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

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Michael Alperyn

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Factors Affecting the Community Ecology of Predacious Diving Beetles

(Coleoptera: Dytiscidae) in Boreal and Prairie Ponds Across Southern Manitoba

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

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Abstract

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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.

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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 cooccurrence 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 $\mu S\ cm^{-1}$ to as high as 472 000 $\mu S\ cm^{-1}$ (LaBaugh 1989). In a survey of Manitoban wetlands, Barica (1978) found conductivity to range from 220 to 12 070 $\mu S\ cm^{-1}$. 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 $\mu S\ cm^{-1}$), oligosaline (800 - 8000 $\mu S\ cm^{-1}$), mesosaline (8 000 – 30 000 $\mu S\ cm^{-1}$), polysaline (30 000 – 45 000 $\mu S\ cm^{1}$), eusaline (45 000 – 60 000 $\mu S\ cm^{-1}$) and hypersaline (>60 000 $\mu S\ cm^{-1}$).

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