ground cover following riparian clearcutting. Leaf-litter plays an important role in slowing erosion, and France (1997) reports a positive relationship between the amount of forest floor litter and the amount of sedimentation in lakes.

Leaf-litter is important as an energy source in forest wetlands. When leaf-litter inputs change, aquatic invertebrates may be influenced directly and indirectly (Batzer and Sion 1999). Leaf-litter influx has been estimated to vary between 300 and 1825 g dry mass $\cdot$ $m^{-2} \cdot y^{-1}$ for forested streams and wetlands (Petersen and

Cummins 1974, Cummins et al. 1989) and may be reduced to 7 - 65 $g \cdot m^{-2} \cdot yr^{-1}$ during the 4-10 years following clear-cutting (France 1997).

Another major impact of forest harvesting on aquatic systems is the tempered effect of flood mitigation. Verry (1986) describes increased flooding in the upper Mississippi River following major deforestation in the early 20th century. Compared to the Red River at Grand Forks, North Dakota, flood peak increased 43% in the upper Mississippi. Verry (1986) reported that stream flow following rainstorms in harvested aspen stands is doubled for at least five years after cutting. Related research has also focused on functional connectivity between seasonal wetlands and adjacent forests (Verry 1986). Removal of trees immediately adjacent to wetlands reduces evapotranspiration and may lengthen hydroperiods, causing invertebrate taxa fluctuations (Dube and Plamondon 1995, Verry and Boelter 1979, Verry 1997).

Due to increasing demands for wood fiber, timber harvest will increase, with or without ecologically based management. Current harvest guidelines suggest leaving greater than five % tree cover in areas surrounding wetlands, but I am aware of no research or empirical evidence to indicate that this is the best management approach. It is possible that the most beneficial tree cover for invertebrates, and other animals utilizing forest wetlands, consists of a buffer zone with residual patches of trees in the upland adjacent to the wetland.

Organic matter in wetlands

In forest wetlands, trees may form a complete or near-complete canopy enclosing the small pool, providing shade and large inputs of leaf-litter (allochthonous organic matter) during annual leaf fall. Within a given geographical area, litterfall in forest wetlands exceeds rates in non-wetland forested areas, but continuous flooding may lead to reduced production because of tree mortality (Conner and Day 1992). Because canopy-induced light limitation inhibits growth of emergent plants within seasonal wetlands, large inputs of leaf-litter are usually the predominant energy source and may support animal communities living in these wetlands (Oertli 1993, Cummins et al. 1973, Wetzel 1975, Hessen 1992). In terrestrial systems, litterfall values have been used to estimate net primary productivity (Bray and Gorham 1964).

Decomposition of organic matter makes energy or nutrients available for animals and plants in the wetlands. Initial decomposition of leaf-litter occurs by nutrient leaching, which increases with temperature in terrestrial systems (Andersson et al. 2000). Peterson and Cummins (1974) showed that trembling aspen (*Populus tremuloides*) leaves in woodland streams lost about 20% of their weight from leaching and the remainder from other forms of physical processing. Because of a paucity of invertebrate shredders in seasonal forest wetlands from north-central Minnesota, the remaining decomposition is generally accomplished through microbial activity as the biodegradable dissolved organic carbon (BDOC) is obtained from leaf-litter. As defined by Boissier and Fontvieille (1993), BDOC is that portion of the dissolved organic carbon that is assimilated by autochthonous bacteria during a short-term incubation. In seasonal wetlands, decomposition rates exceed those in other systems because alternation of wet and dry periods facilitates rapid microbial colonization (Brinson et al. 1981). Indirectly through the decompositional process and directly as a food source, microbial action is believed to provide the basis for the diverse invertebrate community in the seasonal wetlands (Barlocher et al. 1978).

In a woodland wetland study by Oertli (1993), 81% of decomposing leaf-litter was transformed by fungal and bacterial processes. The readily available fine particulate organic matter (FPOM) and dissolved organic matter (DOM) are then used quickly by algae and invertebrates (Mulholland and Hill 1997, Higgins and Merritt 1999) and by other microbes (Tranvik 1992). Tranvik (1992) states that DOM exists in many states of lability and that different species of bacteria are involved in a “microbial loop” as the recalcitrant organic matter is broken down for use by other bacterial species. The cycling of wet and dry periods in seasonal wetlands promotes the rapid microbial decomposition of the leaf litter. As previously stated, tree removal can not only reduce the amounts of litterfall entering the wetland, it may also modify hydroperiods (Dube and Plamondon 1995), breaking the wet and dry cycle. Increased length of inundation can decrease the decomposition rate of allochthonous organic matter (Conner and Day 1992).

Barlocher et al. (1978) reported that detritus that remained dry over winter increased in protein concentration due to microbial colonization. Following spring flooding, protein levels dropped sharply as invertebrates consumed the microbes. In a study by Lawson et al. (1984), fungal and bacterial community structure on leaf-litter had a significant influence on Tipulidae (*Tipula abdominalis*) consumption rates, assimilation efficiency, and growth. Many other invertebrates show preferences for leaf types that are directly or indirectly mediated by the type of microbial flora on the leaves (Cummins et al. 1973).

Changes in the type and abundance of organic matter have been shown to alter macroinvertebrate communities (France 1998). Oertli (1993) showed that woodland ponds in Switzerland that have a predominance of allochthonous organic input have efficient energy conversion (2-2.5%) between consumer levels (detritus + primary producers). Compared to aquatic macrophytes, terrestrial leaf-litter seems to provide a higher nutritional potential for invertebrate production (Oertli 1993). Allochthonous dissolved organic matter is known to be an important carbon source for bacteria and algae (Tranvik 1992; Hessen 1992; Jones et al. 1998). Hessen (1992) found that 90% of the carbon required to support bacterial growth came from allochthonous matter. In turn, these algal and bacterial communities have been shown to be important food sources for microinvertebrates (zooplankton) and macroinvertebrates (insects and crustaceans) in seasonal aquatic environments (Hamilton et al. 1992) as well as in lakes (Hessen 1992; Keough et al. 1998). Rau (1980) determined that approximately 38% of the 51 kg carbon of insect biomass emerging annually from Findley Lake in Washington originated from terrestrial plant sources. In a small-order stream, Kaushik and Hynes (1968) found that 66% of the net production of primary consumers was derived from allochthonous organic matter. A substantial part of this organic matter is known to be autumn-shed leaves. Campeau et al. (1994) have shown that herbivore and detritivore densities fluctuate when autochthonous matter is manipulated. It is also clear that, at times, leaf-litter is favored over available emergent macrophytes as an energy source for invertebrates, presumably because of the extent of microbial activity and consequent rapid breakdown (Oertli 1993; Cummins et al. 1973; Peterson and Cummins 1974; Cornelissen 1996).

When light availability increases in response to canopy removal, emergent vegetation increases in density (Higgins and Merritt 1999; personal observation). When the canopy is removed, there is often a shift from a system fueled by allochthonous matter to one that is dominated predominately by autochthonous matter in the form of emergent hydrophytes. Emergent and submerged vegetation have been shown to alter the growth of algae negatively through shading and competition (Sand-Jensen and Borum 1991), thus depleting possible invertebrate food sources.

Decomposition rates have been shown to differ among different plant types. Cornelissen (1996) experimentally demonstrated that monocots decompose more slowly than dicots in aquatic environments. Plants that are lower to the ground (monocots) have evolved greater resistance to herbivory with more anti-browser defenses such as lignins, tannins, and defensive chemicals (Cornelissen 1996). Slower decomposition of emergent vegetation may mean less available organic carbon in wetlands. Without canopy closure, it is plausible that increased accumulation of recalcitrant organic matter from emergent vegetation could eventually lead to accelerated sedimentation. Watt and Golladay (1999) demonstrated that terrestrial leaf-litter in forested wetlands of the southern United States lasts just over two years. This reference to decomposition rate may indicate that leaf-litter also accumulates in forest wetlands but perhaps not as rapidly as detritus from emergent vegetation. Increased accumulation and sedimentation will ultimately accelerate the ontogeny of the wetland, i.e., the rate of conversion of the aquatic system to a terrestrial one (Wetzel 1975). This process would be expected to be faster in a wetland dominated by autochthonous organic matter. It is also possible that increased light promotes transformation of detritus from particulate to dissolved forms through photochemical degradation (Denward et al. 1999, Buffam et al. 1996) if sunlight is not blocked by emergent vegetation.

Algae in wetlands

Algae are the most important primary producers in seasonal forest wetlands. Algae provide a very labile food source for the majority of primary consumers (Wetzel 1975, Goldsborough and Robinson 1996). Other autotrophs, such as macrophytes, are available in detrital form (Campeau et al. 1994), but the small clusters of cells characteristic of algae allow for easy assimilation (Goldsborough and Robinson 1996). Campeau et al. (1994) have shown that benthic algae from wetlands are a major food resource for cladocerans, copepods, chironomid larvae, amphipods, oligochaetes, and planorbid snails. Algae affect the growth, reproduction, survival, and development in all of these taxa.

Diatoms, green algae, and cyanobacteria grow well and are often abundant in forested wetlands where DOM levels are usually high (Brinson et al. 1981). They also play roles in nutrient cycling as sources of dissolved organic matter and other nutrients such as nitrogen and phosphorous for consumers like zooplankton and other herbivorous invertebrates (Goldsborough and Robinson 1996, Wetzel 1975).

Algae of different growth forms often inhabit the same wetland through spatial or temporal separation (Wetzel 1975). Certain algae proliferate under certain conditions, and, as the growing season progresses, temporal fluctuations of light intensity, temperature, and nutrient availability influence the dominant form of algae. Herbivores have the potential to limit algal abundance, which implies "top-down" control of algae by grazing. Top down control is possible across a wide gradient of water trophic state (Scheffer et al. 1993).

Temporal and spatial separations are not the only factors that may influence the success of algae in wetlands. In shallow, seasonal wetlands with sufficient light, macrophytic vegetation can proliferate and out-compete algae for nutrients and light, or release chemicals that inhibit algal growth (Goldsborough and Robinson 1996, Elakovich and Wooten 1989). In a semi-permanent shallow lake, Hanson and Butler (1994) allude to mechanisms that describe a dramatic drop in phytoplankton biomass after an epiphyte/macrophyte-dominated system is reestablished in a shallow prairie lake. Minimum light requirements for macrophytes are believed to be up to tenfold greater than those of most phytoplankton (Sand-Jensen and Borum 1991), so strong competition is probably not typical in small, forest wetlands unless trees are removed through fire, storm damage, or forestry practices.

Nutrient availability plays a large role in determining algal biomass and productivity. It is generally accepted that primary productivity in freshwater systems is often phosphorus limited (Underwood and Kromkamp 1999), although nutrient limitation may not exist in forest wetlands where phosphorus concentrations are typically high but light is limiting. In highly eutrophic aquatic systems, where nitrogen to phosphorous ratios are low due to farming runoff or human waste, phytoplankton is the dominant autotroph. The density of phytoplankton can become so great that light is blocked to rooted macrophytes and periphyton, reducing their biomass (Hansson 1988), with the caveat that water depth be great enough to allow for algal accumulation sufficiently dense enough to block light to macrophytes.

Herbivory can also have an impact on the abundance and species composition of wetland algae. Hann (1991) reported that herbivorous grazing by cladocerans, copepods, and ostracods reduced algal biomass and altered species composition in a prairie wetland. Other lake studies have demonstrated substantial grazing effects of large-bodied cladocerans and other zooplankton on algal biomass (Carpenter et al*.* 1985, 1995; McQueen et al. 1986) and analogous influences seem likely in forest wetlands.

Invertebrates in seasonal wetlands

Although there is an abundance of literature dealing with permanent aquatic habitats, little is actually known about the seasonal wetlands in forest landscapes (Oertli 1993), and there is little current research on these sites (Batzer and Sion 1999, Schneider 1999).

Factors that influence habitat utilization by aquatic insects and other invertebrates, in general, include physiological constraints, such as oxygen acquisition, osmoregulation, and temperature effects; water trophic status, as it relates to food acquisition (Wiederholm 1984); and physical constraints, i.e., coping with habitat fluctuations and biotic interactions, such as predation and competition (Wallace and Anderson 1996). All of these factors have discrete effects, but all interact as well.

Species composition in very ephemeral habitats primarily reflect physical constraints imposed by a highly variable habitat, i.e., fluctuating hydroperiods (Wiggins et al. 1980, Welborn et al. 1996, Brooks 2000). Animals inhabiting aquatic habitats with slightly longer hydroperiods are influenced more by biotic interactions, e.g., primary invertebrate predators (Schneider and Frost 1996; Welborn et al. 1996). Short hydroperiods typical of seasonal wetlands have a major influence on resident invertebrates due to a rapidly changing environment. Some taxa are limited by this variation in habitat, but others benefit from it. Wiggins et al. (1980) suggest categories, or "groups," of animals inhabiting seasonal pools based on life-cycle strategies for tolerating/avoiding drought and freezing, and also, recruiting to the ecosystem. Some insects become dormant to survive drought periods and others enter a "true diapause" stage (Butler 1984). Several species depend on periodic drying and reflooding to stimulate the hatch of resistant egg stages. Also, periodic drying lessens the likelihood that fish and large invertebrate predators colonize sites and persist to cause extinctions of vulnerable invertebrate prey.

In seasonal wetlands, vulnerable species such as fairy and tadpole shrimp take advantage of a low predator environment to hatch and reproduce before larger invertebrate predators recolonize the wetlands. Invertebrate community composition, behavior, and size structure in seasonal wetlands is influenced by the presence of large invertebrate predators (Herwig and Schindler 1996, Peckarsky 1984). Typically, aquatic insects rely on mechanical or tactile cues to detect prey, but some species in the orders Odonata and Coleoptera possess well-developed eyes and supplement tactile cues with visual ones while hunting (Peckarsky 1984). Peckarsky (1984) states that the use of visual cues for predation is not common because most insects are “negatively phototactic,” hiding under substrate during periods of high light intensity.

Aquatic invertebrates were initially used to assess water quality in Germany in the early part of the 20th century (Rosenberg and Resh 1996), and have been used successfully as disturbance indicators in streams and recently in the prairie pothole region (Adamus 1996). Lists of “indicator species” have been compiled, which identify species that are both intolerant and tolerant of pollution (Rosenberg and Resh 1996). Biomonitoring with aquatic insects is commonly used as a before-and-after-impact assessment tool. Batzer and Sion (1999) proposed that aquatic invertebrates could be useful in wetlands for the same purposes, especially for determining disturbance due to agriculture and current forestry practices. Species of several taxa, such as anostracans, amphipods, and conchostracans, require specific hydroperiods (Wiggins et al. 1980) that may be modified following timber harvest (Dube and Plamondon 1995). Aquatic invertebrates such as filter feeders cannot tolerate high levels of sedimentation such as those that often result from farming and forestry practices (Wiederholm 1984). Wiederholm (1984) reported that invertebrates in streams adjacent to timber harvest areas were less diverse, with taxa intolerant to sedimentation reduced. Such responses have been shown to persist for up to 15 years after logging (Batzer et al. 2000). Other factors, such as increased water temperatures, changes in litter substrate, and altered water chemistry, may also be detrimental to invertebrates (Merritt and Cummins 1996). In streams, macroinvertebrates have been shown to associate strongly with specific leaf types (Cummins et al. 1973).

MATERIALS AND METHODS

Study sites

The study area was located near Remer, MN, in the Minnesota Drift and Lake Plain Section (north-central MN), and was covered by mixtures of deciduous and coniferous forests. The land was characterized by deep, but variable, glacial till with large areas of lakes and wetlands. All study wetlands were located in old-growth (70-90 years since harvest), Aspen-dominated stands. Before treatment, Aspen canopies covered at least 75% of each experimental wetland. Sixteen study sites were chosen in the winter of 2000 and 2001 from Cass County land and land owned by the Potlatch Paper Company. All 16 study wetlands were in close proximity to a permanent water body of some kind, either lentic or lotic (Figure 1). The wetlands were selected on the basis of criteria that included size, hydroperiod, age of surrounding forest, and landscape features; and were then each assigned to one of four experimental groups. The wetlands are located in one of four clusters or groups, each of which includes one of the following wetland types (Figure 2):

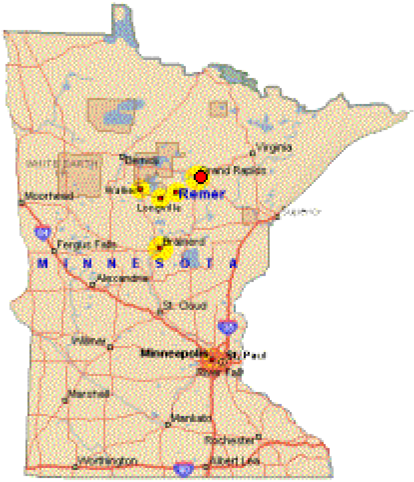
A. *One uncut control;*

B. *One 50-ft uncut buffer strip around pond with no residual trees;*

C. *One 50-ft partially cut buffer around pond with no residual trees;*

D. *One upland clear-cut with residual upland trees;*

Figure 1. Maps showing location of study wetlands. Detailed image shows study wetland proximity to permanent water; the faint lines represent permanent streams and rivers. The dark bodies represent permanent lakes.


WHITE EARTH
Virginia
Bemidji
Grand Rapids
Walker
Remer
Longville
Moorhead
Superior
Fergus Falls
Brainerd
M I N N E S O T A
Alexandria
St. Cloud
Willmar
Minneapolis
St. Paul
River Falls
Marshall
Mankato
Rochester
Worthington
Albert Lea

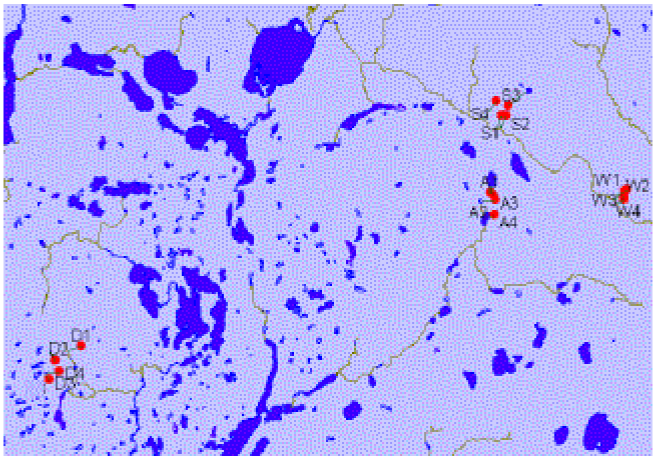
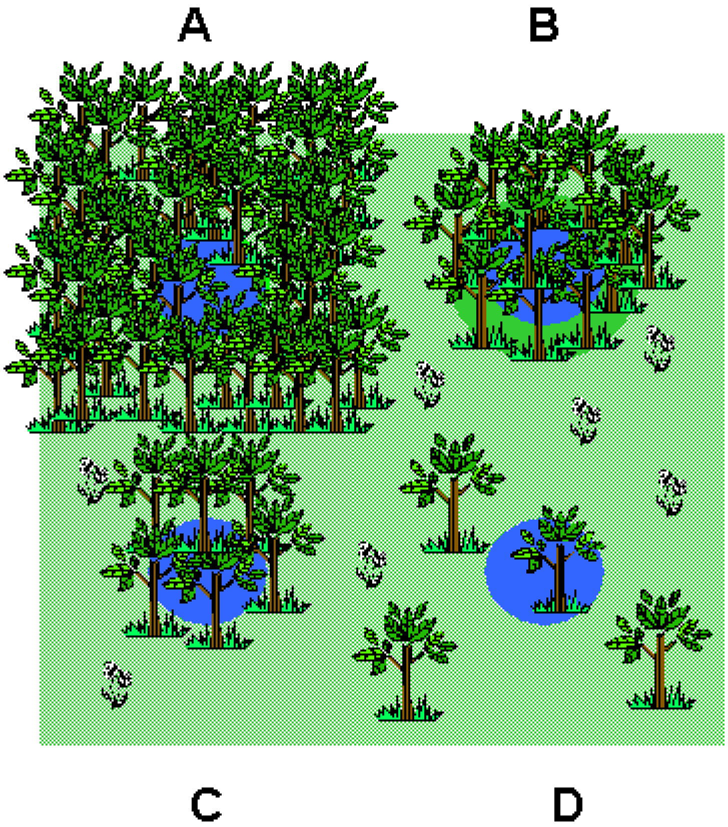

S3
S4
S2
S1
A1
A3
A5
A4
W1
W2
W3
W4
D1
D2
D4
D3

Figure 2. Types of logging treatments imposed on the 16 study wetlands. This drawing represents one of the four clusters. Treatments A, B, C, and D are uncut control, complete 50-ft. buffer, partially cut 50-ft. buffer, and clear-cut with residual upland trees, respectively. Note: clear-cut wetlands retained those trees that were in the basin proper (typically black ash).


A
B
C
D

The Soo Line, Lake Ahsebun, and Dog Lake clusters all had identical cutting assignments as related to the wetland number. Wetlands 1, 2, 3, and 4 were assigned the treatment of partially cut buffer, clear-cut buffer, full buffer, and control, respectively. The Willow River cluster treatment assignments differed slightly because of logging contractor miscommunication. Wetlands 1, 2, 3, and 4 in the Willow River cluster were assigned full buffer, partial buffer, clear-cut, and control, respectively.

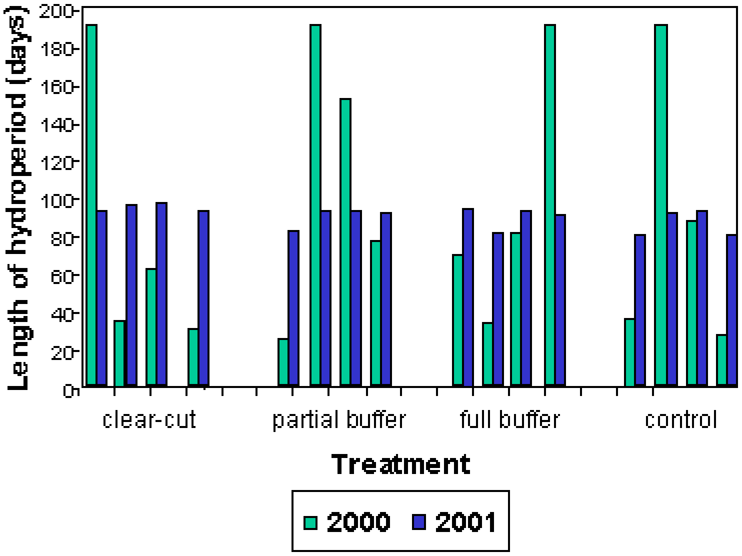
Invertebrate sampling

Samples of aquatic and semi-aquatic invertebrates were collected from wetlands adjacent to harvest (or control) areas at two-week intervals beginning approximately two-three weeks after ice-out and ending when the wetlands dried, or when four to five sample runs had been completed. Five transects in each wetland were chosen randomly for sampling. To quantify invertebrate assemblages, I used surface-associated activity traps (SATs) (Hanson et al. 2000) to sample invertebrates associated with shallow wetland margins and the water surface. Traps were deployed for 24 hr by attachment to PVC frames fastened in sediments along the 5 randomly chosen transects in each study wetland. In the field, all trap contents were condensed by passing through a 0.4 mm diameter mesh and preserved in 70% ethanol. SATs have proven useful for sampling wetland invertebrate communities because they gather representative, clean samples, thus facilitating more intensive sampling and reducing the magnitude of within wetland variance estimates (Brinkman and Duffy 1996, Hanson et al. 2000). Invertebrates were sorted, identified to the lowest feasible taxonomic level (typically family for insects and genus for crustaceans), and enumerated in the lab using stereomicroscopes. See Appendix A for a complete listing of invertebrate taxa from 2000 and 2001.

Invertebrate communities in seasonal wetlands undergo broad shifts in composition from “ice-out” to drying. (See page 42.) All inhabitants have evolved some strategy for surviving seemingly inhospitable conditions, but shifts are seen because different taxa have evolved different life-cycle strategies to minimize predation or, adversely, to seek out prey (Wiggins et al. 1980). As a result, the timing of invertebrate sampling is critical in order to obtain an overall estimate of wetland invertebrate communities.

In 2000, ice-out in most sites occurred approximately 15 April. The first sampling week began on 1 May, two weeks after ice-out, in order to allow invertebrates to recover from diapause stages or hatch from desiccation resistant eggs deposited the previous year. The first sampling date of the 2000 field season did not incorporate all 16 wetlands due to late identification of some sites. By mid May all wetlands were identified by forest service personnel. The second sampling week, occurring on 15 May, did involve all 16 wetlands. Because of extreme differences in regional rainfall, hydroperiod was highly variable in 2000 (Figure 3), which led to rapid drying in some wetlands. As a result of these fluctuations, only one sampling run was completed (15 May). This set of samples was subsequently used for the majority of between-year comparisons.

Figure 3. Hydroperiod duration (initial days of inundation) of study wetlands in pre- (grey) and post-treatment (black) years.


Length of hydroperiod (days)
0
20
40
60
80
100
120
140
160
180
200
clear-cut
partial buffer
full buffer
control
Treatment
2000
2001

Ice-out in 2001 was more variable as a result of increased light intensity in the harvested wetlands (See page 64.), but sampling began on the same calendar week (30 April). Four sample runs were completed during the post-treatment year. Regional rainfall was more uniform in 2001, which resulted in sampling of all 16 wetlands for each sampling effort.

Water quality parameters

During the 2000 and 2001 field season, U.S. Forest Service (USFS) personnel took water samples from each wetland once after initial flooding and once before drying, although results from only the first samples from 2001 were made available to me because of lengthy sample processing. In 2001, I took water samples on 17 May and 28 May during the invertebrate sampling runs to obtain an estimate of chlorophyll *a* biomass. USFS water samples were processed at the North-Central Research Station for approximately 19 water parameters. Water was stored in 0.5-liter polyethylene bottles under refrigeration at 4ºC for a maximum of 30 days before analysis for water chemistry. From the unfiltered samples, solution pH was measured by glass electrode and conductivity using a Yellow Springs Instruments model 35 conductance meter. Alkalinity was determined by auto-titration to pH 4.5 (Metler DL20 titrator) followed by Gran plot analysis. Nitrate-N (0.02 mg/L), ammonium-N (NH_4N) (0.02 mg/L), and total P (0.5mg/L) were determined by colorimetric procedures on a Lachet Quik Chem 8000 flow injection system, with in-line persulfate digestion for total P. Total organic carbon was measured using a Dorhmann DC-190 carbon analyzer. Color (as absorbance) was measured using a Spectronic 21D. Water temperature was recorded hourly with data loggers and was uploaded at the end of each field season. The resultant water parameters (Appendix B) were used selectively in statistical analyses to assess possible correlations with the invertebrate and algal communities.

Algae sampling

Phytoplankton

Biomass estimates of phytoplankton, using chlorophyll *a* concentrations, were made two times during the 2001 field season, coinciding with the last two invertebrate sampling runs. Approximately 300-1000 ml of water was filtered separately through two 0.45-μm membrane filters in the field using a hand-pump filtration system. Filters were then placed in individual petri dishes, stored in an aluminum foil covered container, and transported back to the lab on ice for absorbance analysis on a Beckman DU-64 spectrophotometer. Samples were prepared and analyzed according to methods described by Lind (1985). Absorbance was measured at 750 and 665 nm as an estimate of chlorophyll *a* concentration. Correction for the presence of phaeophytin *a* was also preformed according to Lind (1985).

Relative abundance of phytoplankton was determined by direct counts. A 200-ml water sample was brought back to the lab where a subsample was then poured into a 40-ml borosilicate vial and preserved with 4 drops of Lugol's solution and 80-μl of formalin (Throndsen 1978). For enumeration, 20 ml of each preserved sample was filtered through 0.8-μm membrane filters and mounted on a microscope slide following the methods of Lind (1985). Phycologists at North

Dakota State University counted algal cells until approximately 500 cells were counted. I then extrapolated counts to 20 ml (volume of sample) by dividing each count by the fraction of the filter counted. Phytoplankton were identified to phylum or class.

Periphyton

To estimate the relative abundance of attached forms of algae, six acrylic rods were placed in each wetland, shortly after ice-out, and collected after four weeks to allow for sufficient colonization time (Hann 1991). Samples were taken from each wetland on 28 May 01 and 18 June 01, coinciding with the phytoplankton and invertebrate samples. Two rods were removed at each sampling period. A three-centimeter section was cut off each rod and transported back to the lab in a whirl-pack. There, the periphyton was cleaned off the rods using a toothbrush to a 25-ml dilution, rinsed into a 40 ml scintillation vial, and preserved with 4 drops of Lugol's and 40 μl of formalin. Slides for enumeration were prepared as above for phytoplankton according to Lind (1985). NDSU personnel identified algae to phylum or class and counted cells as described above for phytoplankton.

Wetland physical features

Hydroperiod was determined as the time that wetlands held standing water, from complete ice-out to initial drying. Depth sticks were placed in each wetland, and depth was recorded weekly to estimate water fluctuations due to rain events.

USFS personnel estimated canopy cover using canonical densiometers at the water surface, in the upland, and halfway between the water and canopy.

Statistical analysis

The fauna of seasonal forest wetlands is not well known and is often highly variable. This variability makes determining a possible response in the invertebrate community from a treatment (removal of trees) very difficult. To best account for these problems, we used exploratory multivariate analysis techniques to determine natural variation in invertebrate communities and to identify environmental variables that were significantly correlated with this variation.

Multi-Response Permutation Procedure (MRPP) tests were performed using PC-ORD for Windows (McCune and Mefford 1997) to determine differences in the invertebrate community based on treatments and to find the most similar sampling periods between years based on aquatic invertebrates. MRPP is a distribution-free permutation technique, based on Euclidean distances; it is data-dependent and provides analysis for completely randomized designs in a multivariate framework (Biondini et al. 1988). MRPP works well with asymmetric or non-normal data, which often results from ecological studies. The most similar sampling dates between years, based on MRPP testing (largest P value), were subsequently compared to assess possible changes in invertebrate communities due to harvest effects. Also, MRPP was used to find possible difference in species communities in the pre- and post-treatment invertebrate samples.

Principal components analysis (PCA), redundancy analysis (RDA), and partial RDA ordinations were performed using CANOCO 4 analysis software (ter

Braak and Smilauer 1998). Linear multivariate ordination techniques were chosen for analysis because initial testing with detrended correspondence analysis showed short gradient lengths on all tests (<2 SD), indicating that invertebrates increased or decreased in abundance in a linear fashion and not unimodally (Verdonschot and ter Braak 1994).

Partial RDAs were performed to account for, or “partial out,” the residual temporal variation when comparing samples between years and also to decompose the % of variation (variance partitioning) explained by each environmental variable (Borcard et al. 1992, ter Braak & Wiertz 1994, Rodriguez and Magnan 1995). PCA was used in conjunction with RDA to best account for the strengths and shortcomings of each test in describing communities and relating them to environmental variables. RDA is very useful because it allows Monte Carlo significance testing of the relationship of environmental variables to community structure. However, as stated by McCune (1997) and ter Braak (1995), output from direct multivariate techniques, such as RDA and CCA, can be misleading when “noisy” or irrelevant data are included in the analysis and can distort representation of true community structure. PCA is, therefore, useful when environmental data are subsequently analyzed with the ordination results to determine if relationships exist. The shortfall of PCA is that relationships between environmental variables and community structure cannot be directly assessed with Monte Carlo tests as described for RDA. This combination of the two tests limits potential for erroneous data interpretations.

Instead of performing the RDA with all environmental variables at once, I used forward selection to determine which environmental variables were significantly correlated with the invertebrate data (P<0.10) using Monte Carlo tests based on 1000 permutations (ter Braak and Smilauer 1998). Because of the high degree of variability in invertebrate community data, a P value of 0.10 was used for significance testing to lessen the likelihood of committing a type I error, although most environmental variables were significant at the more conventional P<0.05 level. The ordination was then performed using chosen significant environmental variables. Statistical significance (P<0.05) of all canonical axes was also evaluated with the Monte Carlo tests with 1000 permutations.

To determine whether the relationships between selected environmental variables and invertebrate community structure were valid, PCA was then performed. Then the indirect ordination was plotted in conjunction with the chosen variables. If the indirect PCA triplot was similar to the direct RDA triplot, the constrained RDA was affirmed and interpreted to relate the actual relationships among wetlands, species, and environmental variables. In other words, relationships among chosen environmental variables and species were determined to be valid.

Data for all multivariate tests were natural log transformed (ln x+1) to prevent high values from excessively influencing our results (ter Braak 1995). Environmental variables were relativized by the maximum to standardize for different measurement scales. Ordinations were centered by species, and scaling was based on inter-species correlations in most cases.

Differences in hydroperiod and chlorophyll *a* concentrations between treatment wetlands were compared by ANOVA using Excel 2000 spreadsheet data analysis (Microsoft Corporation, 1999). Taxon diversity was calculated for all sampling periods and for each treatment per year using the Shannon-Wiener index:

$$H' = \sum_{i=1}^{s} (p_i)(log_{10} p_i)$$

where H' = Index of species diversity

S = Number of species

p_i = Proportion of total sample belonging to *i*th species.

Statistical comparisons of diversity were made between treatments and sampling dates using ANOVA in Excel 2000 (Microsoft Corporation 1999). As a result of extremely short hydroperiods in 2000, invertebrate diversity between treatments was averaged before testing. Also, to evaluate diversity between years, diversity was averaged to account for the unbalance sampling from 2000. These analysis methods should help clarify general wetland features influencing wetland communities and will be useful for assessing results of specific harvest strategies implemented in adjacent uplands.

RESULTS

Pre-treatment (2000)

Invertebrates

Five bi-weekly sample runs were completed during the 2000 field season (1 May – 5 July). Appendix A gives a complete account of the taxa collected. Average taxon diversity was found to be highest at the beginning of the year, dropping after the middle of May and increasing toward the end of the hydroperiod (Figure 4). Grouping the wetlands by treatment resulted in no significant differences in a priori diversity (F=1.43, P=0.28; see Appendix C). Also, there were no significant differences in hydroperiod based on the pre-assigned treatment classes (F=0.14, P=0.93).

As predicted, temporal variation of wetland invertebrate communities was great. The PCA diagram of the first four sampling weeks shows how the wetlands spread out along axis one based on temporal changes in the invertebrate community (Figure 5).

Principal components analysis (PCA) from 15 May (Figure 6) shows a random distribution of the wetlands in the ordination, based on the sampled invertebrate taxa, with respect to their assigned treatment (clear-cut, full buffer, etc.), and MRPP showed no difference according to treatment assignment (P=0.92) (Table 1). This random distribution indicates that the invertebrate taxon composition between wetlands varied randomly among the assigned treatments. The Eigenvalues of the first 2 PCA axes from 15 May were 0.286 and 0.221,

Figure 4. Annual changes in invertebrate taxon diversity for 2000 and 2001 in 16 seasonal forest wetlands. Taxon diversity was calculated for all sampling periods and for each treatment per year using the Shannon-Wiener diversity index. Five samples were taken in 2000 and four in 2001.

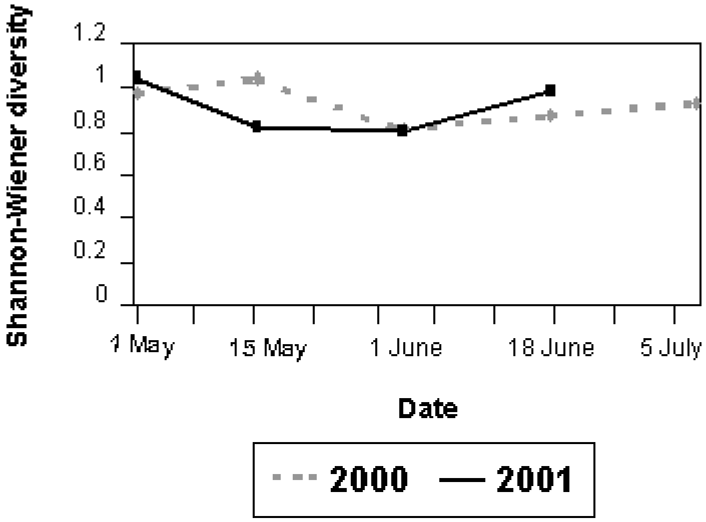

Shannon-Wiener diversity
1.2
1
0.8
0.6
0.4
0.2
0
1 May
15 May
1 June
18 June
5 July
Date
2000
2001

Figure 5. PCA relating temporal changes in invertebrate communities from seven wetlands common to the first four sampling periods from 2000. Wetlands sampled during the same week are connected by lines. Darker dots represent later sampling period. Vectors represent sampled taxa (not labeled due to spatial constraints). Circles represent wetlands. The letter of the label describes the cluster location (Soo line, S; Ahsebun Lake, A; and Dog Lake, D). The first number in the label represents pond 1-4 in each cluster, pond 1 being the northernmost and pond 4 being the southernmost in each cluster. The last number indicates which sampling period is represented, 1 being the earliest and 4 being the latest.

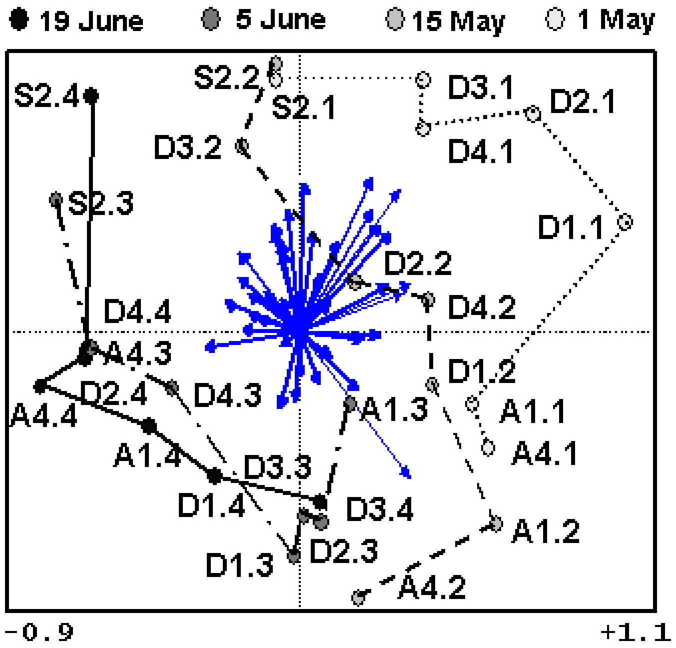
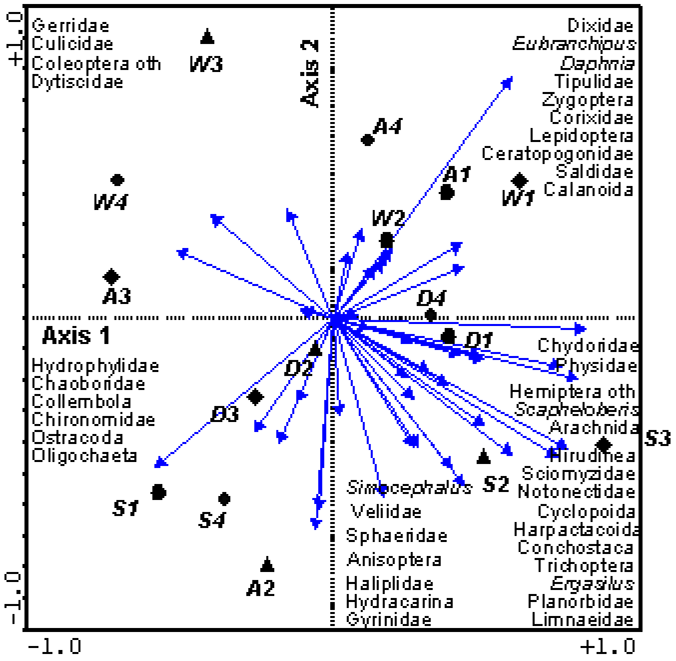

● 19 June
● 5 June
● 15 May
○ 1 May
S2.4
S2.2
S2.1
D3.1
D2.1
D4.1
D3.2
S2.3
D1.1
D2.2
D4.2
D4.4
A4.3
D1.2
A1.1
A4.4
D2.4
D4.3
A1.3
A4.1
A1.4
D3.3
D1.4
D3.4
A1.2
D2.3
D1.3
A4.2
-0.9
+1.1

Figure 6. PCA of invertebrate communities in 16 wetlands on 15 May 2000 showing taxa with r^2>0.20 for either axis. Vectors (arrows) represent taxa sampled. Wetland treatments are designated by shape: circle, controls; triangle, clear-cut; hexagon, partially cut buffer; and diamond, full buffer. Vectors point toward wetlands where taxa are found in greatest abundance. Longer vectors indicate stronger correlations between the taxon vector and the axis.



+1.0
Gerridae
Culicidae
Coleoptera oth
Dytiscidae
W3
Axis 2
Dixidae
Eubranchipus
Daphnia
Tipulidae
Zygoptera
Corixidae
Lepidoptera
Ceratopogonidae
Saldidae
Calanoida
A4
A1
W1
W4
W2
A3
D4
Axis 1
D1
D2
Chydoridae
Physidae
Hydrophylidae
Chaoboridae
Collembola
Chironomidae
Ostracoda
Oligochaeta
D3
Hemiptera oth
Scapheloberis
Arachnida
S3
Hirudinea
Sciomyzidae
Notonectidae
Simocephalus
S2
S1
S4
Veliidae
Sphaeridae
Anisoptera
Haliplidae
Hydracarina
Gyrinidae
Cyclopoida
Harpactacoida
Conchostaca
Trichoptera
Ergasilus
Planorbidae
Limnaeidae
A2
-1.0
-1.0
+1.0

respectively, cumulatively explaining 51% of the total variance in the species data with the complete model (4 axes) explaining 71%. Axis one Eigenvalues of 0.3-0.4 are quite common in other ecological applications (ter Braak and Smilauer 1988), so with these data, results from direct ordination may be used to represent the invertebrate community in the search for significant correlations with chosen environmental variables.

Table 1. Results from multi-response permutation procedure (MRPP) assessing differences among invertebrate communities in a priori treatment wetlands (2000)

Test	R	P
All treatment types	-0.0383	0.920†

†Lack of significance in overall test negated any further individual treatment tests.

Forward selection in RDA was used to choose environmental variables that portrayed significant correlations with changes in species composition (ter Braak and Smilauer 1998) and to remove irrelevant or “noisy” environmental data (McCune 1997). Appendix B lists all of the environmental variables used in forward selection. Those environmental variables found to be significant at the $P<0.05$ level were block, hydroperiod (hydro), total organic carbon (TOC), and NH_4N. Tadpole capture rate (tadpoles) was included in the analysis at the $P<0.07$ level of significance. Further RDA was performed with block as a covariable (partial RDA) to cancel out the significant variance that resulted from spatial differences that could possibly mask other weaker, but significant, correlations.

Partial redundancy analysis performed with these significant variables yielded Eigenvalues of 0.265 for axis one and 0.203 for axis two. The Monte Carlo significance test gave a P value of 0.001 for the first and for all canonical axes while permutating freely among all samples (Table 2).

Table 2. Results of RDA on invertebrate communities and significant environmental variables sampled on 15 May 2000

Axis summary statistics	Axis 1	Axis 2	Axis 3	Total variance
Eigenvalue	0.265	0.203	0.102	1.000
Species-environment correlations	0.968	0.965	0.955	
Total variance explained (sum of all axis)				.703
Summary of Monte Carlo tests	**F ratio**	**P***		
Axis 1	2.892	0.001		
All canonical axes	2.711	0.001		

*Significance was determined with Monte Carlo tests (1000) permutations.

Figure 7 shows the relationship between the invertebrate community and the chosen environmental variables. Using variance partitioning in partial RDA, I was able to determine that the significant environmental variables (including block) cumulatively explained 70.3% of the variation in the species community, leaving approximately 30% of total variation unexplained. Of the explained variation, variance partitioning indicated that block was associated with 27.2% of the variation; hydroperiod, 17.8%; TOC, 16.5%; NH_4N, 9.9%; and tadpole abundance, 8.5% (Figure 8). Variables were tested for interaction effects, most of which were found to be <2.2%. Although still considered negligible, cluster and total organic carbon had an interaction effect of 7.6%. All of the cumulative interaction effects were found to be 9.6% as seen in Figure 8.

The majority of the species vectors were positively correlated with wetlands having longer hydroperiods, and higher concentrations of total organic carbon and NH_4N (Figure 7). Exceptions to the overall pattern were Hydrophylidae, Culicidae, Collembola, and Chaoboridae, which exhibited a negative correlation to longer hydroperiod wetlands. Those taxa in the Coleoptera-other category (rare families, e.g., Scirtidae, Staphylanidae, etc.) showed negative correlations with wetlands having higher concentrations of NH_4N.

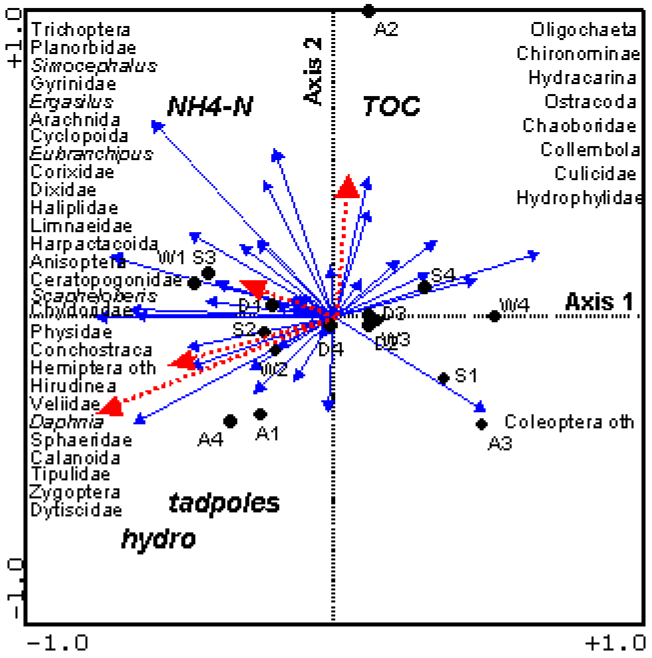
Correlations among species, wetlands and environmental variables from the RDA triplot were nearly identical to the PCA diagram resulting from analysis with chosen environmental variables (Figure 9). This similarity confirms the relationships found to be statistically significant with the Monte Carlo tests in the aforementioned RDA.

Post-treatment 2001

Physical features

There were immediate responses to the removal of trees in the experimental wetlands in the year following treatment. On 10 April 2001, as temperatures rose, there were significant differences in the degree of ice-out between treatments (F=9.60, P=0.002) (Figure 10). The four clear-cut wetlands were nearly 100% open, whereas the control wetlands

Figure 7. Partial RDA of invertebrate communities in 16 wetlands from 15 May 2000 with cluster as covariable. Solid vectors represent invertebrate taxa sampled. The dashed vectors represent the four environmental variables that were found to be significantly correlated ($P<0.07$) with changes in the invertebrate community by forward selection using Monte Carlo permutations. The chosen environmental variables are hydroperiod (hydro), wood frog tadpole capture rate (tadpoles), NH_4N, and total organic carbon concentration (TOC). Vectors point in the direction of increasing value for species and environmental variables. Areas opposite of arrow directions are the areas of lowest concentration or number. Longer vectors indicate stronger correlations between the vector and the axis.



+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
NH4-N
TOC
tadpoles
hydro
Trichoptera
Planorbidae
Simocephalus
Gyrinidae
Ergasilus
Arachnida
Cyclopoida
Eubranchipus
Corixidae
Dixidae
Haliplidae
Limnaeidae
Harpactacoida
Anisoptera
Ceratopogonidae
Scapheloberis
Chydoridae
Physidae
Conchostraca
Hemiptera oth
Hirudinea
Veliidae
Daphnia
Sphaeridae
Calanoida
Tipulidae
Zygoptera
Dytiscidae
Oligochaeta
Chironominae
Hydracarina
Ostracoda
Chaoboridae
Collembola
Culicidae
Hydrophylidae
Coleoptera oth
A2
W1
S3
S4
W4
D1
D3
S2
D4
D2
W3
W2
S1
A4
A1
A3

Figure 8. Histogram showing the partitioning of variance in the invertebrate communities by variables from 15 May 2000. Environmental variables are wood frog tadpole capture rate (tadpole CR), NH_4N, total organic carbon concentration (TOC), hydroperiod (hydro) and wetland cluster or block (block). Interaction variation is equal to the accumulation of interaction effects between the significant explanatory variables.

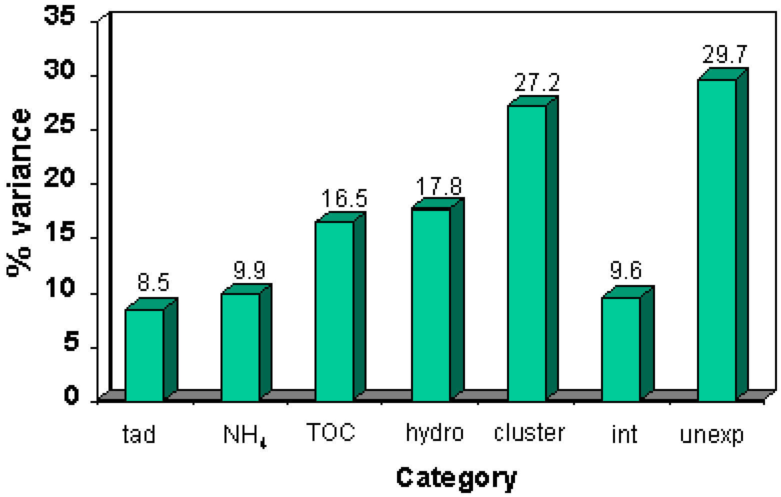

% variance
35
30
25
20
15
10
5
0
8.5
9.9
16.5
17.8
27.2
9.6
29.7
tad
NH4
TOC
hydro
cluster
int
unexp
Category

Figure 9. PCA on invertebrate communities and joint plot with those environmental variables chosen as significant in partial RDA from 15 May 2000. Solid vectors represent invertebrate taxa sampled. Dashed vectors represent environmental variables that were chosen using forward selection in RDA.

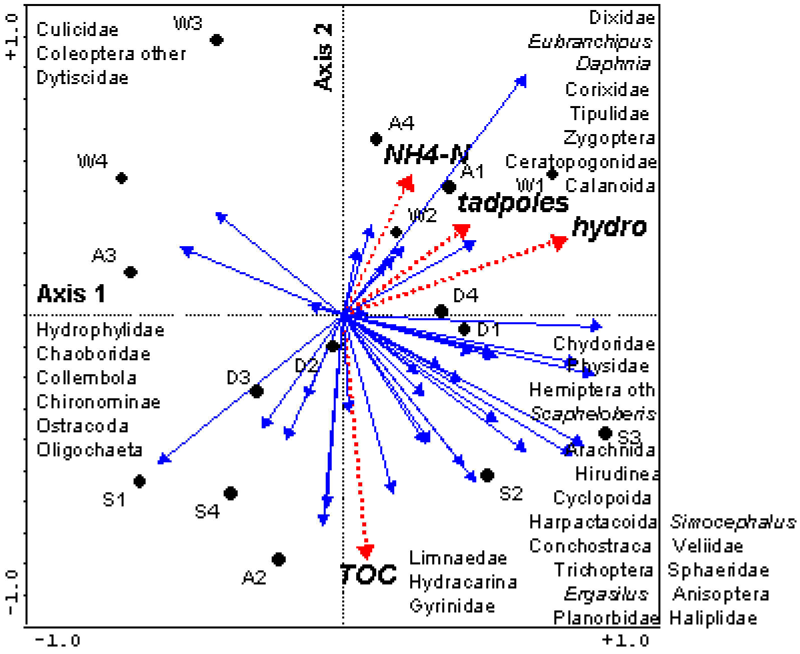
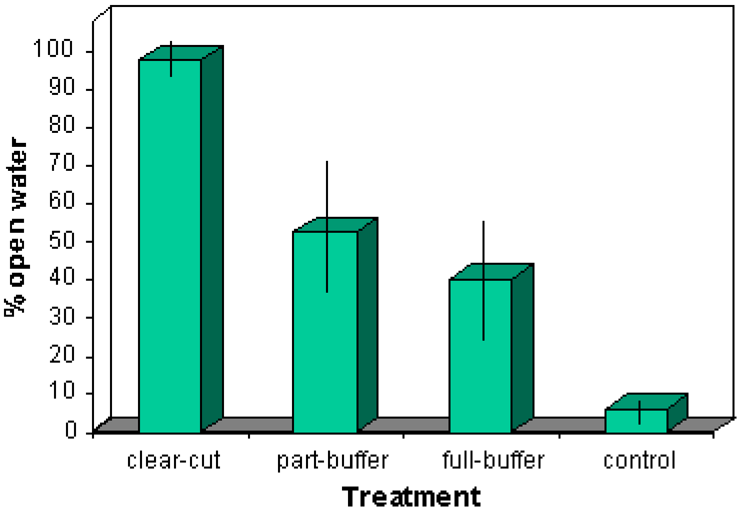

+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
Culicidae
Coleoptera other
Dytiscidae
W3
W4
A3
A4
A1
W1
W2
D4
D1
D3
D2
S1
S4
S2
S3
A2
NH4-N
tadpoles
hydro
TOC
Dixidae
Eubranchipus
Daphnia
Corixidae
Tipulidae
Zygoptera
Ceratopogonidae
Calanoida
Hydrophylidae
Chaoboridae
Collembola
Chironominae
Ostracoda
Oligochaeta
Chydoridae
Physidae
Hemiptera oth
Scapheloberis
Arachnida
Hirudinea
Cyclopoida
Harpactacoida
Conchostraca
Trichoptera
Ergasilus
Planorbidae
Simocephalus
Veliidae
Sphaeridae
Anisoptera
Haliplidae
Limnaedae
Hydracarina
Gyrinidae

Figure 10. Ice-out differences related to treatments in 16 study wetlands in 2001. ANOVA revealed that the clear-cut wetlands were significantly more open than the full-buffer and control wetlands at the alpha of 0.01. Clear-cut wetlands were significantly more open than the partially cut wetlands at a more liberal $P<0.06$, as well as full-buffer wetlands were more open than controls and partially cut wetlands were more open than full buffer treatment wetlands. USFS personnel used visual estimation to determine the percentage of openness.



100
90
80
70
60
50
40
30
20
10
0
% open water
clear-cut
part-buffer
full-buffer
control
Treatment

averaged only 6.25% open water (determined by USFS personnel). The thinned, or partial-buffer, wetlands and full-buffer wetlands showed an intermediate degree of thawing, but with large differences between wetlands in each treatment. The amount of cover provided by the partial buffer and full buffer would be expected to vary with manipulations of this magnitude due to variation in buffer width and also the size of trees surrounding each wetland. This variation probably caused the differences in thaw phenology within the buffer cut wetlands.

A shift in hydroperiod following treatment was also apparent. PCA with only treatment and hydroperiod as response variables revealed no apparent pattern in hydroperiod related to the assigned cuts in 2000 (Figure 11). After the winter tree harvest in 2000-01, similar PCA showed hydroperiod having a strong positive association with the clear-cut wetlands and a negative association with the control sites (Figure 12).

Invertebrates

Four bi-weekly sampling runs were completed in the post-treatment year (30 April - 18 June). Appendix A lists all invertebrate taxa collected during the 2001 field season. Diversity was similar to 2000, being highest at the beginning of the year (30 April 2001), dropping sharply through May, and increasing as summer progressed (Figure 4). Diversity among treatments was also similar to 2000 in that there were no significant differences (F=0.55, P=0.66; Appendix D) between treatment. No significant differences were detectable between years (F=1.69, P=0.21; Appendix D). Since species could have shown positive or negative

Figure 11. PCA showing the relationship between hydroperiod and the pre-treatment assignment on 16 study wetlands from 2000. Dashed vectors represent the treatments (clear cut, control, partial buffer, full buffer). Solid vector represents hydroperiod.

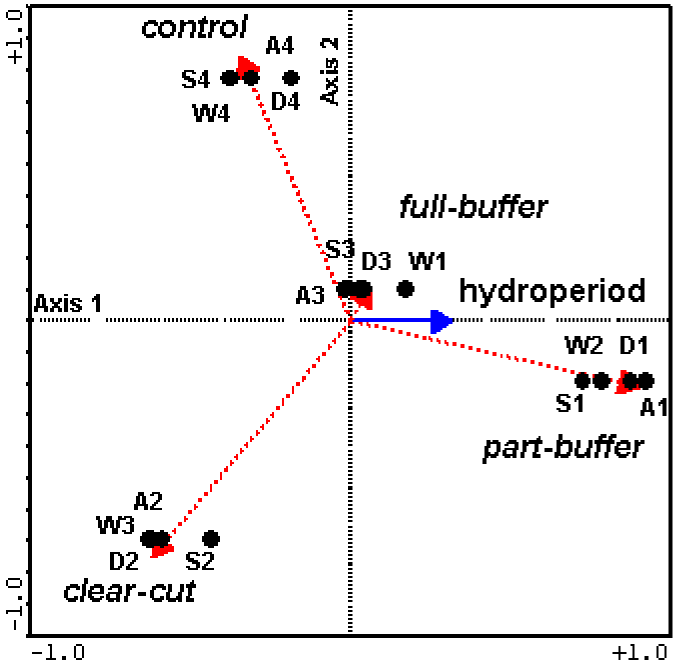
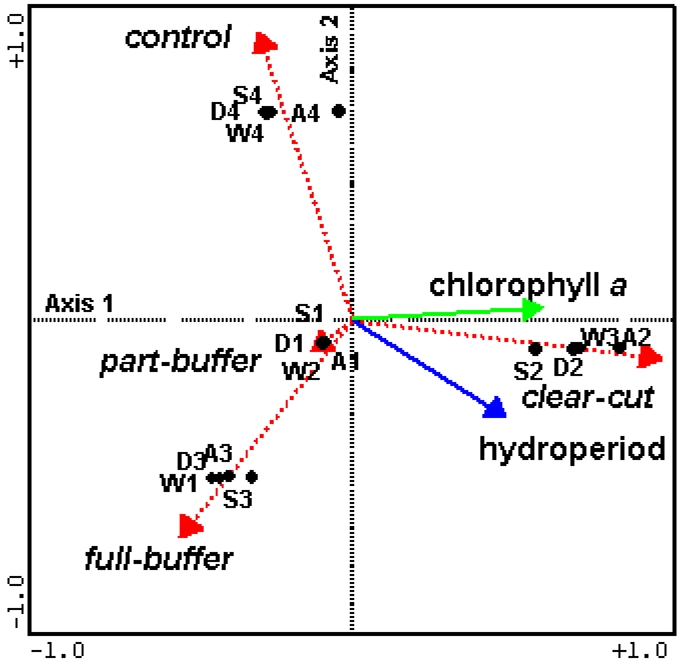

control
A4
S4
W4
D4
Axis 2
full-buffer
S3
D3
W1
A3
Axis 1
hydroperiod
W2
D1
S1
A1
part-buffer
A2
W3
D2
S2
clear-cut
+1.0
-1.0
-1.0
+1.0

Figure 12. PCA showing the relationship among hydroperiod, chlorophyll *a* concentration, and the post-treatment wetlands (17 May 2001). Dashed vectors represent the treatments (clear cut, control, partial buffer, full buffer). Solid vectors represent hydroperiod and chlorophyll *a*.


control
Axis 2
S4
D4
A4
W4
Axis 1
chlorophyll *a*
S1
D1
W3
A2
part-buffer
W2
A1
S2
D2
clear-cut
hydroperiod
D3
A3
W1
S3
full-buffer
+1.0
-1.0
-1.0
+1.0

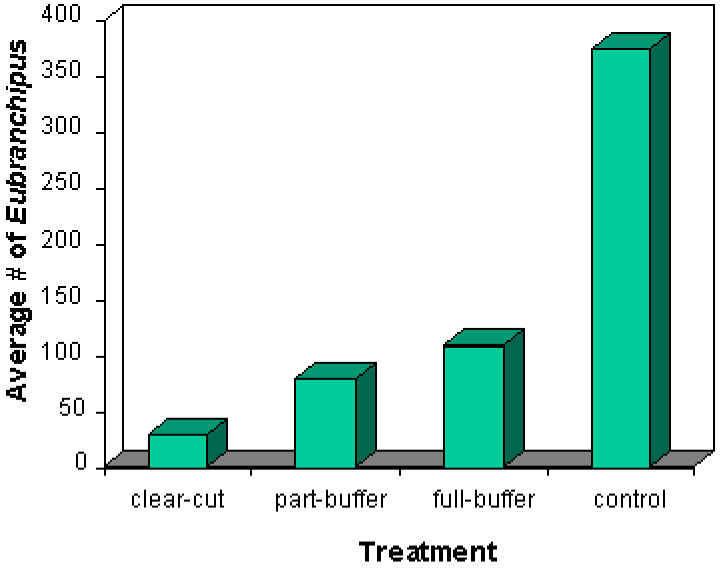
changes in association with treatment, diversity indices may not accurately portray treatment effects, but for our purposes, they function well to relate temporal shifts in invertebrate community composition.

An immediate invertebrate response was seen in the numbers of *Eubranchipus* among treatment types (Figure 13). Although, large standard deviations negate any statistical significance, a trend of fewer fairy shrimp in the clear-cut wetlands could accurately portray the small crustacean's negative response to the reduced canopy in the treatment wetlands as thawing was faster which facilitated an earlier completion of the fairy shrimp's short life cycle.

RDA from 13 May 2001(Figure 14) detected very similar, significant environmental correlations compared to 15 May 2000. The prominent exception was that "cluster" had no significant effect on species distributions. As with the 2000 RDA, hydroperiod and total carbon had strong influences on the community, but additionally, many invertebrates were positively associated with the absorbance attenuation vector, which is defined as the attenuation of light at 360 nm. Absorbance attenuation was negatively correlated with hydroperiod, and these opposing variables (along with total carbon) served to spread out the invertebrate community along axes 1 and 2. Eigenvalues for axes 1 and 2 were 0.158 and 0.102, respectively. The Monte Carlo test yielded a P value of 0.002 for the model (Table 3). All 4 axes of the model explained 34.6% of the variance in the species community.

Variation associated with each significant environmental variable was found using variance partitioning in partial RDA. Of the explained invertebrate

Figure 13. Mean numbers of *Eubranchipus* in relation to treatment type. Large standard deviations from the mean negate any statistical significance between treatments.



Average # of *Eubranchipus*
400
350
300
250
200
150
100
50
0
clear-cut
part-buffer
full-buffer
control
Treatment

Figure 14. RDA on invertebrate communities and significant environmental variables from 16 study wetlands (13 May 2001). The significant environmental variables chosen using manual forward selection are hydroperiod (hydro), total carbon (TC), and absorbance attenuation (abs attn). Vectors point in the direction of increasing value for species and environmental variables. Directions opposite of vectors indicate lower concentration or number. Longer vectors indicate stronger correlations between the vector and the axes.

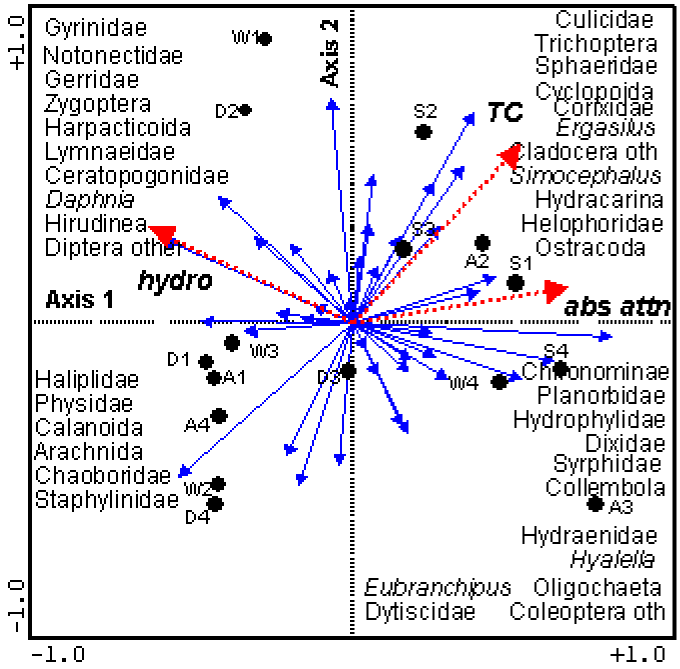

+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
hydro
TC
abs attn
Gyrinidae
Notonectidae
Gerridae
Zygoptera
Harpacticoida
Lymnaeidae
Ceratopogonidae
Daphnia
Hirudinea
Diptera other
Culicidae
Trichoptera
Sphaeridae
Cyclopoida
Corixidae
Ergasilus
Cladocera oth
Simocephalus
Hydracarina
Helophoridae
Ostracoda
Haliplidae
Physidae
Calanoida
Arachnida
Chaoboridae
Staphylinidae
Chironominae
Planorbidae
Hydrophylidae
Dixidae
Syrphidae
Collembola
Hydraenidae
Hyalella
Eubranchipus
Oligochaeta
Dytiscidae
Coleoptera oth
W1
D2
S2
S3
A2
S1
W3
D1
A1
D3
A4
W2
D4
S4
W4
A3

Table 3. Results of RDA on invertebrate communities and significant environmental variables sampled on 13 May 2001

Axis summary statistics	Axis 1	Axis 2	Axis 3	Total variance
Eigenvalue	0.158	0.102	0.087	1.000
Species-environment correlations	0.826	0.826	0.857	
Total variance explained (sum of all axis)				34.6

Summary of Monte Carlo tests	F ratio	P*
Axis 1	2.244	0.0609
All canonical axes	2.116	0.0020

*Significance was determined with Monte Carlo test (1000) permutations.

community variance, hydroperiod was associated with 11.4%; total carbon, 10.2%; and absorbance attenuation, 9.8% (Figure 15). The model failed to explain 68.6% of the invertebrate variance, making this model much weaker than the 15 May 2000 model.

Sporadic hydroperiods during 2000 resulted in only 1 complete sample (including all 16 wetlands), thus averaging data across each season was not feasible for statistical comparisons between years. To best assess the possible changes in invertebrate communities resulting from treatment, I decided to compare the most similar sampling periods between years. Using the invertebrate samples from the control wetlands (S4, A4, D4, and W4), I compared the one complete year 2000 sample (15 May) to each 2001 sample using MRPP to find the most similar weeks between years (Table 4). I looked for the largest P value to predict the most similar (or least dissimilar) sampling period. The 28 May 2001

Figure 15. Percentages of variance in invertebrate communities explained by significant variables from 13 May 2001 based on variance partitioning in partial RDA. Environmental variables are absorbance attenuation (abs attn), total carbon (TC), and hydroperiod (hydro).

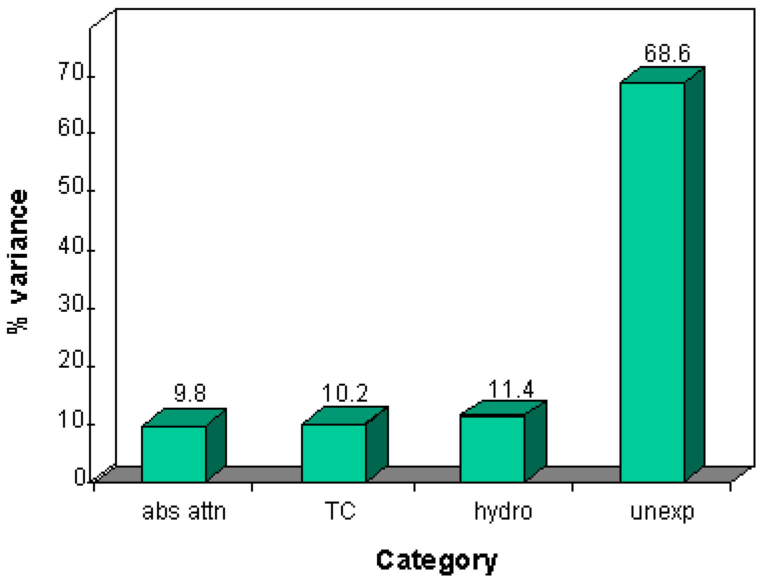

% variance
0
10
20
30
40
50
60
70
9.8
10.2
11.4
68.6
abs attn
TC
hydro
unexp
Category

Table 4. Results from multi-response permutation procedure (MRPP) to find the most similar sampling periods between year (highest P value)

Test	R	P
15 May 00 versus 30 April 01	0.113	0.016
15 May 00 versus 13 May 01	0.031	0.099
15 May 00 versus 28 May 01	-0.023	0.712[†]
15 May 00 versus 18 June 01	-0.017	0.618

[†] Because a high P value indicates the greatest lack of dissimilarity between sampling dates, 28 May 01 was chosen for between-year comparison of treatment effect on invertebrate communities.

date was found to be most similar to 15 May 2000 with a P value of 0.71. Comparisons between treatments were then made between the two sampling periods using MRPP. No significant differences were found between treatments in the invertebrate communities (R=-0.001 and P=0.49) in this early stage of the wetland community.

Also, PCA on invertebrate communities from 28 May only (Figure 16) did not show any apparent distribution of the wetlands on the ordination with respect to their assigned treatment (clear-cut, full buffer, etc.), and MRPP, again, showed no significant difference according to treatment assignment (P=0.163) on this early sampling date (Table 5), yet the P value was approaching significance at an alpha level of 0.05. The Eigenvalues of the first 2 PCA axes from 28 May were 0.32 and 0.17 respectively, which explain 49% of the total variance in the species data, with the complete model (four axes) explaining 75% of species variance. As with the 15 May 2000 PCA, these Eigenvalues were high enough to indicate that species composition was correctly constrained by environmental variables in RDA.

Figure 16. PCA from 28 May 2001, indicating no immediate apparent differences in the invertebrate communities based on treatment. Wetland treatments are designated by shape: circle, controls; triangle, clear-cut; hexagon, partially cut buffer; and diamond, full buffer. Vectors represent sampled invertebrate taxa.

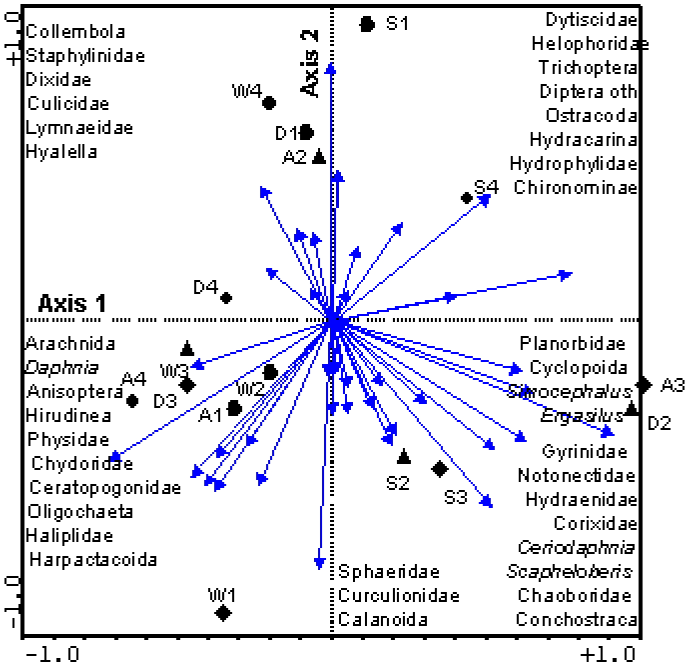

+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
Collembola
Staphylinidae
Dixidae
Culicidae
Lymnaeidae
Hyalella
Dytiscidae
Helophoridae
Trichoptera
Diptera oth
Ostracoda
Hydracarina
Hydrophylidae
Chironominae
Arachnida
Daphnia
Anisoptera
Hirudinea
Physidae
Chydoridae
Ceratopogonidae
Oligochaeta
Haliplidae
Harpactacoida
Planorbidae
Cyclopoida
Simocephalus
Ergasilus
Gyrinidae
Notonectidae
Hydraenidae
Corixidae
Ceriodaphnia
Scapheloberis
Chaoboridae
Conchostraca
Sphaeridae
Curculionidae
Calanoida
S1
W4
D1
A2
S4
D4
W3
A4
D3
W2
A1
A3
D2
S2
S3
W1

Table 5. Results from multi-response permutation procedure (MRPP) assessing differences in invertebrate communities in treatment wetlands from 28 May 2001

Test	R	P
All treatment types	0.012	0.163[†]

[†] Lack of significance in overall test negated any further individual treatment tests.

RDA forward selection on the species from 28 May found three significant variables to be included in the full ordination: hydroperiod, total phosphorous (tP), and total nitrogen (tN) (Figure 17). The first 2 axes of this model explained 17.9% and 10.5% of the variance in the species community, with all 4 axes explaining 34%. To determine the model's reliability the constrained RDA was compared to the unconstrained PCA diagram (Figure 18). Correlation disagreements were seen between wetlands and species, which reflected the lack of significance seen in the direct ordination (Figure 17). Monte Carlo testing yielded significance (P=0.008) for the complete RDA model from 28 May, but axis 1 was not significant at the acceptable alpha of 0.05 (P=0.085) (Table 6). As stated previously, the analysis for my project is exploratory, so non-significant results may still be useful for preliminary biological interpretations. The lack of significance of first RDA axis after Monte Carlo testing, combined with the disagreement between the constrained (RDA) and unconstrained (PCA) ordination makes interpretation of the

Figure 17. RDA on invertebrate communities and environmental variables in 16 wetlands sampled on 28 May 2001. Environmental variables are represented by dotted vectors: hydroperiod (hydro) and ammonium-N (NH_4N). Invertebrate taxa are represented by solid vectors.

Figure 17. RDA on invertebrate communities and environmental variables in 16 wetlands sampled on 28 May 2001. Environmental variables are represented by dotted vectors: hydroperiod (hydro) and ammonium-N (NH_4N). Invertebrate taxa are represented by solid vectors.

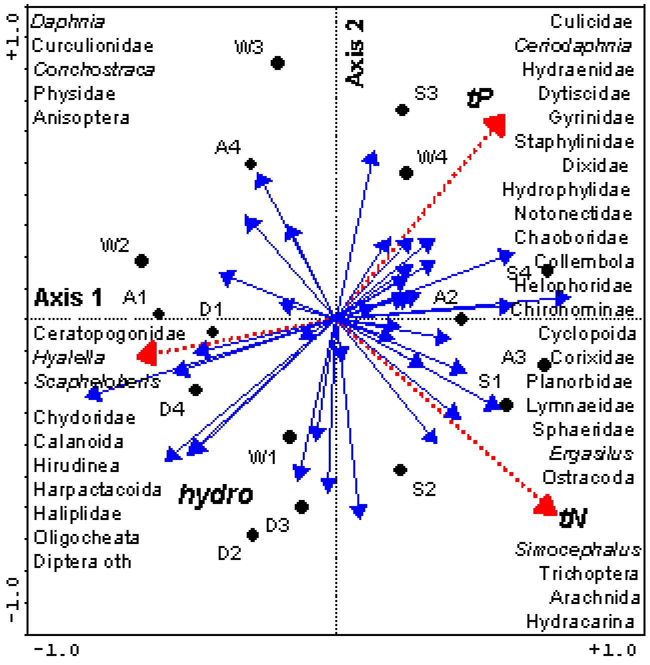
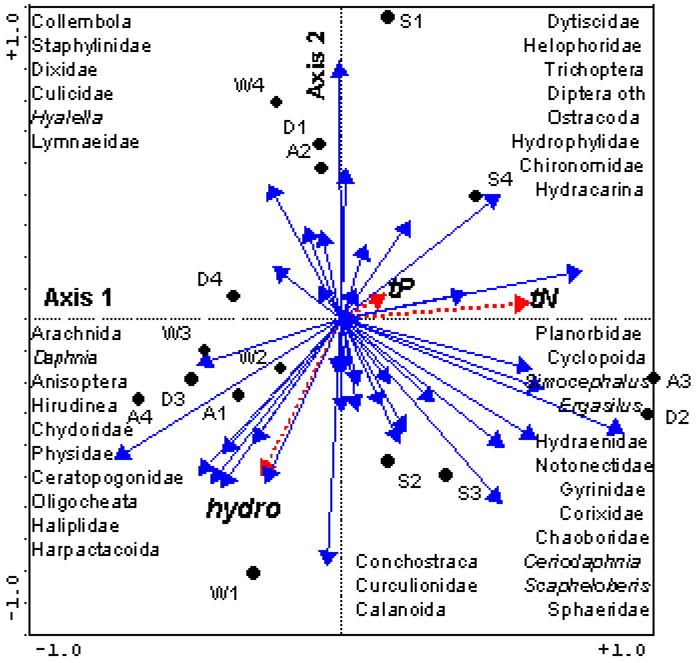

+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
tP
tN
hydro
W1
W2
W3
W4
A1
A2
A3
A4
D1
D2
D3
D4
S1
S2
S3
S4
Daphnia
Curculionidae
Conchostraca
Physidae
Anisoptera
Ceratopogonidae
Hyalella
Scapholeberis
Chydoridae
Calanoida
Hirudinea
Harpactacoida
Haliplidae
Oligocheata
Diptera oth
Culicidae
Ceriodaphnia
Hydraenidae
Dytiscidae
Gyrinidae
Staphylinidae
Dixidae
Hydrophylidae
Notonectidae
Chaoboridae
Collembola
Helophoridae
Chironominae
Cyclopoida
Corixidae
Planorbidae
Lymnaeidae
Sphaeridae
Ergasilus
Ostracoda
Simocephalus
Trichoptera
Arachnida
Hydracarina

Figure 18. PCA from 28 May 2001 on invertebrate communities and joint plot with those environmental variables found to be significantly correlated with changes in the invertebrate community with forward selection in RDA. Solid vectors represent sampled invertebrate taxa. Dashed vectors represent environmental variables.



+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
Collembola
Staphylinidae
Dixidae
Culicidae
Hyalella
Lymnaeidae
Dytiscidae
Helophoridae
Trichoptera
Diptera oth
Ostracoda
Hydrophylidae
Chironomidae
Hydracarina
Arachnida
Daphnia
Anisoptera
Hirudinea
Chydoridae
Physidae
Ceratopogonidae
Oligocheata
Haliplidae
Harpactacoida
Planorbidae
Cyclopoida
Simocephalus
Ergasilus
Hydraenidae
Notonectidae
Gyrinidae
Corixidae
Chaoboridae
Ceriodaphnia
Scapheloberis
Sphaeridae
Conchostraca
Curculionidae
Calanoida
S1
W4
D1
A2
S4
D4
tP
tN
W3
W2
D3
A4
A1
A3
D2
S2
S3
hydro
W1

Table 6. Results of RDA on invertebrate communities and significant environmental variables sampled on 28 May 2001

Axis summary statistics	Axis 1	Axis 2	Axis 3	Total variance
Eigenvalue	0.179	0.105	0.057	1.000
Species-environment correlations	0.856	0.745	0.725	
Total variance explained (sum of all axis)				0.34

Summary of Monte Carlo tests	F ratio	P*
Axis 1	2.609	0.0859
All canonical axes	2.066	0.0080

*Significance was determined with Monte Carlo test (1000) permutations.

28 May invertebrate data unreliable and was not used for further ecological interpretation.

Although most of the invertebrate communities showed little or no initial response to the treatment, forward selection in RDA on the invertebrates sampled during the week of 18 June 2001 did select the clear-cut treatment as being a significant environmental variable (Figure 19). The large Eigenvalues associated with axes 1 and 2 (Table 7) probably reflect the strength of this latter model.

Six invertebrates that show a strong positive relationship with the clear-cut wetlands are three non-wintering spring immigrant insects (Zygoptera, Anisoptera, Notonectidae, Corixidae, Dytiscidae, and Gerridae). Several invertebrates portrayed a negative association with the clear-cut vector. Variance partitioning determined that hydroperiod, cluster, sulfate concentration, and the clear-cut treatment were associated with 30.7%, 23.4%, 13.4%, and 9.5%, respectively, of

Figure 19. Partial RDA on invertebrate communities and significant environmental variables from 18 June 2001. Invertebrate taxa are represented by solid vectors. Environmental variables (dotted vectors) include hydroperiod (hydro), clear-cut treatment (clear-cut), and sulfate concentration (SO_4). Cluster was included in the model as a covariable.

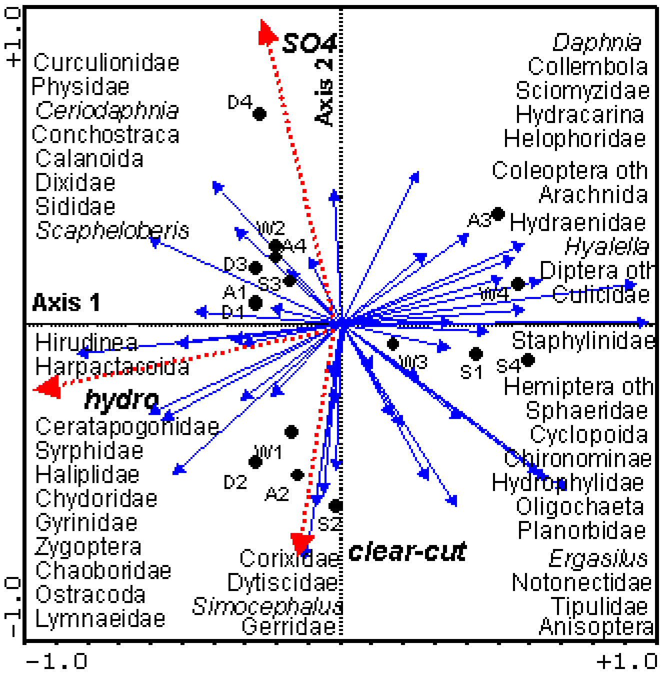

+1.0
-1.0
-1.0
+1.0
Axis 1
Axis 2
SO4
hydro
clear-cut
Curculionidae
Physidae
Ceriodaphnia
Conchostraca
Calanoida
Dixidae
Sididae
Scapheloberis
Daphnia
Collembola
Sciomyzidae
Hydracarina
Helophoridae
Coleoptera oth
Arachnida
Hydraenidae
Hyalella
Diptera oth
Culicidae
Hirudinea
Harpactacoida
Ceratapogonidae
Syrphidae
Haliplidae
Chydoridae
Gyrinidae
Zygoptera
Chaoboridae
Ostracoda
Lymnaeidae
Corixidae
Dytiscidae
Simocephalus
Gerridae
Staphylinidae
Hemiptera oth
Sphaeridae
Cyclopoida
Chironominae
Hydrophylidae
Oligochaeta
Planorbidae
Ergasilus
Notonectidae
Tipulidae
Anisoptera
D4
W2
A4
D3
S3
A1
D1
A3
W4
W3
S1
S4
W1
D2
A2
S2

Table 7. Results of partial RDA on invertebrate communities and significant environmental variables sampled on 18 June 2001

Axis summary statistics	Axis 1	Axis 2	Axis 3	Total variance
Eigenvalue	0.257	0.113	0.050	1.000
Species-environment correlations	0.960	0.956	0.785	
Total variance explained (sum of all axis)				0.766

Summary of Monte Carlo tests	F ratio	P*
Axis 1	4.561	0.001
All canonical axes	3.643	0.001

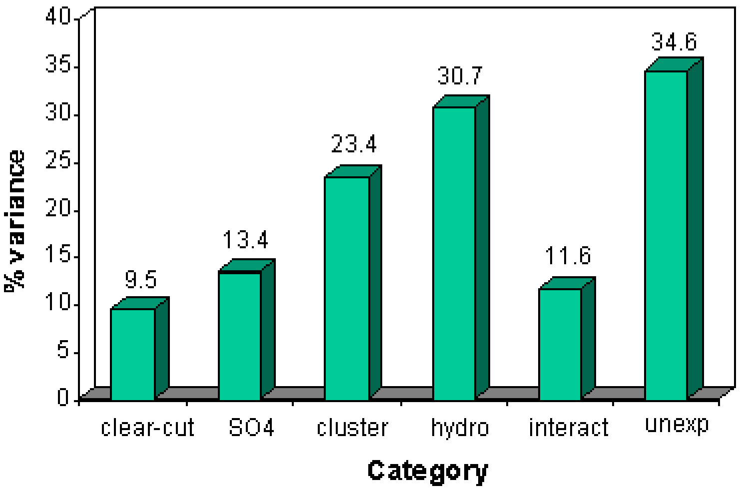
*Significance was determined with Monte Carlo tests (1000) permutations

the 77% of explained variation in the invertebrate community (Figure 20). Interaction among significant environmental variables accounted for a residual of 23%.

Algae

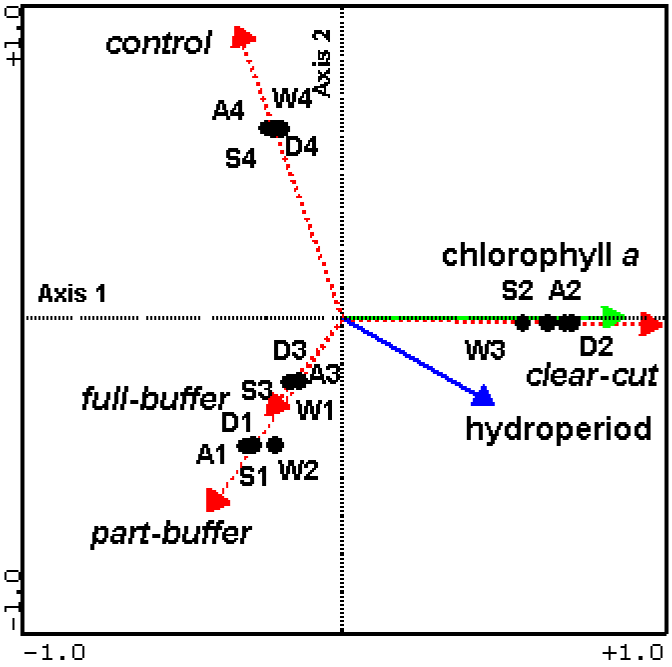
Total algal cell counts of sampled periphyton and phytoplankton (per 20 ml sample) are listed by phylum and class in Appendix C from the week of 28 May 2001 and 18 June 2001. Multivariate analysis detected few significant trends in the periphyton and phytoplankton data. The strongest trend of algal response to treatment is shown in Figures 11 and 20. Chlorophyll *a* levels were highest in the reduced canopy, clear-cut wetlands during the week of 17 May. Two weeks later (Figure 21), correlations between chlorophyll *a* and clear-cut wetlands intensified in clear-cut versus all other treatment wetlands and became significantly more abundant (F=8.28 and P=0.003, among all treatments).

Figure 20. Histogram showing the partitioning of variance in the invertebrate communities by variables from 18 June 2001. Variables include tadpole abundance (tad), ammonium-N (NH_4N), total organic carbon (TOC), hydroperiod (hydro), cluster, interaction (int), and unexplained (unexp).



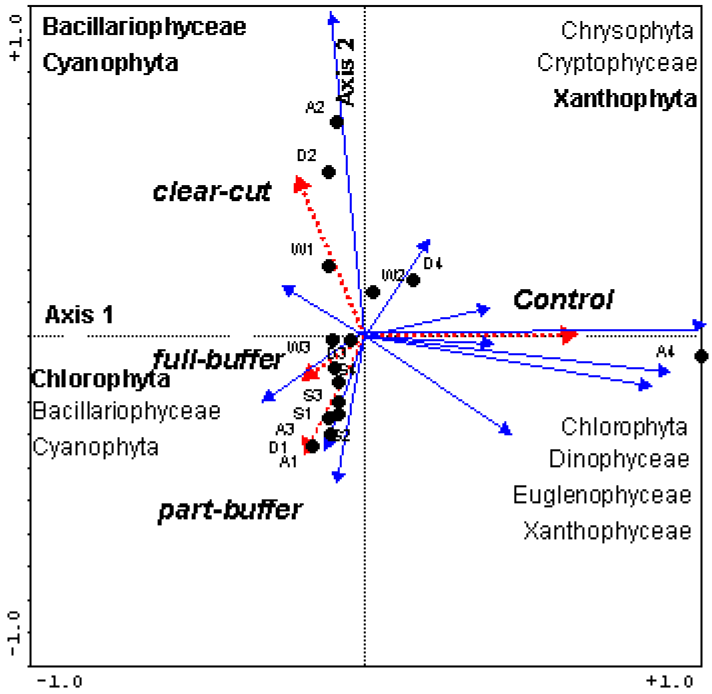
40
35
30
25
20
15
10
5
0
% variance
9.5
13.4
23.4
30.7
11.6
34.6
clear-cut
SO4
cluster
hydro
interact
unexp
Category

Figure 21. PCA showing the relationship among hydroperiod, chlorophyll *a* concentration, and the post-treatment wetlands (28 May 2001). Logging treatment is represented by dotted vectors. Chlorophyll *a* and hydroperiod are represented by solid vectors.


+1.0
control
Axis 2
W4
A4
D4
S4
chlorophyll *a*
Axis 1
S2
A2
D3
W3
D2
A3
clear-cut
full-buffer
S3
W1
D1
hydroperiod
A1
S1
W2
part-buffer
-1.0
-1.0
+1.0

Algal samples taken for taxonomic identification during the week of 28 May exhibited no significant trends with respect to treatment or any of the measured physical and chemical variables (Appendix B). Samples taken during the week of 18 June did indicate general relationships with respect to treatment (Figure 22). Phytoplankton appeared to be most abundant in the control wetlands with the exception of the Xanthophytes. Periphyton was found to be most abundant in the treatment wetlands. Periphytic diatoms (Bacillariophyceae) were most pronounced in the clear-cut wetlands while the phytoplankontic diatoms were most abundant in the partial buffer cut wetlands. No other significant trends in algae, resulting from chemical or physical differences, were apparent in the experimental wetlands.

Figure 22. PCA jointplot from 18 June 2001 of algal communities in relation to treatments. Solid vectors represent algal taxa. Dashed vectors represent logging treatments. Taxon names in bold represent periphyton, and non-bold names are phytoplankton. W4 is not included in the analysis due to loss of sample.



Bacillariophyceae
Cyanophyta
Chrysophyta
Cryptophyceae
Xanthophyta
Axis 2
A2
D2
clear-cut
W1
W2
D4
Control
Axis 1
W3
D3
full-buffer
S4
Chlorophyta
Bacillariophyceae
Cyanophyta
S3
S1
A3
S2
D1
A1
A4
Chlorophyta
Dinophyceae
Euglenophyceae
Xanthophyceae
part-buffer
+1.0
-1.0
-1.0
+1.0

DISCUSSION

Sources of natural variation in invertebrate communities

Faunal inhabitants of the study wetlands exhibited a large natural variation in composition and abundance associated with site-specific spatial, temporal, physical, and chemical characteristics. Competition and predator-prey interactions were also suspected of playing a role in shaping aquatic communities within these variable environments.

Natural variation in invertebrate communities from the 16 experimental wetlands in the pre-treatment year was largely explained by normal chronology of these populations. As described by Wiggins et al. (1980), taxonomic composition changes dramatically throughout the annual cycle of a temporary or seasonal wetland as over-wintering residents (e.g., Anostraca, Cladocera, Copepoda, etc.) are supplemented and sometimes replaced by non-wintering spring immigrants (e.g., Coleoptera, Hemiptera, etc.). As shown in Figure 3, invertebrate diversity in my study wetlands was found to peak at the beginning of the year and again before the end of the primary wet phase of the wetland. This fluctuation in diversity demonstrates the change in community composition as described by Wiggins et al. (1980).

Within each sampling period, spatial differences between wetland clusters were the largest cause of variation in invertebrates in 2000. Using variance partitioning in partial RDA, I was able to determine that the block, or cluster, where each wetland was located was associated with 27.2% of the explained variation in the invertebrate community from 15 May 2000 (Figure 7). Such variation may reflect the wetland's proximity to permanent water bodies (Sheldon 1984). Distance to permanent water (meters) was also used as a variable in the multivariate analysis and did show significant correlations with some of the individual tests. Obviously, distance from the seasonal wetland to the permanent water source would influence both colonization ability and rate for invertebrates considered to be non-wintering spring immigrants. Alexander and Syrdahl (1992) describe how regional diversity is often greater than diversity within any one pool because of the ability of individuals to move or disperse from pool to pool, so small scale spatial variability would be expected to be large.

Regional weather patterns and variation in groundwater-wetland connectivity are other possible causes of spatial differences. Summer thunderstorms struck locally and randomly among the four clusters and caused large variation in hydroperiods among the wetlands. Although not measured in my experiment, differences in conductivity between wetlands could reflect variation in each wetland's relationship to the water table, which can alter hydroperiods as well as water chemistry.

Several physical and chemical variables neared, or in some cases exceeded, the variation associated with spatial and temporal changes as seen in the variance partitioning results (Figures 7 and 19). Hydroperiod is the primary constraint on shaping community composition in seasonal wetlands (Wiggins et al. 1980), and this influence was obvious in my study wetlands. Throughout the pre-treatment season, hydroperiod was second only to spatial differences in shaping the invertebrate community as found by my multivariate analysis. For example, variance partitioning from 15 May 2000 revealed that hydroperiod was associated with 17.8% of the explained variation in the entire invertebrate community. In temporary aquatic environments, longer-lasting pools develop a greater diversity of individuals as more time is available for hatching endemic taxa and colonization by transient species (Wiggins et al. 1980, King et al. 1996).

Another possible explanation for the higher invertebrate densities found in relation to longer hydroperiods is that these wetlands are typically larger than the shorter lasting wetlands. This idea would concur with MacArthur and Wilson's (1963), and MacArthur's (1967) classic work with island biogeography. This theory describes how habitat area and distance from other (source) habitats can have direct effects on species richness. In larger wetlands, there is a greater amount of substrate available for utilization by invertebrates (King et al. 1996). I believe that the response seen by the invertebrate community in my study could be attributed to a combination of size and permanence, but hydroperiod is not always directly related to size. Water availability would ultimately be the shaping constraint for most obligate aquatic taxa (Bilton et al. 2001).

Concentration of total organic carbon was another significant wetland characteristic that was positively associated with invertebrate density, associated with 16.5% of explained invertebrate variation in data from 15 May 2000. Invertebrates would be expected to reach greatest densities where organic carbon levels are highest because of carbon's necessity for sustainable life and production. I initially expected that carbon concentrations could be a direct result of microbial decomposition. Wetlands with the highest carbon levels would be expected to support high densities of fungi and bacteria responsible for the majority of leaf-litter processing. Interestingly, results from the ordinations suggest that carbon is completely unrelated, or “orthogonal,” to hydroperiod in the experimental wetlands. In contrast, I expected decomposition to be highest in the shortest hydroperiod wetlands (Day and Megonigal 1993) where moist leaf-litter is exposed to the air for the longest periods, providing the most ideal environment for microbial metabolism. This contradiction in rationale may reflect another pathway for carbon in these wetlands. It is possible that sites with high concentrations of organic carbon have a greater degree of allochthonous matter input and that an increased leaching of carbon from leaf-litter is responsible for the elevated levels of carbon. In combination or separately, these wetlands could also have a greater degree of run-off from the surrounding upland, which would cause elevated carbon levels. A third possibility, although more remote, is that the elevated TOC levels are an artifact of invertebrate processing of organic matter. Given the paucity of invertebrate shredders in my study wetlands, this assumption seems less likely.

The significant correlation of NH_4N with high invertebrate densities from 15 May 2000 may also be an artifact of high invertebrate densities. NH_4 is acommon form of nitrogen in water (Wetzel 1975), and is a common waste product in most aquatic insects (Chapman 1982) and other aquatic invertebrates living in freshwater (Wetzel 1975, Ruppert and Barnes 1996). It is possible that NH_4N was elevated as a result of invertebrate waste production or possibly bioturbation. Bioturbation due to the activities of some species of *Chironomous* larvae has been shown to increase the concentration of NH_4^+ in the water (Ganapati 1949, Edwards

1958). Although ammonia is a major excretory product of aquatic animals, this source is considered minor in comparison to the amounts formed in decomposition by heterotrophic bacteria (Wetzel 1975). I expect that bacterial decomposition is the probable reason for elevated NH_4N levels in the experimental wetlands. High ammonia production from bacteria leads me to believe that the longer hydroperiod wetlands possibly have a greater rate of microbial decomposition and that TOC levels were elevated by another means.

It seems unlikely that the positive correlation of wood frog tadpoles and invertebrate taxa is a direct interaction as portrayed in Figure 6. The most probable explanation is that the longer hydroperiod wetlands that are the most ideal invertebrate habitats are also prime wood frog tadpole habitat because of similar life-cycle adaptations in the larval stages and time needed for development. There are indications that, within these habitats, there are other competitive or predator-prey interactions taking place between the tadpoles and invertebrates that would cause a negative interaction between the tadpole larvae and aquatic invertebrates.

Wetland physical and community response to treatment

An immediate response to logging treatment was a distinct difference in thawing or ice-out (Figure 9) in the wetlands. Those wetlands that had a reduced canopy (increased solar incidence) exhibited the fastest thawing.

I also detected an alteration in wetland hydroperiod as an immediate response to logging (Figures 12-13). Previous work (Verry 1986, Dube and Plamondon 1996) has shown that the removal of trees causes lengthened hydroperiods in lentic and lotic systems as a direct result of reduced evapotranspiration. Reduced evapotranspiration from tree removal is apparently the cause of the longer hydroperiods seen in my study wetlands evident when comparing the clear-cut wetlands and controls (Figure 11). In more arid regions, the opposite may happen if increased evaporation (resulting from reduced canopy cover) exceeded moisture loss from trees. Lengthening wetland hydroperiods is a possible concern for inhabitants of these sites, and changes in hydroperiod due to logging could interfere with natural hydroperiod fluctuations, causing life cycles of sensitive taxa to be altered. Aquatic taxa have evolved to persist in these ephemeral habitats where natural fluctuations in hydroperiod can be extreme (Figure 3). As seen in my study, anthropogenic alterations in wetland hydroperiod induced by logging could cause persistent changes in the temporary aquatic ecosystems that occur too rapidly for invertebrate taxa to adapt. If hydroperiods were found to be consistently longer in the clear-cut wetlands, a disturbance is likely within resident invertebrate communities. Another possible concern is that extended periods of inundation in forest wetlands have been shown to slow decomposition rates and, thus, nutrient availability (Day and Megonigal 1993), which can cause disturbance to wetland invertebrate communities (Golladay et al. 1997).

Early thawing of the treatment wetlands seemed to accelerate biotic processes in the pools. One of the most ephemeral taxa, anostracans, exhibited the strongest response to the early ice-out (Figure 10). In clear-cut and other treatment wetlands, fairy shrimp were approaching the end of their life cycle just as populations from the control wetlands were reaching peak density. Wiggins et al. (1980) suggest that the hatching of fairy shrimp quickly follows the first appearance of free water as eggs respond specifically to the lowered oxygen tension. Ultimately, this premature emergence would seem to present advantages to these animals that are prone to predation by larger invertebrates if life cycles can be completed before the predators that over-winter in still-frozen permanent water migrate to the temporary/seasonal wetlands.

A fourth response to treatment was elevated concentrations of chlorophyll *a*. Clear-cut wetlands were found to have significantly higher concentrations of chlorophyll *a* than the other treatments. The increase in this estimate of primary production is not surprising and can be attributed to the increased sunlight in the clear-cut wetlands.

Early in the sampling season, invertebrate communities exhibited no generalized response to the changes in wetland condition resulting from the imposed treatments. Although spatial differences were not a significant contributor in the early post-harvest year, hydroperiod and TOC still exhibited a profound effect in the early invertebrate community samples (Figures 14-15). An additional significant variable was absorbance attenuation. This measurement could represent abundance of tannins that give the water a dark, stained appearance. Increased absorbance attenuation, resulting from higher tannin concentrations, could lead to increased water temperature, which is known to influence invertebrate density and abundance in both positive and negative ways (Wiederholm 1984). I expect that effects of temperature elevation would be most pronounced early in the year when water temperatures are still low. Water temperatures were not available at the time of analysis, so this is only speculation.

Early in the post-harvest year (30 April, 13 May, and 28 May), there was no apparent treatment effect evident in the invertebrate communities and also no spatial differences. This lack of effect led me to believe that some other (unmeasured) variables were influencing these communities, which seems likely given that spatial variation was so pronounced in 2000. Also, discrepancies between the direct (RDA) and indirect analysis (PCA) from 28 May may reflect misrepresentation of significant environmental variables (Figures 16-17).

Although not significant in the early samples, two variables were found to be significant on the last sampling date. Invertebrates sampled during the week of 18 June began to show a response to the clear-cut harvesting treatment (Figure 19), and pronounced spatial effects were again evident. By 18 June 2001, invertebrate communities were not as strongly associated with longer hydroperiods as in the pre-treatment year. This delayed invertebrate response may indicate a latent shift in the community as a direct result of the logging treatments. The treatment effect on invertebrates seen on 18 June would most likely be a response to other factors that were impacted by the reduction in upland tree cover. It is probable that the reduction in canopy cover opened the wetlands to increased predatory pressure from colonizing invertebrates.

Effects of hydroperiod on invertebrates, although always a significant influence, were even more pronounced on 18 June than early in the season (associated with 30.7% of the explained invertebrate variation). It is probable that the strong hydroperiod association with invertebrate communities was a delayed reaction from 2000. Large natural hydroperiod variations in the pre-treatment year (Figure 3) may have influenced invertebrate communities in ways that did not show up in my samples until the 2001 sampling season.

Reasons for the significance of the sulfate (SO_4) correlation are unclear. Sulfates are a common end product of iron-oxidizing autotrophic bacteria, but typically, these bacteria inhabit eutrophic lakes, not small wetlands (Wetzel 1975). Bacteria typically endemic to oligotrophic water are heterotrophic and reduce SO_4 to hydrogen sulfide (Wetzel 1975). I can think of no other ecological reason for the influence of sulfate on invertebrate composition. A reason to question this statistically significant result is that the water chemistry samples were collected a month prior to the 18 June invertebrate samples and that sulfate levels would be expected to vary significantly within that time period. Additional water samples were collected by USFS personnel during the week of 4 June, but results were not made available to me in time for this analysis. Regardless of the effect of SO_4, the large amount of invertebrate variance explained with only the physical variables (hydroperiod, cluster, and clear-cut; Figure 19) would reinforce the validity of the results presented here.

Six invertebrate taxa (Dytiscidae, Corixidae, Gerridae, Anisoptera, Zygoptera, and Notonectidae) that were closely correlated with the clear-cut vector in the 18 June RDA are described as spring migrants by Wiggins et al. (1980). This positive association might be expected if removal of the surrounding trees made the wetlands easier to find for these predacious taxa when recolonizing from their over-wintering habitat. As described by Sheldon (1984), reflectance plays a key role in the discrimination of site colonization by aquatic insects, noting that Belostomatidae have been observed attempting to colonize parking lots wet by rain. Increases in water surface reflectance in my experimental wetlands due to logging could explain the increased numbers of these spring immigrants in the clear-cut wetlands.

Six of the taxa that exhibited a strong negative response to the clear-cut treatment (Curculionidae, *Daphnia,* Physidae, *Ceriodaphnia*, Conchostraca, and Calanoida) are all generally small and considered to be herbivores. It would be expected that herbivorous taxa would achieve maximum abundance where algal biomass is greatest, shown in this experiment to occur in the clear-cut wetlands. My results, showing small herbivorous taxa to be least abundant in the clear-cut wetlands, are inconsistent with explanations pertaining to food abundance.

A possible explanation for this paradox can be found in the recent mesocosm study by Sterner et al. (1998). Incident light was manipulated in large towers that contained algae, microbes, and herbivores. Results indicated that food chain production was lower in the towers with the highest light intensity. It appears that, in this experiment, higher light intensity increased algal abundance yet raised its carbon:phosphorus ratio. Here algae, although abundant, had excess cellular carbon and inhibited the growth of the herbivorous invertebrate *Daphnia,* which has a high metabolic demand for phosphorus. Algal C:P ratios were not measured in my experiment, but the similar responses of *Daphnia* and other herbivores could help explain their negative response to the clear-cut treatment.

I propose another plausible explanation for the trend of fewer herbivores and other small invertebrates found in the clear-cut wetlands. Many abundant spring migrants are predatory species that colonize the seasonal wetlands to take advantage of the abundant prey. It is possible that the clear-cut treatment promoted colonization rates of the migrant predators and subsequently increased predation rates in the seasonal ponds. Over-wintering residents of seasonal ponds are often not able to withstand high predation, which is reflected in their reliance on ephemeral habitats. Invertebrate predation on species such as fairy shrimp has been shown to be up to twice the maximum rate of population increase in these small crustaceans (Schneider and Frost 1996). It is very likely that high numbers of predators found in the clear-cut wetlands reduced the density of the smaller invertebrate prey as shown in Figure 19.

Algal communities did not respond strongly to the treatment. Responses that were detailed in the Results chapter did not follow my expectations based on accepted principles of algal ecology. I predicted an opposite response to treatment in that the bottom dwelling periphyton might have been shaded out in the clear-cut wetlands after phytoplankton increases. As the opposite was seen, I do not have a clear understanding of the response I observed. It is possible that nutrients, not only light, are important for phytoplankton growth, but periphyton, because of their attachment to nutrient rich detritus, are more strongly limited by light. This aspect of their ecology would explain the trend of increased periphyton abundance in the logged, reduced canopy treatments. The shallow depth in my study wetlands is most likely responsible for a lack of shading seen by phytoplankton on the periphyton. In deeper aquatic systems, light can be completely utilized by phytoplanktonic algae in the water column, leaving little light to reach bottom- dwelling periphytic algae, but in shallow systems, like seasonal wetlands, light probably penetrates the entire water column, regardless of phytoplankton density.

Variation in algal diversity and abundance between wetlands did not appear to have an effect on the herbivorous invertebrate community. Using the identified periphyton and phytoplankton as environmental variables in RDA, no significant correlation was found with the invertebrates. It is possible that higher taxonomic resolution would be necessary to identify algal community responses to the measured environmental variables and treatment effect.

Subsequent sampling in the post-treatment years could help to clarify and reinforce the findings presented here and to determine, if actual, the duration of the treatment effect on the invertebrate and algal communities.

CONCLUSIONS

Because of their small size and degree of embeddedness in the landscape, seasonal forest wetlands are influenced by changes in the adjacent upland. Evidence from this short experiment gives substantial clues to the consequences of upland alteration on aquatic communities.

My initial thought was that adjacent tree removal would result in sufficient physical change in the wetlands to sharply alter invertebrate and algal communities. Physical changes were evident: reduced canopies, faster ice-out, longer hydroperiods, and increased primary productivity were seen, and these changes did alter many aspects of invertebrate community dynamics. The changes in the invertebrate community attributed to the treatments, seen at the end of the first post-treatment year, appear to reflect an alteration in biotic interactions. Removing trees and opening wetland canopies made study wetlands more visible from above and possibly more prone to colonization by large, predatory invertebrates. I believe that the number of predacious insects increased to a density high enough to substantially reduce the number of small invertebrates. Thus, tree removal was indirectly responsible for altering community dynamics of invertebrates.

The vulnerability of smaller invertebrates to increased predation would be expected to diminish as quick-growing aspen trees decreased the visibility of wetland as canopies re-grew. Even with fast-growing aspen trees, the openness of the wetlands could affect invertebrate predator-prey ratios for 10-20 years through an increase in predator colonization. This community alteration could have long-term implications such as species extinctions through cumulative, large-scale forest alternation adjacent to seasonal wetlands. Although all invertebrates exhibit active or passive means of dispersal to surrounding aquatic systems, large-scale and long-term anthropogenic disturbance could have profound impacts on current wetland communities.

Another possible concern is the apparent shift in wetlands from an open water system to a macrophyte-choked pool when canopies are removed. This physical shift is common throughout the logged landscape, but is seen to reverse as canopies re-grow. Although dominance by emergent vegetation is only seen for 15-20 years, I believe that the repeated, long-term effect of macrophyte dominance in the seasonal pool might result in a substantial slowing of decomposition (Cornelissen 1996), subsequently speeding rates of basin filling. Based on past literature, emergent sedge should last approximately twice as long as deciduous aspen leaves (Cornelissen 1996). Based on this literature, I suggest that cumulative, repeated tree removal could shorten the life of the wetland through increased deposition of the more recalcitrant, slowly decomposing, emergent macrophyte. Obviously, this alteration in habitat would be expected to have a profound influence on those animals and plants utilizing seasonal wetlands in northern forest wetlands.

Results from this study suggest that leaving a partially thinned 50-ft. buffer immediately adjacent to the wetland is sufficient to protect the integrity of the invertebrate and plant communities residing therein, as long as canopies remain complete enough to inhibit emergent macrophyte growth and prevent increased colonization by invertebrate predators.

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APPENDIX A
INVERTEBRATES

<DATA NOT INCLUDED>

APPENDIX B
ENVIRONMENTAL VARIABLES

<DATA NOT INCLUDED>

APPENDIX C
ALGAE

<DATA NOT INCLUDED>

APPENDIX D
ANOVA RESULTS

Table 8. Year 2000 comparison between diversity

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between treatments	0.0548	3	0.0183	1.4259	0.2836	3.4903
Within treatments	0.1537	12	0.0128			
Total	0.2084	15				

Table 9. Year 2001 comparison between diversity

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between treatments	0.0271	3	0.0090	0.5460	0.6602	3.4903
Within treatments	0.1986	12	0.0165			
Total	0.2257	15				

Table 10. Diversity comparison between years

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Year	0.0248	1	0.0248	1.6919	0.2057	4.2597
Treatment	0.0693	3	0.0231	1.5743	0.2215	3.0088
Interaction	0.0126	3	0.0042	0.2855	0.8354	3.0088
Within	0.3522	24	0.0147			
Total	0.4589	31				

Table 11. Ice-out comparison between treatments

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between treatments	17092.1875	3	5697.395	9.6040	0.0016	3.4903
Within treatments	7118.75	12	593.2292			
Total	24210.9375	15				

Table 12. Chlorophyll a comparison between treatments (28 May 2001)

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between treatments	2044.1452	3	681.3817	8.2768	0.0030	3.4903
Within treatments	987.8886	12	82.3240			
Total	3032.0338	15				