FACTORS AFFECTING THE COMMUNITY ECOLOGY OF PREDACIOUS DIVING BEETLES (COLEOPTERA: DYTISCIDAE) IN BOREAL AND PRAIRIE PONDS ACROSS SOUTHERN MANITOBA

A Thesis

Submitted to the Faculty

of

Graduate Studies

by

Michael Alperyn

In Partial Fulfillment of the

Requirement for the Degree

of

Masters of Science

2004

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION PAGE

Factors Affecting the Community Ecology of Predacious Diving Beetles (Coleoptera: Dytiscidae) in Boreal and Prairie Ponds Across Southern Manitoba

BY

Michael Alperyn

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree

of

MASTER OF SCIENCE

Acknowledgments

I would like to express my deepest appreciation to Dr. R. E. Roughley for providing me with bountiful amounts of time, and wisdom throughout this project. My thanks go out to Dr. T. D. Galloway for his support, encouragement, editorial help, and for teaching, 038.428 Aquatic Entomology, a course that addresses all the reasons why I decided to become an entomologist. I would like to thank the other committee members Dr. N. Kenkel, Dr. D. M. Rosenberg, and Dr. D. A. Wrubleski for all their advice and encouragement throughout this project.

The technical support provided by Ms. Lisa Babey and Mr. David Holder is appreciated. I thank Ms. Liz Punter for her assistance in the identification of aquatic plants. Field assistance provided by Adam Carrière is appreciated. From the Freshwater Institute, I thank Mr. Ron Schade for his assistance in the water analysis and Mr. Len Henzel for instructing me on chlorophyll analysis and editing the description of this procedure. I thank Ms. Tonya Mouseau and Mr. David Wade for their advice, help and continuous support. Thanks go to Ms. Nicole Lauro for hours of volunteered help in the field, keeping me inquisitive, and most of all for her support. Thanks to Dr. N. J. Holliday for all of his talents in multi-tasking, which made him seem always available for my questions, despite the competition for his time. Thanks to everyone in the Department of Entomology who made being a graduate student a wonderful experience. I would like to thank everyone enrolled in the community residence program at the St. Amant Centre for being a constant source of inspiration in their efforts to overcome adversity each and every day. Thanks to Ms. Kimberly Spiers for her editing and patience, both of which

must have been required to wade through my atrocious grammar to get at my thoughts, and for supporting me through the final chapter of this degree.

Thanks go out to those that I have met along this transect of Manitoba including: Clint, whose talks about life and war stories made me look forward to coming to Dand; property owners such Mr. Paul Oaks whose commitment to the preservation of wetland habitats is inspiring, and Mr. Donnie Millar and Ms. Thelma Millar for welcoming me into their ponds and their home. I also would like to thank all the friends that I have made in Manitoba throughout this journey, for living up to our license-plate motto, "Friendly Manitoba", and welcoming me. Finally, I would like to thank my friends back in Toronto, Ontario, for their continuous support, especially Christina Masters, Sheila Masters, Katie McDonald, Nanci Karrandjas, Steve Thorne, and Michael Rowe.

Abstract

Alperyn, M., M.Sc., University of Manitoba, 2004.

Factors affecting the community ecology of predacious diving beetles (Coleoptera: Dytiscidae) in boreal and prairie ponds across southern Manitoba.

Major professor: R. E. Roughley

Bottle-traps and volume-sampling were effective techniques for collecting dytiscids. A total of 17 060 dytiscids were collected in two years among 30 ponds, using both sampling methods. Conclusions about the factors that organize dytiscid communities were similar, based on the results obtained from both methods of sampling. However, bottle-traps collected elusive, rare, or large species effectively whereas volume-sampling was better at collecting small species. Recommendations for the sampling regimes of future studies are provided.

A primary objective of this study was to relate and rank the environmental variables of boreal and prairie ponds that influence dytiscid diversity. This objective was accomplished by measuring various environmental variables for each pond including pH, conductivity, chlorophyll *a* density, pond permanence, pond area, macrophyte density, emergent vegetation density, and presence of fish and tiger salamanders. The environmental profiles of ponds were compared with their respective dytiscid communities. Multivariate analysis was used to determine the affinities of pond communities and species to the respective environmental variables. Environmental variables important for discriminating between boreal and prairie ponds included macrophyte diversity, pH, water conductivity, chlorophyll *a* density, and pond permanence. Among these variables, macrophyte diversity was considered a particularly good indicator of dytiscid communities. Ponds that were high in conductivity or that varied in hydroperiod also produced a number of strong associations. Adults of *Hygrotus salinarius* Wallis and *Hygrotus masculinus* Crotch were found only in the most conductive of the ponds examined. Ponds with unstable hydroperiods were inhabited by *Agabus bifarius* Kirby, *Agabus canadensis* Fall, *Agabus punctulatus* Aubé, and *Rhantus consimilis* Motschulsky.

An additional objective was to examine the extent that predatory guilds, including odonate larvae, fish, and grey tiger salamanders (*Ambystoma tigrinum diaboli* Dunn), contributed to the community structure of predacious diving beetles. Boreal ponds had higher densities of odonate larvae than prairie ponds, although predatory pressure by odonates in the boreal ecozone could not be demonstrated. Brook sticklebacks (*Culaea inconstans* Kirtland) and fathead minnows (*Pimephales promelas* Rafinesque) were the two most abundant fish species. Tiger salamanders were found in more than half of the prairie ponds examined. Ponds that were inhabited by tiger salamanders or fish could not be differentiated, based on dytiscid assemblages, from ponds that had neither of these vertebrates.

The final purpose of this study was to compare and contrast the species of dytiscids in boreal and prairie ponds. This objective was addressed by sampling 30 ponds among eight regional localities along a transect across southern Manitoba each month, May through September, over two years. Ponds in boreal plains and boreal ecozones shared more species than boreal plains and prairie communities. Boreal plains ponds were thus treated as boreal ponds. Dytiscid communities in prairie ponds were made up of ecological generalists. Species found in 25 or more of the 30 ponds included *Hygrotus sayi* Balfour-Browne, *Laccophilus maculosus* Say, *Liodessus obscurellus* LeConte, *Ilybius fraterculus* LeConte, *Coptotomus longulus* LeConte, *Rhantus sericans* Sharp, and *Graphoderus perplexus* Sharp. Boreal ponds had a higher frequency of ecological specialists, including *Desmopachria convexa* Aubé, *Hygrotus farctus* LeConte, *Graphoderus liberus* Say, and *Uvarus granarius* Aubé. Prairie ponds contained more species in greater abundance than boreal ponds.

Table of Contents

List of Tables

List of Figures

List of Appendices

INTRODUCTION

Predacious diving beetles (Coleoptera: Dytiscidae) are a diverse family with members adapted to many different types of water bodies. The species richness and abundance of dytiscids within lentic ecosystems are thought to be dependent on a number of variables, including predation, permanence and stability, macrophyte diversity, emergent vegetation, pH, and salinity (Galewski 1971; Larson 1985; Cuppen 1986; Lancaster and Scudder 1987; Larson 1990; Juliano 1991; Nilsson *et al.* 1994; Nilsson and Söderberg 1996; Fairchild *et al.* 2003).

Characteristics of water bodies, such as water chemistry, are generally attributed to the surrounding region. A region can be broadly categorized as an ecozone and defined as an area with characteristic physical features and biota (Wilken 1986). Within its provincial boundary, Manitoba contains a total of five ecozones. A latitudinal transect through the southern portion of the province cuts through three of these ecozones including (from east to west) boreal shield, boreal plains, and prairie (Wilken 1986). In the prairie ecozone, lakes and ponds are typically, ecologically productive waters that are nutrient rich, alkaline, and have varying salinities. Such water also may have unstable hydroperiods due to the arid climate. In contrast, boreal waters are generally less productive, poorer in nutrient content, and acidic. The hydroperiod of boreal waters is more stable than their prairie counterparts. The boreal plains is a transitional ecozone, thus a mixture of environmental features of either adjacent ecozones may influence associated waters. In addition, the proximity of water bodies to neighbouring prairie or boreal ecozones will dictate how close their environmental features resemble the waters of each ecozone.

Interestingly, some of the same environmental variables noted by authors to affect dytiscid communities vary between prairie and boreal waters (Larson 1985). Therefore, the existing environmental variation between prairie and boreal water bodies presents an excellent opportunity to investigate the ecology of these water beetles. The major objective of this study was to compare the composition of dytiscid communities in boreal and prairie ponds. A second goal was to relate and rank the influence of environmental variables within boreal and prairie ponds on dytiscid diversity. The last objective was to examine the extent that predatory guilds, including odonate larvae, fish, and tiger salamanders contributed to community ecology of predacious diving beetles.

LITERATURE REVIEW

Introduction

Ponds are fascinating and important ecosystems. These standing waters serve not only as wildlife habitats but also have significant hydrologic functions (Reimold 1994). Murkin (1998) outlined four functions of standing water in the maintenance and renewal of freshwater supplies, including: (1) control and storage of surface water; (2) recharge of groundwater supplies; (3) sinks for excess nutrients; and (4) filters for sediments and a wide variety of chemicals. Ponds also are recognized as being centres of biological activity (Gerald *et al.* 1984). Ecologists have capitalized on their manageable size and used ponds as models to analyze the interactions of abiotic and biotic factors on community structure (Heino 2000). However, before delving into the ecology of ponds, it is important to consider a definition and classification of these habitats.

What is a pond? A "small lake" is one definition (Reid 1961), referring to the common element of size. Roughley and Larson (1991) also based their definition on surface area, to account for the effect of wave action on the shoreline. Ponds have been defined as bodies of water in which the water temperature does not dramatically vary from the surface to the bottom (Gerald *et al.* 1984). Another definition points out a ponds' typically shallow depth, "...a body of water that has rooted plants growing across it..." (Reid 1961; p. 13). The littoral zone, or the zone occupied by rooted vascular aquatic plants, is a dominant feature of ponds (Reid 1961).

Ponds also can be classified according to the way they were formed. Potholes or sloughs in the prairie region are examples of water-filled hollows formed by retreating glaciers (Winter 1989). Flowing waters can be converted to ponds. For example, ox-bow ponds are formed by areas that are cut off from rivers and streams. Ponds can be man-made, as is the case of dug-outs for such purposes as aquaculture or to supply water for fire fighting (Gerald *et al.* 1984).

Zoltai and Vitt (1995) classified ponds based on three gradients important to the ecological processes of these habitats: pH, nutrients (particularly nitrogen and phosphorus), and water fluctuation. Zoltai and Vitt's classification implied that an aquatic community is predictable and that by understanding its constituents, the organization of these communities can be realized. Southwood (1977) adopted the notion of the habitat as an ecological templet, where the most prominent features of the templet would dictate the nature of the community. Thinking in this format poses interesting questions. What are the most important factors of the pond templet? What about other factors that contribute to organizing a community, such as predation producing top-down effects, or limits in primary production producing bottom-up effects? Can some of these factors be generalized and applied to a wider ecological scale, perhaps such as across an entire ecozone?

To answer such questions, ecologists generally use a study group from which patterns can be extrapolated based on the presence, absence, and abundance of certain members of the study group. The Dytiscidae (Coleoptera) is a family that has caught the attention of pond ecologists for their potential utility in understanding some of these questions. Predacious water beetles, or dytiscids, are numerically dominant predators and are taxonomically well known (Larson *et al.* 2000). Sampling in a given aquatic habitat, it is possible to find many species of varying sizes (Larson *et al.* 2000). The co-occurrence of similar size classes of water beetles also is cause for contemplation into the organizational forces that structure these communities.

The purpose of this literature review is for the reader to gain an understanding of: (1) dytiscid biology, life history and ecology as it applies to their community ecology; (2) to review some of the factors (water chemistry, aquatic macrophytes, predation by fish and odonate larvae) that determine dytiscid community structure; and (3) to predict and examine factors [salinity, algal density, fathead minnows (Cypriniformes: Cyprinidae: *Pimephales promelas* Rafinesque), and grey tiger salamanders (Caudata: Ambystomatidae: *Ambystoma tigrinum diaboli* Dunn)] specific to lentic waters of southern Manitoba that determine aquatic invertebrate communities and also may influence dytiscid communities.

Dytiscid biology, life history, and ecology

Dytiscids inhabit various aquatic habitats (Larson *et al.* 2000). In standing waters, they can often be found in very shallow water, partly because larvae and adults respire at the air-water interface. Adults store air beneath the elytra where the abdominal spiracles are located. They use the air for respiration and sometimes to control their buoyancy (Larson *et al.* 2000). Larvae store air throughout their tracheal trunks. In addition, larvae obtain oxygen through cuticular exchange, and members of one genus, *Coptotomus* Say, possess gills (Larson *et al.* 2000).

Most adult dytiscids have an oval body form that is dorsal-ventrally flattened. This form is streamlined and well suited for swimming. In some species, the body takes on a more globular form, presumably adapted for manoeuvrability, rather than speed

(Ribera *et al.* 1997). In other groups, the body is further dorsal-ventrally flattened, to permit beetles access among vegetation or under rocks (Larson *et al.* 2000).

Adults swim by moving their hind legs in unison. The legs are equipped with setae that increase the surface area of the power stroke. On the return stroke, setae are retracted to reduce drag. Species that are not powerful swimmers have reduced setation on their hind legs, and the overall hind leg is reduced in size. Many adult dytiscids are buoyant and, therefore, need to hold onto substrate or swim to stay submerged. In contrast, most larvae have a specific gravity greater than water, although larvae of species of Dytiscinae are neutrally buoyant (Larson *et al.* 2000).

Many dytiscids are early colonists of aquatic habitats and/or may inhabit temporary habitats, so dispersal by flight is an important aspect of their existence. Wings may not always be functional, depending on the condition of the flight muscles. Muscles may be absorbed depending on the species, populations, and season (Larson *et al.* 2000). Dytiscids cannot fly directly out of water, but have to exit the water before attempting flight (Larson *et al.* 2000).

The life histories of dytiscids vary (Larson *et al.* 2000). Typically, temperate species are univoltine, adults overwinter, mate, oviposit in the spring, and larvae develop during the summer, pupating, and emerging as adults in late summer. Oviposition strategies among dytiscids are diverse. Eggs may be scattered, attached to the substrate, deposited into crevices, or inserted into plant tissue. Female dytiscids that deposit eggs into plants possess a serrated ovipositor (some species of *Agabus* Leach, *Coptotomus* Say, *Cybister* Curtis, *Dytiscus* Linnaeus, *Ilybius* Erichson, *Laccophilus* Leach, and

Thermonectus Dejean) used for cutting (Larson *et al.* 2000). Larvae develop through three larval instars before crawling out of the water to pupate on land.

Predacious diving beetles are carnivorous as larvae and adults. The larvae seize their prey and inject pre-oral digestive enzymes through their large mandibles (Larson *et al.* 2000). The mouth of most dytiscid larvae is sealed. Their liquefied meal is sucked through the mandibles and into the digestive tract (Larson *et al.* 2000). The larvae feed on a variety of prey items, limited by what is available and what they can overpower (Larson *et al.* 2000). There are examples of specialized feeding in dytiscid larvae. For example, some members of Hydroporinae feed on microcrustacea (Matta 1983), and some species of *Dytiscus* are specialized for feeding on caddisfly larvae and tadpoles (Leclair *et al.* 1986). The larvae tend to be stealthy hunters, but adult dytiscids operate more as scavengers than predators, with dead or injured prey making up the greater portion of their diet (Hicks 1994).

Adult beetles are the life stage least affected by predators (Larson *et al.* 2000). Adults are fast swimmers, have hardened bodies, cryptic colouration, and chemical defences that, combined, help them evade predation (Larson *et al.* 2000). Despite these defences, adults are still heavily preyed on by insectivorous fish, which often results in reductions or the absence of dytiscids in waters where fish are present (Larson *et al.* 2000). The larvae of dytiscids have fewer defences and as a result are the food items of a variety of different predators, particularly dragonfly larvae (Larson 1990). Leaving the water makes dytiscids a target of terrestrial predators (e.g. ants and carabid beetles) and parasites (e.g. mites and parasitic wasps) (Larson *et al.* 2000).

Water chemistry in southern Manitoba

Prairie wetlands are unique in their levels of pH and salinity (LaBaugh 1989). These wetlands are typically alkaline with pH values greater than 7.4. The chemical factor responsible for elevating pH in this region is salinity (Hammer 1986). In contrast, in the southeastern portion of the province, in the boreal plains and boreal shield ecozones, waters are more acidic (McKillop 1985). Wetlands in this region typically are low in conductivity (McKillop 1985). Conductivity in prairie wetlands is typically high, but values may range from as low as 42 μS cm^{-1} to as high as 472 000 μS cm^{-1} (LaBaugh 1989). In a survey of Manitoban wetlands, Barica (1978) found conductivity to range from 220 to 12 070 μS cm^{-1}. Dissolved salts, principally chloride and bicarbonate-carbonate salts of sodium tend to be responsible for elevating conductivity values in prairie ponds (Euliss *et al.* 1999). Cowardin *et al.*'s (1979) classification of saline wetlands, proposed the following categories: fresh (< 800 μS cm^{-1}), oligosaline (800 - 8000 μS cm^{-1}), mesosaline (8 000 – 30 000 μS cm^{-1}), polysaline (30 000 – 45 000 μS cm^{1}), eusaline (45 000 – 60 000 μS cm^{-1}) and hypersaline (>60 000 μS cm^{-1}).

Aquatic insect response to salinity and pH

Some aquatic insects are able to exploit novel habitats by tolerating adverse hydrological conditions, such as extremes in pH and salinity. These habitats result in low intensities of predation, parasitism, and/or competition (Ward 1992a). For example, *Cenocorixa expleta* Uhler (Hemiptera: Corixidae) was found in saline waters but was excluded from lakes of low salinity (Scudder 1983). Scudder (1983) suspected that this species' preference for saline lakes was an avoidance of parasites, which were excluded from these habitats. Coping mechanisms for surviving adverse conditions may include a combination of behavioural (e.g. burrowing into substrate), physiological (e.g. increased absorption of water across midgut wall), and structural (e.g. waterproof secretions) adaptations (Scudder 1987). The distribution of species along pH or saline gradients is not always caused by a physiological response (Ward 1992a) but may represent a response to habitat stability, microhabitats, food resources, and/or the availability of oviposition sites (Ward 1992a).

Species richness is typically low in saline habitats but abundance of tolerant taxa may be high (Ward 1992a). Insect orders that possess saline specialists include Hemiptera (especially Corixidae), Coleoptera, Odonata, Trichoptera, and Diptera (Ward 1992a). Rawson and Moore (1944), in a survey of Saskatchewan saline lakes, found that flies and beetles possessed the greatest number of saline specialists. Dytiscids are especially adapted to tolerate saline waters as indicated by their high species richness (Rawson and Moore 1944). A number of authors have indicated that salinity is a good predictor of dytiscid composition (Balfour-Browne 1940; Galewski 1971; Larson 1985; Cuppen 1986). In fact, there is often very little overlap of dytiscid species between fresh and saline waters (Rawson and Moore 1944; Larson 1985). *Hygrotus salinarius* Wallis is the most notable example of a saline specialist in which larvae and adults can live in water more saline than seawater (Tones 1978).

There are few studies of aquatic insects in naturally acidic lentic waters (Ward 1992a). The response of aquatic insect communities to pH is quite similar to salinity: there is an increase in the abundance of a reduced number of taxa toward the endpoints of the pH continuum (Ward 1992a). Galewski (1971) noted that *Hydroporus* Clairville species seem well adapted for inhabiting acidic *Sphagnum* bogs where the pH may be as low as 4 to 5. Other selected species from the genera *Laccophilus*, *Agabus*, *Ilybius*, *Rhantus* Dejean, *Acilius* Leach, and *Dytiscus* also inhabit acidic bog pools (Galewski 1971). Among pond sites in The Netherlands, pH was a better predictor than conductivity of *Hydroporus* species distribution (Cuppen 1986). However, the response of invertebrate communities to pH is often not direct (Ward 1992a). Associated factors of acidic water, which may have a direct effect on the insect fauna, include changes in physicochemistry (e.g. oxygen deficiency, see Jewell and Brown 1929) and food resources (e.g. reduced algae, see Sutcliffe and Carrick 1973). This phenomenon is probably equally true for dytiscid species. For example, in lab experiments, larvae of *Dytiscus verticalis* Say were unaffected in acidic waters as low as pH 3.0 (Frisbie and Dunson 1987). This species is known to inhabit acidic bogs, but it typically is found in ponds with a rich diversity of macrophytes (Larson *et al.* 2000). This pattern of occurrence suggests that *Dytiscus verticalis* may be responding to factors such as macrophyte diversity in its habitat selection.

Aquatic vegetation

Aquatic macrophytes are vascular plants that grow principally on or below the surface of the water. They are differentiated from emergent vegetation, which grows around the periphery of aquatic habitats (Sharitz and Batzer 1999). Rooted macrophytes grow at a variety of depths although they are restricted to the photic zone (Sharitz and Batzer 1999). Aquatic macrophytes and other aquatic vegetation such as green algae, liverworts, and mosses, may play an equal ecological role in contributing to the structural complexity of the aquatic habitat. Therefore any reference to aquatic vegetation will also include these non-vascular plant groups.

Dytiscids and aquatic vegetation

A number of authors have commented on the positive correlation between dytiscid diversity and aquatic vegetation diversity (Larson 1985; Nilsson *et al.* 1994; Fairchild *et al.* 2003). Indirectly, aquatic vegetation attracts other invertebrates, which supply dytiscids with a variety of prey items. Macrophytes are attractive to invertebrates for a number of reasons: (1) they serve as a refuge from predators (Gilinsky 1984); (2) they serve as a substrate, allowing invertebrates to use a greater portion of the water column (Rabe and Gibson 1984); (3) they provide an indirect food source for invertebrates that feed on periphyton that grows on the plants (Rabe and Gibson 1984); and (4) they provide a direct food source for a small proportion of invertebrates (Newman 1991). In addition, macrophytes are tapped for oxygen by invertebrates such as mosquitoes, in the genus *Mansonia* Blanchard (Diptera: Culicidae), and the aquatic syrphid, *Chrysogatser* sp. Meigen (Diptera: Syrphidae) (Ward 1992b).

Exactly how dytiscids benefit from aquatic vegetation has not been examined, but dytiscids probably gain shelter from predators within aquatic vegetation. In addition, aquatic vegetation satisfies an important role in the life history of many dytiscid species by serving as oviposition sites (Larson *et al.* 2000).

Algae and aquatic communities

Wetlands are extremely productive habitats (Crumpton 1989). An important contributor to this productivity is algae. It is becoming clear that algae are a far more important food source for primary consumers than macrophytes (Neill and Cornwell 1992; Euliss *et al.* 1999). The low importance of macrophytes in food webs has been known for some time; macrophytes function primarily as substrate. Shelford (1918, p. 47) suggested that one could probably, "substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations". There are four algal assemblages: plankton, metaphyton, epiphyton and epipelon. Planktonic algae are often referred to as phytoplankton; these algae are suspended in the water column. Periphyton is made up of diatoms, cyanobacteria, flagellates, and unicellular, colonial, and some filamentous algae. Metaphyton is unattached, but loosely associated with the substrate. These algae are the most conspicuous, growing in floating mats and are made up of filamentous algae and cyanobacteria. Periphyton (attached algae) are either epiphytic or epipelic. Epiphytic algae grow attached on plants, whereas epipelic algae grow on sediment.

The production of algae in fertile lakes may be equal to or even surpass that of macrophytes in the littoral zones (Jones 1984; Allen 1971). Unlike macrophytes, algae can respond quickly to nutrient fluctuations. Without root systems, algae obtain their nutrients directly from the surrounding water. Nutrient pulses can lead to an explosive population increase in algal abundance, the so-called "algal bloom". This can be extensive enough to shade out macrophytes (Hann and Goldsborough 1997). In the prairie region, the seasonal pattern of algae generally involves as many as three blooms, occurring in the spring, summer, and fall. The spring bloom occurs when temperature and light conditions become ideal, resulting in a surge in the production of diatoms. Chlorophytes and cyanobacteria give rise to blooms in the mid-summer months. Algal blooms are often exacerbated by agricultural practices which contribute nutrients in the form of run-off (Crumpton 1989).

Algal density is a function of nutrient availability and it is correlated with invertebrate communities (Murkin *et al.* 1994; Hann and Goldsborough 1997; Sandilands *et al.* 2000). Algal density has been positively correlated with invertebrate abundance (Campeau *et al.* 1994). As predators, dytiscids would be terminal units in many of the associated food webs. Although the relationship between dytiscids and algal density has not been examined, it is probable that elevated primary production is met with increases in abundance at higher trophic levels (Campeau *et al.* 1994; Hann and Goldsborough 1997).

Predator guilds

Dragonfly larvae

Odonates are divided into two suborders: Zygoptera (damselflies) and Anisoptera (dragonflies) (Walker 1953). Within littoral zones, dragonflies are often the dominant predators (Benke and Benke 1975) and are taxonomically well known for Canada (Walker 1958, Walker and Corbet 1975). One-hundred and forty-three species of adult odonates are known for Canada; the immature, aquatic stages (larvae) are known for 133 species (Corbet 1979). Ninety-five species are known from Manitoba (Walker 1958, Walker and Corbet 1975, Conroy and Kuhn 1978; Hughes and Duncan 2003).

The immature stages of dragonflies advance through 10-15 instars and are exclusively aquatic during this period (Westfall and Tennessen 1996). Dragonflies are uni- and semi-voltine, although dragonflies in northern latitudes tend to be semi-voltine. Some larvae may take more than five years to complete their life cycle (Westfall and Tennessen 1996). Thus, dragonfly larvae tend to be excluded from habitats that are subject to seasonal drying (Larson and House 1990).

Dragonfly larvae are often the most diverse predacious insects (>1000/m^2; 10-20 coexisting species) in the littoral zone of permanent lentic habitats (Wissinger 1989). In the absence of fish, dragonfly larvae may be keystone predators (Larson and House 1990). Several authors have examined the change in community ecology of various invertebrate groups as a result of odonate predation (Pritchard 1964; Benke 1978; Thorp and Cothran 1984; Wissinger 1989; Larson and House 1990; McPeek 1990). Predation by odonates generally results in a decline in species abundance rather than species richness within invertebrate communities (Larson and House 1990; Larson 1990; Thorp and Cothran 1984).

Odonates are regarded as keystone predators in fishless, permanent ponds, but dytiscids occupy this ecological role in temporary water bodies (Larson 1990). It is suspected that this habitat partitioning has evolved, in part, by the predatory pressure by odonates on dytiscids (Larson 1990). As a result, dytiscids have adapted to colonize unstable habitats that do not favour odonate survivorship. However, ecological relationships are rarely sharply defined; thus dytiscids do co-occur with odonates to varying degrees in various habitats. To what extent does the predatory pressure exerted by odonate larvae affect the community ecology of dytiscids? This question was posed by

Larson and Colbo (1983) who suggested that odonates may be important predators of dytiscids, and the question was further investigated by Larson (1990). Larson's (1990) examined Newfoundland bog pools and found that: (1) dytiscid and odonate densities were inversely correlated; (2) size of adult dytiscids was positively correlated to pool size, in which odonates were speculated to exclude small dytiscids from large pools; and (3) at least one specimen of all species of dragonfly larvae examined had dytiscid larvae in their guts. These findings provide support for the hypothesis that odonate larvae may alter dytiscid communities.

Fish

Freshwater fish are generally the keystone predator in aquatic habitats and thus are the major organizing force within a community (Connell 1975). However, the predatory force that fish exert on an invertebrate community varies with the species (both fish and invertebrate), the season and habitat (Gilinsky 1984).

The ecological role of various fish species in relationship to invertebrates (at least in the higher trophic levels) probably represents a continuum, from predator to competitor to prey. Insectivory may approach 100% in some species of trout (Duffield and Nelson 1993). Brook sticklebacks (Gasterosteiformes: Gasterosteidae: *Culaea inconstans* Kirtland) compete with many predacious aquatic insects for prey items such as chironomid larvae, an important dietary component of sticklebacks (Tompkins and Gee 1983). Even the early life stages of large game fish, such as northern pike (Esociformes: Esocidae: *Esox lucius* Linnaeus) are often susceptible to predation by aquatic insects (notonectids, naucorids, odonate larvae, and dytiscid adults) (Louarn and Cloarec 1997).

The predatory pressure that fish exercise tends to be seasonal. In northern latitudes fish may be piscivorous in the winter and then feed almost exclusively on invertebrates in the summer (Jacobsen *et al.* 2002). This relationship is a result of a decrease in availability of invertebrates during winter months (Jacobsen *et al.* 2002).

Habitat complexity plays an important factor governing predation efficiency and also the type of prey that is seized. In aquatic habitats, macrophytes increase spatial complexity (Crowder and Cooper 1982; Gilinsky 1984). Crowder and Cooper (1982) found that bluegill sunfish (Perciformes: Centrarchidae *Lepomis macrochirus* Rafinesque) predation on invertebrates at low and intermediate macrophyte densities was greater than in high densities of macrophytes. In addition, bluegills were more likely to capture larger (odonate larvae) or more mobile prey (corixids) in high-density treatments.

Fish in southern Manitoba

There are over 95 species of freshwater fishes in Manitoba (Stewart and Watkinson 2004). However, conditions in shallow pond environments in southern Manitoba, generally, do not favour fish (Euliss *et al.* 1999). Many fish are prevented from establishing permanent populations in Manitoba ponds due to frequent drying, nonintegrated watersheds, and harsh winter conditions (Euliss *et al.* 1999). Brook sticklebacks (*Culaea inconstans*) and fathead minnows (*Pimephales promelas*) are the most common, naturally occurring species in prairie regions (Peterka 1989). Fatheads are also introduced deliberately into ponds in this region for the baitfish industry (Hanson and Riggs 1995).

The southeastern portion of Manitoba is a transition into the southern reaches of the boreal plains and, further east, into the boreal ecozone. In comparison to the prairie region, boreal wetlands are equivalently harsh habitats for fish, being characteristically acidic and oxygen-limited during winter months. The fish assemblage in these shallow water bodies includes central mudminnows [Esociformes: Umbridae: *Umbra limi* (Kirtland)], Iowa darter [Perciformes: Percidae: *Etheostoma exile* (Girard)], and redbelly dace (Cypriniformes: Cyprinidae: *Phoxinus eos* Cope), along with brook stickleback and fathead minnows (Tompkins and Gee 1983). Brook sticklebacks and fathead minnows appear to be the dominant fish in the wetlands of this region (M. Alperyn, personal observation).

In habitats where fathead minnows and brook sticklebacks co-occur, fatheads are usually dominant in terms of numbers of individuals and biomass and are often the keystone predator (Zimmer *et al.* 2000). A number of authors have examined the effects of fatheads minnows on invertebrate communities (Price *et al.* 1991; Hanson and Riggs 1995; Duffy 1998; Zimmer *et al.* 2001). Fathead minnows affect wetlands because of their diverse diets and dense populations (Duffy 1998; Zimmer *et al.* 2000). Fathead minnows alter a wetland directly through their consumption of prey and indirectly through the cascading effects of their excrement and nutrient transport (Zimmer *et al.* 2001). Wetlands supporting fathead minnow populations show increases in turbidity, chlorophyll *a* and phosphorus and have lowered aquatic macrophyte abundance (Zimmer *et al.* 2001). Fathead minnows reduce the abundance of invertebrates and may play a major role in structuring invertebrate communities (Zimmer *et al.* 2000, Zimmer *et al.* 2001).

The effect of other small-bodied fish, such as brook sticklebacks and mudminnows, on invertebrate communities is less clear. In comparison to fathead minnows, brook sticklebacks, feed on smaller invertebrates, such as *Daphnia* (Cladocera: Daphnidae), and appear to be more prey selective (Winn 1960; Laurich *et al.* 2003). Mudminnows are similar to fatheads, feeding as generalists on a wide variety of invertebrates (Peckham and Dineen 1957). In addition, mudminnows are tolerant of harsh conditions, surviving hypoxic and extreme temperature conditions (Peckham and Dineen 1957; Rahel and Nutzman 1994). These characteristics predispose the mudminnow to exert a predatory force on wetland communities.

Wilson (1923) extensively examined the influence of fish predation on dytiscid communities in fishponds. He found that species richness and abundance were negatively impacted by fish predation (Wilson 1923). This finding agrees with other authors who have observed reductions in dytiscid diversity from large water bodies (Galewski 1971; Larson 1990). A possible explanation for this phenomenon is that large bodies of water are more likely to be permanent and thus more likely to contain fish than smaller, less hydrologically stable habitats. Wilson (1923) examined predation by bluegills (*Lepomis macrochirus*), black crappie [Perciformes: Centrarchidae: *Pomoxis nigromaculatus* (Lesueur)], largemouth bass (Perciformes: Centrarchidae: *Macrochirus salmoides* (Lacépedé), and other large carnivorous fish on aquatic invertebrates. Such species can hardly be compared to smaller-bodied fish such as fathead minnows, brook sticklebacks, and central mudminnows, most common in wetlands of southern Manitoba. Central mudminnows and probably fathead minnows consume dytiscids (Peckham and Dineen 1957; K. D. Zimmer, North Dakota State University, personal communication 2004). Zimmer *et al.* (2000) examined invertebrate communities and found that dytiscid community structure was affected by the presence of fathead minnows. However, Zimmer *et al.* (2000) and other studies (Price *et al.* 1990; Mallory *et al.* 1994; Zimmer *et al.* 2001) were designed to examine the gross effects of fish predation, and therefore to examine the inhabitants of aquatic communities at a low taxonomic resolution. Therefore, potential shifts of taxa in the community structure within a particular family of invertebrates, such as Dytiscidae, have been overlooked.

Tiger salamanders

The grey tiger salamander (*Ambystoma tigrinum diaboli*) is the more common of the two subspecies occurring in southern Manitoba (USGS 2003; Larson 1968). The grey tiger salamander is distributed across much of southwestern Manitoba, while the eastern tiger salamander, *Ambystoma tigrinum tigrinum* (Green) occupies a small portion of the southeastern corner of the province (USGS 2003).

Metamorphic (terrestrial) tiger salamanders overwinter in surrounding forested areas of nearby aquatic habitats (Whiteman *et al.* 1994). In late spring, they migrate to permanent and semipermanent ponds where they mate and remain until autumn before returning to overwintering sites. Eggs are deposited on aquatic vegetation and hatch in mid-July. Development of the larvae into metamorphic and sexually mature salamanders may take two to five growing seasons (Wissinger *et al.* 1999). However, some individuals forgo metamorphosis completely and become sexually mature as larvae (i.e. become paedomorphic adults) (Whiteman *et al.* 1994).

Tiger salamanders are nocturnal, floating up from their benthic retreats to feed on invertebrates in the water column (Anderson and Graham 1967). They are opportunistic predators (Norris 1989). Wissinger *et al.* (1999) found that almost all pond invertebrates sampled with aquatic nets were represented in the stomach contents of tiger salamanders. When describing their feeding habits, Zaret (1980, p. 44) called tiger salamanders "fish in amphibian garments". In Manitoba, their ecological role has been compared with dabbling ducks (Benoy *et al.* 2002) and rainbow trout (Salmonidae: Salmoniformes: *Oncorhynchus mykiss* Walbaum; Olenick and Gee 1981). Maximum annual production of tiger salamanders was estimated at 565 $kg \cdot ha^{-1}$ in prairie lakes of North Dakota (Deutschman and Peterka 1988). This production is comparable to the production estimates of fathead minnows (144 – 482 $kg \cdot ha^{-1}$), which are known to alter invertebrate communities (Duffy 1998). Similar to fish and ducks, tiger salamanders are capable of affecting invertebrate communities through predation (Dobson 1970; Sprules 1972; Holomuzki *et al.* 1994). Tiger salamander densities were correlated negatively with mayfly and odonate larvae abundance (Holomuzki *et al.* 1994). In enclosure experiments, tiger salamanders reduced the density of zooplankton (Holomuzki *et al.* 1994).

Dytiscid and tiger salamander predator-prey interactions have been reported (Holomuzki 1986). Tiger salamander larvae altered their microhabitat usage in the presence of *Dytiscus dauricus* Gebler larvae (Holomuzki 1986). This behaviour was suspected to be an attempt to avoid predation by beetle larvae (Holomuzki 1986). However, large dytiscids such as *D. dauricus* make up a small percentage of a typical community (Larson 1985). In addition, numerous authors have reported adults and larvae of water beetles in the guts of tiger salamanders (Dobson and Dobson 1971; Olenick and Gee 1981; Collins and Holomuzki 1984; Holomuzki and Collins 1987; Benoy *et al.* 2002). Therefore, it is more likely that the predatory pressure is enforced by tiger salamanders. Studies involving tiger salamanders, like fish, have been focused on the predatory effects at higher taxonomic levels. Therefore, a potential alteration in the community structure of Dytscidae due to tiger salamander predation is probable, but has been overlooked.

Summary

Predacious diving beetles communities in ponds are governed by various environmental factors. Salinity and pH are factors that primarily affect species richness. Ponds at the extremes of these variables have a modified or selected fauna. Predation and primary productivity mainly regulate dytiscid species abundance by affecting the community through top-down and bottom-up interactions, respectively. Environmental factors such as diversity in aquatic vegetation are positively correlated with dytiscid species richness and abundance.

The factors that influence dytiscid communities can be examined on a broader ecological scale. What are the factors influencing dytiscid communities in ponds across southern Manitoba? Brook sticklebacks and fathead minnows occur in ponds across southern Manitoba and, therefore, so does their potential to impact dytiscid communities. The influence of other factors may be more localized. Odonate larvae, for example, can be found in high densities in ponds with stable hydroperiods. Such ponds are typically found in the boreal region of the province, so the impact of odonate as predators of dytiscids would be expected to be more pronounced in this ecoregion than in other ecoregions. Finally, factors such as pH may be dichotomously represented across the province and correspondingly affect dytiscid communities. For example, ponds in the eastern, boreal region are generally more acidic, favouring acidophilic species, whereas western, prairie ponds have higher pH values favouring species adapted to such waters.

Ponds can be viewed as experimental replications due to their differences and similarities in environmental variables. This variability allows the experimenter to select ponds that are similar in many respects but differ in relation to a few environmental variables. By sampling the dytiscid communities of ponds and comparing them with particular environmental variables, maybe it is possible to account for differences in species diversity. Southern Manitoba is an excellent region for such a study due to its large number of ponds, dytiscid diversity, and contrasting boreal and prairie ecozones.

MATERIALS AND METHODS

Survey design

Dytiscid communities were examined in ponds across southern Manitoba. The study was designed to examine some of the environmental factors within a given pond that influence dytiscid diversity. Environmental factors that were evaluated were pond size, pH, conductivity, aquatic vegetation diversity, emergent vegetation density, algal density, presence of certain fish species, presence of tiger salamanders, and odonate larval density.

Description of the general study area

The sampling was conducted in 2001 and 2002 in the southern region of Manitoba between latitudes 49°17'N and 49°43'N. A transect across southern Manitoba was subdivided into eight regional localities. In this study, a locality was designated as an area in which a number of ponds were: (1) close in proximity (all ponds within a 5 km radius) and (2) varied in terms of size and/or the presence/absence of fish. Each locality consisted of three to five ponds for a total of 30. Two localities were located within the boreal ecozone, one in the boreal plains ecozone and five localities were located in the prairie ecozone of southern Manitoba (Fig. 1).

Pond selection

A pond was defined by Roughley and Larson (1991; p. 27) as a "small permanent body of water; with small enough surface area that wave action does not significantly affect shoreline so that fringing organic matter and emergent plants occur; generally with an open-water central area". By this definition aquatic habitats that are typically known as 'small lakes' (which will subsequently be referred to as ponds) were included for comparison purposes to smaller water bodies (traditionally known as ponds). A large variety of water bodies are classified as ponds using this definition, including reservoirs (e.g. Paterson and Fernando 1969), aestival ponds (Daborn 1974), and saline ponds (Hammer *et al.* 1975).

In May, 2001, survey trips located and assessed ponds for inclusion in the study. The initial selection of localities was made with Energy, Mines and Resources Canada 1:50 000 maps to find areas with clusters of neighbouring ponds. A global positioning system (GPS; Garmin® 12 XL model) was used to find their locations. Over 60 ponds were considered for the study, and from these, 30 ponds among eight localities were selected (Table 1). Ponds within a locality were selected so that they could be compared within a locality and compared to ponds in other localities. Criteria for ponds included accessibility, size, distance to other ponds within a given locality, minimal impact by agricultural practices and/or other anthropogenic activities, and presence/absence of fish (seven of the eight localities included at least one pond in which at least one fish species was present).

Pond specifications

The geographical co-ordinates and elevation of each pond were recorded using the GPS. Pond surface area was calculated by walking the perimeter of the pond, entering waypoints around the pond margin and using the "calculate area" function contained in the GPS. Surface area of ponds >500 m^2 was extrapolated from maps. Water samples were taken from each pond each month, from May through September, and measured in the laboratory for conductivity and pH. A Hanna Instruments model 9812® portable pH meter was used to measure pH. Conductivity was measured using a Bach-Simpson model CDM3® conductivity metre.

Algal collection and quantification

Water samples were collected and filtered for algae each month, from May through September in 2001 only. Samples were collected by dipping a one-litre Nalgene™ bottle near the surface in open areas of the ponds. Generally 0.4 L of water provided a sufficient biomass, although on occasions when algal densities were low, greater volumes of water were needed. Water samples were filtered in the field through 47 mm, glass fiber filters (Whatman® GFC) using a Nalgene™ vacuum filtering apparatus with a hand operated Nalgene™ vacuum pump at approximately 100 mm Hg vacuum. Filtered volumes were recorded. After filtration, filters were folded and placed into 20 mL glass vials. Filtered samples were stored in the dark and kept frozen. These filtered samples were transferred to 20 x 150 mm test tubes and extracted in 6 mL of 90% methanol. Test tubes were covered with Parafilm M™ and refrigerated at 4-5 °C in the dark for at least 12 hours. Chlorophyll extracts were then filtered through 25 mm diameter glass fibre filters. Glass fibre sample filters were rinsed with 4 mL of 90% methanol, combined with the extract and the final volume was adjusted to 10 mL with methanol. An aliquot of each filtered extract was pipetted into a 10 cm path length cuvette and the optical density (OD) was read using a Jenway® model 6300 spectrophotometer at three different wavelengths [650, 665, and 750 nanometers (nm)]. Any interference due to sample extract turbidity was corrected by subtracting the OD at 750 nm from the OD readings at 650 and 665 nm, respectively. Algal density was expressed as micrograms of chlorophyll *a* per litre (μg chlorophyll *a*/L) and calculated from the OD measured readings using the following equation and extinction coefficients (MacKinney, 1941):

$$\mu\text{g chlorophyll } a/\text{L} = \frac{(1.65 \text{ x } OD_{665} - 0.83 \text{ x } OD_{650})(\text{vol. of extract, mL})}{(\text{vol. of sample, L})},$$

where $\mathbf{OD_{665}}$ is the optical density reading at 665 nm and $\mathbf{OD_{650}}$ is the optical density reading at 650 nm. The extinction coefficients 1.65 at 665 nm and 0.83 at 650 nm were according to MacKinney (1941). The **vol. of extract, mL** equalled 10 mL for all the samples and the **vol. of sample, L** was the volume of water, in litres, that was initially filtered in the field.

Between samples, the cuvette was rinsed with 90% methanol to avoid cross contamination. In addition, the spectrophotometer was re-calibrated after every five samples using a blank sample (cuvette filled with only methanol).

Pond permanence

Efforts were made to include only permanent ponds in the study; that is, ponds that would contain water throughout the entire year, for at least both study years. However, some ponds dried out at some point in the sampling period, either in the first or the second study year or both. Therefore, pond permanence was ranked on a 6 point scale (0-5). A point was given for each sampling month that each pond contained water. Ponds were ranked separately for each study year.

Survey of submergent vegetation and emergent vegetation

Submergent vegetation was defined as macro-vegetation that was partially or completely submerged. This definition was not limited to vascular plants, so macroalgae and liverworts also were considered. Emergent vegetation was defined as rooted plants that had parts extending above the water surface, such as *Typha latifolia* Linnaus (Typhales: Typhaceae). Representative samples of aquatic plants were pressed with a plant-press and returned to the laboratory for identification. All aquatic plants were identified to species. Submergent vegetation and emergent vegetation were surveyed in all 30 ponds once in August, 2001.

Submergent vegetation was assessed on a 6-point scale (0-5) to determine its diversity for the entire pond. For example, ponds that had either one or two dominant aquatic plant species were scored a “1”, ponds that had either three or four dominant plant species were scored a “2” and so forth. The entire pond was visually scanned and scored for the number of dominant aquatic plant species present. For ponds that were >500 m^2 and, therefore, sub-sampled, only the sub-sampled portion was surveyed for submergent vegetation. Dominant aquatic plant species were classified as plants that were present throughout the entire pond and in relatively high densities.

Emergent vegetation was assessed on an 11-point scale (0-10). The entire pond shoreline was visually scanned and the proportion of emergent vegetation bordering the pond was scored. For ponds that were >500 m^2 and, therefore, sub-sampled, only the sub-sampled portion was surveyed for emergent vegetation.

Faunal sampling techniques

Pond were divided into four sectors (A, B, C, and D) corresponding to compass points (N, E, S, and W) prior to sampling (Fig. 2). Ponds that were >20 000 m^2 in size were sub-sampled in such a way that a smaller, representative portion of the pond was selected and divided into the same four sectors. Larger ponds were sampled only in the these smaller sectors.

Bottle-trap sampling

Bottle-trap sampling was conducted each month, May through September, for years 2001 and 2002. Bottle-traps were used to collect adult dytiscids. These bottle-traps were constructed out of two, two-litre soft drink bottles (Fig. 3). Each bottle-trap was weighted with a piece of lead, and floating cork markers were attached with fishing line to aid in its retrieval. One bottle-trap was placed into each sector (A to D) of the pond at a depth of ~20 cm and oriented parallel with the shoreline (Aiken and Roughley, 1985). The bottle- trap contents were collected after a 24 h period. Dytiscid catches were preserved in a 70% ethanol and returned to the laboratory for identification.

This method samples large, mobile species that may be elusive and in low abundance when sampled with discrete volumetric methods. However, bottle-trapping has several drawbacks when compared to volumetric methods: the abundance of guilds of large-sized dytiscids are overestimated; small, less mobile dytiscid species are underestimated; and odonate larvae are sampled ineffectively (Gundersen *et al.* 2002). To overcome these shortcomings, volumetric sampling was employed in conjunction with bottle-trap sampling.

Volumetric sampling

Volume-sampling was conducted each month, May through September, for year 2001 only. This method was used to obtain accurate, quantitative samples of adult dytiscids and odonate larvae. Volumetric samples were taken with an aluminium garbage can (diameter = 42 cm; length = 90 cm), the bottom of which was cut out and reinforced with a steel band. When the bottom of the apparatus was placed firmly into the substrate of the pond it created a cylinder of defined volume (Fig. 4). With the volume-sampler in place, the contents were swept with a D-frame aquatic net (400 x 800 μm mesh size) and placed into a sorting tray. This procedure was repeated until no more dytiscids and odonate larvae were collected. Dytiscids and odonate larvae were then sorted, preserved in a 70% ethanol and returned to the laboratory for identification. These samples provided a comparison to the data provided by the bottle-traps. Two volume-samples were taken from each pond sector (A to D) at different depths, following a stratified random approach. One sample was taken at the pond margin and the second was taken at an approximate water depth of 60 cm (+/- 15 cm).

Seine net sampling

Seine net samples were used to determine the relative abundance of fish and tiger salamanders in each of the study ponds. Seine net sampling was done once in August, 2001 for all 30 sites. The seine net used was 1.8 m by 12.24 m and the mesh size was 1.27 cm. Seine netting was conducted with two people, in which one person at the bank would be unravelling the net while another person in snorkelling gear would tow the net out. The leading end of the net was then brought back to the same bank, forming a horseshoe, the net was then brought to shore, and the catch was transferred to a holding bin. Specimens were killed by a tricaine methane sulfonate (MS-222) overdose (2 g/L) (University of Manitoba Animal Care permit #F01-028). Salamanders were also pithed to ensure humane death. All specimens were preserved in 70% ethanol and returned to the laboratory for identification.

Identifications

All organisms were identified in the laboratory, using a Heerbrugg Wild M3B (40x) dissecting microscope. Adult dytiscids were identified to species using Larson *et al.* (2000). Odonate larvae were identified to family level using Westfall and Tennessen (1996). Salamanders and fish were identified to species. Fish were identified using Fedoruk (1971). A voucher collection of dytiscids, odonate larvae, fish, and salamanders is deposited in the J. B. Wallis Museum, Department of Entomology, University of Manitoba.

Data analysis

Dytiscid species diversity index and evenness

Dytiscid diversity for each pond was examined to understand how it varied in ponds among selected (boreal, boreal plains and prairie) ecozones. Among the three ecozones, boreal ponds and boreal plains ponds were the most similar based on dytiscid species composition. Therefore, in all subsequent analyses in which ecozone was treated as a grouping variable, boreal and boreal plains ponds were treated as one, and compared to prairie ponds. Dytiscid diversity was calculated for each pond and each sampling technique using Hill's reformulation for Renyi's entropy of order two:

$$N2 = [\sum_{i=1}^{s} p_i^2]^{-1},$$

where p_i is the proportion of individuals belonging to the *i*th species and $\sum$ denotes the summation from $i = 1$ to $i = s$, with s being the number of species in the sample (Kvålseth 1991).

Dytiscid evenness was calculated for each pond and each sampling technique using the evenness measure that was used was proposed by Kvålseth (1991):

$$E = (N2-1)/(N1-1),$$

where N1 is calculated by the following formula,

$$N1 = \exp(-\sum p_i \log_e p_i).$$

To quantify and qualify the similarities and differences between boreal and prairie ponds based on dytiscid diversity and evenness, two group t-tests were performed on all three data sets using SYSTAT version 10.

Cluster Analysis

Cluster analysis was used to determine how ponds grouped together based on similarity in dytiscid species abundance, richness, and composition. Cluster analysis was done using SYN-TAX 2000 software, within the Hierclus module. The clustering method used was sum of squares, based on chord distance, performed on all three logarithmically transformed species data sets.

Multivariate Analysis

A multivariate approach, using CANOCO version 4.5 for Windows (ter Braak and Šmilauer 1998), was used to determine: (1) how specific environmental variables (e.g. pH, macrophyte diversity, etc.) in each pond influenced the corresponding dytiscid communities, and (2) how attributes of the ecozone influenced the dytiscid communities of each pond.

Redundancy analysis (RDA) was done on all three logarithmically transformed dytiscid data sets. The environmental variables that were used with the volume and bottle-trap dytiscid data sets in 2001, included pH, $\log_{10}$ (conductivity), $\log_{10}$ (chlorophyll *a* density), pond permanence, pond area, macrophyte density, emergent vegetation density, and presence of fish and tiger salamanders. Fish and tiger salamanders were considered present if they were collected either by volume, bottle-trap, or seine net sampling. Presence of fish and of tiger salamanders were the only environmental variables that were not treated as continuous variables. All environmental variables, except chlorophyll *a* density, that were used with the 2001 data sets, were also used in the single 2002 dytiscid data set. In the RDA, three environmental variables were forward selected to determine which variables best explained the trends in the species data. Monte Carlo permutation tests were used to determine the significance of the relationships among the three environmental variables and the species data. For each Monte Carlo test, 199 permutations were used (ter Braak and Šmilauer, 1998).

Redundancy analysis was also used to examine the potential effect of odonate larvae on dytiscid communities in prairie and boreal ponds. The odonate larval data set was logarithmically transformed, treated as an environmental variable, and included the abundances of six families of Odonata collected: Lestidae, Coenagrionidae, Gomphidae, Aeshnidae, Corduliidae, and Libellulidae.

RESULTS

Dytiscid species data set

Species of adult dytiscids collected by volume-sampling were combined (eight samples per pond) for all four months of collecting (May – August). Collections by bottle-trap sampling were also combined (four samples per pond) for all five months of collecting (May – September). The result was two dytiscid data sets obtained from 2001, corresponding to collecting techniques, bottle-traps (Appendix I) and volume-sampling (Appendix II) from 30 ponds. The collections by bottle-trap sampling for 2002 were also combined (four samples per pond) for all five months of collecting (May – September) (Appendix III).

Dytiscid diversity

Dytiscids collected using volume-sampling and bottle-traps in 2001 and bottle-traps in 2002 are summarized in Table 2. A total number of 17 060 dytiscids were collected representing 74 species during this study. The ten most common species made up 79.5 % of the total number of dytiscids collected. These ten species included (in descending order of abundance): *Hygrotus sayi* Balfour-Browne, *Laccophilus biguttatus* Kirby, *Rhantus sericans* Sharp, *Agabus antennatus* Leech, *Laccophilus maculosus* Say, *Liodessus obscurellus* (LeConte), *Agabus ajax* Fall, *Neoporus superioris* (Balfour-Browne), *Coptotomus longulus* LeConte, and *Neoporus undulatus* (Say).

There were 26 species found only in prairie ponds and 13 species that were only in boreal ponds (Table 3). Among the set of species that was unique to boreal ponds was *Hydrovatus pustulatus* (Melsheimer). This find is the first published occurrence of this species in Manitoba. For the three boreal plains and eight boreal ponds, a total of 2285 dytiscids were collected. The top ten species of that total made up 87.4% and included species, in descending order: *Hygrotus sayi*, *Coptotomus longulus*, *Laccophilus maculosus*, *Acilius semisulcatus* Aubé, *Liodessus obscurellus*, *Desmopachria convexa* (Aubé), *Hygrotus farctus* (LeConte), *Neoporus undulatus*, *Uvarus granarius* (Aubé), and *Graphoderus liberus* (Say). In prairie ponds, a total of 14775 dytiscids were collected. The top ten species of that total made up 82.8% and included (in descending order of abundance): *Laccophilus biguttatus*, *Hygrotus sayi*, *Rhantus sericans*, *Agabus antennatus*, *Laccophilus maculosus*, *Liodessus obscurellus*, *Agabus ajax*, *Neoporus superioris*, *Hygrotus impressopunctatus* (Schaller), and *Neoporus undulatus*.

Volume-sampling of dytiscids, 2001

A total of 5080 dytiscid specimens was collected using volume-sampling for all 30 ponds in 2001. The ten most common species made up 81.2 % of the total number of dytiscids collected. The ten most common species collected included (in descending order of abundance): *Hygrotus sayi*, *Liodessus obscurellus*, *Neoporus undulatus*, *Laccophilus biguttatus*, *Rhantus sericans*, *Agabus antennatus*, *Coptotomus longulus*, *Neoporus superiorus*, *Laccophilus maculosus*, and *Hygrotus impressopunctatus*. A total of 1273 dytiscids was collected in the boreal ponds. The top ten species of that total made up 91.4% and included (in descending order of abundance): *Hygrotus sayi*, *Coptotomus longulus*, *Desmopachria convexa*, *Liodessus obscurellus*, *Laccophilus maculosus*, *Hygrotus farctus*, *Uvarus granarius*, *Neoporus undulatus*, *Acilius semisulcatus*, and *Hydroporus dentellus* Fall. A total of 3807 dytiscids was collected from the prairie ponds.

The top ten species of that total made up 84.2% and included the following species (in descending order of abundance): *Liodessus obscurellus*, *Hygrotus sayi*, *Laccophilus biguttatus*, *Neoporus undulatus*, *Agabus antennatus*, *Rhantus sericans*, *Neoporus superioris*, *Laccophilus maculosus*, *Hygrotus impressopunctatus*, and *Hydroporus fuscipennis* Schaum.

Species richness was averaged for boreal and prairie ponds. The two groups of ponds were compared using a two-group t-test with a confidence of 95%. Boreal ponds, on average, had fewer species (s=14 ±4.3) than prairie ponds (s=17 ±5.0), although the difference was not significant (t=-1.7, df=24, p=0.10)(Fig. 5). The Hill's effective species richness diversity index (N2) was calculated for each pond. Prairie ponds, on average, had an N2 value of 6.0 ±1.8, whereas boreal ponds on average were less diverse, N2 = 4.0 ±1.6. Prairie ponds were significantly more diverse than boreal ponds (t=-3.1, df=23, p=0.0051)(Fig. 6). Prairie ponds, on average, had a Kvålseth evenness value of 0.67 ±0.066 compared to 0.59 ±0.12 in boreal ponds. The difference between these two groups of ponds was not significant (t=-2.1, df=14, p=0.051) (Fig. 7).

Bottle-trap sampling of dytiscids, 2001

A total of 5391 dytiscid specimens was collected using bottle-traps for all 30 ponds in year 2001. The ten most common species made up 81.3 % of the total dytiscids collected. The ten most collected species using bottle-traps included (in descending order abundance): *Hygrotus sayi*, *Laccophilus biguttatus*, *Rhantus sericans*, *Agabus ajax*, *Agabus antennatus*, *Laccophilus maculosus*, *Ilybius fraterculus* (LeConte), and *Graphoderus perplexus* Sharp, *Neoporus superioris*, and *Coptotomus longulus*. A total of

608 dytiscids were collected in the boreal ponds. The top ten species of that total made up 89.1% and included the following species (abundances in descending order): *Hygrotus sayi*, *Coptotomus longulus*, *Acilius semisulcatus*, *Liodessus obscurellus*, *Laccophilus maculosus*, *Graphoderus liberus*, *Graphoderus perplexus*, *Neoporus undulatus*, *Ilybius subaeneus* (Erichson), and *Rhantus binotatus* (Harris). A total of 4783 dytiscids was collected from the prairie ponds. The top ten species of that total made up 85.5% and included the following species (in descending order of abundance): *Laccophilus biguttatus*, *Rhantus sericans*, *Hygrotus sayi*, *Agabus ajax*, *Agabus antennatus*, *Laccophilus maculosus*, *Ilybius fraterculus*, *Graphoderus perplexus*, *Neoporus superiorus*, and *Graphoderus occidentalis* Horn.

Boreal ponds had an average species richness of 9 ±4.0 compared to an average species richness of 20 ±3.6 in prairie ponds. This difference was significant (t=-7.3, df=20, p>0.001)(Fig. 8). Prairie ponds on average had an N2 value of 6.2 ±2.3, whereas boreal ponds on average were less diverse, N2=4.2 ±1.7. Prairie ponds were significantly more diverse than boreal ponds (t=-2.7, df=27, p=0.013) (Fig. 9). Prairie ponds, on average, had an evenness value of 0.62 ±0.12 compared to 0.70 ±0.12 in boreal ponds. This difference was not significant (t=1.8, df=21, p=0.080) (Fig. 10).

Bottle-trap sampling of dytiscids, 2002

A total of 5666 dytiscid specimens was collected using bottle-traps for all 30 ponds in 2002. The ten most common species made up 85.9 % of the total dytiscids collected. The ten most frequently collected species using bottle-traps included (in descending order of abundance): *Laccophilus biguttatus*, *Hygrotus sayi*, *Rhantus sericans*, *Agabus antennatus*, *Laccophilus maculosus*, *Neoporus superiorus*, *Hygrotus* *impressopunctatus*, *Coptotomus longulus*, *Hygrotus sellatus* (LeConte), and *Graphoderus perplexus*. A total of 404 dytiscids was collected in the boreal ponds. The top ten species of that total made up 86.6% and included the following species (in descending order of adundance): *Coptotomus longulus*, *Hygrotus sayi*, *Laccophilus maculosus*, *Acilius semisulcatus*, *Graphoderus liberus*, *Graphoderus perplexus*, *Rhantus wallisi* (Hatch), *Ilybius fraterculus*, *Dytiscus harrisii* Kirby, and *Agabus anthracinus* Mannerheim.

Prairie ponds had a significantly greater species richness (*s*=17 ±6.8) than boreal ponds (9.1 ±4.3)(t=-4.1, df=28, p>0.001) as with bottle-trap sampling in 2002 (Fig. 11). Boreal ponds on average were less diverse (N2 = 4.8 ±2.4) than prairie ponds (N2 =5.0 ±2.3), but the difference was not significant (t=-0.44, df=27, p=0.66)(Fig. 12). Boreal ponds on average had a significantly higher evenness value (0.74 ±0.16) than prairie ponds (0.60 ±0.11)(t=2.6, df=17, p=0.018)(Fig. 13).

Dytiscid species abundance

To determine whether there were differences in productivity between prairie and boreal ponds, ponds were examined based on their dytiscid abundances for all three data sets. To quantify the differences between these two groups, group t-tests were performed within all three data sets. An average of 200 ±204 specimens of dytiscids were collected using volume-sampling in prairie ponds, in comparison to 116 ±92 specimens of dytiscids in boreal ponds. The difference in abundance between groups of ponds was not significant (t=-1.6, df=27, p=0.13)(Fig. 14). An average of 252 ±195 dytiscid specimens was collected in bottle traps in 2001 in prairie ponds, and 55 ±89 dytiscid specimens in boreal ponds. The difference in abundance between groups of ponds was significant (t=-3.8, df=27, p<0.001)(Fig. 15). In 2002, an average of 326 ±278 dytiscids was collected in bottle traps in prairie ponds and 37 ±46 dytiscids collected in boreal ponds. The difference in abundance between them was significant (t=-4.4, df=20, p<0.001)(Fig. 16).

Cluster analysis of ponds based on the dytiscid data sets

The clustering method used was sum of squares, based on chord distance. All three data sets were transformed logarithmically. Cluster analysis of the 30 ponds based on similarity of occurrences of dytiscids produced two well-defined clusters, These two representing ponds located in prairie sites and boreal sites (including boreal plains sites). Ponds represented in both clusters had short pectinate runs suggesting that the first division represented two discrete groups.

Volume-sampling of dytiscids, 2001

The dendrogram formed by the communities of dytiscids sampled using volume-sampling in 2001 formed two main clusters, representing prairie ponds and boreal ponds (Fig. 17). The prairie ponds clustered together at a lower level of similarity than the boreal ponds, which suggested that the prairie ponds had more variable dytiscid communities than boreal ponds. There were some regional locality affinities among boreal ponds. Examples of ponds from the same general locality clustered together, included all three ponds from the Richer locality (2E, 3E, 4E), two of three ponds from the East Braintree locality (19E, 21E), and four of five ponds from the Prawda locality

(8E, 9E, 12E, 14E). In contrast, prairie ponds showed less of an affinity to regional locality, except for the Miami locality, which formed a unique cluster (2W, 4W, 5W).

Bottle-trap sampling of dytiscids, 2001

The dendrogram formed by the communities of dytiscids sampled using bottle-traps in 2001 also formed two main clusters consisting of prairie ponds and boreal ponds (Fig. 18). The clustering of boreal ponds showed less affinity to their respective localities than in Fig. 17. One prairie pond (2W) clustered together with the boreal ponds. All the ponds near Baldur (12We, 12Ww, 13We, 13Ww) formed a cluster that also included ponds 23W and 25Wn.

Bottle-trap sampling of dytiscid specimens, 2002

The cluster diagrams of dytiscids collected using bottle-traps in 2002 showed more variability in the boreal ponds that either of the previous two dendrograms (Fig. 19). All three ponds from the Miami region (2W, 4W, 5W) grouped within the predominately boreal pond cluster. Prairie ponds 30W, 31W, 32W, and 103W were closely associated and are from the same region. Ponds 12We (Baldur) and 24W (Dand) formed a group separate from all the other prairie ponds.

Redundancy analysis of dytiscid species

Volume-sampling of dytiscids, 2001

The redundancy analysis (RDA) of the dytiscid species collected using volume-sampling in 2001 produced an ordination diagram in which 60.2 % of the variation in the species data was explained by axis 1, and 19.6 % was explained by axis 2 (Fig. 20). The species-environment relation for axis 1 was 52.2% and 17.0% for axis 2.

Forward selection was used to determine which variables were most significant in explaining the trends in dytiscid communities. Three variables were forward selected and included in the ordination diagram. The first axis separated the ponds based on macrophyte diversity and chlorophyll *a* density. Using a Monte-Carlo test, the relationship between these two environmental variables and the species data was significant (chlorophyll *a* density, F=6.72, p=0.005; macrophyte diversity, F=1.66, p=0.08). The second axis separated the ponds based on pH. A Monte-Carlo test showed that the relationship between pH and the species data was significant (F=2.22, p=0.02). Most of the prairie ponds were positively correlated with conductivity and chlorophyll *a* density. Ponds that were the exceptions to this trend included prairie ponds 12We, 20W, and 23W, which grouped closer to boreal and boreal plains ponds. Boreal and boreal plains ponds showed limited displacement along axis 2, which is correlated to pH. Boreal and boreal plains ponds that were most correlated with high and low pH values were ponds 21E and 4E, respectively. Ponds 12We, and 103W were at the positive end of the pH environmental vector, while ponds 30W, 5W, and 4W were at the negative end. As a group, dytiscid species showed a bipolar association with axis 1, being either correlated positively or negatively with chlorophyll *a* and macrophyte diversity. Some species, such as *Hygrotus sayi*, *H. picatus* (Kirby), *Neoporus undulatus*, and *Agabus phaeopterus* (Kirby), were exceptions and were negatively correlated with pH values, whereas *H. sellatus* was positively correlated with pH.

Bottle-trap sampling of dytiscid specimens, 2001

The RDA of the dytiscid species collected using bottle-trap sampling in 2001 produced an ordination diagram in which 59.9% of the variation in the species data is explained by axis 1, and 11.2% is explained by axis 2 (Fig. 21). The species-environment relation for axis 1 is 76.6% and 14.8% for axis 2.

The same set of environmental variables used for the volume-sampling 2001 ordination was included in the bottle-trap sampling 2001 ordination. Three environmental variables were again forward selected. Conductivity, macrophyte, and pond permanence were the most significant in explaining the trends in the dytiscid communities. The first axis separated the ponds based on conductivity and macrophyte diversity. Using a Monte-Carlo test, the relationship between these two environmental variables and the species data was significant (conductivity, F=8.01, p=0.05; macrophyte diversity, F=4.7, p=0.005). The second axis separated the ponds based on permanence and using a Monte-Carlo test, this relationship was significant (F=3.89, p=0.025). Boreal and boreal plains ponds were all located at the negative end of axis 1 and were negatively correlated with conductivity and macrophyte diversity. These ponds were not evenly distributed along axis 2. Most prairie ponds were positively correlated with conductivity and macrophyte diversity, except for ponds 20W and 23W. *Hygrotus punctilineatus* (Fall), *H. masculinus* (Crotch), and *Hydroporus columbianus* Fall exclusively co-occurred within prairie pond 12We. Prairie ponds as a whole also do not show a strong correlation to permanence. Pond 24W was an outlier and was negatively correlated to permanence. A number of dytiscids also were negatively correlated to permanence and closely associated with pond 24W, including, *Agabus punctulatus* Aubé, *Agabus canadensis* Fall, and *Agabus bifarius*

(Kirby). Others species of dytiscids that were negatively correlated with permanence include *Hygrotus infuscatus* (Sharp), *Hygrotus turbidus* (LeConte), *Agabus ajax*, *Hygrotus sellatus*, *Hydroporus tenebrosus* LeConte, *Liodessus obscurellus*, *Hygrotus patruelis* (LeConte), *Hygrotus marklini* (Gyllenhal), *Hygrotus impressopunctatus*, *Colymbetes exaratus* LeConte, *Graphoderus occidentalis*, and *Ilybius angustior* (Gyllenhal).

Bottle-trap sampling of dytiscids, 2002

The RDA of dytiscid species collected using bottle-traps in 2002 produced an ordination diagram in which, 65.5% of the variation in the species data was explained by axis 1, and 3.9% was explained by axis 2 (Fig. 22). The species-environment relation for axis 1 was 90.2% and 5.3% for axis 2.

Environmental variables used for bottle-trap sampling in the 2002 ordination were similar to those used for volume-sampling of the 2001 ordination, except chlorophyll *a* data were unavailable. Macrophyte diversity, pH, and bordering vegetation were forward-selected and were most significant in explaining trends in the species data. The first axis separated the ponds based on macrophyte diversity and pH. Using a Monte-Carlo test, the relationship between the species data and macrophyte diversity ($F=5.83$, $p<0.002$) and pH was significant ($F=4.98$, $p<0.004$). Bordering vegetation separated the ponds along axis 2 and using a Monte-Carlo test this relationship was significant ($F=5.76$, $p<0.002$). Boreal, boreal plains, and prairie ponds 24W, 13Ww, 12We, 2W, and 4W were negatively correlated with pH and macrophyte diversity. The remaining prairie ponds were positively correlated with both pH and macrophyte diversity. Approximately half of the boreal, boreal plains, and prairie ponds were positively correlated with bordering vegetation. Ponds 13Ww, 24W, and 12We were outliers and negatively correlated with bordering vegetation. *Hygrotus salinaris* (Wallis) and *Hygrotus punctilineatus* were only found in pond 12We.

Boreal ponds, dytiscids and odonates from volume-sampling, 2001

The RDA of boreal ponds using the dytiscid species and odonate larvae (Table 4) collected by volume-sampling in 2001 produced an ordination diagram in which 36.1 % of the variation in the dytiscid species data was explained by axis 1, and 17.8 % was explained by axis 2 (Fig. 23). The dytiscid species-odonate relationship for axis 1 was 56.0 % and 83.5 % for axis 2.

Forward selection was used to determine which odonate families were most significant in explaining trends in dytiscid species. Three odonate families (Aeshnidae, Libellulidae and Gomphidae) were forward-selected and included in the ordination. However, using a Monte-Carlo test, the relationship between these three odonate families and the dytiscid species data was not significant (Aeshnidae F=1.45, p=1.54; Libellulidae F=1.17, p=0.348; Gomphidae F=1.60, p=0.078).

Prairie ponds, dytiscids and odonate specimens from volume-sampling, 2001

The RDA of prairie ponds using the dytiscid species and odonate larvae (Table 5) collected by volume-sampling in 2001 produced an ordination diagram in which 36.3 % of the variation in the species data was explained by axis 1, and 13.2 % was explained by axis 2 (Fig. 24). The dytiscid species-odonate relationship for axis 1 was 60.7 % and 83.0 % for axis 2.

Forward selection with the six odonate families included revealed that Gomphidae, Lestidae, and Coenagrionidae were the most significant in explaining trends in dytiscid species. Using a Monte-Carlo test, the relationship between only Gomphidae and the species of dytiscid was significant (Gomphidae F=3.51, p=0.002; Lestidae F=1.20, p=0.284; Coenagrionidae F=1.48, p=0.134). Ponds 2W and 4W from the Miami region were positively correlated with Gomphidae. Dytiscid species correlated with Gomphidae included *Hygrotus acaroides*, *Neoporus undulatus*, *Colymbetes sculptilis*, *Coptotomus longulus*, *Liodessus obscurellus*, *Hydaticus aruspex*, *Neoporus superioris*, *Laccophilus maculosus*, *Ilybius fraterculus*, *Hygrotus turbidus*, *Hygrotus patruelis*, *Colymbetes exaratus*, and *Hygrotus impressopunctatus*.

Table 1: Reference number, locality, water body name, ecozone, and selected environmental variables of ponds selected for sampling in 2001 and 2002 across southern Manitoba. Ponds are arranged east to west.

Ref. #	Locality	GPS coordinates	Water body name	Ecozone (boreal plains=BPL; boreal=BOR; prairie=PRA)	Area (m^2)	pH		Conductivity (µS/cm)		Chlorophyll *a* density 2001	Permanence scale 0-5		Macrophyte diversity scale 0-5		Emergent vegetation scale 0-10		Tiger salamanders presence=1 absence=0	Fish presence=1 absence=0
						2001	2002	2001	2002		2001	2002	2001	2002	2001	2002		
16E	East Braintree	49°38’05.8”N, 95°31’17.7”W	n/a	BOR	120	8.4	7.7	331	402	2.0	5	5	2	2	3	3	0	1
19E	East Braintree	49°37’54.4”N, 95°30’42.1”W	Strawberry Pond	BOR	111	8.3	8.1	331	377	1.9	5	5	2	2	6	6	0	1
21E	East Braintree	49°38’12.6”N, 95°27’33.3”W	Saskatoon Pond	BOR	119	8.5	8.0	243	312	2.4	5	5	1	1	4	4	0	0
8E	Prawda	49°38’48.5”N, 95°45’51.4”W	n/a	BOR	43	7.8	7.8	545	609	1.8	5	5	1	1	10	10	0	1
9E	Prawda	49°38’49.6”N, 95°45’49.4”W	n/a	BOR	74	8.2	7.9	328	337	1.5	5	5	1	1	10	10	0	1
12E	Prawda	49°38’50.9”N, 95°45’32.7”W	n/a	BOR	42	8.1	7.9	338	361	1.3	5	5	2	3	8	8	0	0
13E	Prawda	49°38’50.8”N, 95°45’33.4”W	n/a	BOR	49	8.3	8.1	324	354	1.6	5	5	1	1	10	10	0	1
14E	Prawda	49°38’48.1”N, 95°44’48.8”W	n/a	BOR	27	8.1	8.3	343	399	1.2	5	5	1	1	10	10	0	0
2E	Richer	49°43’28.4”N 95°15’35.9”W	n/a	BPL	57	8.3	8.2	286	365	2.8	5	5	2	3	5	5	0	0
3E	Richer	49°43’43.7”N, 96°16’02.4”W	Reynolds Pond	BPL	141	8.0	7.8	318	340	4.1	5	5	1	3	3	3	0	1
4E	Richer	49°43’01.9”N, 96°14’25.9”W	n/a	BPL	28	7.7	8.0	255	298	1.7	5	5	2	2	6	7	0	0
2W	Miami	49°17’03.4”N, 98°15’21.1”W	n/a	PRA	85	8.0	8.0	817	790	14.9	5	5	3	3	7	7	0	1
4W	Miami	49°17’20.1”N, 98°14’18.1”W	n/a	PRA	44	7.7	7.6	890	846	37.6	5	5	3	3	10	10	1	0
5W	Miami	49°17’18.9”N, 98°14’11.2”W	n/a	PRA	43	7.5	8.3	1192	1356	23.7	5	5	2	2	10	10	0	1
12We	Baldur	49°25’30.7”N, 99°94’51.3”W	Cobbes Lake (east side)	PRA	3500	9.1	9.1	9500	10572	3.8	5	5	1	1	1	1	1	1
12Ww	Baldur	49°25’44.7”N, 99°15’18.6”W	Cobbes Lake (west side)	PRA	625	8.7	8.7	6075	7000	16.0	5	5	2	2	8	8	1	1
13We	Baldur	49°26’24.1”N 99°14’48.8”W	Taylors Lake (east side)	PRA	80	8.6	8.7	3094	3321	28.6	5	5	3	3	4	5	1	1
13Ww	Baldur	49°26’24.3”N, 99°14’49.5”W	Taylors Lake (west side)	PRA	625	8.7	8.7	3250	3499	24.4	5	5	1	3	0	0	1	1
14W	Baldur	49°27’45.8”N, 99°14’43.9”W	n/a	PRA	625	8.8	9.0	1218	1306	36.6	5	5	3	3	2	4	0	1

Table 1: continued

Ref. #	Locality	GPS coordinates	Water body name	Ecozone (boreal plains=BPL; boreal=BOR; prairie=PRA)	Area (m^2)	pH		Conductivity (µS/cm)		Chlorophyll *a* density 2001	Permanence scale 0-5		Macrophyte diversity scale 0-5		Emergent vegetation scale 0-10		Tiger salamanders presence=1 absence=0	Fish presence=1 absence=0
						2001	2002	2001	2002		2001	2002	2001	2002	2001	2002		
18W	Ninette	49°24'47.2"N, 99°37'56.3"W	Grass Lake	PRA	10000	8.5	8.5	781	880	9.2	5	5	3	3	10	10	0	1
19W	Ninette	49°21'38.5"N, 99°39'11.7"W	n/a	PRA	206	8.1	8.3	987	1137	15.6	5	5	2	3	10	10	1	1
20W	Ninette	49°20'38.7"N, 99°39'15.4"W	n/a	PRA	225	8.0	8.1	900	954	3.1	5	5	2	3	10	10	1	1
23W	Dand	49°20'26.6"N, 100°27'37.6"W	n/a	PRA	24	8.3	9.0	883	1053	3.6	5	5	1	1	10	10	1	0
24W	Dand	49°20'25.8"N, 100°28'21.8"W	n/a	PRA	42	9.0	9.1	862	1286	92.5	3	4	1	1	10	0	1	0
25Wn	Dand	49°21'51.3"N, 100°29'29.3"W	Chain Lakes (north side)	PRA	3000	8.1	8.4	754	700	21.2	5	5	4	4	4	6	1	1
25Ws	Dand	49°21'47.6"N, 100°29'32.4"W	Chain Lakes (south side)	PRA	80	8.2	8.5	843	998	6.0	5	2	3	3	9	9	0	1
30W	Reston	49°31'43.3"N, 101°09'54.2"W	n/a	PRA	25	7.6	7.8	2043	3000	28.3	5	4	2	3	10	10	0	0
31W	Reston	49°33'47.1"N, 101°10'01.8"W	n/a	PRA	52	8.4	9.3	1132	1553	21.2	5	4	3	3	3	4	1	0
32W	Linklater	49°35'48.4"N, 101°12'47.1"W	n/a	PRA	64	8.5	8.2	1493	1898	5.4	5	5	4	4	8	9	1	0
103W	Linklater	49°36'38.5"N, 101°12'49.4"W	n/a	PRA	80	9.1	8.9	1114	1422	2.0	5	5	4	4	5	7	0	0

Table 2: Dytiscid species (Coleoptera: Dytiscidae) collected using volume-sampling in 2001, bottle-traps in 2001, and bottle-traps in 2002, and the sum of dytiscids collected by all three sampling methods at 30 ponds across southern Manitoba. Taxa are arranged in accordance with Larson *et al.* (2000).

Species name	Total collected in 2001 using volume-sampling	Total collected using bottle-traps		SUM
		2001	2002	
Laccophilus biguttatus Kirby	398	865	1462	**2725**
L. maculosus Say	250	268	621	**1139**
Desmopachria convexa (Aubé)	69	1	12	**82**
Liodessus cantralli (Young)	2	0	0	**2**
L. fuscatus (Crotch)	1	0	0	**1**
L. obscurellus (LeConte)	718	117	74	**909**
Uvarus granarius (Aubé)	49	0	1	**50**
Hygrotus acaroides (LeConte)	4	0	1	**5**
H. farctus (LeConte)	51	7	6	**64**
H. impressopunctatus (Schaller)	136	63	235	**434**
H. infuscatus (Sharp)	0	3	2	**5**
H. laccophilinus (LeConte)	4	1	1	**6**
H. marklini (Gyllenhal)	57	24	75	**156**
H. masculinus (Crotch)	0	1	0	**1**
H. patruelis (LeConte)	102	34	52	**188**
H. picatus (Kirby)	22	8	7	**37**
H. punctilineatus (Fall)	0	1	5	**6**
H. salinarius (Wallis)	0	0	1	**1**
H. sayi Balfour-Browne	1148	923	1067	**3138**
H. sellatus (LeConte)	26	32	125	**183**
H. tumidventris (Fall)	5	4	18	**27**
H. turbidus (LeConte)	50	20	81	**151**
Neoporus superioris (Balfour-Browne)	253	134	317	**704**
N. undulates (Say)	413	26	24	**463**
Hydroporus columbianus Fall	4	1	1	**6**
H. dentellus Fall	15	0	0	**15**
H. fuscipennis Schaum	102	9	11	**122**
H. larsoni Nilsson	50	6	1	**57**
H. notabilis LeConte	5	1	10	**16**
H. pervicinus Fall	2	0	3	**5**
H. rectus Fall	1	0	0	**1**
H. striola (Gyllenhal)	2	0	0	**2**
H. tartaricus LeConte	0	0	1	**1**
H. tenebrosus LeConte	33	6	2	**41**
H. tristis (Paykull)	7	0	0	**7**
Laccornis conoideus (LeConte)	9	1	1	**11**
Hydrovatus pustulatus (Melsheimer)	0	1	1	**2**
Agabus ajax Fall	48	644	71	**763**
A. ambiguous (Say)	1	0	0	**1**
A. antennatus Leech	272	307	647	**1226**
A. anthracinus Mannerheim	7	8	10	**25**
A. bifarius (Kirby)	2	1	0	**3**
A. canadensis Fall	0	2	18	**20**
A. erichsoni Gemminger & Harold	0	2	0	**2**
A. phaeopterus (Kirby)	6	4	2	**12**
A. punctulatus Aubé	2	2	6	**10**

Table 2: continued

Species name	Total collected in 2001 using volume-sampling	Total collected using bottle traps		SUM
		2001	2002	
Ilybius angustior (Gyllenhal)	5	23	2	**30**
I. fraterculus (LeConte)	53	174	98	**325**
I. picipes (Kirby)	0	1	2	**3**
I. pleuriticus (LeConte)	1	1	2	**4**
I. subaeneus (Erichson)	10	45	16	**71**
Colymbetes exaratus LeConte	29	69	24	**122**
C. sculptilis Harris	7	5	6	**18**
Rhantus binotatus (Harris)	2	9	2	**13**
R. consimilis Motschulsky	1	1	1	**3**
R. sericans Sharp	280	772	928	**1980**
R. sinuatus (LeConte)	0	1	0	**1**
R. suturellus (Harris)	3	0	1	**4**
R. wallisi (Hatch)	8	4	13	**25**
Coptotomus longulus LeConte	256	123	139	**518**
Dytiscus alaskanus Balfour-Browne	4	60	53	**117**
D. circumcinctus Ahrens	0	1	0	**1**
D. cordieri Aubé	4	90	12	**106**
D. dauricus Gebler	0	7	8	**15**
D. harrisii Kirby	1	8	10	**19**
D. hybridus Aubé	0	0	2	**2**
D. verticalis Say	2	3	1	**6**
Hydaticus aruspex Clark	8	38	7	**53**
H. piceus LeConte	4	26	39	**69**
Acilius semisulcatus Aubé	25	94	54	**173**
A. sylvanus Hilsenhoff	0	2	2	**4**
Graphoderus liberus (Say)	10	13	23	**46**
G. occidentalis Horn	23	122	47	**192**
G. perplexus Sharp	18	172	125	**315**
Total species abundance	**5080**	**5391**	**6589**	**17060**
Total species richness	**60**	**60**	**62**	**74**

Table 3: Dytiscid species (Coleoptera: Dytiscidae) collected using volume-sampling in 2001, bottle-traps in 2001, and bottle-traps in 2002 from boreal and prairie ponds and ecozone preference. Ecozone preference is denoted for species that were only collected in either boreal or prairie ponds for all samples. Boreal preference represents species that were collected predominantly in either boreal plains or boreal ponds.

Species name	Volume-sampling 2001		Bottle-trap sampling				Ecozone preference
			2001		2002		
	Ponds						
	Boreal	Prairie	Boreal	Prairie	Boreal	Prairie	
Laccophilus biguttatus Kirby	1	397	0	865	2	1460	-
L. maculosus Say	54	196	49	219	48	573	-
Desmopachria convexa (Aubé)	68	1	1	0	5	7	-
Liodessus cantralli (Young)	2	0	0	0	0	0	boreal
L. fuscatus (Crotch)	1	0	0	0	0	0	boreal
L. obscurellus (LeConte)	67	651	56	61	5	69	-
Uvarus granarius (Aubé)	48	1	0	0	1	0	-
Hygrotus acaroides (LeConte)	0	4	0	0	0	1	prairie
H. farctus (LeConte)	51	0	7	0	6	0	boreal
H. impressopunctatus (Schaller)	3	133	2	61	0	235	-
H. infuscatus (Sharp)	0	0	0	3	0	2	-
H. laccophilinus (LeConte)	4	0	1	0	1	0	boreal
H. marklini (Gyllenhal)	1	56	0	24	0	75	-
H. masculinus (Crotch)	0	0	0	1	0	0	prairie
H. patruelis (LeConte)	2	100	0	34	0	52	-
H. picatus (Kirby)	9	13	2	6	2	5	-
H. punctilineatus (Fall)	0	0	0	1	0	5	prairie
H. salinarius (Wallis)	0	0	0	0	0	1	prairie
H. sayi Balfour-Browne	582	566	219	704	78	989	-
H. sellatus (LeConte)	0	26	0	32	0	125	prairie
H. tumidventris (Fall)	0	5	0	4	0	18	prairie
H. turbidus (LeConte)	0	50	0	20	1	80	-
Neoporus superioris (Balfour-Browne)	2	251	0	134	0	317	-
N. undulates (Say)	46	367	8	18	4	20	-
Hydroporus columbianus Fall	0	4	0	1	0	1	prairie
H. dentellus Fall	15	0	0	0	0	0	boreal
H. fuscipennis Schaum	0	102	0	9	0	11	-
H. larsoni Nilsson	3	47	0	6	0	1	-
H. notabilis LeConte	1	4	0	1	1	9	-
H. pervicinus Fall	0	2	0	0	0	3	prairie
H. rectus Fall	0	1	0	0	0	0	prairie
H. striola (Gyllenhal)	0	2	0	0	0	0	prairie
H. tartaricus LeConte	0	0	0	0	0	1	prairie
H. tenebrosus LeConte	2	31	0	6	0	2	-
H. tristis (Paykull)	7	0	0	0	0	0	boreal
Laccornis conoideus (LeConte)	0	9	0	1	0	1	boreal
Hydrovatus pustulatus (Melsheimer)	0	0	1	0	1	0	boreal
Agabus ajax Fall	0	48	0	644	0	71	prairie
A. ambiguous (Say)	0	1	0	0	0	0	prairie
A. antennatus Leech	0	272	0	307	0	647	prairie
A. anthracinus Mannerheim	7	0	2	6	9	1	-
A. bifarius (Kirby)	0	2	0	1	0	0	prairie
A. canadensis Fall	0	0	0	2	0	18	prairie
A. erichsoni Gemminger & Harold	0	0	0	2	0	0	prairie
A. phaeopterus (Kirby)	1	5	0	4	0	2	-
A. punctulatus Aubé	0	2	0	2	0	6	prairie
Ilybius angustior (Gyllenhal)	0	5	1	22	0	2	-
I. fraterculus (LeConte)	12	41	6	168	10	88	-

Table 3: continued

Species name	Volume-sampling 2001		Bottle-trap sampling 2001		Bottle-trap sampling 2002		Ecozone preference
	Ponds						
	Boreal	Prairie	Boreal	Prairie	Boreal	Prairie	
I. picipes (Kirby)	0	0	0	1	0	2	prairie
I. pleuriticus (LeConte)	1	0	1	0	2	0	boreal
I. subaeneus (Erichson)	3	7	8	37	2	14	-
Colymbetes exaratus LeConte	2	27	2	67	1	23	-
C. sculptilis Harris	5	2	0	5	0	6	-
Rhantus binotatus (Harris)	1	1	8	1	1	1	-
R. consimilis Motschulsky	0	1	0	1	0	1	prairie
R. sericans Sharp	8	272	6	766	2	926	-
R. sinuatus (LeConte)	0	0	1	0	0	0	boreal
R. suturellus (Harris)	3	0	0	0	1	0	boreal
R. wallisi (Hatch)	8	0	0	4	11	2	-
Coptotomus longulus LeConte	208	48	90	33	106	33	-
Dytiscus alaskanus Balfour-Browne	0	4	0	60	0	53	prairie
D. circumcinctus Ahrens	0	0	0	1	0	0	prairie
D. cordieri Aubé	1	3	1	89	3	9	-
D. dauricus Gebler	0	0	7	0	8	0	boreal
D. harrisii Kirby	1	0	8	0	10	0	boreal
D. hybridus Aubé	0	0	0	0	0	2	prairie
D. verticalis Say	2	0	3	0	1	0	boreal
Hydaticus aruspex Clark	1	7	5	33	1	6	-
H. piceus LeConte	1	3	4	22	3	36	-
Acilius semisulcatus Aubé	24	1	84	10	42	12	-
A. sylvanus Hilsenhoff	0	0	1	1	0	2	-
Graphoderus liberus (Say)	10	0	11	2	19	4	-
G. occidentalis Horn	2	21	4	118	0	47	-
G. perplexus Sharp	3	15	9	163	17	108	-
SUM	1273	3807	608	4783	404	6185	Total # of species unique to boreal = 13; prairie ponds= 26.

Table 4: Numbers of odonate larvae (Insecta: Odonata) arranged by family collected in boreal ponds using volume-sampling, 2001. Site locations as in Table 1.

Odonate family	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	**SUM**
Lestidae	0	0	1	4	2	19	0	21	7	0	172	**226**
Coenagrionidae	81	77	116	76	108	187	26	46	134	50	134	**1035**
Gomphidae	9	5	9	0	0	0	4	0	2	3	0	**32**
Aeshnidae	29	24	25	41	54	34	19	12	6	6	26	**276**
Corduliidae	4	27	8	5	7	24	18	14	0	2	2	**111**
Libellulidae	71	179	420	102	211	165	170	223	135	90	186	**1952**

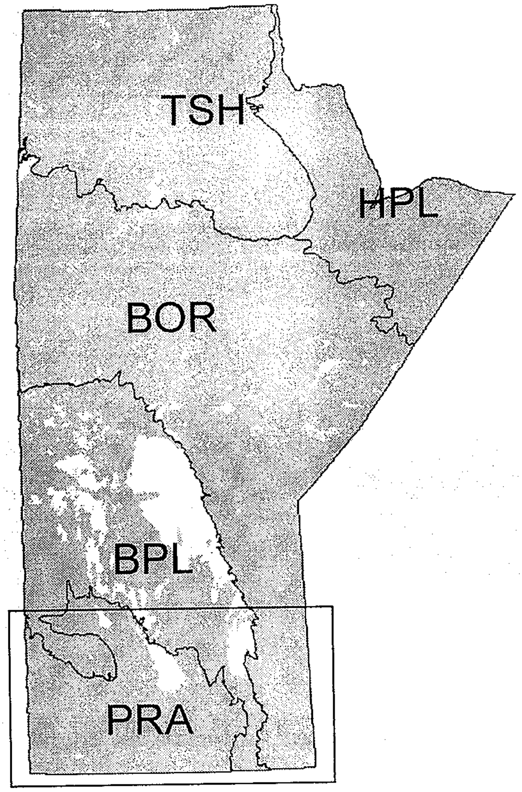
Table 5: Numbers of odonate larvae (Insecta: Odonata) arranged by family collected in prairie ponds using volume-sampling, 2001. Site locations as in Table 1.

Odonate family	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	**SUM**
Lestidae	35	35	0	0	3	0	0	0	1	52	13	18	134	2	8	3	45	82	13	**445**
Coenagrionidae	294	13	6	50	63	275	108	219	22	21	19	6	29	224	37	45	177	19	73	**1816**
Gomphidae	18	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**30**
Aeshnidae	62	31	0	0	3	2	0	0	4	2	10	2	13	17	14	0	10	8	4	**207**
Corduliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**8**
Libellulidae	16	54	1	0	9	0	0	0	5	33	6	12	96	3	20	1	42	74	47	**839**

Table 6: Pond reference number, dytiscid species richness, Hill's effective species richness (N2), and Kvålseth evenness, for volume-sampling 2001, bottle-trap sampling 2001, and bottle-sampling 2002 for each of the 30 pond sampled in southern Manitoba. Site locations as in Table 1.

Ponds	Volume-sampling 2001			Bottle-trap sampling					
				2001			2002		
	Species richness	Hill's effective species richness (N2)	Kvålseth evenness	Species richness	Hill's effective species richness (N2)	Kvålseth evenness	Species richness	Hill's effective species richness (N2)	Kvålseth evenness
14E	12	6.362	0.786	11	5.261	0.532	8	5.158	0.818
16E	13	3.810	0.571	9	2.977	0.565	5	3.846	0.849
19E	13	3.256	0.571	4	2.613	0.748	7	6.400	0.943
8E	19	2.121	0.371	7	2.738	0.684	11	4.670	0.641
9E	11	3.331	0.636	11	2.895	0.540	11	7.024	0.764
12E	21	3.195	0.407	10	5.507	0.763	11	6.443	0.797
13E	7	2.109	0.626	5	2.750	0.744	6	5.261	0.929
2E	16	4.744	0.674	18	4.414	0.616	19	4.547	0.609
3E	13	3.219	0.510	6	4.000	0.797	5	1.914	0.534
4E	10	4.839	0.694	6	4.765	0.866	5	3.522	0.796
21E	19	7.087	0.614	11	8.036	0.868	12	3.320	0.474
2W	19	4.314	0.637	14	8.640	0.759	13	6.000	0.680
4W	20	6.026	0.592	21	10.394	0.743	13	9.959	0.875
5W	16	5.210	0.631	16	8.605	0.767	22	6.503	0.583
12We	5	3.024	0.769	16	3.974	0.553	11	3.220	0.489
12Ww	12	5.618	0.718	18	7.822	0.764	9	2.632	0.531
13We	17	7.257	0.654	18	6.382	0.720	19	3.515	0.499
13Ww	11	3.151	0.662	18	2.063	0.401	9	2.855	0.568
14W	20	5.262	0.621	21	3.548	0.501	24	2.135	0.404
18W	20	8.074	0.741	21	8.096	0.668	16	4.892	0.625
19W	25	6.396	0.589	25	6.826	0.607	22	4.038	0.615
20W	25	8.285	0.666	22	5.625	0.520	20	8.012	0.750
23W	19	7.220	0.673	14	2.962	0.468	31	8.502	0.654
24W	16	8.547	0.786	25	2.559	0.375	1	1.000	n/a
25Wn	18	8.126	0.763	17	6.431	0.651	20	2.558	0.476
25Ws	12	3.438	0.529	18	5.140	0.552	19	7.224	0.694
30W	23	7.640	0.705	27	9.009	0.619	22	3.863	0.482
31W	16	5.459	0.681	19	5.943	0.634	23	6.415	0.599
32W	12	3.973	0.655	22	5.763	0.669	20	4.052	0.586
103W	16	6.560	0.702	19	7.069	0.737	18	4.568	0.680

Figure 1: Distribution of the five ecozones within the Province of Manitoba: taiga shield (TSH), Hudson Bay plains (HPL), boreal (BOR), boreal plains (BPL), and prairie (PRA) (Wilken 1986). Inset map indicates the general location (◉) of all eight localities which represent groups of ponds: Reston/Linklater (1), Dand (2), Ninette (3), Baldur (4), Miami (5), Richer (6), Prawda (7), and East Braintree (8).


TSH
HPL
BOR
BPL
PRA

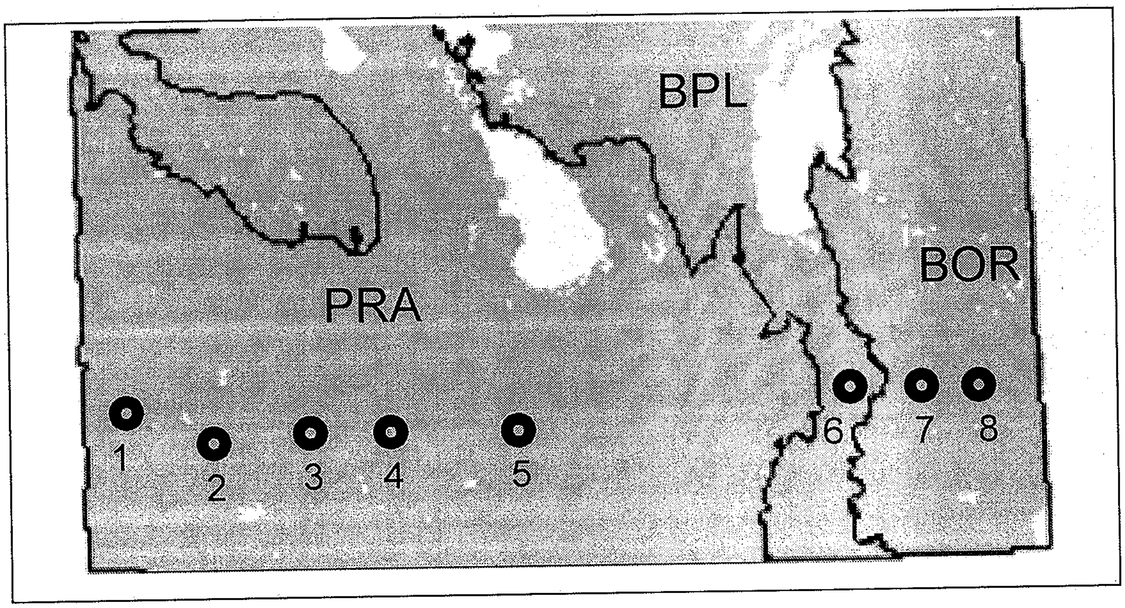

BPL
BOR
PRA
1
2
3
4
5
6
7
8

Figure 2: Sampling protocol in ponds across southern Manitoba illustrating the placement of bottle-traps and where volume-samples were taken within the four sectors of a hypothetical pond.

○ volume-sample

▬ bottle-trap

▨ pond depth 0 – 60 cm

☐ pond depth >60 cm

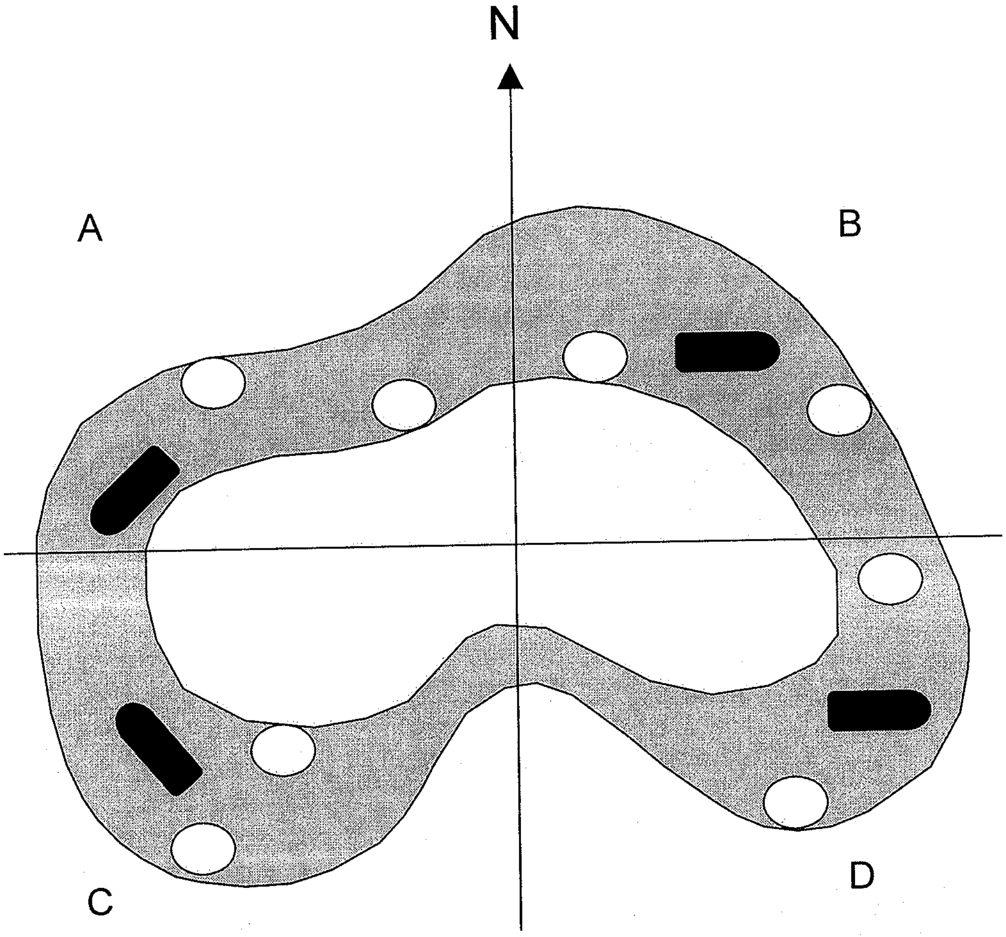
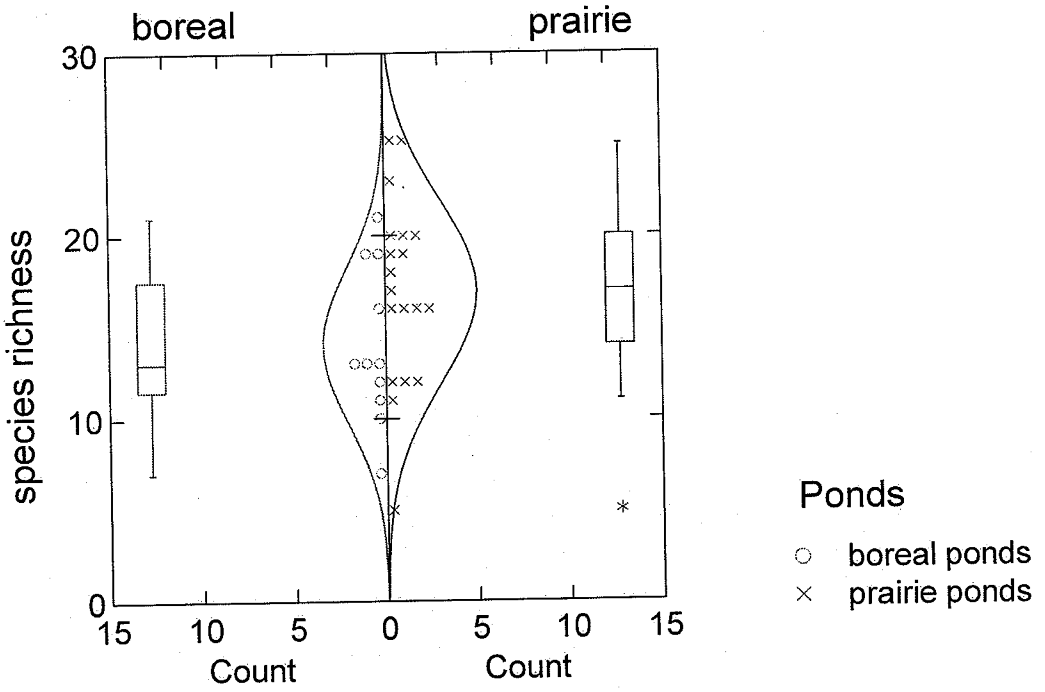

N
A
B
C
D

Figure 3: A bottle-trap (inset) being submerged in a pond for sampling of invertebrates. See Figure 2 for placement of bottle traps within the pond.

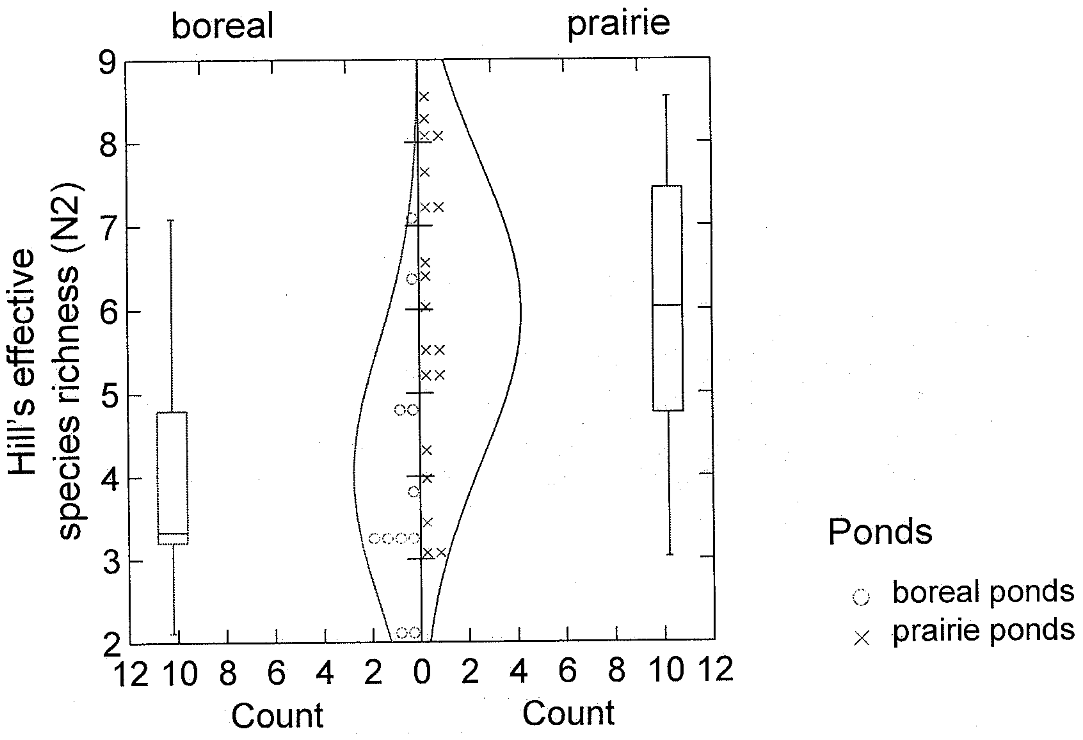
Figure 4: Use of a volume-sampler and a D-net for sampling invertebrates from a pond. See Figure 2 for placement of samples within a pond.

Figure 5: Group t-test comparing species richness of dytiscids (Coleoptera: Dytiscidae) collected by volume-sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species richness in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



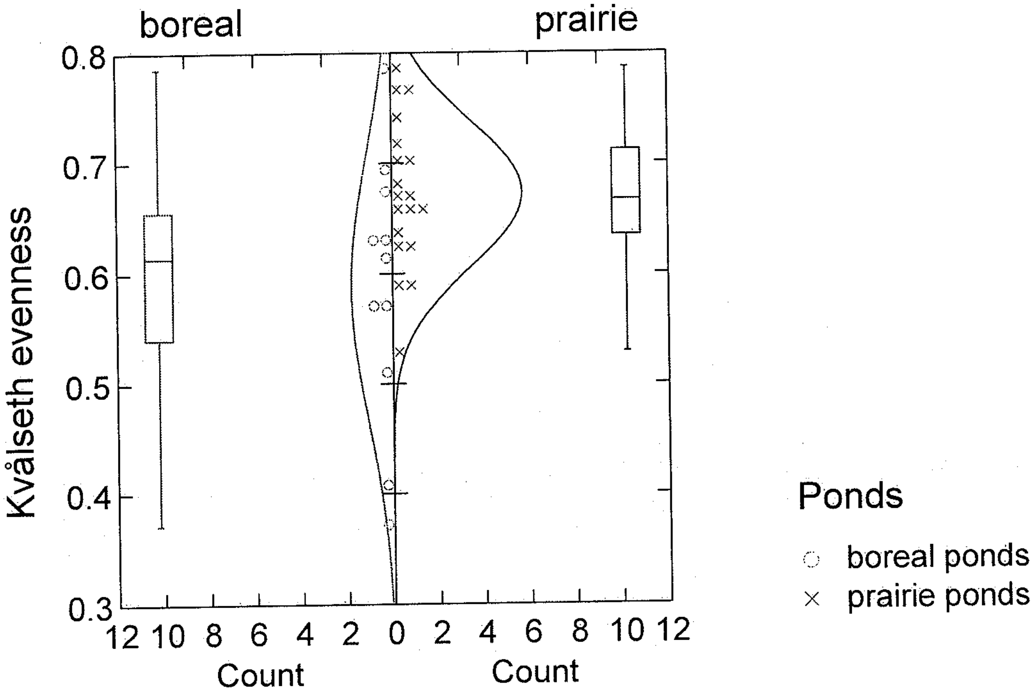
t=-1.7 df=24 p=0.10

Figure 6: Group t-test comparing Hill's effective species richness (N2) of dytiscids (Coleoptera: Dytiscidae) collected by volume-sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Hill's effective species richness (N2) in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



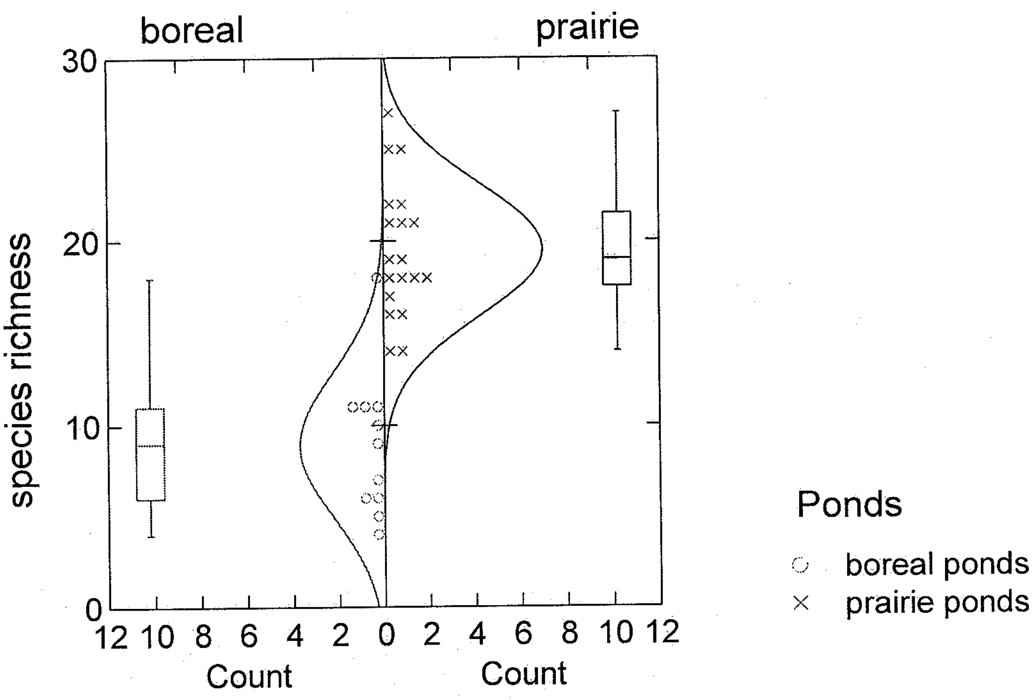
t=-3.1 df= 23 p=0.0051

Figure 7: Group t-test comparing Kvålseth evenness index of dytiscids (Coleoptera: Dytiscidae) collected by volume-sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Kvålseth evenness index in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



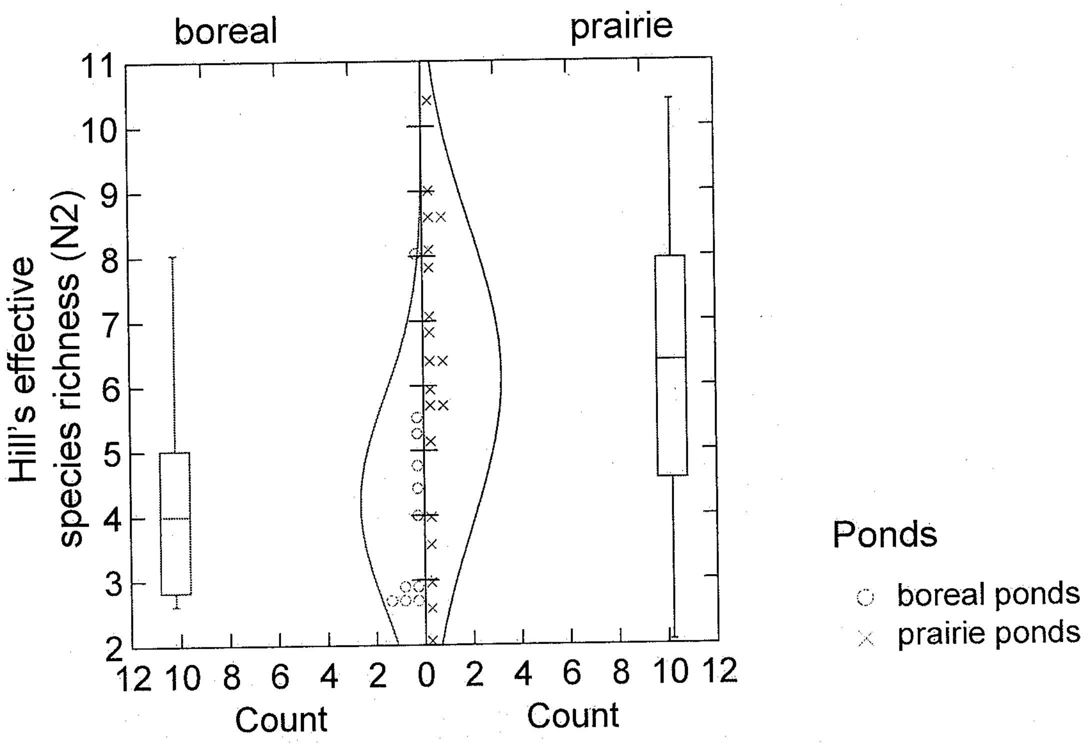
t=-2.1 df=14 p=0.051

Figure 8: Group t-test comparing species richness of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species richness in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



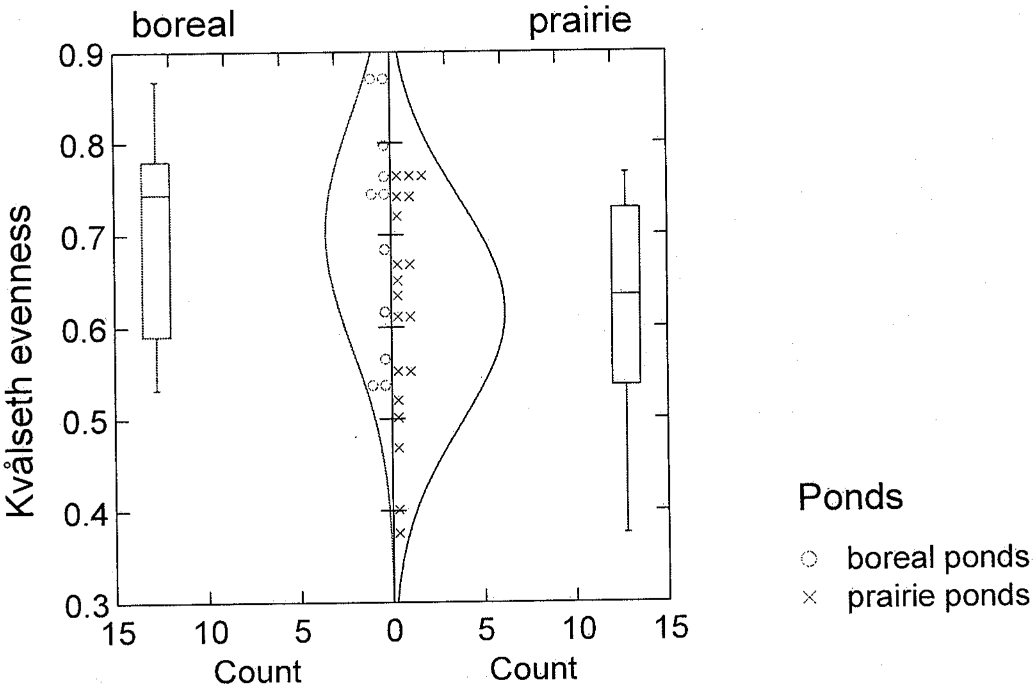
t=-7.3 df= 20 p<0.001

Figure 9: Group t-test comparing Hill's effective species richness (N2) of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Hill's effective species richness (N2) in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



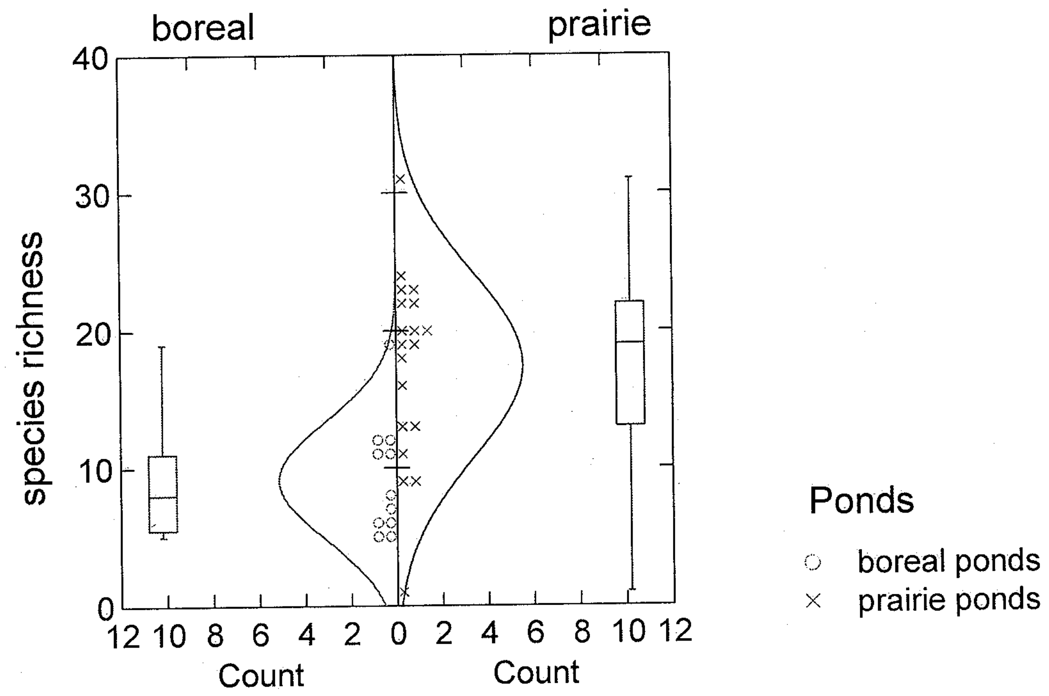
t=-2.7 df=27 p=0.013

Figure 10: Group t-test comparing Kvålseth evenness index of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap in 2001 in sampling in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Kvålseth evenness index in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



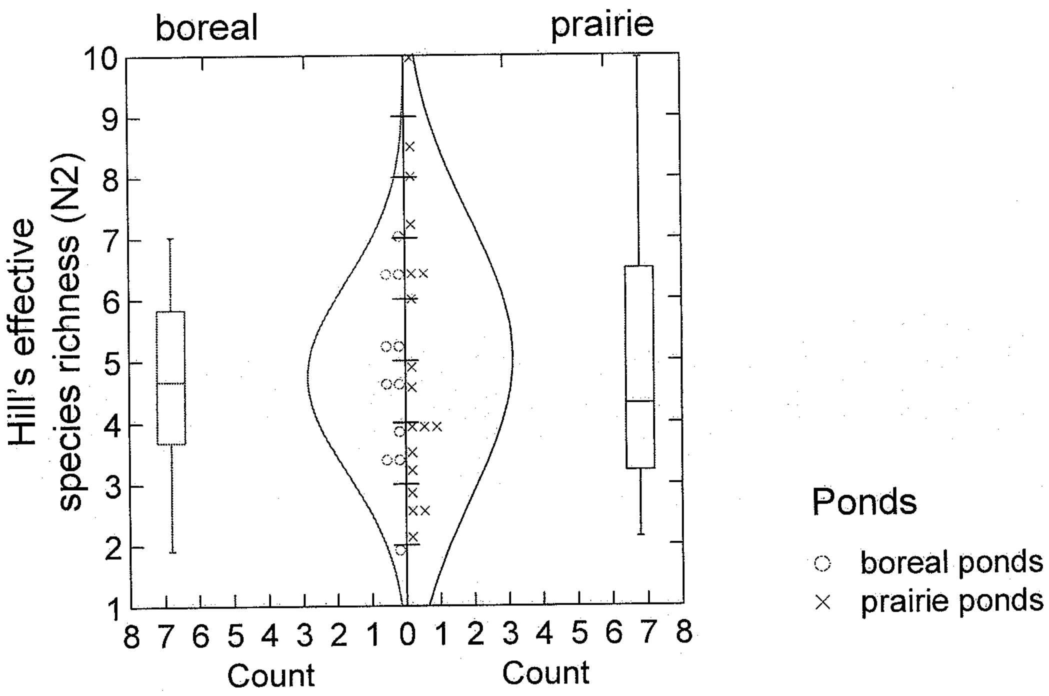
t=1.8 df=21 p=0.080

Figure 11: Group t-test comparing species richness of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2002 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species richness in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



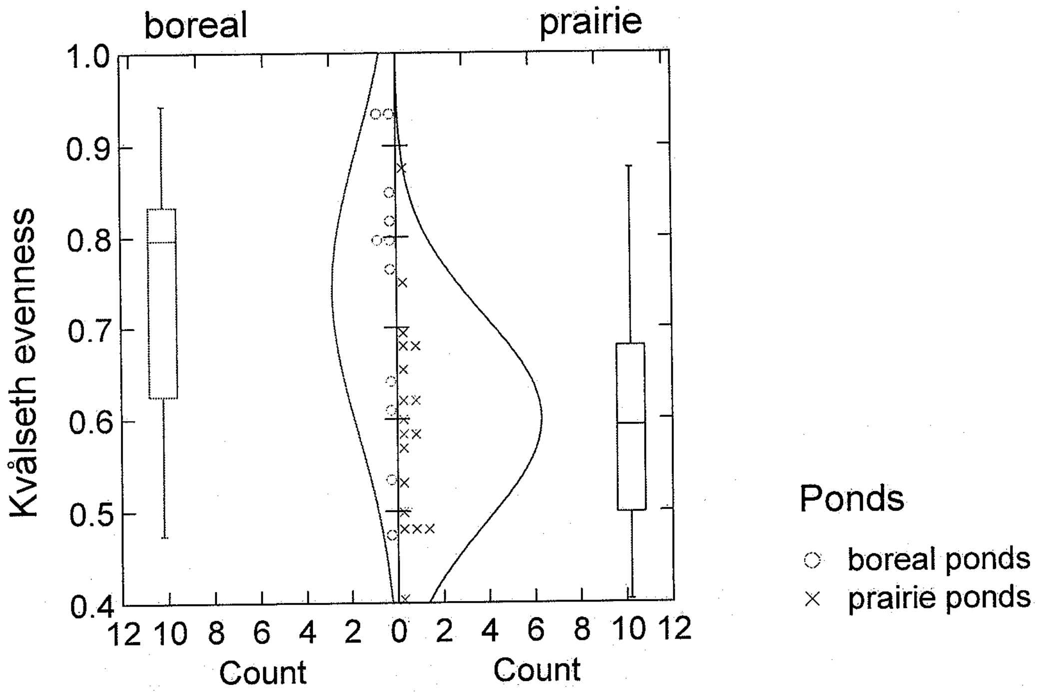
t=-4.1 df=28 p<0.001

Figure 12: Group t-test comparing Hill's effectiveness species richness (N2) of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2002 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Hill's effectiveness species richness (N2) in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



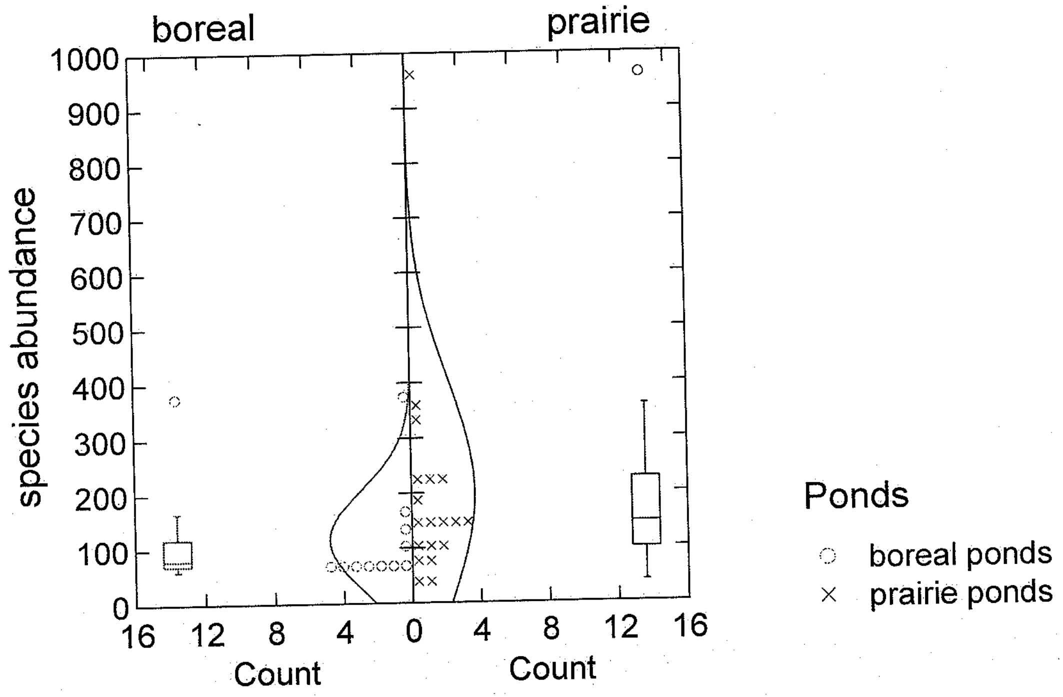
t=-0.44 df=27 p=0.66

Figure 13: Group t-test comparing Kvålseth evenness index of dytiscids (Coleoptera: Dytiscidae) collected by bottle trap in 2002 sampling in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate Kvålseth evenness index in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



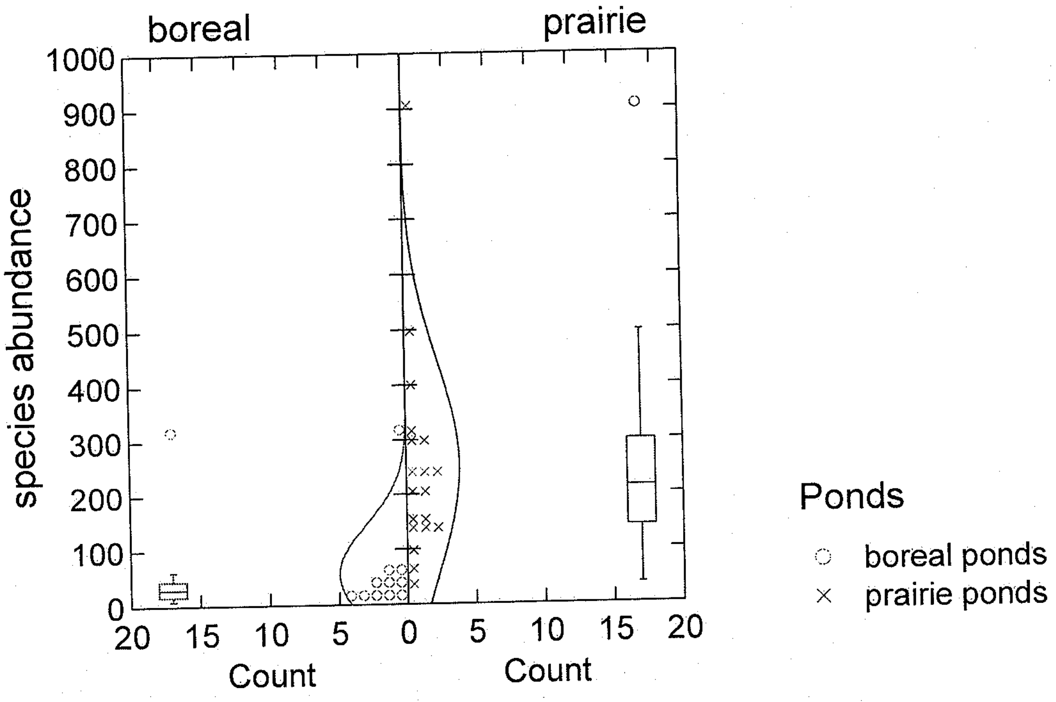
t=2.6 df=17 p=0.018

Figure 14: Group t-test comparing species abundance of dytiscids (Coleoptera: Dytiscidae) collected by volume-sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species abundance in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



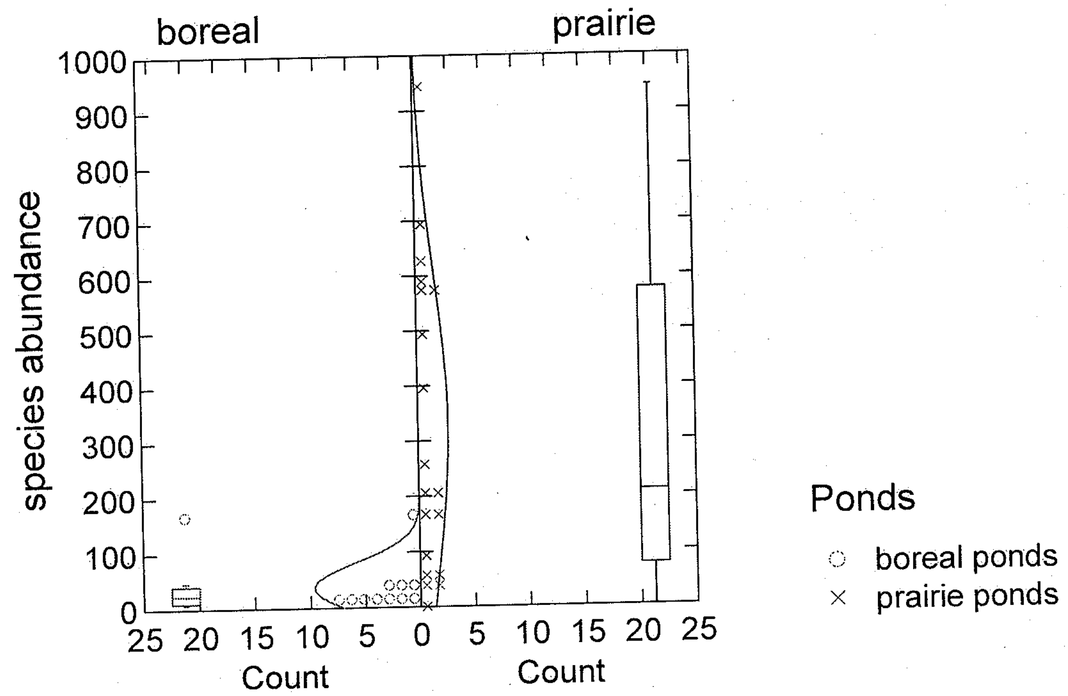
t=-1.6 df=27 p=0.13

Figure 15: Group t-test comparing species abundance of dytiscids (Coleoptera: Dytiscidae) collected by bottle trap sampling in 2001 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species abundance in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



t=-3.8 df=27 p<0.001

Figure 16: Group t-test comparing species abundance of dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2002 in boreal ponds and prairie ponds across southern Manitoba with a confidence of 95%. Box and whisker plots indicate species abundance in boreal and prairie ponds. Upper and lower ends of boxes represent 75th and 25th percentiles. The median is depicted with a solid line between the upper and lower end of the boxes. Whiskers represent 90th and 10th percentiles, and the stars (*) represent any outliers.



t=-4.4 df= 20 p<0.001

Figure 17: Sum of squares (chord) cluster analysis dendrogram of ponds across southern Manitoba based on dytiscids (Coleoptera: Dytiscidae) collected by volume-sampling in 2001. Site locations as in Table 1.

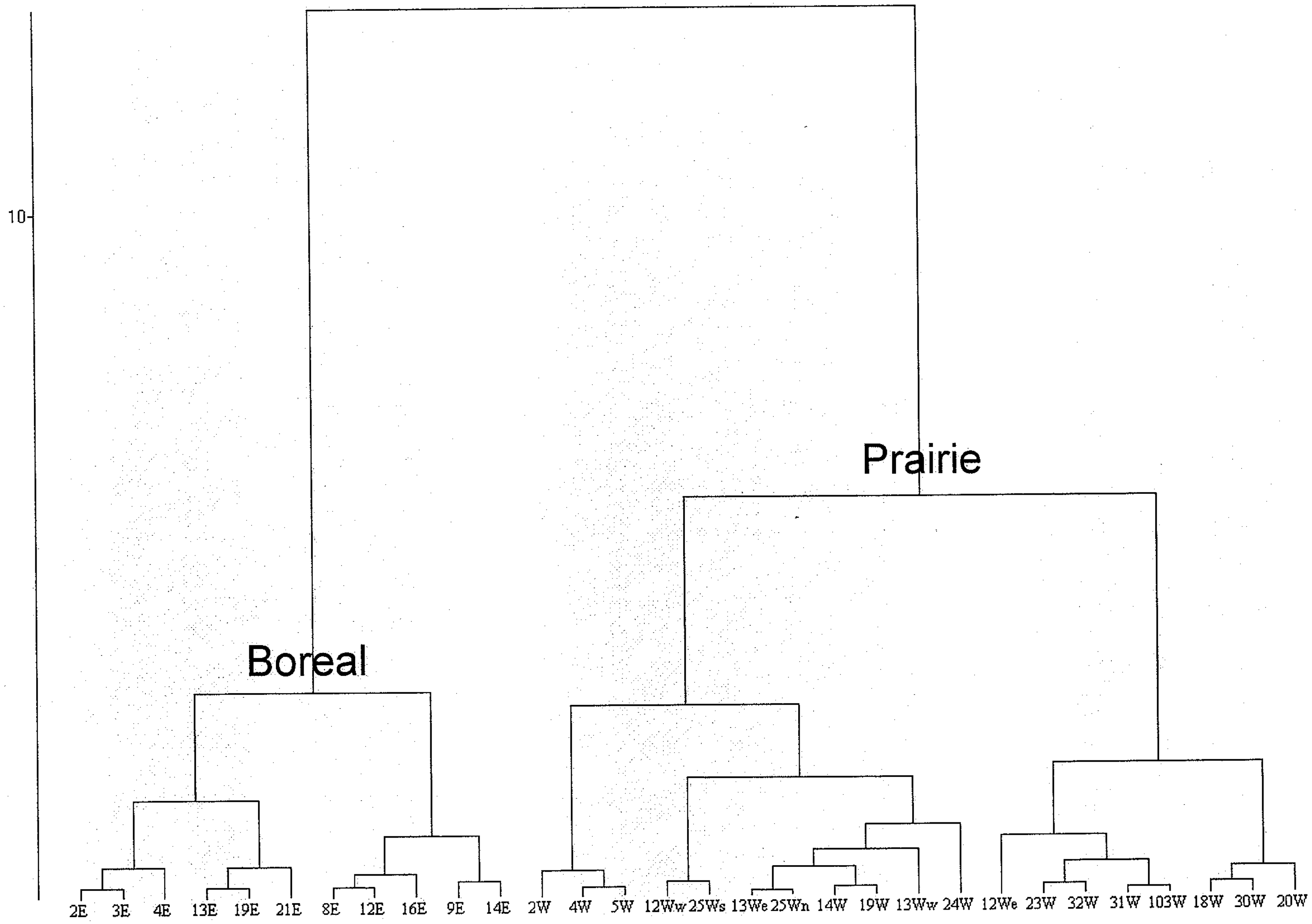

10
Boreal
Prairie
2E
3E
4E
13E
19E
21E
8E
12E
16E
9E
14E
2W
4W
5W
12Ww
25Ws
13We
25Wn
14W
19W
13Ww
24W
12We
23W
32W
31W
103W
18W
30W
20W

Figure 18: Sum of squares (chord) cluster analysis dendrogram of ponds across southern Manitoba based on dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2001. Site locations as in Table 1.

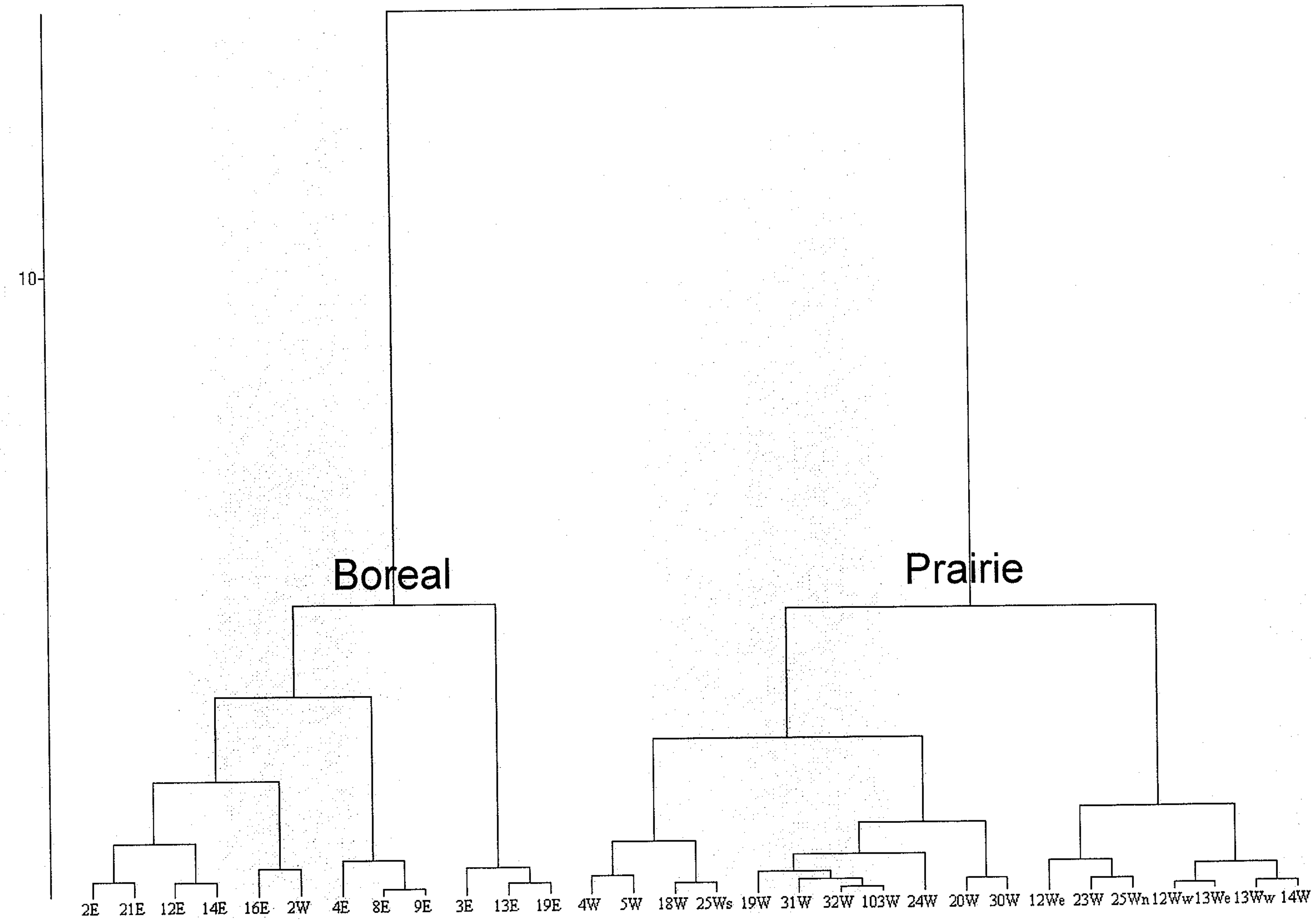

10
Boreal
Prairie
2E
21E
12E
14E
16E
2W
4E
8E
9E
3E
13E
19E
4W
5W
18W
25Ws
19W
31W
32W
103W
24W
20W
30W
12We
23W
25Wn
12Ww
13We
13Ww
14W

Figure 19: Sum of squares (chord) cluster analysis dendrogram of ponds across southern Manitoba based on dytiscids (Coleoptera: Dytiscidae) collected by bottle-trap sampling in 2002. Site locations as in Table 1.

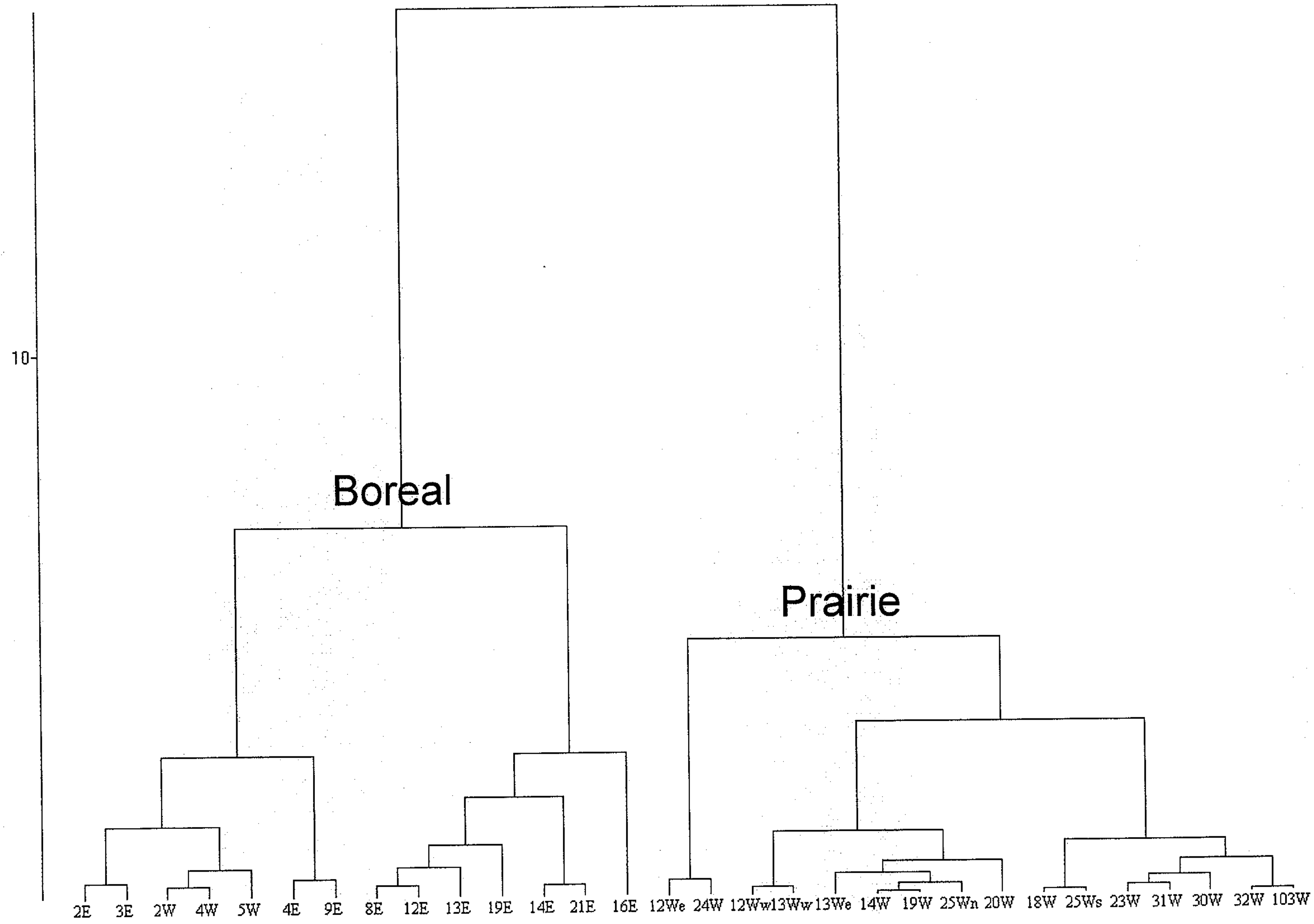
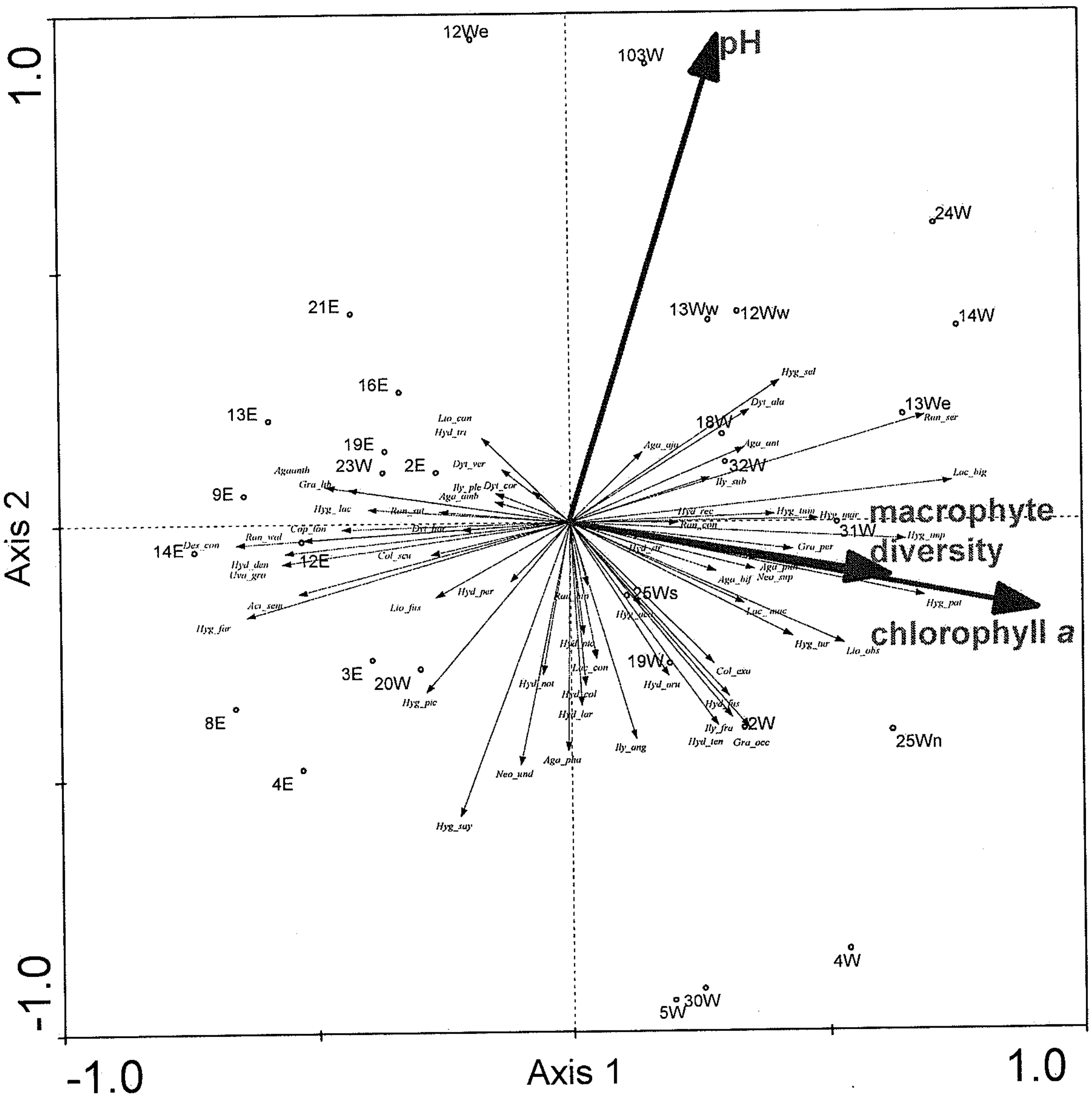

10
Boreal
Prairie
2E
3E
2W
4W
5W
4E
9E
8E
12E
13E
19E
14E
21E
16E
12We
24W
12Ww
13Ww
13We
14W
19W
25Wn
20W
18W
25Ws
23W
31W
30W
32W
103W

Figure 20: Redundancy analysis ordination diagram with site scores (⊙), species scores (→), and environmental vectors (→). The first axis (horizontal) has an eigenvalue of 0.239=60.2%, and the second axis (vertical) has an eigenvalue of 0.078=19.6%. Site locations as in Table 1. Acronyms for dytiscid species (Coleoptera: Dytiscidae): specimens were collected from ponds across southern Manitoba using volume-sampling for 2001.

Aci_sem = *Acilius semisulcatus*
Aga_aja = *Agabus ajax*
Aga_amb = *Agabus ambiguus*
Aga_ant = *Agabus antennatus*
Aga_bif = *Agabus bifarius*
Aga_can = *Agabus canadensis*
Aga_pha = *Agabus phaeopterus*
Aga_pun = *Agabus punctulatus*
Agaanth = *Agabus anthracinus*
Col_exa = *Colymbetes exaratus*
Col_scu = *Colymbetes sculptilis*
Cop_lon = *Coptotomus longulus*
Des_con = *Desmopachria convexa*
Dyt_ala = *Dytiscus alaskanus*
Dyt_cor = *Dytiscus cordieri*
Dyt_har = *Dytiscus harrisii*
Dyt_ver = *Dytiscus verticalis*
Gra_lib = *Graphoderus liberus*
Gra_occ = *Graphoderus occidentalis*
Gra_per = *Graphoderus perplexus*
Hyd_aru = *Hydaticus aruspex*
Hyd_col = *Hydroporus columbianus*
Hyd_den = *Hydroporus dentellus*
Hyd_fus = *Hydroporus fuscipennis*
Hyd_lar = *Hydroporus larsoni*
Hyd_not = *Hydroporus notabilis*
Hyd_per = *Hydroporus pervicinus*
Hyd_pic = *Hydaticus piceus*
Hyd_rec = *Hydroporus rectus*
Hyd_str = *Hydroporus striola*
Hyd_ten = *Hydroporus tenebrosus*
Hyd_tri = *Hydroporus tristis*
Hyg_aca = *Hygrotus acaroides*
Hyg_far = *Hygrotus farctus*
Hyg_imp = *Hygrotus impressopunctatus*
Hyg_lac = *Hygrotus laccophilinus*
Hyg_mar = *Hygrotus marklini*
Hyg_mas = *Hygrotus masculinus*
Hyg_pat = *Hygrotus patruelis*
Hyg_pic = *Hygrotus picatus*
Hyg_pun = *Hygrotus punctilineatus*
Hyg_say = *Hygrotus sayi*
Hyg_sel = *Hygrotus sellatus*
Hyg_tum = *Hygrotus tumidiventris*
Hyg_tur = *Hygrotus turbidus*
Ily_ang = *Ilybius angustior*
Ily_fra = *Ilybius fraterculus*
Ily_ple = *Ilybius pleuriticus*
Ily_sub = *Ilybius subaeneus*
Lac_big = *Laccophilus biguttatus*
Lac_con = *Laccornis conoideus*
Lac_mac = *Laccophilus maculosus*
Lio_can = *Liodessus cantralli*
Lio_fus = *Liodessus fuscatus*
Lio_obs = *Liodessus obscurellus*
Neo_sup = *Neoporus superioris*
Neo_und = *Neoporus undulatus*
Ran_bin = *Rhantus binotatus*
Ran_con = *Rhantus consimilis*
Ran_ser = *Rhantus sericans*
Ran_sut = *Rhantus suturellus*
Ran_wal = *Rhantus wallisi*
Uva_gra = *Uvarus granarius*



12We
103W
pH
24W
21E
13Ww
12Ww
14W
16E
13E
19E
23W
2E
9E
14E
12E
18W
13We
32W
31W
25Ws
19W
2W
25Wn
3E
20W
8E
4E
4W
5W
30W
macrophyte diversity
chlorophyll a
Lio_can
Hyd_tri
Dyt_ver
Ily_ple
Dyt_cor
Aga_amb
Agaanth
Gra_lib
Hyg_lac
Ran_sut
Cop_lon
Dyt_lap
Ran_wal
Des_con
Hyd_den
Uva_gra
Col_scu
Aci_sem
Hyg_far
Hyd_par
Lio_fus
Hyg_pic
Hyg_say
Neo_und
Aga_pha
Hyd_not
Hyd_nig
Lac_con
Hyd_col
Hyd_lar
Ran_uni
Hyg_aeq
Ily_ang
Hyd_oru
Hyd_fus
Ily_fra
Hyd_ten
Gra_occ
Col_exu
Hyg_tur
Lio_obs
Lac_mac
Hyg_pal
Aga_bif
Neo_sup
Aga_pau
Hyd_str
Gra_per
Hyg_imp
Hyg_mar
Hyg_tum
Hyd_rec
Ran_con
Lac_big
Ily_sub
Aga_ant
Aga_aju
Dyt_ala
Hyg_sel
Ran_ser
1.0
-1.0
Axis 2
Axis 1
-1.0
1.0

Figure 21: Redundancy analysis ordination diagram with site scores (○), species scores (—►), and environmental vectors (—►). The first axis (horizontal) has an eigenvalue of 0.338=59.9%, and the second axis (vertical) has an eigenvalue of 0.063=11.2%. Site locations as in Table 1. Acronyms for dytiscid species (Coleoptera: Dytiscidae): specimens were collected from ponds across southern Manitoba using bottle-trap sampling for 2001.

Aci_sem = *Acilius semisulcatus*
Aga_aja = *Agabus ajax*
Aga_amb = *Agabus ambiguus*
Aga_ant = *Agabus antennatus*
Aga_bif = *Agabus bifarius*
Aga_can = *Agabus canadensis*
Aga_pha = *Agabus phaeopterus*
Aga_pun = *Agabus punctulatus*
Agaanth = *Agabus anthracinus*
Col_exa = *Colymbetes exaratus*
Col_scu = *Colymbetes sculptilis*
Cop_lon = *Coptotomus longulus*
Des_con = *Desmopachria convexa*
Dyt_ala = *Dytiscus alaskanus*
Dyt_cor = *Dytiscus cordieri*
Dyt_har = *Dytiscus harrisii*
Dyt_ver = *Dytiscus verticalis*
Gra_lib = *Graphoderus liberus*
Gra_occ = *Graphoderus occidentalis*
Gra_per = *Graphoderus perplexus*
Hyd_aru = *Hydaticus aruspex*
Hyd_col = *Hydroporus columbianus*
Hyd_den = *Hydroporus dentellus*
Hyd_fus = *Hydroporus fuscipennis*
Hyd_lar = *Hydroporus larsoni*
Hyd_not = *Hydroporus notabilis*
Hyd_per = *Hydroporus pervicinus*
Hyd_pic = *Hydaticus piceus*
Hyd_rec = *Hydroporus rectus*
Hyd_str = *Hydroporus striola*
Hyd_ten = *Hydroporus tenebrosus*
Hyd_tri = *Hydroporus tristis*
Hyg_aca = *Hygrotus acaroides*
Hyg_far = *Hygrotus farctus*
Hyg_imp = *Hygrotus impressopunctatus*
Hyg_lac = *Hygrotus laccophilinus*
Hyg_mar = *Hygrotus marklini*
Hyg_mas = *Hygrotus masculinus*
Hyg_pat = *Hygrotus patruelis*
Hyg_pic = *Hygrotus picatus*
Hyg_pun = *Hygrotus punctilineatus*
Hyg_say = *Hygrotus sayi*
Hyg_sel = *Hygrotus sellatus*
Hyg_tum = *Hygrotus tumidiventris*
Hyg_tur = *Hygrotus turbidus*
Ily_ang = *Ilybius angustior*
Ily_fra = *Ilybius fraterculus*
Ily_ple = *Ilybius pleuriticus*
Ily_sub = *Ilybius subaeneus*
Lac_big = *Laccophilus biguttatus*
Lac_con = *Laccornis conoideus*
Lac_mac = *Laccophilus maculosus*
Lio_can = *Liodessus cantralli*
Lio_fus = *Liodessus fuscatus*
Lio_obs = *Liodessus obscurellus*
Neo_sup = *Neoporus superioris*
Neo_und = *Neoporus undulatus*
Ran_bin = *Rhantus binotatus*
Ran_con = *Rhantus consimilis*
Ran_ser = *Rhantus sericans*
Ran_sut = *Rhantus suturellus*
Ran_wal = *Rhantus wallisi*
Uva_gra = *Uvarus granarius*

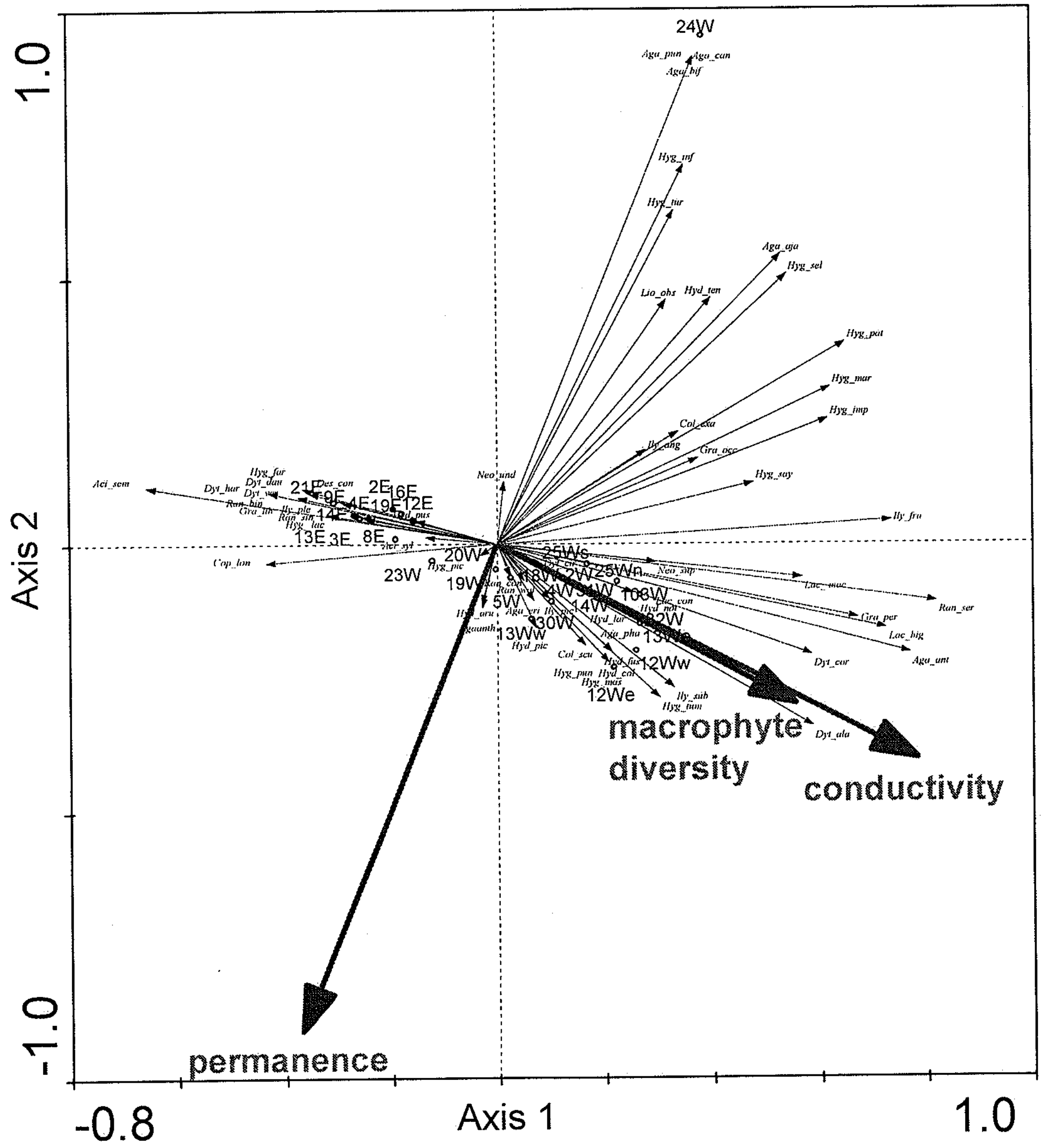

Axis 1
-0.8
1.0
Axis 2
-1.0
1.0
permanence
macrophyte
diversity
conductivity
24W
Aga_pun
Aga_can
Aga_bif
Hyg_inf
Hyg_tur
Aga_aja
Hyg_sel
Lio_obs
Hyd_ten
Hyg_pat
Hyg_mar
Hyg_imp
Col_exa
Ily_ang
Gra_occ
Hyg_say
Ily_fra
Neo_und
Aci_sem
Hyg_far
Dyt_dau
Dyt_har
Des_con
Ran_bin
Gra_lin
Ily_ple
Ran_sin
Hyg_lac
Cop_lon
Hyg_pic
21E
9E
2E
16E
4E
19E
12E
14E
13E
3E
8E
20W
23W
19W
5W
13Ww
30W
Hyd_pic
Ran_con
Ran_wal
Agu_eri
Ily_pic
18W
2W
25Ws
25Wn
Neo_sup
Lac_mac
Ran_ser
Gra_per
Lac_big
Aga_unt
Dyt_cor
Dyt_ala
4W
14W
108W
Lac_con
Hyd_nor
Hyd_lat
32W
Aga_pha
13We
Col_scu
Hyd_fus
12Ww
Hyg_pun
Hyd_col
Hyg_mas
12We
Ily_sub
Hyg_tum

Figure 22: Redundancy analysis ordination diagram with site scores (○), species scores (►), and environmental vectors (—►). The first axis (horizontal) has an eigenvalue of 0.386=65.5%, and the second axis (vertical) has an eigenvalue of 0.023=3.9%. Site locations as in Table 1. Acronyms for dytiscid species (Coleoptera: Dytiscidae): specimens were collected from ponds across southern Manitoba using bottle-trap sampling for 2002.

Aci_sem = *Acilius semisulcatus*
Aga_aja = *Agabus ajax*
Aga_amb = *Agabus ambiguus*
Aga_ant = *Agabus antennatus*
Aga_bif = *Agabus bifarius*
Aga_can = *Agabus canadensis*
Aga_pha = *Agabus phaeopterus*
Aga_pun = *Agabus punctulatus*
Agaanth = *Agabus anthracinus*
Col_exa = *Colymbetes exaratus*
Col_scu = *Colymbetes sculptilis*
Cop_lon = *Coptotomus longulus*
Des_con = *Desmopachria convexa*
Dyt_ala = *Dytiscus alaskanus*
Dyt_cor = *Dytiscus cordieri*
Dyt_har = *Dytiscus harrisii*
Dyt_ver = *Dytiscus verticalis*
Gra_lib = *Graphoderus liberus*
Gra_occ = *Graphoderus occidentalis*
Gra_per = *Graphoderus perplexus*
Hyd_aru = *Hydaticus aruspex*
Hyd_col = *Hydroporus columbianus*
Hyd_den = *Hydroporus dentellus*
Hyd_fus = *Hydroporus fuscipennis*
Hyd_lar = *Hydroporus larsoni*
Hyd_not = *Hydroporus notabilis*
Hyd_per = *Hydroporus pervicinus*
Hyd_pic = *Hydaticus piceus*
Hyd_rec = *Hydroporus rectus*
Hyd_str = *Hydroporus striola*
Hyd_ten = *Hydroporus tenebrosus*
Hyd_tri = *Hydroporus tristis*
Hyg_aca = *Hygrotus acaroides*
Hyg_far = *Hygrotus farctus*
Hyg_imp = *Hygrotusimpressopunctatus*
Hyg_lac = *Hygrotus laccophilinus*
Hyg_mar = *Hygrotus marklini*
Hyg_mas = *Hygrotus masculinus*
Hyg_pat = *Hygrotus patruelis*
Hyg_pic = *Hygrotus picatus*
Hyg_pun = *Hygrotus punctilineatus*
Hyg_say = *Hygrotus sayi*
Hyg_sel = *Hygrotus sellatus*
Hyg_tum = *Hygrotus tumidiventris*
Hyg_tur = *Hygrotus turbidus*
Ily_ang = *Ilybius angustior*
Ily_fra = *Ilybius fraterculus*
Ily_ple = *Ilybius pleuriticus*
Ily_sub = *Ilybius subaeneus*
Lac_big = *Laccophilus biguttatus*
Lac_con = *Laccornis conoideus*
Lac_mac = *Laccophilus maculosus*
Lio_can = *Liodessus cantralli*
Lio_fus = *Liodessus fuscatus*
Lio_obs = *Liodessus obscurellus*
Neo_sup = *Neoporus superioris*
Neo_und = *Neoporus undulatus*
Ran_bin = *Rhantus binotatus*
Ran_con = *Rhantus consimilis*
Ran_ser = *Rhantus sericans*
Ran_sut = *Rhantus suturellus*
Ran_wal = *Rhantus wallisi*
Uva_gra = *Uvarus granarius*

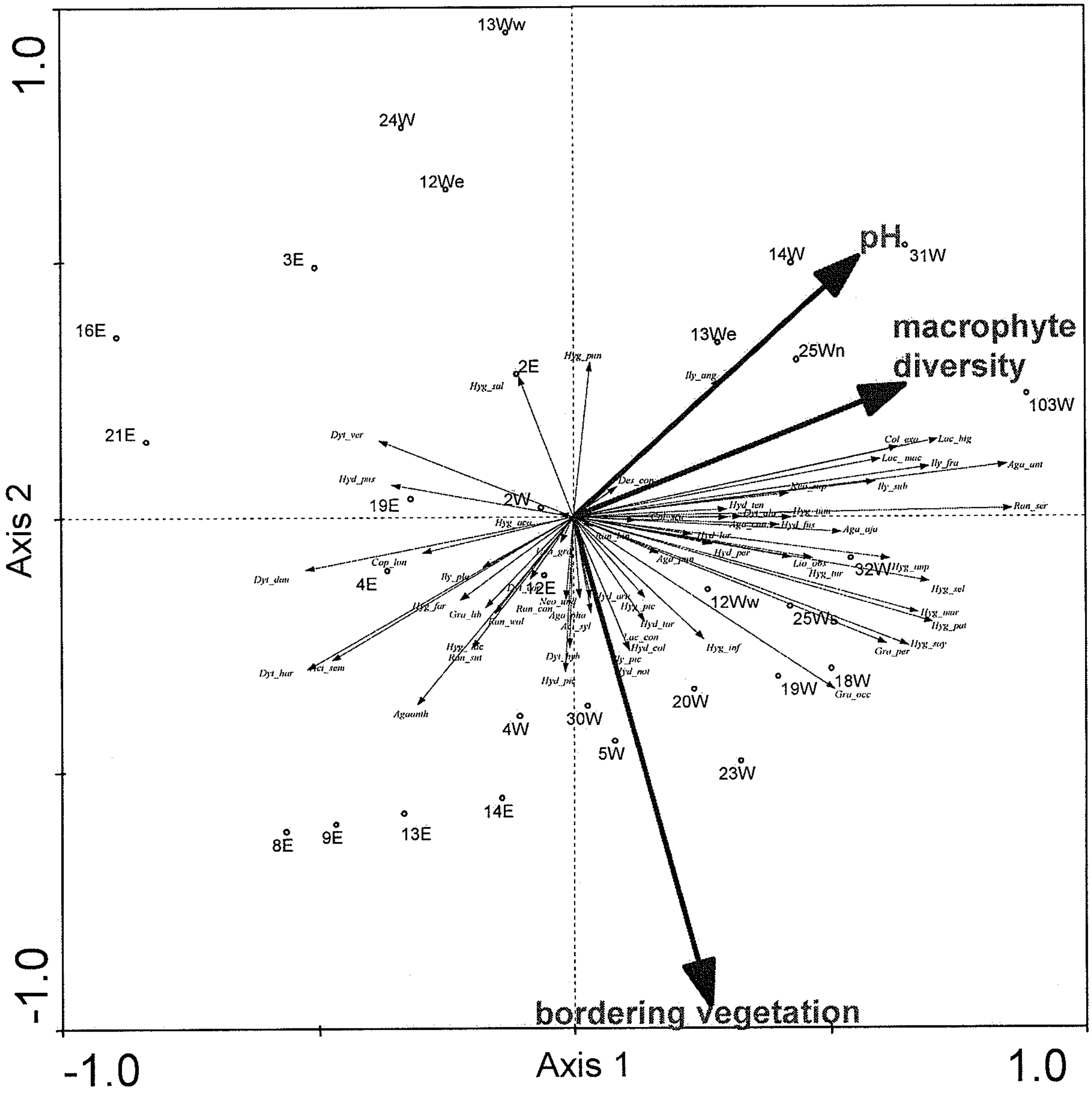

Axis 2
1.0
-1.0
Axis 1
-1.0
1.0
pH
macrophyte diversity
bordering vegetation
13Ww
24W
12We
3E
16E
21E
14W
31W
13We
25Wn
2E
103W
2W
19E
4E
12E
12Ww
25Ws
32W
18W
19W
20W
4W
30W
5W
23W
14E
13E
9E
8E
Hyg_pun
Hyg_sal
Ily_ang
Dyt_ver
Hyd_pus
Des_con
Col_exa
Luc_big
Luc_mac
Ily_fra
Aga_ant
Neo_sup
Ily_sub
Hyd_ten
Ran_ser
Dyt_ala
Hyg_tum
Aga_con
Hyd_fus
Aga_aja
Hyg_acu
Ran_bin
Hyd_per
Aga_pun
Lio_obs
Hyg_tur
Hyg_imp
Hyg_sel
Hyg_mar
Hyg_pat
Hyg_say
Gra_per
Gra_occ
Cop_lon
Dyt_dau
Ily_pla
Hyg_far
Gra_lit
Ran_wal
Hyg_lac
Ran_sut
Dyt_har
Aci_sem
Agaanth
Neo_und
Ran_con
Aga_pha
Aci_syl
Dyt_hyb
Hyd_pic
Hyd_ari
Hyg_pic
Hyd_tar
Luc_con
Hyd_col
Ily_pic
Hyd_not
Hyg_inf

Figure 23: Redundancy analysis (RDA) ordination diagram with site scores (◉), species scores (→), and odonate family abundance as environmental vectors (→). The first axis (horizontal) has an eigenvalue of 0.215=36.1%, and the second axis (vertical) has an eigenvalue of 0.106=17.8%. Site locations as in Table 1. Acronyms for dytiscid species (Coleoptera: Dytiscidae): specimens were collected from boreal ponds using volume-sampling for 2001.

Aci_sem = *Acilius semisulcatus*
Aga_aja = *Agabus ajax*
Aga_amb = *Agabus ambiguus*
Aga_ant = *Agabus antennatus*
Aga_bif = *Agabus bifarius*
Aga_can = *Agabus canadensis*
Aga_pha = *Agabus phaeopterus*
Aga_pun = *Agabus punctulatus*
Agaanth = *Agabus anthracinus*
Col_exa = *Colymbetes exaratus*
Col_scu = *Colymbetes sculptilis*
Cop_lon = *Coptotomus longulus*
Des_con = *Desmopachria convexa*
Dyt_ala = *Dytiscus alaskanus*
Dyt_cor = *Dytiscus cordieri*
Dyt_har = *Dytiscus harrisii*
Dyt_ver = *Dytiscus verticalis*
Gra_lib = *Graphoderus liberus*
Gra_occ = *Graphoderus occidentalis*
Gra_per = *Graphoderus perplexus*
Hyd_aru = *Hydaticus aruspex*
Hyd_col = *Hydroporus columbianus*
Hyd_den = *Hydroporus dentellus*
Hyd_fus = *Hydroporus fuscipennis*
Hyd_lar = *Hydroporus larsoni*
Hyd_not = *Hydroporus notabilis*
Hyd_per = *Hydroporus pervicinus*
Hyd_pic = *Hydaticus piceus*
Hyd_rec = *Hydroporus rectus*
Hyd_str = *Hydroporus striola*
Hyd_ten = *Hydroporus tenebrosus*
Hyd_tri = *Hydroporus tristis*
Hyg_aca = *Hygrotus acaroides*
Hyg_far = *Hygrotus farctus*
Hyg_imp = *Hygrotus impressopunctatus*
Hyg_lac = *Hygrotus laccophilinus*
Hyg_mar = *Hygrotus marklini*
Hyg_mas = *Hygrotus masculinus*
Hyg_pat = *Hygrotus patruelis*
Hyg_pic = *Hygrotus picatus*
Hyg_pun = *Hygrotus punctilineatus*
Hyg_say = *Hygrotus sayi*
Hyg_sel = *Hygrotus sellatus*
Hyg_tum = *Hygrotus tumidiventris*
Hyg_tur = *Hygrotus turbidus*
Ily_ang = *Ilybius angustior*
Ily_fra = *Ilybius fraterculus*
Ily_ple = *Ilybius pleuriticus*
Ily_sub = *Ilybius subaeneus*
Lac_big = *Laccophilus biguttatus*
Lac_con = *Laccornis conoideus*
Lac_mac = *Laccophilus maculosus*
Lio_can = *Liodessus cantralli*
Lio_fus = *Liodessus fuscatus*
Lio_obs = *Liodessus obscurellus*
Neo_sup = *Neoporus superioris*
Neo_und = *Neoporus undulatus*
Ran_bin = *Rhantus binotatus*
Ran_con = *Rhantus consimilis*
Ran_ser = *Rhantus sericans*
Ran_sut = *Rhantus suturellus*
Ran_wal = *Rhantus wallisi*
Uva_gra = *Uvarus granarius*

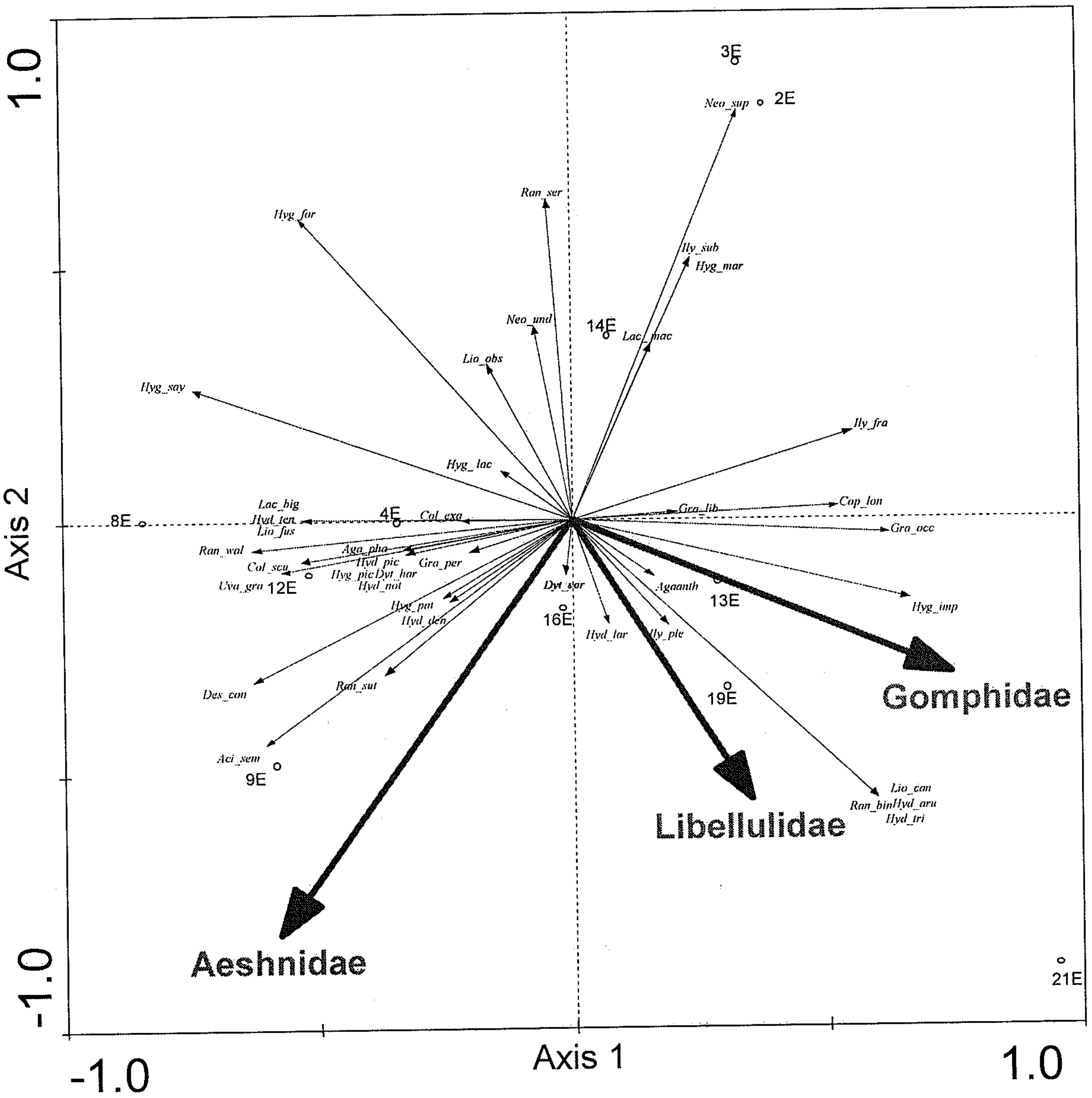

1.0
-1.0
Axis 2
Axis 1
-1.0
1.0
3E
2E
Neo_sup
Ran_ser
Hyg_far
Ily_sub
Hyg_mar
Neo_und
14E
Lac_mac
Lio_obs
Hyg_sav
Ily_fra
Hyg_lac
Gra_lib
Cop_lon
Lac_big
Hyd_ten
Lio_fus
8E
4E
Col_exa
Gra_occ
Ran_wal
Aga_pha
Hyd_pic
Gra_per
Col_scu
Hyg_pic
Dyt_har
Hyd_not
Uva_gra
12E
Dyt_sar
Agaanth
13E
Hyg_imp
Hyg_pat
Hyd_den
16E
Hyd_lar
Ily_ple
Gomphidae
Des_con
Ran_sut
19E
Aci_sem
9E
Lio_can
Ran_bin
Hyd_aru
Hyd_tri
Libellulidae
Aeshnidae
21E

Figure 24: Redundancy analysis (RDA) ordination diagram with site scores (⊙), species scores (→), and odonate family abundance as environmental vectors (➔). The first axis (horizontal) has an eigenvalue of 0.181=36.3%, and the second axis (vertical) has an eigenvalue of 0.066=13.2%. Site locations as in Table 1. Acronyms for dytiscid species (Coleoptera: Dytiscidae): specimens were collected from prairie ponds using volume-sampling for 2001.

Aci_sem = *Acilius semisulcatus*
Aga_aja = *Agabus ajax*
Aga_amb = *Agabus ambiguus*
Aga_ant = *Agabus antennatus*
Aga_bif = *Agabus bifarius*
Aga_can = *Agabus canadensis*
Aga_pha = *Agabus phaeopterus*
Aga_pun = *Agabus punctulatus*
Agaanth = *Agabus anthracinus*
Col_exa = *Colymbetes exaratus*
Col_scu = *Colymbetes sculptilis*
Cop_lon = *Coptotomus longulus*
Des_con = *Desmopachria convexa*
Dyt_ala = *Dytiscus alaskanus*
Dyt_cor = *Dytiscus cordieri*
Dyt_har = *Dytiscus harrisii*
Dyt_ver = *Dytiscus verticalis*
Gra_lib = *Graphoderus liberus*
Gra_occ = *Graphoderus occidentalis*
Gra_per = *Graphoderus perplexus*
Hyd_aru = *Hydaticus aruspex*
Hyd_col = *Hydroporus columbianus*
Hyd_den = *Hydroporus dentellus*
Hyd_fus = *Hydroporus fuscipennis*
Hyd_lar = *Hydroporus larsoni*
Hyd_not = *Hydroporus notabilis*
Hyd_per = *Hydroporus pervicinus*
Hyd_pic = *Hydaticus piceus*
Hyd_rec = *Hydroporus rectus*
Hyd_str = *Hydroporus striola*
Hyd_ten = *Hydroporus tenebrosus*
Hyd_tri = *Hydroporus tristis*
Hyg_aca = *Hygrotus acaroides*
Hyg_far = *Hygrotus farctus*
Hyg_imp = *Hygrotus impressopunctatus*
Hyg_lac = *Hygrotus laccophilinus*
Hyg_mar = *Hygrotus marklini*
Hyg_mas = *Hygrotus masculinus*
Hyg_pat = *Hygrotus patruelis*
Hyg_pic = *Hygrotus picatus*
Hyg_pun = *Hygrotus punctilineatus*
Hyg_say = *Hygrotus sayi*
Hyg_sel = *Hygrotus sellatus*
Hyg_tum = *Hygrotus tumidiventris*
Hyg_tur = *Hygrotus turbidus*
Ily_ang = *Ilybius angustior*
Ily_fra = *Ilybius fraterculus*
Ily_ple = *Ilybius pleuriticus*
Ily_sub = *Ilybius subaeneus*
Lac_big = *Laccophilus biguttatus*
Lac_con = *Laccornis conoideus*
Lac_mac = *Laccophilus maculosus*
Lio_can = *Liodessus cantralli*
Lio_fus = *Liodessus fuscatus*
Lio_obs = *Liodessus obscurellus*
Neo_sup = *Neoporus superioris*
Neo_und = *Neoporus undulatus*
Ran_bin = *Rhantus binotatus*
Ran_con = *Rhantus consimilis*
Ran_ser = *Rhantus sericans*
Ran_sut = *Rhantus suturellus*
Ran_wal = *Rhantus wallisi*
Uva_gra = *Uvarus granarius*

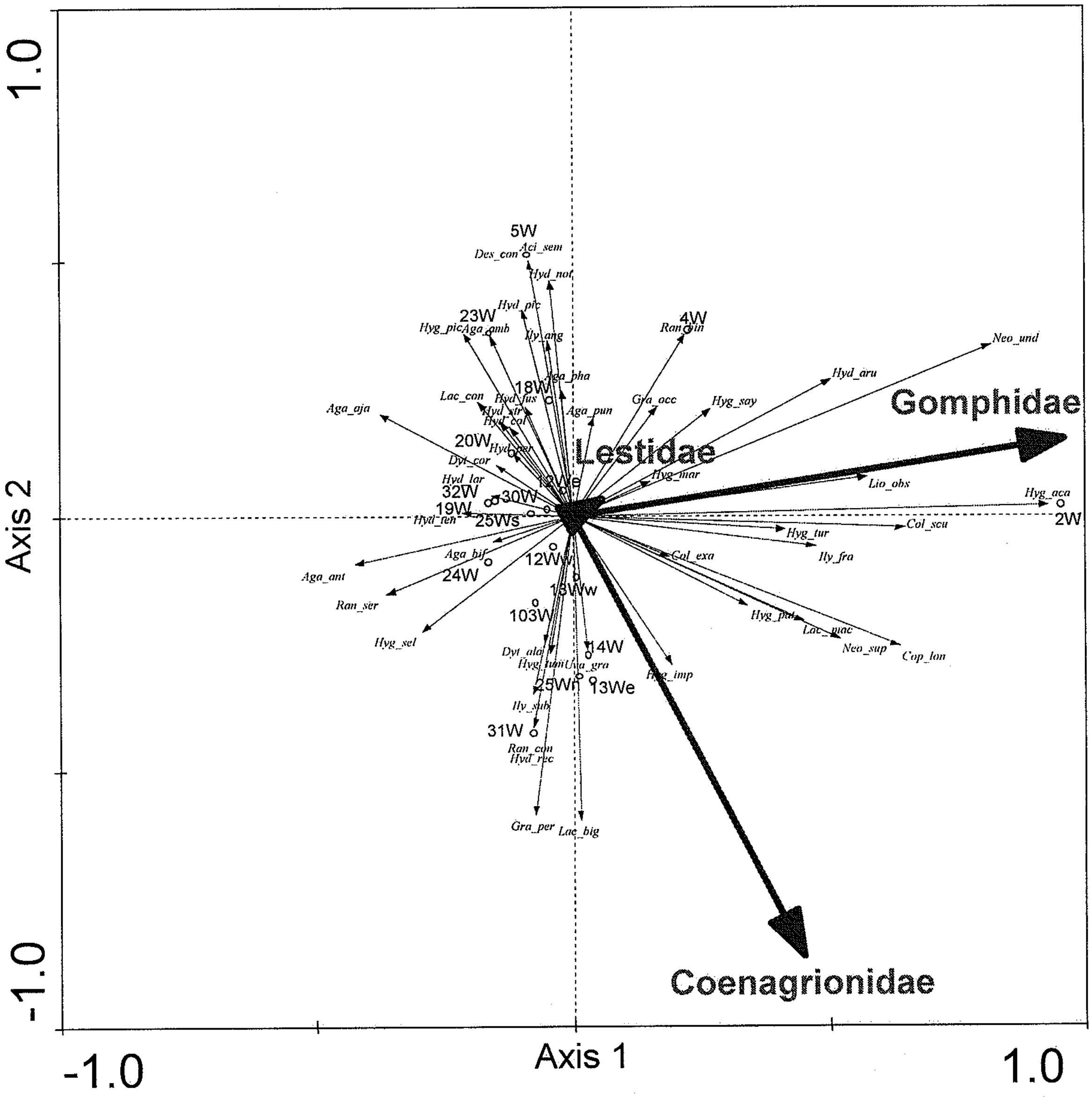
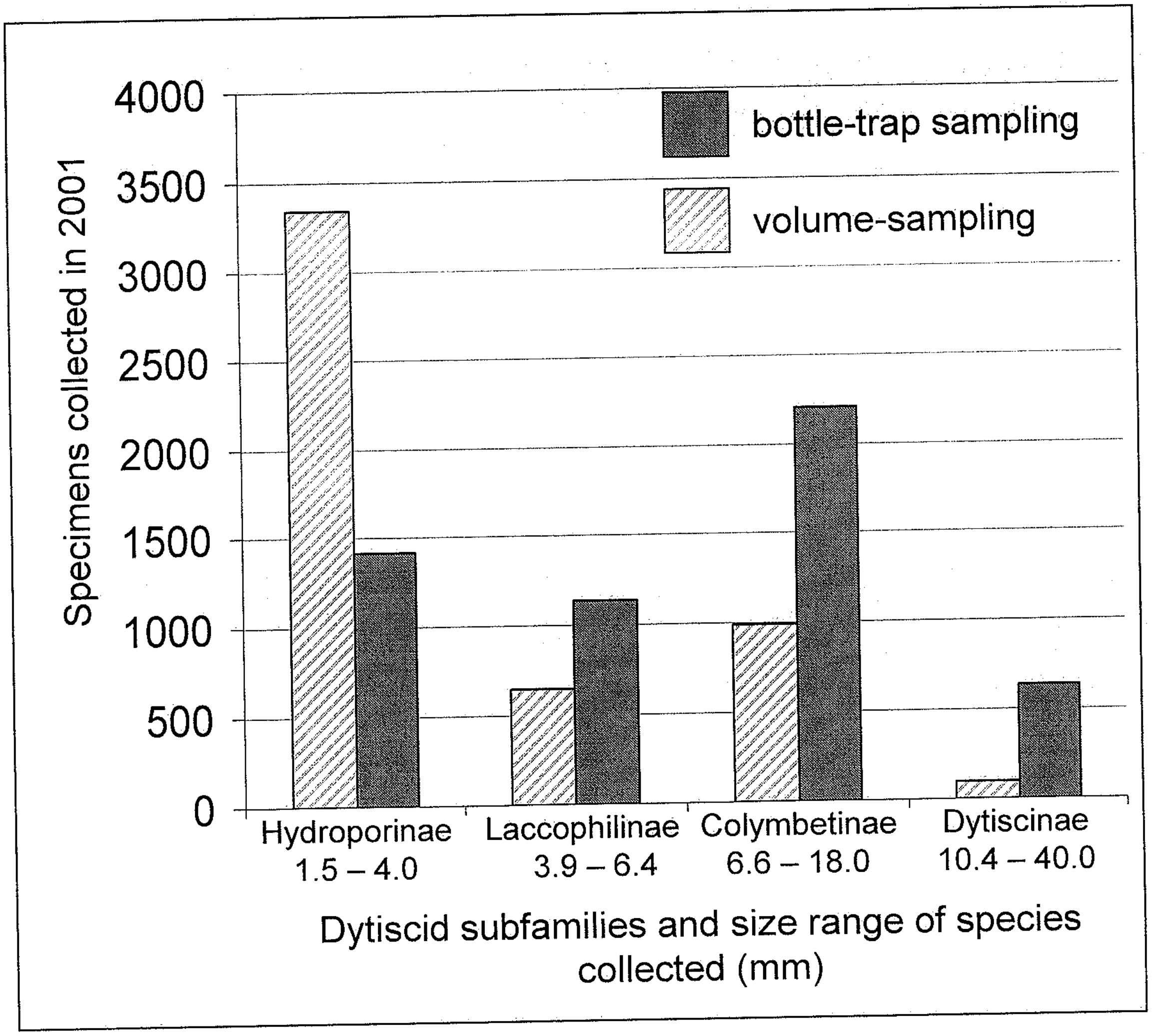

5W
Des_con
Aci_sem
Hyd_not
Hyd_pic
23W
Hyg_pic
Aga_amb
Ily_ang
4W
Ran_bin
Neo_und
Hyd_aru
Aga_pha
18W
Lac_con
Hyd_fus
Hyd_str
Hyd_col
Aga_pun
Gra_occ
Hyg_say
Gomphidae
Aga_aja
20W
Hyd_per
Lestidae
Dyt_cor
Hyd_lar
13We
Hyg_mar
Lio_obs
32W
30W
19W
Hyd_ren
25Ws
Hyg_aca
2W
Hyg_tur
Col_scu
Aga_bif
Col_exa
Ily_fra
Aga_ant
12Ww
24W
Ran_ser
13Ww
103W
Hyg_pul
Lac_mac
Neo_sup
Cop_lon
Hyg_sel
14W
Dyt_alo
Hyg_tum
Una_gra
Hyg_imp
25Wn
13We
Ily_sub
31W
Ran_con
Hyd_rec
Gra_per
Lac_big
Coenagrionidae
1.0
-1.0
Axis 2
Axis 1
-1.0
1.0

Figure 25: Bar graph comparing the total dytiscid (Coleoptera: Dytiscidae) specimens collected from each subfamily by bottle-trap and volume sampling in 2001. Size (mm) indicates the range of body lengths of dytiscid species collected from each subfamily.


bottle-trap sampling
volume-sampling
Specimens collected in 2001
4000
3500
3000
2500
2000
1500
1000
500
0
Hydroporinae
1.5 – 4.0
Laccophilinae
3.9 – 6.4
Colymbetinae
6.6 – 18.0
Dytiscinae
10.4 – 40.0
Dytiscid subfamilies and size range of species collected (mm)

DISCUSSION

The organization of dytiscid communities can be examined at various ecological levels, from small-scale differences among ponds to expansive, shared factors within an ecozone. The interpretation of any results from any study must first be considered within the context of the sampling methods. Collecting dytiscids using bottle-traps or volume-sampling and potential biases of each sampling method will be considered in the first section. In the second section, the focus will be on which of the environmental variables examined are the most influential in organizing dytiscid communities. The third section will investigate the impact of predator guilds (e.g. fish, dragonfly larvae, and tiger salamanders) on predacious diving beetle communities. In the final section, I compared and contrasted boreal and prairie ponds in southern Manitoba based on their environmental characteristics and the diversity of dytiscids that inhabit them.

Sampling methods

Comparison of volume-sampling and bottle-trap sampling

In 2001, bottle-traps and volume-sampling each collected 60 species of dytiscids and total catches of 5391 and 5080 specimens, respectively. Both sampling techniques were, therefore, effective means of collecting dytiscids; however, each sampling technique comes with its own set of biases.

Bottle-traps are an efficient, inexpensive, and easy way of collecting mobile aquatic insects in lentic habitats (Hilsenhoff 1987; Hilsenhoff 1991; Gundersen *et al.* 2002). Aquatic beetles have been collected using these techniques for almost one hundred years (Aiken and Roughley 1985). Bottle-traps are more effective at collecting large species of aquatic Coleoptera compared to active sampling techniques (Hilsenhoff 1987; Hilsenhoff 1991; Gundersen et al. 2002). Large species tend to swim horizontally within the water column, which makes them more likely to be collected by horizontally oriented bottle-traps (Hilsenhoff 1987). Small species, however, tend to swim vertically from the bottom to the surface (Hilsenhoff 1987). In my study, bottle-traps were more effective than volume-sampling at collecting specimens of large species within the subfamilies Laccophilinae, Colymbetinae, and Dytiscinae (Fig. 25). Volume-sampling collected smaller specimens, typical of species of Hydroporinae, in greater numbers particularly species of *Desmopachria* Babington, *Liodessus* Guignot, and *Uvarus* Guignot. Hilsenhoff (1991) also found that bottle-traps were particularly biased against specimens of *Desmopachria*, *Liodessus*, and *Uvarus* when compared to aquatic net sampling. Gundersen *et al.* (2002) acknowledged the inequality in catches between bottle-trap, and active sampling techniques, such as volume-sampling. Gundersen *et al.* (2002) found that a vertically oriented bottle-trap captured small species in much greater abundances than a bottle-trap oriented horizontally (Table 5 in Gundersen *et al.* 2002). Including horizontally and vertically oriented bottle-traps in a sampling regime, a better representation of the dytiscid community can be obtained.

Collecting dytiscids with active sampling techniques, such as volume-sampling, has several advantages. Volume-sampling is useful when a density measurement is required. In my study, I used volume-sampling not only to get estimates of dytiscid densities (including smaller species), but also to sample odonate larval densities. Odonate larvae are "sit and wait" or ambush predators, and are not well-collected with activity traps such as bottle-traps (Larson 1990). Volume-sampling addressed my objectives by effectively sampling dytiscid and odonate densities. However, this sampling technique is time consuming, because of the need for sorting insects from the debris that is collected. I chose to sift through the samples with a hand-held sifter. Some researchers choose to carry this out passively with a separator tray in which debris is spread over a screen that is set onto a collecting pan (Gundersen *et al.* 2002). Insects work their way through the debris and fall through the screen into the collecting pan. Gundersen *et al.* (2002) found that this separation technique collected 90% of the adult insects and 55% of the immature insects (including odonate larvae). My separation technique was more laborious but was probably more effective, particularly at collecting odonate larvae. In the end, however, I found separating insects from debris so time consuming that volume-sampling was eliminated in the second field year. For improved efficiency, I recommend a passive separation regime similar to those suggested by Gundersen *et al.* (2002). One way to circumvent the issue of specimen loss when using the separator is to increase the number of samples. Although this may appear to be a time-consuming counter method, it would be a practical option because there is no need to sort the samples manually as would otherwise be the case.

Volume-sampling techniques also poorly sample elusive or nocturnal and rare species. Typically, these types of techniques are conducted during the daylight hours; therefore, species that are active at night could be missed. Several species of *Agabus*, *Ilybius*, *Rhantus* Dejean, *Dytiscus*, and *Hydaticus* Leach are nocturnal and spend the day buried in the bottom substrate (Hilsenhoff 1987). In addition, rare species also might not be collected. Hilsenhoff (1987) noted that *Rhantus sinuatus* (LeConte) was a rare species that was difficult to collect with an aquatic net. This species, along with other rare dytiscids, are often collected effectively using bottle-traps (Aiken and Roughley 1985; Hilsenhoff 1987). I found specimens of *R. sinuatus* only in bottle-trap catches. Bottle-traps also are useful for collecting species that are elusive during the daylight hours. Most traps are emptied after at least one night, allowing nocturnal species to be caught. Bottle-traps thus are a good supplement to any dytiscid sampling regime that intends to collect representation of the entire community.

Dytiscid collections from volume-sampling and bottle-traps were able to accomplish most of my study objectives equally well. Both sampling technique collections allowed me to distinguish the differences between prairie and boreal pond communities and to identify the factors that were correlated with these differences. There are three reasons for the similarities in interpretation, despite the potential biases discussed above: (1) there was considerable overlap of species diversity and composition between both sampling techniques; (2) ecological generalists, which dominated the data analysis, were equally collected in high abundance by both sampling techniques; (3) species that were missed by one sampling technique tended to be rare and, therefore, not influential in the data analysis.

Sampling effort

Gross differences between prairie and boreal dytiscid communities were easily recognized, but finer scale differences within an ecozone or region could not be shown. Sampling effort may have been to blame for the lack of resolution. Since, more intensive sampling would lead to more specimens collected per habitat and therefore greater statistical relevance. For example, Gundersen *et al.* (2002) recommended that, at least ten but preferably 20 bottle-traps, be used to sample a lentic habitat adequately. I sampled each pond with only four bottle-traps per month, which was not enough to collect an adequate number of dytiscids. An increase in the number of volume-samples was also thought to be necessary, especially to extract finer scale effects. Larson and House (1990) sampled at least 4 m^2 per bog pool per month and obtained significant results examining predatory pressure of odonate larvae on dytiscids. I sampled 1.1 m^2 of each pond per month and was not able to find evidence of predatory pressure. Dytiscid communities are influenced by many factors that may have contributed to their variation. This variation certainly would have obscured the effects of predation by odonates. Larson and House's bog pools were probably more homogeneous, varying only in size. However, additional sampling effort from volume-sampling would certainly have helped in differentiating the effects on dytiscid assemblages in my study.

Increased sampling effort also would have been beneficial in habitats that were characterized by low dytiscid abundance, such as in saline ponds. Although saline specialists were found, they often occurred in small numbers. Larson (1985) surveyed 11 saline ponds with an aquatic net and collected on average fewer than ten dytiscids per pond. These abundances were similar to those I obtained with volume-sampling and bottle-traps combined. More effort should have been directed to habitats that typically have few dytiscids, such as saline habitats.

Composition of dytiscid assemblages in relation to environmental factors

Several environmental factors influenced dytiscid communities across southern Manitoba. Macrophyte diversity was represented in the ordination biplots of all three data sets. The finding that aquatic vegetation influences macroinvertebrates such as predacious water beetles is consistent with the literature (Ranta 1985; Nilsson *et al.* 1994; Nilsson and Söderberg 1996; Heino 2000; Whiteman and Sites 2003). Low percentage cover of aquatic plants in Finnish ponds and lakes was responsible for low species richness of aquatic macroinvertebrates (Heino 2000). In an examination of various lentic habitats, Ranta (1985) found that ponds rich in aquatic vegetation had diverse communities of aquatic beetles. The association between the abundance of aquatic vegetation and dytiscids could not be easily extrapolated from my study. Aquatic macrophyte richness rather than abundance varied in my study ponds. However, some of the saline and temporary ponds had limited abundances of aquatic vegetation and unique dytiscid communities. These ponds are best thought of as a separate set of ponds. They will be examined separately when discussing salinity and permanence.

Species diversity of aquatic vegetation and macroinvertebrate diversity have been positively correlated. Palmer (1981) found that several macroinvertebrate groups, including aquatic Coleoptera, were positively correlated with diversity in aquatic vegetation. Dytiscid communities in Swedish lakes increased in species richness and abundance with increasing aquatic vegetation diversity (Nilsson *et al.* 1994). Prairie ponds, with their relatively higher macrophyte diversity compared to boreal ponds, had a greater species richness and abundance of dytiscids.

The species composition of submerged vegetation influences macroinvertebrate communities. The composition of submerged vegetation influenced the dytiscid communities in my study ponds. Boreal ponds were generally dominated by *Chara* sp. Linnaeus (Charales: Characeae), whereas an assortment of aquatic macrophytes grew in prairie ponds. Therefore, the differences in species composition of dytiscids between prairie and boreal ponds could be partially attributed to the difference in species composition of submerged vegetation. Lakes with extensive *Chara* sp. beds were compared to those dominated by *Potamogeton* sp. in The Netherlands (van den Berg 1997). Densities of macroinvertebrates in *Chara* beds were significantly higher. Hanson (1990) found that different size classes of macroinvertebrates varied in accordance with vascular aquatic plant weedbeds or *Chara* beds. The labyrinth of *Chara* beds seems to be an ideal refuge for smaller dytiscids such as *H. sayi*, *D. convexa* and *U. granarius* and may explain the preference of these species for *Chara*-dominated, boreal ponds. Fairchild *et al.* (2003) assessed microhabitat influences on aquatic beetle assemblages. Some dytiscids were closely associated with submerged vegetation. For example, adult *Celina hubelli* Young and *D. convexa* and larvae of *Hydaticus* Leach and *Matus* spp. Aubé were positively associated with aquatic herbaceous plants (Fairchild *et al.* 2003).

Water pH accounted for some of the variation in dytiscid communities. Most of the species found associated with the low pH values were species typically found in boreal ponds. Alairie and Leclair (1988) examined dytiscid communities in three acidic (pH 3.9-4.3) and three non-acidic (pH 5.8-7.0) temporary habitats in southern Quebec. Many of the species that responded to low pH in my study ponds had a high frequency of occurrence in Alairie and Leclair's (1988) non-acidic ponds rather than their acidic ponds. This finding is not surprising considering the pH of my boreal ponds was never found to be less than neutral. Alairie and Leclair (1988) labeled 11 species as acidophilic, including *A. bifarius* and *H. rectus* Fall. In addition, *H. tristis* (Paykull) was thought to inhabit a wider pH range but preferred acidic waters. Interestingly, these species did not show a preference to pH whenever a significant pH gradient was established in the ordination analysis of my study. This finding could be a product of both the analysis and the ecology of these species. Fewer than ten individuals of any one of these species were collected in my study. Therefore, the habitat affinities of these species should be weighted accordingly. In addition, these species could have been responding to variables other than pH. Juliano (1991) examined the influence of pH on the abundance of various *Hydroporus* spp., including *H. tristis*, and found that pH was not the most important factor in organizing species assemblages.

Water conductivity and chlorophyll *a* density also influenced dytiscid communities. Prairie ponds were typically more conductive and had higher chlorophyll *a* densities than did boreal ponds. Conductivity was positively correlated (excluding saline ponds) with chlorophyll *a* density. Thus, chemical constituents elevating the conductivity values were assumed to be nutrients such as phosphorus and/or nitrogen. It was believed that prairie ponds were higher in such nutrients, which promoted algal growth. The prairie landscape is dominated by agricultural land that may contribute nutrients from runoff (Kantrud *et al.* 1989). Phytoplankton is known to respond quickly to pulses in nutrients, especially in shallow water bodies (Hann and Goldsborough 1997). The combination of these factors makes prairie ponds dynamic and productive. Prairie ponds had a significantly greater abundance of dytiscids than boreal ponds in my study. This result further supports the notion that prairie ponds are productive habitats.

Conductivity did not always correlate with chlorophyll *a* density. Prairie pond 12We (Cobbes Lake, eastside), near Baldur, had the highest conductivity value among all ponds. It also had the highest salinity (2.4 g l^{-1} Na^+) among the five ponds selected for further chemical analysis in the Baldur region. However, its chlorophyll *a* density was found to be average in comparison to the rest of the prairie ponds. Hammer *et al.* (1983) found that elevated salinity was detrimental to algal species diversity in Saskatchewan lakes. The lakes studied by Hammer *et al.* (1983) were more saline than the Baldur ponds in my study. Nevertheless, phytoplankton growth was probably limited, in at least pond 12We, due to high salinity. The remaining ponds examined in the Baldur region also had elevated salinities. Collectively the ponds at this locality formed a salinity gradient. Dytiscid communities decreased in species richness and abundance with increasing salinity. For example, 20 species (N= 208) of dytiscids were collected in the most saline pond (12We), whereas there were 29 species (N= 1483) collected in pond 14W, the least saline pond in the Baldur region. Pond 12We had two species, *H. salinarius* and *H. masculinus* not found in any other pond in my study. Both species are described as saline specialists (Larson *et al.* 2000). Lancaster and Scudder (1986), working in British Columbia, sampled lakes within a similar range of salinity as the Baldur ponds. They also found that species diversity of aquatic Coleoptera and Hemiptera decreased with increasing salinity. Timms and Hammer (1988) examined water beetle communities in saline Saskatchewan lakes. They found that macrophyte abundance was more predictive of water beetle species richness than salinity. Macrophyte diversity was also an important variable among my saline ponds. For example, 13We and 13Ww are adjacent ponds that were comparable in salinity, but four more species were collected in 13We. The difference in species richness was correlated to a difference in macrophyte diversity and abundance of emergent vegetation. Timms and Hammer (1988) arranged species of *Hygrotus* Stephens according to saline tolerance, from greatest to least tolerant. This ranking has *H. salinarius* > *H. tumidiventris* (Fall) > *H. impressopunctatus* = *H. patruelis* > *H. masculinus* > *H. canadensis* (Fall) > *H. sayi*. I found the following salinity tolerance for *Hygrotus* species, from greatest to least tolerant: *H. salinarius* = *H. masculinus* = *H. punctilineatus* > *H. tumidiventris* = *H. sayi* = *H. impressopunctatus* > *H. marklini* = *H. patruelis* = *H. turbidus* = *H. sellatus*. I took a more conservative approach in arranging the salinity tolerance of *Hygrotus* species, because of the limited number of individuals collected from my saline habitats.

Hydroperiod is known to be an important variable in the organization of dytiscid communities (Galewski 1971). I compared only ponds with stable hydroperiods, although a few ponds dried at some point during the study. These ponds provided an opportunity to compare permanent and temporary habitats.

Permanence was a major influencing variable in the ordination for bottle-trap collections in 2001. Pond 24W had an unstable hydroperiod and was the main outlier in the analysis. Many dytiscids have evolved strategies to cope with unstable hydroperiods. As a result, the species richness of temporary ponds may not be equivalent to those that are more permanent, but temporary habitats often have a unique community (Larson 1985). Larson (1985) collected 44 species in temporary grassland ponds compared to 79 species in permanent grassland ponds. He found that many of the species in temporary habitats were unique to this habitat. In my study, temporary ponds were among the most diverse habitats. Several species were found almost exclusively in my temporary ponds, including *A. bifarius, A. canadensis, A. punctulatus*, and *R. consimilis*.

The effect of predator guilds on dytiscid communities

Odonate larvae

Despite the use of a variety of analyses, there was no significant relationship between odonates and dytiscids. Larson and House (1990) examined the insect communities in bog pools of four size classes (<1, 1-10, 10-100, and >100 m^2) in Newfoundland. The species abundance of water beetles was negatively correlated ($r = -0.43$, $p = 0.01$) with pool area. This result was attributed to the high densities of odonate larvae found in larger pools. Larson (1990) re-examined the bog pool communities, and focused on odonate predation as it affected dytiscid community structure. He found that dytiscid densities were negatively correlated ($r = -0.39$, $p < 0.01$) with odonate density. Secondly, in examining the gut contents of the five most abundant species of odonates in bog pools, dytiscids were found in individuals of all five species. In these ponds odonates contribute a significant predatory pressure on dytiscids.

I found no significant relationship between pond area, and dytiscid or odonate densities. Larson (1990) hypothesized that habitat stability was a contributing factor in limiting odonate larvae to large pools, so small pools provided a refuge for dytiscids. My ponds fit into the latter half of Larson's (1990) size classes (10-100 m^2 and >100 m^2). If habitat stability is influencing odonate and dytiscid densities, then these differences should be less apparent when examining relatively permanent habitats such as the ones sampled in my study. This would explain why a relationship between pond area, and odonate or dytiscid density could not be found.

Densities of dytiscids and odonates were not correlated with pond size, but both groups varied between prairie and boreal ecozones. In boreal ponds, odonate densities averaged 74.8/m^2 compared to 32.8/m^2 in prairie ponds and this difference was significant ($t = 4.2$, $df = 26.1$, $p<0.0002$). Dytiscid densities were 26/m^2 in boreal ponds, and 45.2 /m^2 in prairie ponds, but this difference was not significant ($t = -1.6.2$, $df = 26.4$, $p<0.09$). Finally, there was no significant relationship between odonates and dytiscids in boreal and prairie ponds. Odonate densities in both my boreal and prairie ponds were similar to odonate densities in Larson's bog pools in size classes 1 - 10 m^2 and 10 - 100 m^2. Within these same size classes, Larson found dytiscid densities to be 23.8/m^2, and 5.1/m^2, respectively. My boreal ponds, although with fewer dytiscids (26/m^2) when compared to my prairie ponds (45.2 dytiscids /m^2), were still denser than Larson's bog pools when comparing these two size classes. My study ponds had a greater abundance of dytiscids than Larson's bog pools. This abundance in my prairie, and boreal ponds could have obscured any variation created from a predator-prey relationship between odonates, and dytiscids.

Fish

Temperate ponds are harsh habitats for vertebrates such as fish. Summer hypoxic conditions, winter kills, chemical gradients, unstable hydroperiods, and temperature extremes make ponds intolerable for many fish species (Zimmer *et al.* 2000; Laurich *et al.* 2003). Despite these environmental challenges, fathead minnows (*P. promelas*), and brook sticklebacks (*C. inconstans*) were found in almost all of the ponds that contained fish. However, sticklebacks were found in all of the saline ponds in the Baldur regional locality, whereas no fathead minnows were found there. Disparate tolerance to salinity may have contributed to this difference (Winn 1960). Between these two species, fathead minnows are said to have a greater influence on invertebrate communities (Zimmer et al. 2000). However, ponds that contained fish including fathead minnows could not be distinguished from fishless ponds based on dytiscid community assemblages.

Zimmer *et al.* (2000) examined invertebrate communities in prairie wetlands in Minnesota. Multivariate techniques were used to detect the differences between invertebrate communities within the context of several environmental variables. They focused on the presence or absence of fathead minnows. In wetlands inhabited by fatheads, Zimmer *et al.* (2000) reported reductions in abundance of all invertebrate taxa examined except Corixidae. However, they felt that reductions in abundance of predatory insects such as dytiscid larvae and adults were not because of predation, but rather were due to competition for food resources. Indirect factors such as competition that affect communities are often more subtle than the direct affects of predation, and thus are often difficult to measure (Morin *et al.* 1988). This could explain why the influence of fish, such as fathead minnows and brook sticklebacks, was not realized in my study. In addition, my ponds that contained fish were often influenced by strong environmental factors that may have been more important in influencing dytiscid communities. For example, all ponds in the Baldur regional locality had brook sticklebacks in varying abundances. The salinity gradient among these ponds and the factors associated with salinity seemed to have a greater influence on the dytiscid communities.

A number of ponds contained fish known to consume dytiscids (Wilson 1923; Price 1963; Soupir *et al.* 2000); however, a predatory effect was not apparent. Rainbow trout, central mudminnow, yellow perch, and northern pike were found in some combination among four ponds including: 3E, 16E, 19E, and 18W. It was expected that the boreal ponds (3E, 16E, and 19E), which contained predatory fish would be closely associated in the RDA, but this was not the case. Boreal ponds were generally low in dytiscid abundances, independent from fish-presence, when compared to prairie ponds. Due to the limited numbers of dytiscids collected, variation caused by predation may have gone undetected.

Tiger salamanders

Tiger salamanders are a common inhabitant of prairie ponds (Deutschman and Peterka 1988; Euliss *et al.* 1999). Therefore it was not surprising that they were found in half of my prairie ponds. In the absence of fish, tiger salamanders are thought to be keystone predators, exerting a strong predatory force on aquatic invertebrate communities (Holomuzki *et al.* 1994). However, the potential influence of tiger salamanders on dytiscid communities in my prairie ponds could not be detected. Low densities of tiger salamanders within ponds was thought to be the principal reason that salamanders were not found to be influential.

Holomuzki *et al.* (1994) examined the effects of tiger salamander predation in experimental enclosures and study ponds. Top-down patterns of trophic control were evident in natural and experimental habitats. Predation by tiger salamanders was found to be more apparent in the enclosures, perhaps because of the limited selection of macroinvertebrates available to salamanders, whereas natural ponds were more diverse, and thus predation effects on any one taxon were reduced. The densities of salamanders in the natural ponds ranged from 2 to 61 per m^2, and five salamanders were confined in the 1.5 m^2 enclosures. In either case, salamander densities were higher than in my study ponds. In my study salamanders were collected using a 50 meter seine net. On average, in ponds that contained salamanders, one salamander was caught per seining. Assuming that all the salamanders were captured within the netted area, this would translate to a density of one salamander for every 201 m^2. This estimate is consistent with underwater observations while snorkelling. Salamanders in my study ponds were probably at densities far too low to be influential on dytiscid communities.

Despite these results, it would be interesting to re-examine the influence that tiger salamanders undoubtedly have at higher densities. In North Dakota lakes, tiger salamander populations may be reach densities of 5000 salamanders per ha^{-1}. It should be noted that such densities probably represent extremes rather than typical occurrences. In prairie ponds in Manitoba, Benoy *et al.* (2002) found that tiger salamander densities ranged from 6.3/ha to 306.3/ha. At the higher end of this range, it would be expected that the predatory pressure exerted by tiger salamanders on invertebrate communities would be significant.

Prairie and boreal ponds in southern Manitoba

Prairie ponds examined in this study were alkaline, as defined by Cowardin *et al.* (1979) (i.e., the pH is generally greater than 7.4). The specific conductance levels of prairie ponds ranged from 700 to 10572 µS/cm, although most ponds were closer to 1000 µS/cm. This range resembles the findings of Barica (1978) who investigated eutrophic prairie lakes in Manitoba (220 – 12 070 µS/cm). Ponds in the Baldur locality are all at the extreme end of this specific conductance range (1218 – 10572 µS/cm). The pond with the highest specific conductance was Cobbes Lake (12We). The dissolved solid attributed to elevating specific conductance values within the ponds of this locality was sodium chloride. For example, Cobbes Lake's sodium concentration was 2350 mg/L in September, 2002.

According to the trophic classification proposed by Reckhow and Capra (1983), based on chlorophyll *a* concentrations (μg/L), the majority of prairie ponds examined were eutrophic, with a few being hypertrophic and even oligotrophic. Prairie ponds typically had a high diversity of aquatic macrophytes and most were completely bordered by emergent vegetation (excluding a few of the saline ponds).

The boreal and boreal plains ponds in this study contrasted with the prairie ponds in respect to some of the environmental variables measured. Boreal and boreal plains ponds had lower chlorophyll *a* concentrations than prairie ponds and most were classified as oligotrophic (Reckhow and Capra 1983). Macrophyte diversity was low in boreal/boreal plain ponds. Ponds were dominated by a single *Chara* sp. that densely covered the entire pond. Ponds were also well bordered with emergent vegetation, generally by *T. latifolia*. Boreal and boreal plains ponds were alkaline (as described by Cowardin *et al.* 1979) and had relatively consistent hydroperiods for both years of the study.

Dytiscid communities in prairie and boreal ponds

The southern portion of Manitoba is rich in species of predacious diving beetles. A total 74 species was collected along a latitudinal transect of the Province. This number of species is quite impressive for several reasons: (1) it represents almost half of the recorded species for the province (N=148, Larson *et al.* 2000; N=151, Shaverdo *et al.*

2002; plus one new provincial recorded during this study, thus N=152), (2) sites represented a narrow latitudinal extent (<26`) and (3) only lentic habitats were sampled. The species richness is a result of sampling in three ecozones. This observation reinforces the fact that ecozones are regions that are ecologically significant. Smaller ecological units such as ponds reside within an ecozone and share a unique combination of abiotic and biotic features (Wilken 1986). Sampling in various ecozones, therefore, increases the potential for collecting different species (Giller *et al.* 1994). The transition in species composition between ecozones can be very dramatic. McKillop (1985) found that the composition of aquatic gastropods in southeastern Manitoba changed significantly with geological substrate when crossing between Ordovician dolomite (96°) into Precambrian granite (95°). The change in geology affected the concentration of elements in the water, such as calcium, known to be important to the development of molluscs. Predacious diving beetles communities are also particular in their association with ecozones. Larson (1975) conducted a survey of the dytiscid fauna across the various faunal zones of Alberta. The assembly of prairie, boreal and Cordillera ecozones within this province, in part, were thought to have contributed to the species richness (N=156).

Cluster analysis and redundancy analyse (RDA) were used to examine the similarity of ponds based on their dytiscid communities. By both analyses, ponds within an ecozone were strongly affiliated. Was the segregation of ponds due to dytiscids that were specialized to a particular ecozone? Are collections of dytiscids from prairie or boreal ponds made up of ecozone specialists? The ten most commonly collected species in prairie ponds made up 84.2% of the total number of dytiscids collected from this ecozone. However, all ten of these species are considered ecological generalists according to Larson *et al.* (2000) and therefore found in many ecozones across their geographic range. The ten most abundant species collected in boreal ponds made up 87.4%. Similarly, most of these were also thought to be ecological generalists. However, four of these ten species were found in habitats typically associated with the boreal ecozone or boreal-like ecozones across their geographic range. These species include *D. convexa*, *H. farctus*, *G. liberus*, and *U. granarius* (Larson *et al.* 2000). Prairie ponds may favour dytiscids that are ecological generalists in comparison to boreal ponds, which have some ecological specialists.

Euliss *et al.* (1999) reviewed the aquatic invertebrates of wetlands in the prairie pothole region (PPR), a belt stretching across the prairie ecozone. Dynamic environmental conditions of this region produced wetlands with varying salinities and/or unstable hydroperiods. Such conditions were thought to inhibit specialists and favour ecological generalists capable of tolerating unfavourable conditions. The description of factors influencing water bodies within the PPR is consistent with the prairie ponds sampled in my study. My prairie ponds varied in specific conductance. A more detailed water analysis was done only for ponds in the Baldur locality, where salinity levels varied considerably among ponds. As for hydroperiod, many ponds adjacent to my study ponds desiccated at some point in the summer. In addition, one pond in 2001 and four ponds in 2002 had varying hydroperiods. Therefore, salinity, hydroperiod and other dynamic variables in my study ponds may have favoured ecological generalists, as expressed in the abundance of these widespread dytiscids in prairie pond samples. Boreal ponds, in contrast, had stable hydroperiods and did not fluctuate in any of the water chemical variables measured either through the year or among ponds. Therefore, boreal ponds may be stable enough in their hydroperiod and water chemistry to allow for specialization. Larson (1985) found a similar pattern among ecological specialists and generalists in his survey examining dytiscid communities among 312 sites across Alberta. Collection sites based on dytiscid occurrences assembled into 13 generalized habitats, including sphagnum bogs and permanent prairie ponds. Sphagnum bogs most resembled the boreal ponds in my study, based on environmental variables and species composition. Larson found that sphagnum bogs contained a distinct fauna made up of ecological specialists, whereas permanent prairie ponds were made up of species that were widespread.

Predacious diving beetles collected in prairie ponds may be generalists, though these ponds possessed a greater species richness and overall greater diversity than boreal ponds. This finding was also consistent with Larson (1985). Larson found that sphagnum bogs contained 57 species of dytiscids, compared with 79 species collected in permanent prairie ponds. In my study, boreal ponds produced a total of 48 species (43.8% similarity of fauna at species levels between Larson's sphagnum bogs and my boreal ponds) compared to 61 species (65.6% similarity of fauna at species levels between Larson's prairie ponds and my prairie ponds) found in prairie ponds. The number of prairie species collected in my ponds is probably closer to 58 (70.0% similarity), once species that occur only in extremely saline ponds (i.e. *Hygrotus salinarius* and *H. masculinus*) and temporary ponds (*Agabus bifarius*) are omitted. In addition, Larson's distribution of sphagnum bogs is not equivalent to my boreal ponds. Sphagnum bogs in Larson's study were surveyed along the entire latitudinal expanse of Alberta, whereas my study focused on boreal ponds in a much narrower north-south span. Species richness of most coleopteran groups increase with latitude (Campbell 1979). Consequently, Larson's account of species inhabiting boreal aquatic habitats was undoubtedly influenced by this latitudinal gradient. Despite these discrepancies, it is clear that the prairie ecozone accounts for a considerable portion of the Canadian fauna. Canada's total number of prairie dytiscids from all habitats is 93 species (Larson *et al.* 2000), despite the fact that this region accounts for less than 5% of the country's total area (Statistics Canada 2002).

Conclusions

Results of any research project are dependant on the precision, nature and quality of samples. In my study, bottle-traps and volume-sampling were effective techniques for collecting adult dytiscids. Collections of dytiscids using both techniques produced similar results about the factors that organize their communities. Although, bottle-traps tended to collect elusive, rare, or large species, whereas volume-sampling is better at collecting small species.

A number of environmental variables differed between prairie and boreal ponds. Pond characteristics that were predictive of dytiscid communities among and within ponds included macrophyte diversity, pH, water conductivity, chlorophyll *a* density, and pond permanence. Among these variables, macrophyte diversity was of particular importance in organizing dytiscid communities. In addition, saline ponds and ponds with unstable hydroperiods were both inhabited by unique communities of dytiscids. Some of the species found in these ponds were found in no other habitats examined.

Predatory guilds, odonate larvae, fishes, and tiger salamanders, differed between prairie and boreal ponds. Odonate larvae occurred in higher densities in boreal ponds than in prairie ponds, whereas, tiger salamanders were found only in prairie ponds. Dytiscid communities, however, did not vary with respect to variations in odonate larvae and tiger salamander abundances. Fathead minnows and brook sticklebacks were the two species most frequently found in ponds containing fish. Dytiscid communities could not be differentiated based on fish presence.

In southern Manitoba, predacious diving beetles in lentic habitats can be divided into two assemblages in accordance to two broad habitat types: boreal and prairie. Prairie ponds are harsh environments for aquatic insects, primarily because of their dynamic nature. Typically these ponds have salinity gradients, varying hydroperiods and may completely dry out. Dytiscids inhabiting these ponds, therefore, must be tolerant of a number of adverse conditions. As a result, dytiscid communities in prairie ponds are composed predominately of ecological generalists complemented by some saline specialists. Boreal ponds are more predictable habitats exhibiting moderate variation in environmental variables important to dytiscid communities. Boreal ponds, therefore, have dytiscid communities that tend to favour ecological specialists. Despite the potential harshness of their environments, prairie ponds have more dytiscid species than boreal ponds. Selected environmental factors also accounted for differences in diversity between prairie and boreal ponds.

Suggestions for future research

The community ecology of dytiscids and other aquatic invertebrate families deserves further research, especially in regions such as in southern Manitoba, which are highly impacted by various disturbances. Conservation efforts are underway to preserve prairie wetlands. Organizations such as Manitoba Conservation and Ducks Unlimited Canada are at the front lines of these operations. To support these efforts, research into the invertebrates of these wetlands is essential, since invertebrates functions as the building blocks of the faunal ecosystem. Fairchild *et al.* (2000) advocated the use of water beetles as wetland bioindicators for the following reasons: (1) their broad array of feeding guilds, which make them sensitive to changes in food resources, including primary consumers (e.g. Haliplidae, Curculionidae and Chrysomelidae), predators (e.g. Dytiscidae, larval Hydrophilidae), omnivores and detritivores (e.g. many Hydrophilidae), (2) their preference for microhabitats which makes them sensitive to habitat structure, especially in those water beetles that are pelagic and/or benthic either in the adult or larval stage, and (3) their wide range of body sizes which makes them suitable for a wide variety of food web interactions. Fairchild *et al.* (2000) suggested that for beetles and water beetles alike to be effective bioindicators, their community ecology requires more attention. I agree that more work needs to be done and I offer some suggestions into the areas that could be targeted.

In light of the results regarding dytiscid communities in prairie and boreal ecozones, it would be interesting to repeat my survey with another beetle family such as Hydrophilidae. Aquatic hydrophilids share many similarities to dytiscids in their biology and life history. The main difference between Hydrophilidae and Dytiscidae is that the former, as a family, includes algivores, detritivores, and predators (Fairchild *et al.* 2000). It would therefore be interesting to see whether their community ecology mimics that of dytiscids.

In the case of specific habitats deserving of further attention, saline habitats and their invertebrate community ecology deserves study. Dytiscid community ecology in saline habitats has been examined primarily as a function of salinity. However, the decrease in species richness from saline habitats is often not due to physiological limitations. Factors such as the absence of aquatic vegetation may limit dytiscids from certain saline habitats. Therefore, it would be interesting to survey habitats of varying salinity and also include an extensive sampling regime of additional variables that are important to dytiscid ecology such as aquatic vegetation.

I recommend that future researchers take some precautions in studying the effect of predator guilds on dytiscids. Simultaneously examining landscape differences and factors affecting an individual pond such as predator guilds is difficult. For example, landscape differences in pond habitats were thought to overshadow the effect of predation on dytiscid communities. Therefore, numerous replicate ponds should be chosen that vary in as few environmental factors, other than predator abundance, as possible (see Larson and House 1990). By doing so, the variation in dytiscid communities can be more easily accounted for by predatory pressure. Fathead minnows, brook sticklebacks and tiger salamanders are ecologically important species in prairie wetlands. All three species in some respects function as prey, predators and competitors, of predacious diving beetles.

Therefore, it would be interesting to determine the nature and extent of the effect of these guilds on the dytiscid fauna.

In addition, the interactions between tiger salamanders and predacious diving beetles would also be interesting to examine, particularly with members of the tribe Aciliini. The ecological role of larvae of *Graphoderus* and *Acilius* closely resembles that of larval tiger salamanders. These water beetles and salamanders are nocturnal, pelagic predators that inhabit the deeper portions of their aquatic habitats (Wilson 1923, Hilsenhoff 1987; Branch and Altig 1981). It would therefore be interesting to examine the trophic dynamic of these two predator guilds. Holomuzuki and Collins (1987) compared the ecological role of tiger salamanders with larval and adult *Dytiscus* spp. They concluded that these interactions were dynamic and complex due to the mutual exchange in predatory pressure depending on the life stage, size, and abundance of both salamanders, and water beetles.

LITERATURE CITED

Aiken, R. B., and R. E. Roughley. 1985. An effective trapping and marking method for aquatic beetles. *Proceeding of the Academy of Natural Sciences of Philadelphia* **137**: 5-7.

Alarie, Y., and R. LeClair, Jr. 1988. Water beetle records from shallow pools in southern Quebec (Coleoptera: Dytiscidae). *Coleopterists Bulletin* **42**: 353-358.

Allen, H. L. 1971. Primary productivity, chemo-organotrophy, and nutrimental interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecological Monographs*. **41**: 91-127.

Andersen, J. D., and R. E. Graham. 1967. Vertical migration and stratification of larval *Ambystoma*. *Copeia* **1967(2)**: 371-374.

Balfour-Browne, F. 1940. British water beetles. Volume I. London: The Ray Society.

Barica, J. 1978. Variability in ionic composition and phytoplankton biomass of saline eutrophic prairie lakes within a small geographic area. *Archiv für Hydrobiologie* **81**:304-326.

Branch, L. C., and R. Altig. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. *Copeia* **1981(4)**: 870-873.

Benke, A. C. 1978. Interactions among coexisting predators: a field experiment with dragonfly larvae. *Journal of Animal Ecology* **47**: 335-350.

Benke, A. S., and S. S. Benke. 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* **56**: 302-317.

Benoy, G. A., T. D. Nudds, and E. Dunlop. 2002. Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. *Hydrobiologia* **481**: 47-59.

Campbell, J. M. 1979. Coleoptera. in: Danks, H. V. (Editor). *Canada and its insect fauna. Memoirs of the Entomological Society of Canada* **108**: 357-387.

Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 681-692.

Collins, J. P., and J. R. Holomuzki. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). *Canadian Journal of Zoology* **62**: 168-174

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. pp. 460-490. *in* Cody, M.L., and J.M Diamond. (Editors). *Ecology and evolution of communities*. Cambridge: Belknap Press.

Conroy, J. C., and J. L. Kuhn. 1978. New annotated records of Odonata from the province of Manitoba with notes on their parasitism by larvae of water mites. *The Manitoba Entomologist* **11**: 27-40.

Corbet, P. S. 1979. Odonata. pp. 308-311 *in* Danks, H. V. (Editor), *Canada and its insect fauna. Memoirs of the Entomological Society of Canada* **108**: 1-573.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Office of Biological Service Rep. 31. Washington, D. C.: Department International.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**: 1802-1813.

Crumpton, W. G. 1989. Algae in northern prairie wetlands. pp. 188-203 *in* A. G. Van der Valk (Editor), *Northern prairie wetlands*. Ames, IA: Iowa State University Press.

Cuppen, J. G. M. 1986. The influence of acidity and chlorinity on the distribution of *Hydroporus* species (Coleoptera, Dytiscidae) in the Netherlands. *Entomologica Basiliensia* **11**: 327-336.

Daborn, G. R. 1974. Biological features of an aestival pond in Western Canada. *Hydrobiologia* **44**: 287-299.

Deutschman, M. R., and J. J. Peterka. 1988. Secondary production of tiger salamanders (*Ambystoma tigrinum*) in three North Dakota Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 691-697.

Dobson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography* **15**: 131-137.

Dobson, S. I., and R. S. Dobson. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. *Copeia* **1971(4)**: 614-624.

Duffield, R. M., and C. H. Nelson. 1993. Seasonal changes in the stonefly (Plecoptera) component of the diet profile of the trout in Big Hunting Creek, Maryland, USA. *Aquatic Insects* **15**: 141-148.

Duffy, W. G. 1998. Population dynamics, production, and prey consumption of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 15-27.

Euliss, Jr., N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the prairie pothole region: invertebrate species composition, ecology and management. pp. 471-514. *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger (Editors), *Invertebrates in freshwater wetlands of North America: ecology and management.* New York: John Wiley and Sons, Inc.

Fairchild, W. G., J., Cruz, and A. M., Faulds. 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. *Journal of the North American Benthological Society* **22**: 224-240.

Fedoruk, A. N. 1971. Freshwater fishes of Manitoba: checklist and keys. Manitoba: Department of Renewable Resources and Transportation Services, Manitoba, for Department of Mines, Resources & Environmental Management.

Frisbie, M. P., and W. A. Dunson. 1987 Sodium and water balance in larvae of the predaceous diving beetle, *Dytiscus verticalis*: an air-breather resistant to acid-induced sodium loss. *Comparative Biochemistry and Physiology* **89**: 409-414.

Galewski, K. 1971. A study on morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). *Polskie Pismo Entomogiczne* **41**: 487-702.

Gerald, T., J. Coldrey, and G. Benard. 1984. The pond. London: William Collins Sons and Co., Ltd.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* **65**: 455-468.

Giller, P. S., A. G. Hildrew, and D. Raffaelli. 1994. Aquatic ecology: scale, pattern and process. Oxford: Blackwell Scientific.

Gundersen, R., S. Sevec, and M. Waite. 2002. Wetland insect sampling techniques. *Occasional papers in Aquatic Biology St. Cloud State University* **5**: 1-33.

Hammer, U. T., J. Shamess, and R. C. Haynes. 1983. The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. *Hydrobiologia* **105**: 1-26.

Hammer, U. T. 1986. Saline ecosystems of the world. Monographiae Biologicae 59. Dordrecht, The Netherlands: Dr. W. Junk Publishers.

Hann, B. J., and L. G. 1997. Goldsborough. Responses of a prairie wetland to press and pulse additions of inorganic nitrogen and phosphorus: invertebrate community structure and interactions. *Archiv für Hydrobiologie* **140**: 169-194.

Hanson, J. M. 1990. Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. *Freshwater Biology* **24**: 481-491.

Hanson, J. M., and M. R. Riggs. 1995. Effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. *Wetlands* **15**. 167-175.

Heino, J. 2000. Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia* **418**: 229-242.

Hicks, B. 1994. Foregut contents of adult *Ilybius* Erichson (Coleoptera: Dytiscidae) from Newfoundland. *The Coleopterists Bulletin* **48**: 199-200.

Hilsenhoff, W. L. 1987. Effectiveness of bottle traps for collecting Dytiscidae (Coleoptera). *The Coleopterists Bulletin* **41**: 377-380.

Hilsenhoff, W. L. 1991. Comparison of bottle traps with a D-frame net for collecting adults and larvae of Dytiscidae and Hydrophilidae (Coleoptera). *The Coleopterists Bulletin* **45**: 143-146.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use of larval tiger salamanders. *Ecology* **67**: 737-748.

Holomuzki, J. R., and J. P. Collins. 1987. Trophic dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae), in lentic community. *Copeia* **1987(4)**: 949-957.

Holomuzki, J. R., J. P. Collins, and P. E. Brunkow. 1994. Trophic control of fishless ponds by tiger salamander larvae. *Oikos* **71**: 55-64.

Hughes, M. L., and J. R. Duncan. 2003. The dragonflies of Manitoba: an updated species list. *Blue Jay* **61**: 168-175.

Jacobsen, L., S. Berg, M. Broberg, N. N. Jepsen, and C. Skov. 2002. Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study. *Freshwater Biology* **47**: 2370-2379.

Jewell, M. E., and H. W. Brown. 1929. Studies on northern Michigan bog lakes. *Ecology* **10**: 427-475.

Jones, F. H. 1984. The dynamics of suspended algal populations in the lower Wye catchment. *Water Research* 18: 25-35.

Juliano, S. A. 1991. Changes in structure and composition of an assemblage of *Hydroporus* species (Coleoptera: Dytiscidae) along a pH gradient. *Freshwater Biology* **25**: 367-378.

Kantrud, H. A., J. B. Millar, and A. G. van der Valk. 1989. Vegetation of wetlands of the Prairie Pothole Region. pp. 132-187 *in* A. G. van der Valk (Editor), *Northern prairie wetlands*. Ames, IA: Iowa State University Press.

Kvålseth, T.O. 1991. Note on biological diversity, evenness, and homogeneity measures. *Oikos* **62**: 123-127.

LaBaugh, J. W. 1989. Chemical characteristics of water in northern prairie wetlands. pp. 56-90 *in* A. G. van der Valk (Editor*), Northern prairie wetlands*. Ames, IA: Iowa State University Press.

Lancaster, J. and G. G. E. Scudder. 1987. Aquatic Coleoptera and Hemiptera in some Canadian saline lakes: patterns in community structure. *Canadian Journal of Zoology* **65**: 1383-1390.

Larson, D. J. 1985. Structure in temperate predaceous diving beetle communities (Coleoptera: Dytiscidae). *Holarctic Ecology* **8**: 18-32.

Larson, D. J. 1990. Odonate predation as a factor influencing dytiscid beetle distribution and community structure. *Quaestiones Entomologicae* **26**: 151-162.

Larson, D.J., Y. Alarie, and R.E. Roughley. 2000. Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the fauna of Canada and Alaska. Ottawa, Ontario: NRC Research Press.

Larson, D. J., and M. H. Colbo. 1983. The aquatic insects: biogeographic considerations. pp. 593-677 *in* G. R. South (Editor). *Biogeography and Ecology of the Island of Newfoundland*. The Hague: Dr. W. Junk Publishers.

Larson, D. J., and N. L. House. 1990. Insect communities of Newfoundland bog pools with emphasis on the Odonata. *The Canadian Entomologist* **122**: 469-501.

Larson, D. W. 1968. The occurrence of neotenic salamanders, *Ambystoma tigrinum diaboli*, in Devils Lake, North Dakota. *Copeia* **(1968)3**: 620-621.

Laurich, L. M., K. D. Zimmer, M. G. Butler, and M. A. Hanson. 2003. Selectivity for zooplankton prey by fathead minnows and brook sticklebacks. *Wetlands* **23**: 416-422.

Leclair, R., Jr., Y. Alarie, and J. P. Bourassa. 1986. Prey choice in larval *Dytiscus harrisii* Kirby and *D. verticalis* Say (Coleoptera, Dytiscidae). *Entomologica Basiliensia* **11**: 337-342.

Louarn, H., and A. Cloarec. 1997. Insect predation on pike fry. *Journal of Fish Biology* **50**: 366-370.

MacKinney, G. 1941. Absorption of light by chlorophyll solutions. *Journal of Biological Chemistry* **140**: 315-322.

Mallory, M. L., P. J. Blancher, P. J., Weatherhead, and D. K. McNicol. 1994. Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia* **279/280**: 345-351.

Matta, J. F. 1983. Description of the larva of *Uvarus granarius* (Aubé) (Coleoptera: Dytiscidae) with a key to the Nearctic Hydroporinae larvae. *The Coleopterists Bulletin* **37**: 203 - 207.

McKillop, W. B. 1985.Distribution of aquatic gastropods across the Ordovician dolomite – Precambrian granite contact in southeastern Manitoba, Canada. *Canadian Journal of Zoology* **63**: 278-288.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* **71**: 83-98.

Morin, P. J., S. P. Lawler, and E. A. Johnson. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* **69**: 1401-1409.

Murkin, H. R. 1998. Freshwater functions and values of prairie wetlands. *Great Plains Research* **8**: 3-15.

Murkin, H. R., J.B. Pollard, M. P. Stainton, J. A. Boughen, and R. D. Titman. 1994. Nutrient addition experiments in wetlands of the Interlake region of Manitoba, Canada: periodic additions throughout the growing season. *Hydrobiologia* **279/280**: 483-493.

Neill, C., and J. C. Cornwell. 1992. Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. *Wetlands* **12**: 217-224.

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* **10**: 89-114.

Nilsson, A. N., J. Elmberg, and K. Sjöberg. 1994. Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography* **21**: 197-206.

Nilsson, A. N., and H. Söderberg. 1996. Abundance and species richness patterns of diving beetles (Coleoptera, Dytiscidae) from exposed and protected sites in 98 northern Swedish lakes. *Hydrobiologia* **321**: 83-88.

Norris, D. O. 1989. Seasonal changes in diet of paedogenetic tiger salamanders (*Ambystoma tigrinum mavortium*). *Journal of Herpetology* **23**: 87-89.

Olenick, R. J., and J. H. Gee. 1981. Tiger Salamanders (*Ambystoma tigrinum*) and stocked rainbow trout (*Salmo gairdneri*): potential competitors for food in Manitoba prairie pothole lakes. *The Canadian Field Naturalist* **95**: 129-132.

Palmer, M. 1981. Relationships between species richness of macrophytes and insects in some waters in the Norfolk Breckland. *Entomologist's Monthly Magazine* **117**: 35-46.

Paterson, C. G., and C. H. Fernando. 1969. The effect of winter drainage on reservoir benthic fauna. *Canadian Journal of Zoology* 47: 589-595.

Peckham, R. S., and Dineen C. F. 1957. Ecology of the central mudminnow *Umbra limi* (Kirtland). *The American Midland Naturalist* **58**: 222-231.

Peterka, 1989. Fishes in northern prairie wetlands. pp. 302-315 *in* A. G. van der Valk (Editor), *Northern prairie wetlands*. Ames, IA: Iowa State University Press.

Price, C., W. M. Tonn, and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. *Canadian Journal of Zoology* **69**: 2109-2115.

Price, J. W. 1963. A study of the food habits of some Lake Erie fish. *Bulletin of the Ohio Biological Survey New Series*. **2**:1-89.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in northern Alberta. *Canadian Journal of Zoology* **42**: 785-800.

Rabe, F. W., and F. Gibson. 1984. The effect of macrophyte removal on the distribution of selected invertebrates in a littoral environment. *Journal of Freshwater Ecology* **2**: 359-370.

Rahel, F. J., and J. W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. *Ecology* **75**: 1246-1253.

Ranta, E. 1985. Communities of water-beetles in different kinds of waters in Finland. *Proceedings of the Academy of Natural Sciences of Philadelphia* **137**: 33-45.

Rawson, D. S., and J. C. Moore. 1944. The saline lakes of Saskatchewan. *Canadian Journal of Forest Research* **22**: 141-201.

Reckhow, K. H., and S. C. Chapra. 1983. Engineering Approaches for Lake Management, Volume 1: Data Analysis and Empirical Modeling. Boston: Butterworth Publishers.

Reid, G. K. 1961. Ecology of Inland Waters and Estuaries. New York: Van Nostrand.

Reimold, R. J. 1994. Wetlands functions and values. pp. 55-78 *in* D. M. Kent (Editor) *Applied Wetlands Science and Technology*. Boca Raton, Florida: CRC Press.

Ribera, I., G. N. Foster, and W. V. Holt. 1997. Functional types of diving beetle (Coleoptera: Hygrobiidae and Dytiscidae), as identified by comparative swimming behaviour. *Biological Journal of the Linnean Society* **61**: 537-558.

Roughley, R. E., and D. J. Larson. 1991. Aquatic Coleoptera of springs in Canada. *Memoirs of the Entomological Society of Canada*. **155**:125-140.

Sandilands, K., B. J. Hann, and L.G. Goldsborough. 2000. The impact of nutrients and submersed macrophytes on invertebrates in a prairie wetland, Delta Marsh, Manitoba. *Archiv für Hydrobiologie* **148**: 441-45

Schalles, J. F., A. A. Gitelson, Y. Z. Yacobi, and A. E. Kroenke. 1998. Estimations of chlorophyll *a* from time series measurements of high spectral resolution reflectance in an eutrophic lake. *Journal of Phycology* **34**: 383-390.

Scudder, G. G. E. 1983. A review of factors governing the distribution of two closely related corixids in the saline lakes of British Columbia. *Hydrobiologia* **105**: 143-154.

Scudder, G. G. E. 1987. Aquatic and semiaquatic Hemiptera of peatlands and marshes of Canada. *Memoirs of the Entomological Society of Canada* **140**: 65-98.

Sharitz, R.S., and D.P. Batzer. 1999. An introduction to freshwater wetlands in North America and their invertebrates. pp. 1-22. *in* D. P. Batzer, R.B. Rader, S.A. Wissinger. *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. New York: John Wiley & Sons, Inc.

Shaverdo, H. V., R. E. Roughley, and T. Mousseau. 2002. New records of Dytiscidae (Insecta: Coleoptera) in Manitoba. *Proceedings of the Entomological Society of Manitoba* **58**: 8-9.

Shelford, V. E. 1918. Conditions of existence. pp. 19-54. *in* H. B. Ward, and G. C. Whipple (Editors) *Freshwater Biology*. New York: John Wiley & Sons, Inc.

Soupir, C. A., M. L. Brown, and L. W. Kallemeyn. 2000. Trophic ecology, largemouth bass and northern pike in allopatric and sympatric assemblages in northern boreal lakes. *Canadian Journal of Zoology* **78**: 1759-1766.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**: 337-365.

Sprules, W. G. 1972. Effects of size-selective predation and food competition of high altitude zooplankton communities. *Ecology* **53**: 375-386.

Statistics Canada. 2002. Canada year book 1999: the environment - the land [online]. Available from http://www.statcan.ca/english/kits/cyb1999/ecozone/art1.htm#section21

Stewart, K., and D. Watkinson. 2004. The freshwater fishes of Manitoba. Winnipeg: University of Manitoba Press.

Sutcliffe, D. W., and T. R. Carrick. 1973. Studies on mountain streams in the English Lake District. I. pH, calcium and the distribution of invertebrates in the River Duddon. *Freshwater Biology* **3**: 437-462.

terr Braak, C. J. F., and P. Šmilauer. 1998. CANOCO Reference Manual and User's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). New York: Microcomputer Power.

Timms, B. V., and U. T. Hammer. 1988. Water beetles of some saline lakes in Saskatchewan. *The Canadian Field-Naturalist* **102**: 246-250.

Thorp, J. H., and M. L. Cothran. 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. *Ecology* **65**: 1546-1555.

Tompkins, A. M., and J. H. Gee. 1983. Foraging behavior of brook sticklebacks, *Culaea inconstans* (Kirtland): optimization of time, space and diet. *Canadian Journal of Zoology* **61**: 2482-2490.

Tones, P. I. 1978. Osmoregulation in adults and larvae of *Hygrotus salinarius* Wallis (Coleoptera: Dytiscidae). *Comparative Biochemistry and Physiology* **60**: 247-250.

U.S. Geological Survey (USGS), Northern Prairie Wildlife Research Center 2003. Tiger Salamander *Ambystoma tigrinum* [online]. Available from http:// www.npwrc.usgs.gov/narcam/idguide/atigrin.htm

van den Berg, M. S., H. Coops, R. Noordhuis, J. van Schie, and J. Simons. 1997. Macroinvertebrate communities in relation to submerged vegetation in two *Chara*-dominated lakes. *Hydrobiologia* **342/343**: 143-150.

Walker, E. M. 1953. The Odonata of Canada and Alaska. Volume 1. Part I: General. Part II: The Zygoptera - damselflies. Toronto: University of Toronto Press.

Walker, E. M. 1958. The Odonata of Canada and Alaska. Volume 2. Part III: The Anisoptera - four families. Toronto: University of Toronto Press.

Walker, E. M. and P. S. Corbet. 1975. The Odonata of Canada and Alaska. Volume 3. Part III: The Anisoptera - three families. Toronto: University of Toronto Press.

Ward, J. V. 1992a. Marine, brackish, and inland salt waters. pp. 169-197. *in* J. V. Ward. *Aquatic Insect Ecology. Vol.1. Biology and Habitat.* New York: John Wiley & Sons, Inc.

Ward, J. V. 1992b. Evolution and adaptation. pp. 29-65. *in* J. V. Ward. *Aquatic Insect Ecology. Vol.1. Biology and Habitat.* New York: John Wiley & Sons, Inc.

Westfall, M. J., Jr., and K. J. Tennessen. 1996. Odonata. pp. 164-211. *in* Merritt, R. W. and K. W. Cummins. *An Introduction to the Aquatic Insects of North America.* 3rd edition. Iowa, Dubuque: Kendall/Hunt Publishing Company.

Whiteman, H. H., Wissinger, S. A., and A. J. Bohonak. 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum* nebulosum. *Canadian Journal of Zoology* **72**: 1780-1787.

Whiteman, N. K., and R. W. Sites. 2003. Lentic beetles of the Missouri prairie region: habitat and regional associations, with keys to the Hydradephaga. *Transactions of the American Entomological Society* **129**: 185-243.

Wilken, E. B. 1986. Terrestrial ecozones of Canada. Ecological land classifications, Series No. 19. Hull, Quebec: Environment Canada.

Wilson, C. B. 1920. Dragonflies and damselflies in relation to pondfish culture, with a list of those near Fairport, Iowa. *Bulletin of the Unites States Bureau of Fisheries, Washington* **36**: 231-345.

Wilson, C. B. 1923. Water beetles in relation to pondfish culture, with life histories of those found in fishponds at Fairport, Iowa. *Bulletin of the U.S. Bureau of Fisheries* (1923-1924), **39** (# 953): 231-345.

Winn, H. E. 1960. Biology of the brook stickleback *Eucalia inconstans* (Kirtland). *The American Midland Naturalist* **63**: 424-437.

Winter, T. C. 1989, Hydrological studies of wetlands in the northern prairie. pp. 16–54. *in* A. G. van der Valk (Editor) *Northern Prairie Wetlands*. Ames, IA: Iowa State University Press.

Wissinger, S. A. 1989. Seasonal variation in the intensity of competition and predation among dragonfly larvae. *Ecology* **70**: 1017-1027.

Wissinger, S. A., J. B. Bohonak, H. H. Whiteman, and W. S. Brown. 1999. Subalpine wetlands in Colorado: habitat permanence, salamander predation, and invertebrate communities. pp. 757-790. *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger (Editors), *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, Inc.

Zaret, T. M. 1980. Predation and freshwater communities. New Haven, Connecticut: Yale University Press.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries of Aquatic Sciences* **57**: 76-85.

Zimmer, K. D., M. A. Hanson, M. G. Butler, and W. G. Duffy. 2001. Size distribution of aquatic invertebrates in two prairie wetlands, with and without fish, with implications for community production. *Freshwater Biology* **46**: 1373-1386.

Zoltai, S. C., and D. H. Vitt. 1995. Canadian wetlands: environmental gradients and classification. *Vegetatio* **118**: 131-137.

Appendix I: Total numbers of dytiscids (Coleoptera: Dytiscidae) collected using volume-sampling for each pond in 2001. Ponds designations as in Table 1 and arranged east to west.

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Laccophilus biguttatus Kirby	0	0	0	1	0	0	0	0	0	0	0	16	1	1	0	7	14	59	109	3	56	4	13	7	23	2	9	31	29	13	**398**
L. maculosus Say	0	3	7	8	0	5	0	0	18	9	4	46	5	4	0	6	28	14	11	0	16	3	5	2	43	4	0	0	6	3	**240**
Desmopachria convexa (Aubé)	7	1	1	14	18	11	2	14	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**60**
Liodessus cantralli (Young)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
L. fuscatus (Crotch)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
L. obscurellus (LeConte)	2	2	2	30	1	2	0	3	24	1	0	279	25	31	10	0	8	49	30	11	17	9	15	30	21	2	83	12	5	14	**712**
Uvarus granarius (Aubé)	0	4	0	6	23	1	0	11	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	**45**
Hygrotus acaroides (LeConte)	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**4**
H. farctus (LeConte)	2	0	0	5	2	8	0	6	6	6	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**49**
H. impressopunctatus (Schaller)	0	1	1	0	0	0	0	0	1	0	0	14	1	0	0	1	2	1	11	13	8	1	3	16	3	0	44	10	1	4	**134**
H. infuscatus (Sharp)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. laccophilinus (LeConte)	1	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
H. marklini (Gyllenhal)	0	0	0	0	0	0	0	0	1	0	0	4	2	0	0	0	0	1	10	13	8	5	1	10	2	0	0	0	0	0	**57**
H. masculinus (Crotch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. patruelis (LeConte)	0	1	0	1	0	0	0	0	0	0	0	12	2	4	0	1	6	0	25	2	1	1	2	15	23	3	2	0	0	1	**101**
H. picatus (Kirby)	1	0	1	5	0	1	0	0	0	1	0	0	0	3	0	0	0	0	0	0	1	5	0	0	0	4	0	0	0	0	**20**
H. punctilineatus (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. salinarius (Wallis)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. sayi Balfour-Browne	32	24	9	253	48	72	20	16	52	36	20	94	20	34	5	13	8	4	20	31	62	31	23	12	23	34	48	48	49	7	**1083**
H. sellatus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	1	0	5	6	0	0	1	5	0	3	**26**
H. tumidventris (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	**5**
H. turbidus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	14	1	0	0	0	0	0	1	1	2	2	0	10	0	0	17	1	0	1	**50**
Neoporus superioris (Balfour-Browne)	0	0	0	0	0	0	0	0	1	1	0	98	0	0	0	0	3	4	99	0	9	28	1	0	9	0	0	0	0	0	**253**
N. undulates (Say)	1	3	2	23	0	1	2	1	4	7	2	338	9	14	0	0	0	0	0	0	2	0	0	0	1	0	0	0	3	0	**407**
Hydroporus columbianus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	**4**
H. dentellus Fall	0	0	3	7	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**12**
H. fuscipennis Schaum	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0	1	0	3	22	3	31	0	0	0	2	30	2	0	2	**102**
H. larsoni Nilsson	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	1	6	0	0	0	0	35	2	0	0	**49**
H. notabilis LeConte	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	**5**
H. pervicinus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	**2**
H. rectus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
H. striola (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	**2**
H. tartaricus LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. tenebrosus LeConte	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	2	5	0	2	1	2	14	1	0	0	**33**
H. tristis (Paykull)	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Laccornis conoideus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	0	0	0	2	0	0	0	**9**
Hydrovatus pustulatus (Melsheimer)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Agabus ajax Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	15	5	0	0	1	0	22	2	**48**
A. ambiguous (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
A. antennatus Leech	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	3	0	4	23	12	35	10	1	0	0	25	32	94	27	**272**
A. anthracinus Mannerheim	0	1	1	0	2	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**
A. bifarius (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	**2**
A. canadensis Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
A. erichsoni Gemminger & Harold	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
A. phaeopterus (Kirby)	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	**6**
A. punctulatus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	**2**
Ilybius angustior (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	**5**
I. fraterculus (LeConte)	0	1	2	0	0	0	1	1	2	1	4	6	6	2	1	1	3	0	0	1	4	1	0	0	10	0	1	2	1	2	**50**
I. picipes (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
I. pleuriticus (LeConte)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
I. subaeneus (Erichson)	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	2	0	0	0	0	1	**10**
Colymbetes exaratus LeConte	0	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	1	1	0	4	0	5	0	4	2	5	1	**29**
C. sculptilis Harris	0	0	0	2	0	2	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**7**
Rhantus binotatus (Harris)	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
R. consimilis Motschulsky	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
R. sericans Sharp	1	0	0	1	0	1	0	0	4	1	0	4	3	8	19	7	8	4	22	13	14	6	41	24	49	13	2	7	9	19	**279**
R. sinuatus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
R. suturellus (Harris)	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
R. wallisi (Hatch)	0	0	0	2	2	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**8**

Appendix I: continued

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Coptotomus longulus LeConte	14	36	19	9	1	13	46	19	46	3	2	23	0	1	0	1	2	1	1	0	2	1	0	2	13	1	0	0	0	0	187
Dytiscus alaskanus Balfour-Browne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	1	0	4
D. circumcinctus Ahrens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. cordieri Aubé	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	3
D. dauricus Gebler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. harrisii Kirby	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D. hybridus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. verticalis Say	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydaticus aruspex Clark	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	7
H. piceus LeConte	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Acilius semisulcatus Aubé	6	1	1	3	2	5	0	0	0	0	6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
A. sylvanus Hilsenhoff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Graphoderus liberus (Say)	0	0	2	0	0	3	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
G. occidentalis Horn	0	0	1	0	0	0	0	0	1	0	0	1	2	2	0	0	2	0	3	0	0	1	4	0	2	0	4	0	0	0	22
G. perplexus Sharp	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	4	0	1	0	1	1	0	0	2	1	0	2	0	1	17
SUM	71	79	64	374	103	134	73	80	166	69	60	961	85	113	39	42	96	139	359	146	228	187	148	144	233	69	333	159	225	101	

Appendix II: Total numbers of dytiscids (Coleoptera: Dytiscidae) collected using bottle-trap sampling for each pond in 2001. Ponds designated as in Table 1 and arranged east to west.

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Laccophilus biguttatus Kirby	0	0	0	0	0	0	0	0	0	0	0	1	1	1	9	27	48	209	240	0	68	20	13	23	19	4	4	25	94	59	866
L. maculosus Say	0	0	5	1	1	0	0	2	38	1	1	0	13	3	5	15	45	21	21	2	17	4	2	13	29	2	2	9	13	3	268
Desmopachria convexa (Aubé)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Liodessus cantralli (Young)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. fuscatus (Crotch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. obscurellus (LeConte)	2	0	0	0	0	0	0	0	54	0	0	2	0	1	0	0	0	1	0	0	0	1	0	32	0	3	3	1	4	13	117
Uvarus granarius (Aubé)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrotus acaroides (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. farctus (LeConte)	0	0	0	0	0	2	0	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
H. impressopunctatus (Schaller)	0	0	0	0	0	0	0	0	2	0	0	2	3	3	2	1	2	0	0	15	1	1	0	13	0	4	6	5	2	1	63
H. infuscatus (Sharp)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	3
H. laccophilinus (LeConte)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H. marklini (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	3	1	0	5	0	0	1	0	7	0	1	0	0	1	0	24
H. masculinus (Crotch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H. patruelis (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	9	1	0	5	0	0	0	0	13	1	0	1	0	1	1	34
H. picatus (Kirby)	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	8
H. punctilineatus (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H. salinarius (Wallis)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. sayi Balfour-Browne	23	0	4	12	25	18	2	7	127	0	1	4	18	10	9	16	22	2	32	16	54	77	5	92	4	38	41	89	108	67	923
H. sellatus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	14	0	4	2	0	3	4	32
H. tumidventris (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
H. turbidus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	11	0	0	1	4	0	0	20
Neoporus superioris (Balfour-Browne)	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	6	14	91	0	5	13	0	2	1	0	0	0	0	0	134
N. undulates (Say)	1	0	2	1	0	0	0	0	4	0	0	2	5	6	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	26
Hydroporus columbianus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H. dentellus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. fuscipennis Schaum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2	1	0	0	0	0	0	4	0	0	0	9
H. larsoni Nilsson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	1	0	6
H. notabilis LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
H. pervicinus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. rectus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. striola (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. tartaricus LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. tenebrosus LeConte	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	0	0	0	0	0	6
H. tristis (Paykull)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccornis conoideus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Hydrovatus pustulatus (Melsheimer)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Agabus ajax Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	2	5	3	24	552	3	0	4	24	21	3	644
A. ambiguous (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. antennatus Leech	0	0	0	0	0	0	0	0	0	0	0	0	1	1	31	27	21	7	4	25	26	16	10	10	2	5	6	5	72	38	307
A. anthracinus Mannerheim	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	3	0	0	0	8
A. bifarius (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
A. canadensis Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
A. erichsoni Gemminger & Harold	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2
A. phaeopterus (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	4
A. punctulatus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Ilybius angustior (Gyllenhal)	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	7	1	2	0	2	0	2	5	0	0	1	23
I. fraterculus (LeConte)	0	0	1	0	0	0	0	0	3	0	2	3	12	0	8	3	6	2	1	9	6	2	16	19	13	4	3	14	19	28	174
I. picipes (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
I. pleuriticus (LeConte)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
I. subaeneus (Erichson)	0	0	0	0	0	1	0	0	7	0	0	0	2	0	2	1	0	1	3	2	9	0	2	0	3	0	1	2	8	1	45
Colymbetes exaratus LeConte	0	0	0	0	0	0	0	0	1	1	0	0	0	3	0	0	0	0	4	5	2	9	18	7	7	2	1	3	1	5	69
C. sculptilis Harris	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	5
Rhantus binotatus (Harris)	0	0	1	0	1	0	0	1	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
R. consimilis Motschulsky	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
R. sericans Sharp	0	0	0	0	0	3	0	0	2	1	0	2	10	13	59	29	55	31	40	35	23	1	132	66	67	41	13	63	28	58	772
R. sinuatus (LeConte)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
R. suturellus (Harris)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R. wallisi (Hatch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	4

Appendix II: continued

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Coptotomus longulus LeConte	8	5	5	0	1	8	11	5	43	4	0	9	1	1	2	1	3	2	1	0	2	0	2	0	8	0	0	1	0	0	123
Dytiscus alaskanus Balfour-Browne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	3	13	1	4	3	0	0	11	3	1	4	5	5	60
D. circumcinctus Ahrens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
D. cordieri Aubé	0	0	0	0	0	0	1	0	0	0	0	4	4	1	0	1	8	1	6	5	1	3	3	1	28	8	5	5	1	4	90
D. dauricus Gebler	1	0	0	0	0	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
D. harrisii Kirby	4	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
D. hybridus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. verticalis Say	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Hydaticus aruspex Clark	0	1	0	1	0	0	0	1	2	0	0	0	0	7	0	0	0	0	0	6	1	6	0	0	0	2	11	0	0	0	38
H. piceus LeConte	0	0	0	1	3	0	0	0	0	0	0	1	3	0	0	3	0	0	4	0	3	7	0	0	0	1	0	0	0	0	26
Acilius semisulcatus Aubé	0	2	5	15	11	15	7	1	21	4	3	2	0	0	0	0	0	0	1	0	3	0	0	0	1	0	2	0	1	0	94
A. sylvanus Hilsenhoff	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Graphoderus liberus (Say)	0	0	2	0	0	5	0	2	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	13
G. occidentalis Horn	0	0	3	0	1	0	0	0	0	0	0	0	8	9	0	0	1	3	5	1	6	19	8	14	6	0	18	9	0	11	122
G. perplexus Sharp	0	0	0	0	0	6	0	2	0	0	1	0	6	2	0	11	8	4	18	3	9	11	0	5	10	3	20	26	14	13	172
SUM	**43**	**9**	**30**	**32**	**47**	**62**	**22**	**24**	**318**	**12**	**9**	**36**	**98**	**64**	**137**	**154**	**233**	**306**	**497**	**145**	**253**	**205**	**237**	**906**	**213**	**131**	**161**	**291**	**400**	**316**	

Appendix III: Total number of dytiscids (Coleptera: Dytiscidae) collected using bottle-trap sampling for each pond in 2002. Ponds are designated as in Table 1 and arranged east to west.

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Laccophilus biguttatus Kirby	0	0	0	0	0	0	0	0	1	1	0	1	2	1	3	34	19	51	420	1	388	15	85	0	69	5	65	4	94	203	**1462**
L. maculosus Say	0	0	3	0	2	0	0	1	30	12	0	10	5	13	1	1	13	9	40	14	35	6	27	0	337	20	5	1	12	24	**621**
Desmopachria convexa (Aubé)	0	0	0	2	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	**12**
Liodessus cantralli (Young)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
L. fuscatus (Crotch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
L. obscurellus (LeConte)	0	1	0	1	0	0	0	0	3	0	0	0	0	8	0	0	4	0	1	2	2	0	11	0	0	0	6	31	4	0	**74**
Uvarus granarius (Aubé)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Hygrotus acaroides (LeConte)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
H. farctus (LeConte)	0	0	0	0	2	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**6**
H. impressopunctatus (Schaller)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	5	2	2	16	0	3	72	0	0	31	57	22	9	11	**235**
H. infuscatus (Sharp)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	**2**
H. laccophilinus (LeConte)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
H. marklini (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	4	1	10	2	32	0	1	3	6	3	6	4	**75**
H. masculinus (Crotch)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. patruelis (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	3	8	6	0	11	0	1	4	4	1	4	5	**52**
H. picatus (Kirby)	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	**7**
H. punctilineatus (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	**5**
H. salinarius (Wallis)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
H. sayi Balfour-Browne	0	1	1	10	7	9	2	0	43	1	4	7	6	65	1	0	125	1	26	20	191	24	109	0	11	38	231	49	30	55	**1067**
H. sellatus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	17	9	1	46	0	10	18	3	11	5	3	**125**
H. tumidventris (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	7	0	4	3	0	0	0	1	**18**
H. turbidus (LeConte)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	14	0	0	4	18	38	2	1	**81**
Neoporus superioris (Balfour-Browne)	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	1	4	6	68	0	164	37	18	0	14	0	0	0	0	1	**317**
N. undulates (Say)	0	1	0	1	0	0	0	1	1	0	0	3	4	8	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	**24**
Hydroporus columbianus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
H. dentellus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. fuscipennis Schaum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	0	0	0	0	5	1	0	**11**
H. larsoni Nilsson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
H. notabilis LeConte	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	0	1	0	3	0	0	0	**10**
H. pervicinus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	**3**
H. rectus Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. striola (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
H. tartaricus LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
H. tenebrosus LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	**2**
H. tristis (Paykull)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Laccornis conoideus (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Hydrovatus pustulatus (Melsheimer)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Agabus ajax Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	0	1	0	0	5	38	6	**71**
A. ambiguous (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
A. antennatus Leech	0	0	0	0	0	0	0	0	0	0	0	0	1	4	17	5	16	2	17	16	48	23	33	1	17	9	7	46	248	137	**647**
A. anthracinus Mannerheim	0	1	0	2	2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**10**
A. bifarius (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
A. canadensis Fall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	6	8	0	0	**18**
A. erichsoni Gemminger & Harold	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
A. phaeopterus (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**
A. punctulatus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0	1	0	**6**
Ilybius angustior (Gyllenhal)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	**2**
I. fraterculus (LeConte)	0	0	3	0	0	0	0	0	7	0	0	3	3	0	0	1	3	2	3	2	3	2	12	0	2	7	6	12	6	21	**98**
I. picipes (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	**2**
I. pleuriticus (LeConte)	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
I. subaeneus (Erichson)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	1	0	0	4	2	2	**16**
Colymbetes exaratus LeConte	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	5	0	1	0	2	0	2	0	5	1	0	2	4	1	**24**
C. sculptilis Harris	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	**6**
Rhantus binotatus (Harris)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
R. consimilis Motschulsky	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**2**
R. sericans Sharp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
R. sinuatus (LeConte)	0	0	0	0	2	0	0	0	0	0	0	2	3	33	2	5	49	17	22	65	53	6	161	0	81	50	34	128	113	102	**928**
R. suturellus (Harris)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
R. wallisi (Hatch)	0	0	0	0	3	3	0	0	3	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**13**

Appendix III: continued

	16E	19E	21E	8E	9E	12E	13E	14E	2E	3E	4E	2W	4W	5W	12We	12Ww	13We	13Ww	14W	18W	19W	20W	23W	24W	25Wn	25Ws	30W	31W	32W	103W	SUM
Coptotomus longulus LeConte	0	2	21	4	0	10	2	7	57	2	1	17	3	3	0	0	1	0	3	0	0	1	0	0	4	1	0	0	0	0	**139**
Dytiscus alaskanus Balfour-Browne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	3	3	2	0	10	24	0	0	1	1	1	0	0	0	**53**
D. circumcinctus Ahrens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
D. cordieri Aubé	2	0	1	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	**12**
D. dauricus Gebler	1	0	1	3	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**8**
D. harrisii Kirby	2	0	1	2	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**10**
D. hybridus Aubé	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
D. verticalis Say	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Hydaticus aruspex Clark	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	**7**
H. piceus LeConte	0	0	1	0	2	0	0	0	0	0	0	1	2	29	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	**39**
Acilius semisulcatus Aubé	4	1	2	18	0	7	2	4	3	1	0	3	0	7	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	**54**
A. sylvanus Hilsenhoff	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Graphoderus liberus (Say)	0	0	3	0	0	2	0	8	6	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	**23**
G. occidentalis Horn	0	0	0	0	0	0	0	0	0	0	0	1	2	10	0	0	0	0	1	1	5	2	7	0	0	2	10	3	1	2	**47**
G. perplexus Sharp	0	0	2	3	0	6	0	4	2	0	0	0	2	3	1	2	2	0	5	1	8	22	5	0	4	4	22	13	9	5	**126**
SUM	**10**	**8**	**40**	**47**	**24**	**43**	**11**	**28**	**167**	**17**	**9**	**54**	**35**	**209**	**32**	**58**	**258**	**93**	**627**	**167**	**944**	**176**	**694**	**1**	**567**	**206**	**494**	**396**	**690**	**584**	