THE INFLUENCE OF HABITAT STRUCTURE ON PEATLAND ODONATA AT LOCAL AND LANDSCAPE SPATIAL SCALES

by

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Abstract

Within the Gros Morne Greater Ecosystem, Newfoundland, I related the distribution of peatland Odonata to habitat measured at the spatial scales of the pool and landscape. I sampled odonate exuviae and larvae from 30 peatlands and determined habitat preferences at the scale of the bog pool for eight odonate species. For five taxa, I determined the effect of non-peatland habitat (forest, scrub, clearcut) and the amount of peatland (<20%, 25-45%, 50-70% of landscape) on their incidence using generalized linear models. Greater amounts of peatland within landscapes had positive effects on incidence of *Aeshna sitchensis*, *Enallagma* spp. and *Cordulia shurtleffi*, but negative effects on *Leucorrhinia hudsonica* and *Somatochlora septentrionalis*. Forest surrounding peatland had a positive effect on *C. shurtleffi* incidence but negative effects on *L. hudsonica* and *Enallagma* spp. I explain these patterns using knowledge of species' life histories and movement behaviours, and surmise how these are influenced by landscape structure.

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General Introduction

Perspective

The present loss of biodiversity is a cause of great concern for many people, and if this destruction is to be addressed, one must discover its cause. It is generally believed that anthropogenic habitat change is the primary reason for the dramatic rate of biodiversity loss. If this is so, it is critical that we understand how habitat influences animal populations, at a variety of spatial scales.

In 1998, a large-scale project was initiated, which was aimed at examining the effect of habitat on animal distribution and movement. Due to its value as a study system, the project was set in the Gros Morne Greater Ecosystem in western Newfoundland. The region is naturally heterogeneous, composed of open peatlands and barrens, stunted scrubland, coniferous forest, and lakes and rivers. Additionally, large portions of the area just outside the borders of Gros Morne National Park are subject to clearcut logging. This has provided a special opportunity to examine how animals respond to naturally heterogeneous landscapes and to landscapes altered by human activity in the same system.

The project's approach has been to investigate the response of a variety of taxa, studying how animals with different life history traits react to natural and human-altered environments. Learning how the animals are distributed in different landscapes has been the first important step in the project, to be followed by more explicit studies of the movement of focus organisms. As part of this project, I attempted to answer how habitat at local and landscape scales influences the incidence and abundance of a collection of related animals, namely dragonflies and damselflies.

Dragonflies and damselflies (Insecta: Odonata) constitute a group of insects commonly found in many habitats, but are tightly linked to aquatic systems. For the first several months to several years, the length depending upon the environmental conditions and the species, the odonate lives underwater as a predatory larva, subsisting on other invertebrates and sometimes even small vertebrates. When sufficiently mature, the odonate crawls out of the water and emerges from its larval skin, flying off as a winged adult and leaving its shed larval skin, or exuviae, behind. The adult disperses from its natal waterbody and matures sexually during the subsequent few days, preying on other insects for sustenance. Upon maturation, the adult returns to a suitable waterbody where it mates and, if female, oviposits. Many species are restricted to the habitats and types of waterbodies that they occupy and must find suitable habitat in the landscape to reproduce successfully.

Odonates are ideal animals for studying the effects of landscape structure. Firstly, species within the group exhibit different degrees of mobility, at a variety of spatial scales. Although they share similarities in life history, differences exist between species with respect to behaviour, mobility and habitat associations. The general requirement for water in which to live as larvae readily identifies a required resource in the environment that can be monitored and measured to examine associations. Also, odonates use different habitats during their lives and are expected to be susceptible to landscape change.

Additionally, odonates are useful for these studies due to the ease with which they can be sampled. They are fairly easy to identify in the field, especially when captured and held in the hand. They are prevalent in the appropriate habitats and exist in sufficient numbers, so target sample sizes can be easily reached. Finally, sampling for exuviae has very limited if no effect on the animals themselves and does not require the collection of any living specimens, yet the exuviae can be identified and counted, and can provide useful information. For example, the presence of an exuviae is evidence for two things: a female chose the waterbody in which to oviposit, and the resulting larva matured and survived through to adult emergence.

The purpose of my study was threefold. Firstly, I wished to examine the natural history of the odonates of the Gros Morne Greater Ecosystem, acquiring knowledge of the composition of the odonate community in the region and learning what general habitat associations existed. Secondly, I intended to determine how a suite of peatland odonate species are influenced by habitat at a local scale, at the scale of the bog pool which they inhabit as larvae. Thirdly, I attempted to discover how peatland odonates are influenced by habitat structure at the landscape scale, examining the effect of surrounding habitat type and availability of peatland on the incidence and abundance of several common species. The knowledge I have acquired through this study can then be used for future research explicitly investigating how odonate movement is altered by landscape structure.

Chapter 1

Dragonflies and Damselflies (Odonata) of the Gros Morne Greater Ecosystem

With Notes on the Effect of Local Habitat Characteristics on Species Incidence in Peatlands

Chapter Abstract

Odonata were observed and collected from within Gros Morne National Park and the surrounding area in western Newfoundland, Canada, during the summers of 1998 and 1999. Thirty odonate species were noted during this survey, over three-quarters of the known fauna of the island of Newfoundland. Most species were found in peatland habitat, but a strong bias towards survey effort in this habitat is at least partly responsible. Within peatlands, distribution of some species was related to habitat variables such as pH, pool size and depth, although no one variable fully explained species incidence. Associations existed between some peatland species, even after controlling for the effects of local habitat variables. Collections and observations from this project are the first published for the Gros Morne Greater Ecosystem.

Introduction

Gros Morne National Park (GMNP) is situated in western Newfoundland, Canada (49°42'N, 57°45'W), at the southern end of the Long Range Mountains. Within its 1805 km^2 area there is a diversity of habitats, including rocky coastline, boreal forest, extensive peatlands and alpine rock barrens. Just outside its borders to the east exist two major river systems, the Main and Humber watersheds. The area east of the park also contains numerous bogs and fens, and boreal forest, dominated by balsam fir (*Abies balsamea*), spruce (*Picea* spp.) and white birch (*Betula papyrifera*).

The region's relief ranges from sea level at the coast up to 807 m at its highest point (Gros Morne) then slowly down to 200-300 m to the east of the Long Range. Climate is strongly affected by terrain, with higher elevations having mean temperatures 2-4 °C colder than lower elevations and with winds and precipitation differing markedly between the coast, the mountains and the east side of the Long Range (Canadian Parks Service 1990). For example, mean annual snowfall near the coast is 300-400 cm less than snowfall on the mountains (Canadian Parks Service 1990). Such range in climate influences the incidence and distribution of native plants and animals.

Despite the generally depauperate flora and fauna of Newfoundland, GMNP hosts many interesting species of plants and animals. There have been extensive surveys of the vegetation within GMNP, and the park boasts upwards of 70 rare plant taxa. Mammal diversity is low, but the Newfoundland populations of many species are considered distinct subspecies, including the endangered Newfoundland Pine Marten (*Martes americana atrata*). Invertebrates have received little attention, but provincial surveys of beetles and molluscs have included collections from the Gros Morne area (e.g. Balfour-Browne 1948, Lindroth 1955, LaRocque 1961).

The natural system found within GMNP is not restricted to its boundaries, but extends well beyond. Although humans recognize the border between the park and the surrounding region, other animals and plants do not. Individual animals move to access food and other resources, and may move freely across the park's boundary. This movement is not only influenced by fine scale features, such as local habitat structure or availability, but also by factors on a much larger scale (e.g. distribution of resources in the landscape).

Results from an ongoing study of forest dynamics (J.H.McCarthy, pers.comm.) indicate that many of the fir and spruce in the area east of the park are much older than elsewhere in the region, with some balsam fir reaching an age of over 250 years. Parts of this area (hereafter referred to as the "Main River area") are being clearcut for pulp. The magnitude of the effect this logging activity will have on the ecosystem dynamics of this previously untouched area is unknown.

A long-term project was initiated in 1998 aimed at answering questions related to the effects of landscape structure (the amount and configuration of different types of habitat at a large scale) on animals in the area encompassing GMNP and surrounding areas. This region, termed the Gros Morne Greater Ecosystem (see Grumbine 1990), does not have set boundaries, but for the purpose of this paper includes the Main River area and coastal areas within 10 km of the northern and southern park boundaries.

One component of this research is an examination of dragonfly and damselfly (odonate) populations in the Greater Ecosystem. Thirty-eight species of dragonflies and damselflies are reported from the island of Newfoundland (Larson and Colbo 1983, Brunelle 1997), compared to 86 species known for nearby Cape Breton Island, Nova Scotia (Brunelle 2000, Holder and Kingsley 2000). The isolation and latitude of Newfoundland have considerable influence on its depauperate odonate fauna (Larson and Colbo 1983); however, Newfoundland has received little attention by odonatists and this undoubtedly reflects on the low species richness. The purpose of this paper is to provide a contribution to the knowledge of Newfoundland's Odonata, building upon the few earlier efforts (e.g. Williamson 1906, Walker 1916, Cannings 1980). This chapter summarizes the results of two years of surveys and presents data on the natural history of odonate species recorded within the Gros Morne Greater Ecosystem.

Odonate Habitat

There have been innumerable studies examining the effects of forest fragmentation, the majority concentrating their efforts on anthropogenic fragmentation and habitat loss (Andrén 1994, Collinge 1996, Fahrig 1997, Harrison and Bruna 1999). In the Gros Morne Greater Ecosystem, habitat is naturally heterogeneous with a mixture of peatland, forest and open water. Indeed, naturally open habitat, such as bog and fen, can rival or exceed the amount of forest in some areas. Although odonates use terrestrial habitats for maturation, foraging and resting (Corbet 1999), much of their life is tightly linked to sources of freshwater for breeding and larval growth. Within the Gros Morne Greater Ecosystem, freshwater habitats include streams and rivers, oligotrophic lakes and peatlands.

Much of the peatland is ombrogenous bog, receiving water from precipitation, and soligenous fen, influenced by flowing surface water (Vitt 1994, Bridgham et al. 1996). Topogenous (stagnant water) and limnogenous (lake-influenced) fens are also present throughout the region. Typically, peatlands in the Greater Ecosystem are composed of solid peat dominated on the surface by *Sphagnum* spp., variably in association with rushes (Juncaceae), sedges (Cyperaceae), grasses (Poaceae) and other herbs (e.g. *Maianthemum trifolium*, *Sarracenia purpurea*). Discrete pools, or flarks (hereafter referred to as "bog pools"), are generally scattered throughout the open peatland, usually with steep or overhanging banks and muddy bottoms, up to 1.5 m deep. Besides sphagnum and herbs, the pools are often bordered by small shrubs (e.g. *Betula michauxii*, *Chamaedaphne calyculata*, *Empetrum nigrum*, *Kalmia angustifolia*, *Ledum groenlandicum*, *Rhododendron canadense*). Stunted black spruce (tuckamore) grows in patches within the open bog. These bogs and fens may be bordered by spruce-fir forest, tuckamore or open water. In the Main River area, clearcut habitat is also present adjacent to some peatlands, and although minimal mechanical disturbance affects these peatlands directly, there are undoubtedly indirect effects caused by the removal of adjacent forest (e.g. changes in pH, solar radiation, water level fluctuations). A more detailed discussion of the effects of landscape structure on odonate populations is presented in Chapter 2.

Although fish inhabit the lakes and rivers of the Greater Ecosystem, bog pools are almost always uninhabited by vertebrates, the exceptions being pools within fens frequently or infrequently connected to lakes or rivers during flooding events. Amphibians in Newfoundland are represented by only a few species of introduced frog, and in only one occasion was green frog (*Rana clamitans*) found in a bog pool, near the coast and far away from any other surveyed peatland. Birds that regularly prey upon odonate larvae, such as herons, Black Tern (*Chlidonias niger*) and Red-winged Blackbird (*Agelaius phoeniceus*) (Kennedy 1950), are essentially absent from the region. The absence of vertebrate predators in the bog pools of the Greater Ecosystem make them very simple systems that are ideal for examining relationships between habitat and odonate populations.

Methods

General Collections

Between 10 June and 10 August, 1998, a preliminary study was conducted that examined the feasibility of future research and gathered data on local odonate species incidence and ecology. Surveying was spread out across the Greater Ecosystem but was concentrated in the coastal lowlands within GMNP. In 1999, surveys were performed primarily in the Main River area, from 4 June to 10 August, but some observations were made during late May in coastal areas. Casual and opportunistic observations were made during both years. Adult specimens were caught using an aerial sweep net and either retained as vouchers or identified in the hand and released. For some species, field identification of adults without capture was possible, provided adequate views were obtained. Larvae were surveyed in bog pools using aquatic dip nets and exuviae were collected from the edge of rivers, lakes and pools. I noted the location, date and habitat for all specimens. Observations of natural history were noted whenever possible.

I identified specimens using Walker (1953), Walker (1958), Walker and Corbet (1975) and Westfall and May (1996). Vouchers have been deposited at Acadia University and the Nova Scotia Museum.

Peatland Associations

During 1999, observations or collections of exuviae and larvae in peatland were done systematically so as to examine the association between odonate incidence and habitat. I adopted a spatially nested study design with the greatest scale being that of a "landscape", which, for my purposes, was a 2 km x 2 km square. I chose fifteen landscapes using criteria outlined in Chapter 2, and within each landscape I randomly selected two peatlands. Ten pools were randomly selected within each peatland and were surveyed if they had an initial depth of at least 10 cm and a minimum surface area of 2 m^2.

At the beginning of the field season (5-17 June 1999), odonate larvae were sampled from a subset of pools: five pools within one peatland for each landscape. An aquatic dip net ('D' shape, 12" x 8", 500 micron netting) was used to sweep submerged vegetation and mud from 0.5 m from the bank towards the sampler, every two or four metres around the perimeter. Larvae were identified on site and returned to the study pool. A set of voucher specimens, taken from pools other than those included in the study design, was retained.

At all 300 study pools, searches for exuviae were made twice during June and July, 1999. Pools were surveyed for exuviae visually and tactually, searching along the pool's perimeter within a band roughly 2 m wide, centred on the discrete pool edge. Only the perimeter along one half of the pool, as estimated by area in the field, was sampled. The section of the pool to be sampled, either the northern, southern, eastern or western half, was chosen randomly, and the same perimeter was sampled during repeat visits. Exuviae were retained and identified in the lab. Additionally, some living and dead adults associated with exuviae were collected for identification purposes.

At each pool, local habitat covariates were measured or estimated: water depth, pH, pool surface area, bank slope, bottom substrate, plant species richness, amount of exposed mud and amount of submerged and emergent vegetation.

Maximum water depth was measured to the nearest centimetre using an incremented wooden stake: the maximum depth of three to five measurements was recorded. The pH of each pool was measured in the field using a portable pH meter (Oakton pH Testr 2 with automatic temperature compensation), accurate to within 0.1 units. For analysis, values were rounded to the nearest 0.5 units. The discrete bank surrounding all pools had either steep or gradually sloping banks, and each pool was scored as either *gradual* or *steep*. Most pool bottoms were generally flat but differed in their dominant substrate material. Pools were categorised as having one of the following substrates, with classifications based on preliminary pool surveys: *mud, mud/moss, mud/detritus*.

Since I believed vegetation to be an important influence on the distribution of odonate adults and larvae, several scores were made with respect to a pool's plant community. The incidence of all vascular plant species observed growing within a pool or along a pool's immediate edge (<10 cm from pool) was noted, as was the incidence of sphagnum either within or alongside a pool. Values of plant species richness were calculated and incorporated into analyses. The amount of plant cover (all species pooled) was also estimated for the extent of emergent and submerged vegetation across the area of the pool, and the amount of pool area with exposed mud.

Each sampled pool was georeferenced using real-time GPS accurate to within 0.5 m and was used to locate individual pools on aerial photos. Pool area was estimated to the nearest 0.3 m^2 using 1:12,500 aerial photos scanned at 600 dpi and a graphics program (Adobe Photoshop 4.0). The resolution at this scale gave a ratio of 0.282 m^2 to each pixel, and by tallying the total number of pixels within each pool, I was able to arrive at an estimate of area. Values were rounded to the nearest 10 m^2.

Frequency distributions for each pool characteristic are presented in Figure 1.1.

Analysis

Associations between habitat variables in sampled peatlands and species incidence, as measured by the presence of larvae and/or exuviae, were examined by fitting generalized linear models (McCullagh and Neldar 1991). Species incidence was set as the response variable and the nine habitat variables were fit as predictors. To enhance the fit of the models, depth and pool area were log-transformed and plant species richness was square-root transformed. I fit Quasi-likelihood models with binomial errors to compensate for under- and over-dispersed data and tested for significance of predictor variables using an F-test (McCullagh and Neldar 1991). I examined the contribution of each predictor to the fit of the model after controlling for the effect of all other predictors, evaluating the presence of a significant association between the habitat variable and species incidence with a maximum probability of Type I error set at 0.1.

Larson and House (1990) examined larval odonate density in an ombrotrophic bog in eastern Newfoundland, and found distinct communities of odonate species in their study pools, with some species showing specific dispositions toward different pool sizes. I wished to examine their findings to determine if the same dispositions existed at two study sites within the same region. To compare data from the two studies, I organized my available data in the same fashion as Larson and House (1990) and examined the dispositions of eight species for three classes of pool area (see Table 2). I fit a generalized model for each of eight species, with incidence as the response and pool size, study and the interaction of the two as predictors. These models were fit as quasi-likelihood models with binomial errors. A significant contribution to the fit of the model for each predictor was evaluated with a maximum probability of Type I error set at 0.1.

Finally, I sought to determine associations between odonate species in bog pools. For each of the eight commonest species, I first controlled for the effect of pool habitat by fitting all pool variables in a generalized linear model. This allowed me to make conservative statements about the ecological similarities between species that were not due to similarities in measured habitat associations. For consistency, I chose to perform an analysis similar to that described earlier, fitting the incidence of each of the other species as predictors in a quasi-likelihood model with binomial errors. Observed p-values were determined using an F-test (McCullagh and Neldar 1989). A significant contribution to the fit of the model by a predictor species indicated that its presence had an influence on the incidence of the response species. A positive coefficient value suggested the presence of the predictor species had a positive influence on the incidence of the response species, whereas a negative value indicated the opposite. To counter an increased Type I error with multiple tests, I determined significance for each test using Holm's (1979) procedure.

Additionally, I performed two cluster analyses to determine species association both before and after removing the effect of pool habitat. Based on species incidence, I used the Jaccard index to illustrate species association without controlling for the effect of pool habitat (Krebs 1989). Using residuals from generalized linear models fitting incidence against pool variables, I calculated "Manhattan" distances between species (Mathsoft 1998). The resulting matrices were used to classify species into groups using the hierarchical agglomeration algorithm (Ward 1963) and the average weighted link method (Mathsoft 1998). Associations apparent in the dendrograms of both analyses were compared visually.

Results and Discussion

Prior to 1998, only six species of Odonata had been collected in GMNP (P.M.Brunelle, pers. comm.). During 1998 and 1999, these six species and an additional 24 others, for a total of 30 species, were found within the Greater Ecosystem (Figure 1.2). Most species were found in peatland habitat, partially due to the prevalence of peatland over all other aquatic habitats in Newfoundland, and partially due to the bias of effort towards surveying in peatlands. One adult dragonfly (*Sympetrum* cf. *internum*) was observed but not captured and could only be identified in the field to subgenus (*Kalosympetrum* Carle 1993); it is included within the species total, as it was the only observed representative of this subgenus, but is excluded from Figure 1.2. Natural history observations of adult odonates, including reproductive behaviour, are presented in Appendix 1.

Adult Flight Periods

Due to the cold climate of the region, adults begin flying later in Newfoundland than in Nova Scotia. The earliest date adults were recorded flying was 31 May during the especially warm spring of 1999, a full two weeks earlier than the earliest record of 1998. Adults of ten species remained active and in flight until after the surveys were finished in early August. One species has a late flight period beginning in early August and is under-represented in my records. Adult flight periods, for 1998 and 1999 combined, are shown in Figure 1.2. Although roughly at the same latitude, different flight periods of some shared species were reported for a bog in Quebec (Hilton 1981), most notably that for *Leucorrhinia hudsonica*. Hilton (1981) recorded this species only during the month of June, whereas we recorded it from early June through to the end of July. Other species, such as *Lestes disjunctus*, *Aeshna interrupta* and *Cordulia shurtleffi*, had comparable flight periods.

Habitats

Rivers and streams are well represented in the Greater Ecosystem, but the odonate populations along these streams were small and relatively species poor. *Ophiogomphus colubrinus* is a lotic species that was found only along fast-flowing rivers and main tributaries in the Main River area, the single species most closely associated with this habitat. Several *Aeshna* species, including *A. eremita*, *A. interrupta*, *A. juncea* and *A. umbrosa*, were found foraging along rivers and streams but were by no means restricted to them. *Enallagma cyathigerum* was the only damselfly species found near streams in the Greater Ecosystem, but reached its highest abundance in peatlands. Finally, *Somatochlora minor* and *S. walshii* were found along streams flowing through fens, agreeing with Walker and Corbet (1975), although my observations of these species were few.

Lakes in the Greater Ecosystem also have fairly low odonate diversity, although greater than that of rivers and streams. *A. eremita*, *A. interrupta*, *A. juncea* and *A. umbrosa* were typically found patrolling the shoreline of oligotrophic lakes, as were *Somatochlora cingulata* and two species of *Enallagma*: *E. cyathigerum* and *E. boreale*. *Ischnura verticalis* was observed near marshy bays of larger lakes and *E. ebrium* was found in abundance at one lake near the coast that appeared to be rich in nutrients judging from the diversity and abundance of aquatic and semiaquatic flora.

The bogs and fens of the Greater Ecosystem had the greatest diversity of odonate species. Indeed, 24 species were found at bog pools, with an additional two species associated with streams in peatlands (see above). These species are listed in Figure 1.2 with notations. *Enallagma ebrium* was found patrolling bog pools on two (of five) occasions and *Ischnura verticalis* was found in peatlands three (of five) times. Although Walker (1953) stated this habitat association is uncommon for these two species, it may not be as unusual as once thought (Holder and Kingsley 2000). Other species recorded in this habitat are generally typical of bogs and fens.

Peatland Associations

Of the 24 species found at bog pools within the Greater Ecosystem, eight were recorded as larvae or exuviae at pools in sufficient numbers (>20 pools occupied) to enable me to make statements about their requirements or dispositions, if any, for different habitat variables.

Depth

Bog pools ranged in depth from a few centimetres to 1.5 m. The summer of 1999 was particularly dry and water levels dropped considerably; many pools dried up, although none of the study pools did so. Some species, such as *Aeshna sitchensis*, *Leucorrhinia hudsonica* and *Libellula quadrimaculata* (Cannings 1982, Valtonen 1986), are known to survive periods of drought where natal ponds dry up, and other species undoubtedly survive this type of event though no data are available.

In pools with standing water, three species were significantly influenced by depth (Table 1.1). *A. interrupta* and *C. shurtleffi* were found in pools deeper than 20 cm with a frequency greater than expected, and *A. sitchensis* was found with greater than expected frequency in pools less than 30 cm in depth.

Associated with depth was the presence of exposed mud within the confines of pools. Considered as a percentage of total pool area to the nearest tenth, the amount of exposed mud had an influence on the incidence of four odonate species (Table 1.1). *A. sitchensis*, a shallow pool species, was found more than expected in pools with 10% exposed mud or more, as was *S. septentrionalis*. *L. hudsonica* and *C. shurtleffi* exhibited an opposite response, being found with a frequency greater than expected in pools with less than 20% exposed mud.

Pool size

For comparison purposes, I present data for eight species in Table 1.2 organized in the same fashion as Larson and House (1990) alongside the available data from their study for which data are comparable. Although 0.1 was chosen as the maximum probability for Type I error, all significant results had a $p<0.001$ unless otherwise stated.

In both studies, *Lestes disjunctus* had a tendency to occur in larger pools (Table 1.2). For another six species, data between the two studies were incongruous. *Libellula quadrimaculata* did not have a preference for pool size in my study, but Larson and House (1990) found the species with a significantly greater frequency and indicated that the dragonfly preferred smaller pools ($p=0.093$) (Table 1.2). Larson and House (1990) also found three other species, *A. eremita*, *C. shurtleffi* and *S. septentrionalis*, significantly more frequently than in my study. These three species occurred more often in the two larger size classes in eastern Newfoundland (Larson and House 1990). However, in the Main River area, *A. eremita* occurred more than expected in the largest pools, *C. shurtleffi* showed no difference between the three size classes and *S. septentrionalis* occurred significantly more than expected in the two smaller size classes (Table 1.2). Larson and House (1990) indicated *A. sitchensis* occurred more in pools smaller than 10 m^2 in area, but my results indicate a broader disposition, for pools smaller than 100 m^2 (Table 1.2). In eastern Newfoundland, pools greater than 10 m^2 in area had more than expected *Leucorrhinia hudsonica* (Larson and House 1990). This species' response was different in the Main River area, occupying pools between 1 m^2 and 100 m^2 more than expected (Table 1.2). No immediate biological explanation arises to explain the discrepancies, but they do indicate that regional variation and differences in sampling design and intensity can alter our perception of ecological processes.

Pool size, to the nearest 10 m^2 instead of the above size classes, contributed significantly to the fit of models for three species (Table 1.1), all occupying pools with surface areas exceeding 10 m^2 more than expected. The tendency for *A. eremita*, *S. septentrionalis* and *L.*

hudsonica to occur more in larger pools agrees with the findings of Larson and House (1990).

Pool structure

Some odonate species show distinct preferences for specific bottom substrates in their larval habitat, especially burrowing Gomphidae (Huggins and DuBois 1982, Suhling 1994), so substrate type could potentially influence the distribution of certain peatland odonates. I tested for the influence of pool bottom substrate by comparing the incidence of species to the occurrence of three classes of pool substrate: mud, mud/detritus and mud/moss. No species showed a significant difference in incidence between any of the substrates after controlling for other habitat variables.

Pool banks were qualitatively classed as either steep or gradually sloping. *A. juncea*, *C. shurtleffi* and *L. hudsonica* had similar tendencies, found more in pools with steep banks than in those with gradual banks (Table 1.1). Although *S. septentrionalis* showed no significant disposition for a particular pool bank slope (p=0.167), Whitehouse (1941) found *S. septentrionalis* only at pools "...with level wet edges,..., not large muskeg pools, with firm peaty banks...." My results show they are not restricted to, or have a disposition for, pools with gradually sloping banks (e.g. present at 49 of 130 steep-banked pools).

pH

The acidity of natal water bodies may affect odonate distribution either directly (e.g. on larval physiology) or indirectly (e.g. incidence of predatory fish or prey species) (Corbet 1999). While there are some species that appear to be little affected by pH, there are others that exhibit different degrees of tolerance, restricted to waters either below or above a certain threshold (e.g. Pollard and Berrill 1992, Corbet 1999). Schmidt (1989, cited in Corbet 1999) postulated the absence of some odonate species from bog pools was due to their intolerance of a pH of 4.5, the approximate level at which damage to aquatic ecosystems can occur (Gorham et al. 1984). However, pH has been shown by some investigators to be relatively unimportant in predicting species incidence compared to other habitat variables, such as habitat structure (Cannings and Cannings 1994, Foster 1995).

In the bog pools of the Greater Ecosystem, odonates were present in pools within a wide range of pH, from 3.9 to 6.9 (Figure 1.3), the minimum and maximum pH values found in the study pools. Statistically speaking, only *L. hudsonica* showed a significant preference to pool water pH (Table 1.1). *L. hudsonica* was present in almost all pH classes for which pools existed (Figure 1.3), but was found with greater than expected frequency in pools with pH lower than 5.5. Since predatory fish were absent from all pools surveyed, the apparent disposition for acidic pools by *L. hudsonica* is not caused by an absence of vertebrate predators (see Corbet 1999), rather by some other force.

Six other species appeared to occupy pools within a restricted range of pH. *A. eremita*, *A. interrupta*, *C. shurtleffi* and *Libellula quadrimaculata* were not found in pools with pH above 6.3, and all but one *A. juncea* were found in pools with pH between 4.0 and 5.4 (Figure 1.3). Also, *L. quadrimaculata* was not found in pools with pH lower than 4.2 (Figure 1.3). These ranges generally agree with results from lake surveys in central Ontario (Pollard and Berrill 1992), although *C. shurtleffi* occupied lakes within a broader range pH in those lakes than in the present study.

Pool vegetation

When one considers the larvae of many odonate species rely on vegetation to hide themselves from potential predators or prey (Walker 1953, Wellborn and Robinson 1987), or to partition space to decrease intra- and interspecific competition (Baker and Dixon 1986), it should be expected that the influence of vegetation on the physical structure of bog pools has an effect on the odonate inhabitants. Vegetation structure may also alter the ability and decision-making of mating and ovipositing adults, offering cues for site suitability (Martens 1993) or substrate for endophytic oviposition (Waage 1987), which will have a direct effect on resulting larval populations within a water body. Some studies have already examined the effects of vegetation on odonate populations (e.g. Buchwald 1992, Sahlen 1999). Therefore, it seemed wise to explore possible relationships between odonate species incidence and the amount of submerged and emergent vegetation.

As a percentage of pool area estimated to the nearest 10%, submerged vegetation ranged from 10-100% while emergent vegetation ranged from 10-90%. Of the eight commonest odonates, amount of vegetation displayed influence on only one species (Table 1.3). Pools where up to a third of the area had submerged vegetation tended to host *L. hudsonica* more often. Amounts of submerged vegetation had no significant influence on other species, and no species appeared to be influenced by the amount of emergent vegetation. This is surprising considering the life history traits of some species, especially the *Aeshna* that oviposit endophytically and are considered claspers (*sensu* Corbet 1999) and would be expected to be influenced by the amount of vegetation.

Plant species richness

The number of plant species surrounding and inhabiting pools ranged from two to 14 species. Three odonates showed a relationship between incidence and plant species richness (Table 1.1), with incidence of *A. interrupta, C. shurtleffi* and *L. hudsonica* being greater than expected in pools hosting richer plant communities. Sahlen (1999) found a positive relationship between the number of aquatic plant species and the richness of dragonflies in boreal lakes, explaining the relationship as being direct, since greater diversity of plant species increases the diversity of plant structure and the chance that conditions for especially selective species will exist somewhere in the habitat. However, this relationship may not be purely causal. For example, a flush of nutrients into a fen could enhance conditions for both macrophytes and algae in pools, and larval odonate populations could be influenced by both a change in plant structure and a change in herbivorous prey levels reacting to increases in algae. Other measures of water chemistry, such as conductivity, may also be confounded with these effects (Cannings and Cannings 1987).

Landscape structure

There is an indication that landscape structure surrounding natal water bodies has an effect on the dynamics of odonate populations (e.g. Taylor and Merriam 1996, Rith-Najarian 1998, Conrad et al. 1999, Jonsen and Taylor 2000). Relationships between landscape-scale habitat variables and odonate species for which adequate data exists were examined also, but these results are presented in Chapter 2.

Species Interactions

Although microhabitat may be a major contribution to niche partitioning in odonates (Johnson and Crowley 1980), habitat features are not the only variables that affect odonate species incidence. Especially in the absence of vertebrate predators, larval odonates may wield a strong influence on the dynamics of pool inhabitants (Larson and House 1990). Inter- and intraspecific predation appears to be regular among larval odonates, especially when densities are high (e.g. Wissinger 1988, 1989a, 1989b), and larger odonates of either different species or the same species can greatly affect the presence of smaller larvae (Wissinger 1988, 1989a, 1989b, Larson and House 1990). Therefore, it is important to consider the incidence of larger odonate species when examining patterns of distribution of larval odonates.

Species associations based on species incidence and calculated Jaccard indices are illustrated in Figure 1.4. Two discrete species groups are apparent in the dendrogram. Firstly, *S. septentrionalis* and *L. hudsonica* are closely associated and together are associated with *A. sitchensis*. Secondly, *A. interrupta* and *C. shurtleffi* are closely associated and together are associated with *A. eremita*. The observed associations may be due to a tendency for species to occupy similar habitats, judging from the results of prior generalized linear models (Table 1.1). Both *S. septentrionalis* and *A. sitchensis* tend to occupy shallow pools (Walker 1958, Walker and Corbet 1975, Dunkle 2000), while both *L. hudsonica* and *S. septentrionalis* are found more frequently in pools greater than 10 m^2 (Table 1.1). *A. interrupta* and *C. shurtleffi* are similarly influenced by pool depth and plant species richness (Table 1.1), which may explain the association observed between these two species (Figure 1.4).

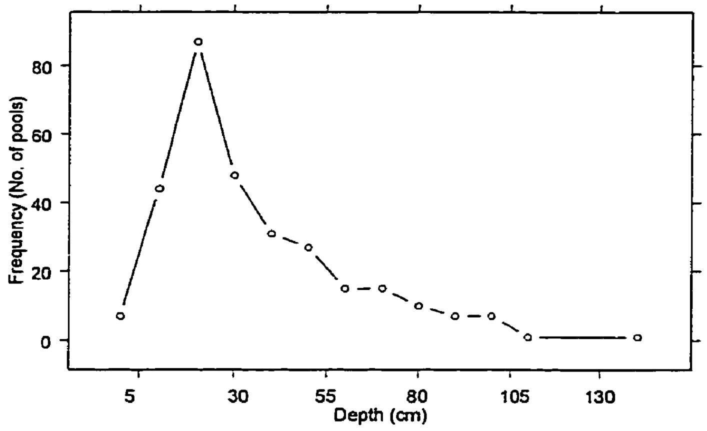
However, removing the effect of local habitat variables helped illuminate the relationships further. Only one group is apparent within the dendrogram, a group showing *A. eremita* and *A. juncea* as being closely associated, but which may be extended to include *L. quadrimaculata*, *A. interrupta* and *C. shurtleffi* (Figure 1.5). These are five species that appear to occupy the same types of pool habitat, judging from my analysis of habitat relationships. However, this association is surprising since Peters' (1998) speculated that *A. eremita*, *A. interrupta* and *A. juncea* are subject to intense interspecific larval competition in British Columbia. Their association may be explained by other variables not directly measured and not included in the models, such as habitat structure at a greater scale than the pool.

Following the procedures described earlier, I determined the effects of species incidence on other odonates using generalized linear models. No species analysed had a negative effect on any other species, although Larson and House (1990) and Van Buskirk (1992) report it may exist in two of the species, *A. juncea* and *Libellula quadrimaculata*. I deemed four positive relationships between odonate species to be statistically significant. After removing the effect of pool habitat, the presence of *S. septentrionalis* in a pool increased the likelihood *A. sitchensis* would be present ($p<0.001$), and the reciprocal relationship was significant also ($p=0.001$). The presence of *A. eremita* increased the likelihood *C. shurtleffi* would be present ($p<0.001$), and if *A. juncea* was present at a pool, it was likely *A. interrupta* would be present also ($p<0.001$). The two latter relationships were unidirectional. These results compare well with those from the cluster analysis and illustrate that species associations within these bog pools are present, even after controlling for the effects of pool habitat variables.

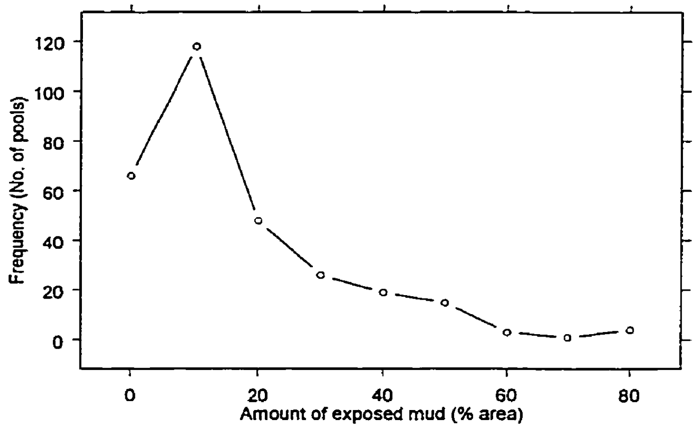
These data help clarify relationships between the habitat of bog pools and some common peatland odonates in western Newfoundland. The relative inaccessibility of boreal regions in northern Canada restrict the number of natural history observations of even common northern species, and these notes provide needed information on the natural history of Newfoundland's odonate fauna. The data on pool habitat associations I have provided also may be used to enhance future research examining the dynamics of peatland odonate populations.

Figure 1.1. Frequency distributions for nine pool characteristics included within models of odonate species incidence. All measurements are from 300 pools, except of pool surface area (N=265). a) depth, b), amount of exposed mud, c) pool surface area, d) pool bottom substrate, e) bank slope type, f) pH, g) amount of emergent vegetation, h) amount of submerged vegetation, i) plant species richness.

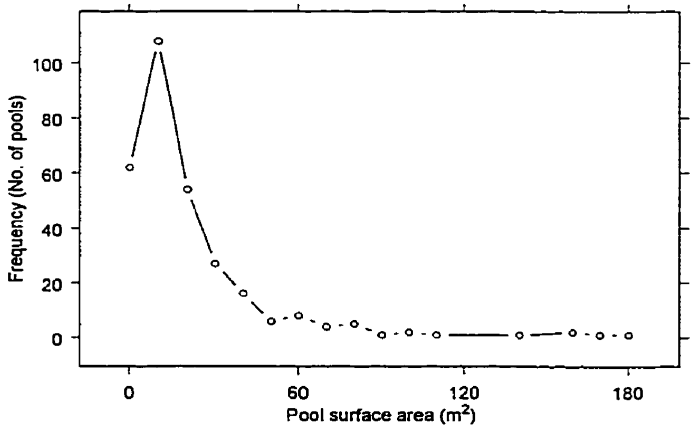
a)


Frequency (No. of pools)
0
20
40
60
80
5
30
55
80
105
130
Depth (cm)

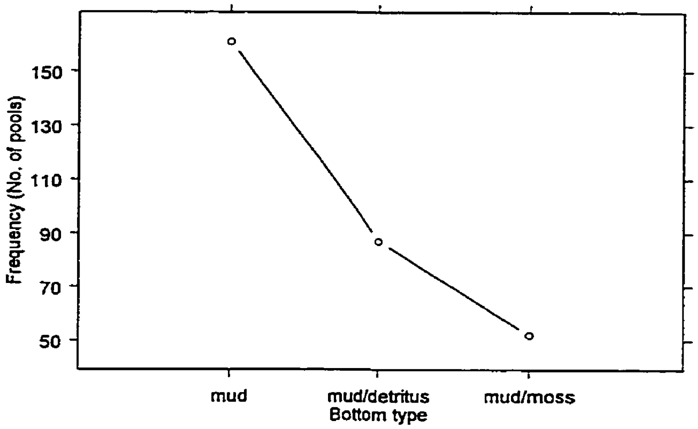
b)


Frequency (No. of pools)
0
20
40
60
80
100
120
0
20
40
60
80
Amount of exposed mud (% area)

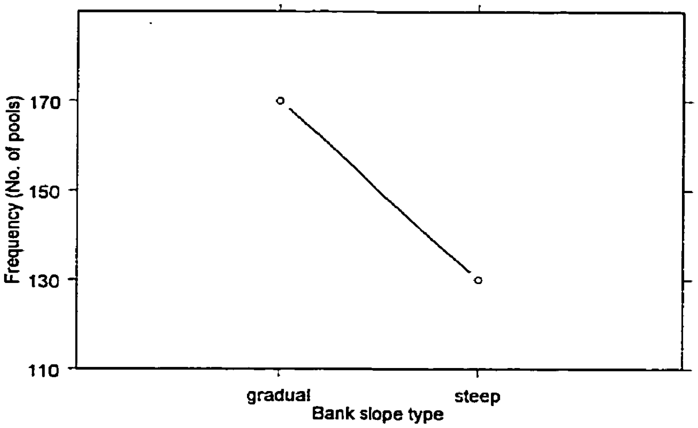
c)


Frequency (No. of pools)
0
20
40
60
80
100
0
60
120
180
Pool surface area (m²)

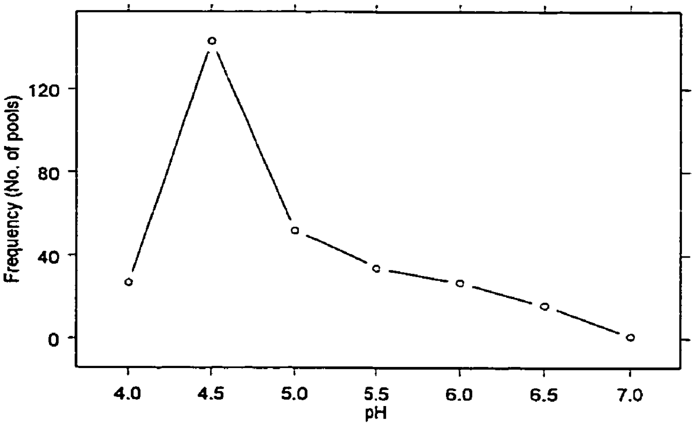
d)


Frequency (No. of pools)
150
130
110
90
70
50
mud
mud/detritus
mud/moss
Bottom type

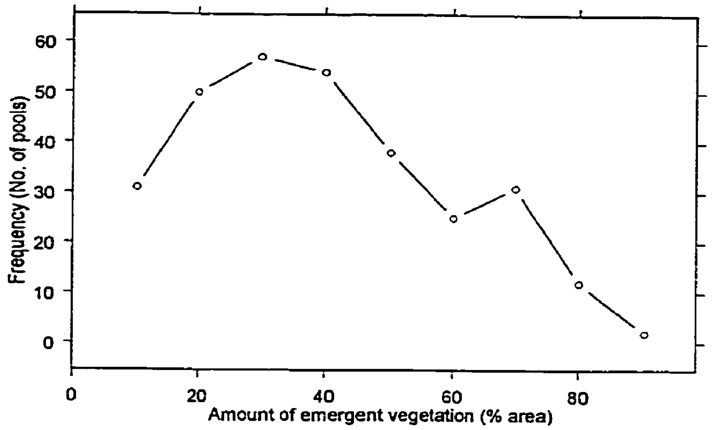
e)


Frequency (No. of pools)
170
150
130
110
gradual
steep
Bank slope type

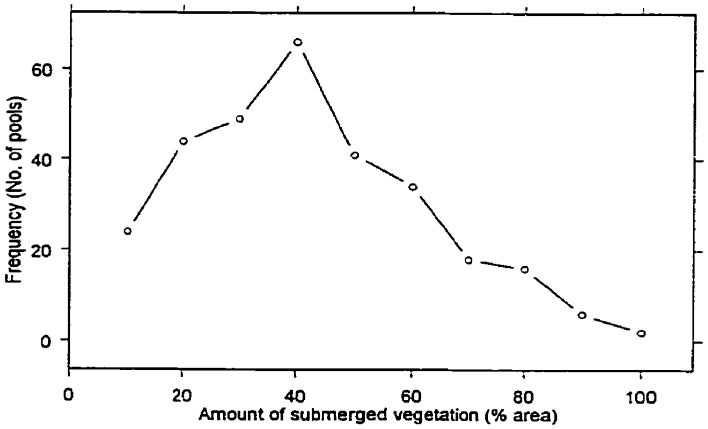
f)


Frequency (No. of pools)
120
80
40
0
4.0
4.5
5.0
5.5
6.0
6.5
7.0
pH

g)


Frequency (No. of pools)
0
10
20
30
40
50
60
0
20
40
60
80
Amount of emergent vegetation (% area)

h)


Frequency (No. of pools)
0
20
40
60
0
20
40
60
80
100
Amount of submerged vegetation (% area)

i)

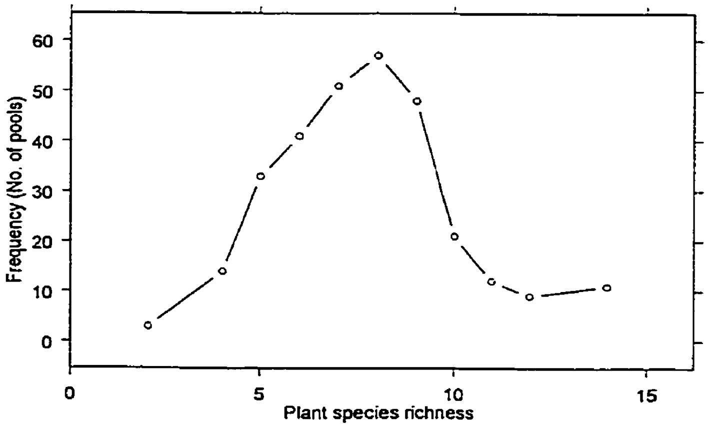

Frequency (No. of pools)
0
10
20
30
40
50
60
0
5
10
15
Plant species richness

Figure 1.2. Flight periods of odonate species in the Gros Morne Greater Ecosystem, based on observations of adults and exuviae. Numbers 1-4 within months refer to week. * denotes species associated with peatlands during surveys.

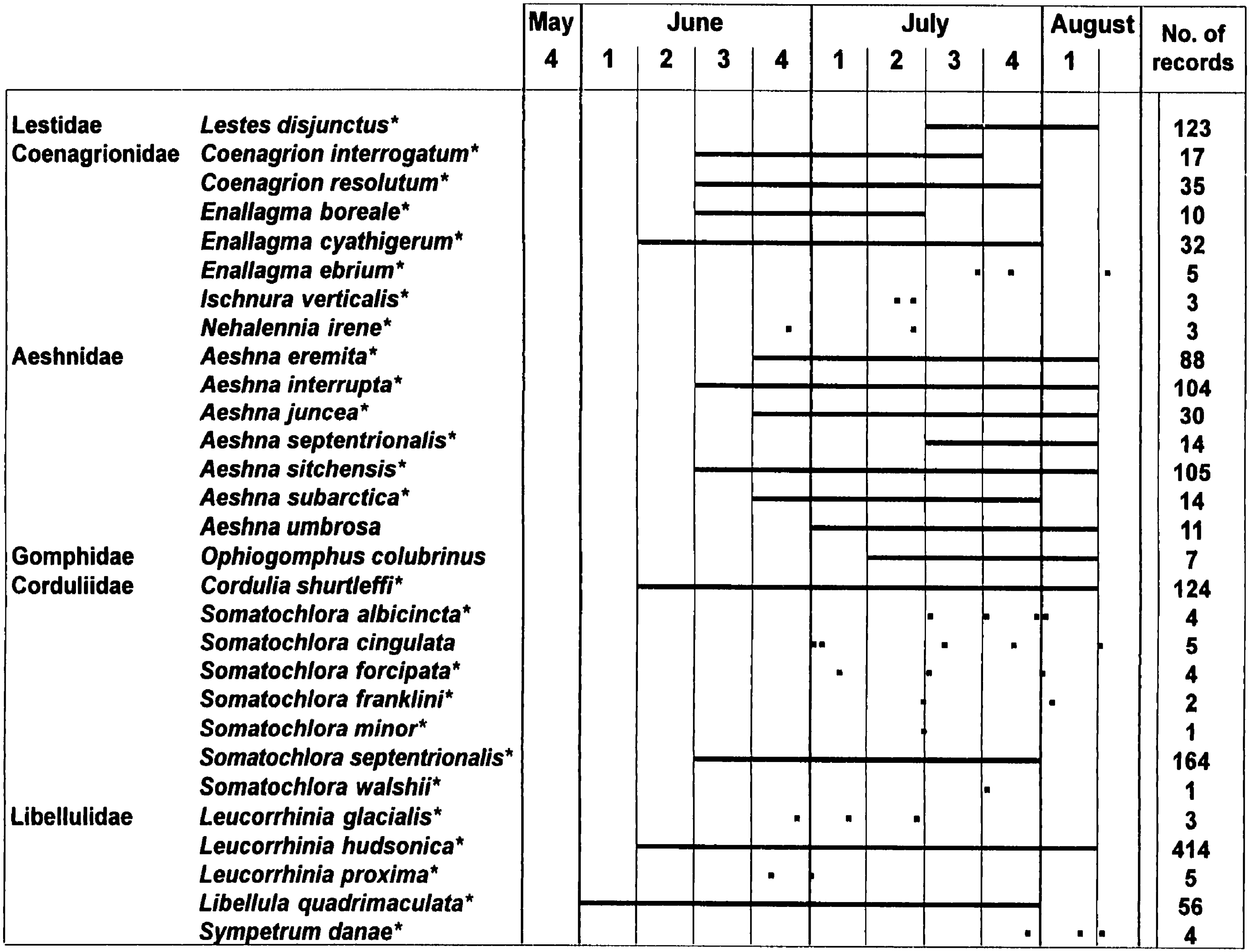

May
June
July
August
4
1
2
3
4
1
2
3
4
1
No. of records
Lestidae
Lestes disjunctus* 123
Coenagrionidae
Coenagrion interrogatum* 17
Coenagrion resolutum* 35
Enallagma boreale* 10
Enallagma cyathigerum* 32
Enallagma ebrium* 5
Ischnura verticalis* 3
Nehalennia irene* 3
Aeshnidae
Aeshna eremita* 88
Aeshna interrupta* 104
Aeshna juncea* 30
Aeshna septentrionalis* 14
Aeshna sitchensis* 105
Aeshna subarctica* 14
Aeshna umbrosa 11
Gomphidae
Ophiogomphus colubrinus 7
Corduliidae
Cordulia shurtleffi* 124
Somatochlora albicincta* 4
Somatochlora cingulata 5
Somatochlora forcipata* 4
Somatochlora franklini* 2
Somatochlora minor* 1
Somatochlora septentrionalis* 164
Somatochlora walshii* 1
Libellulidae
Leucorrhinia glacialis* 3
Leucorrhinia hudsonica* 414
Leucorrhinia proxima* 5
Libellula quadrimaculata* 56
Sympetrum danae* 4

Figure 1.3. Range of pool pH where odonate species were found.

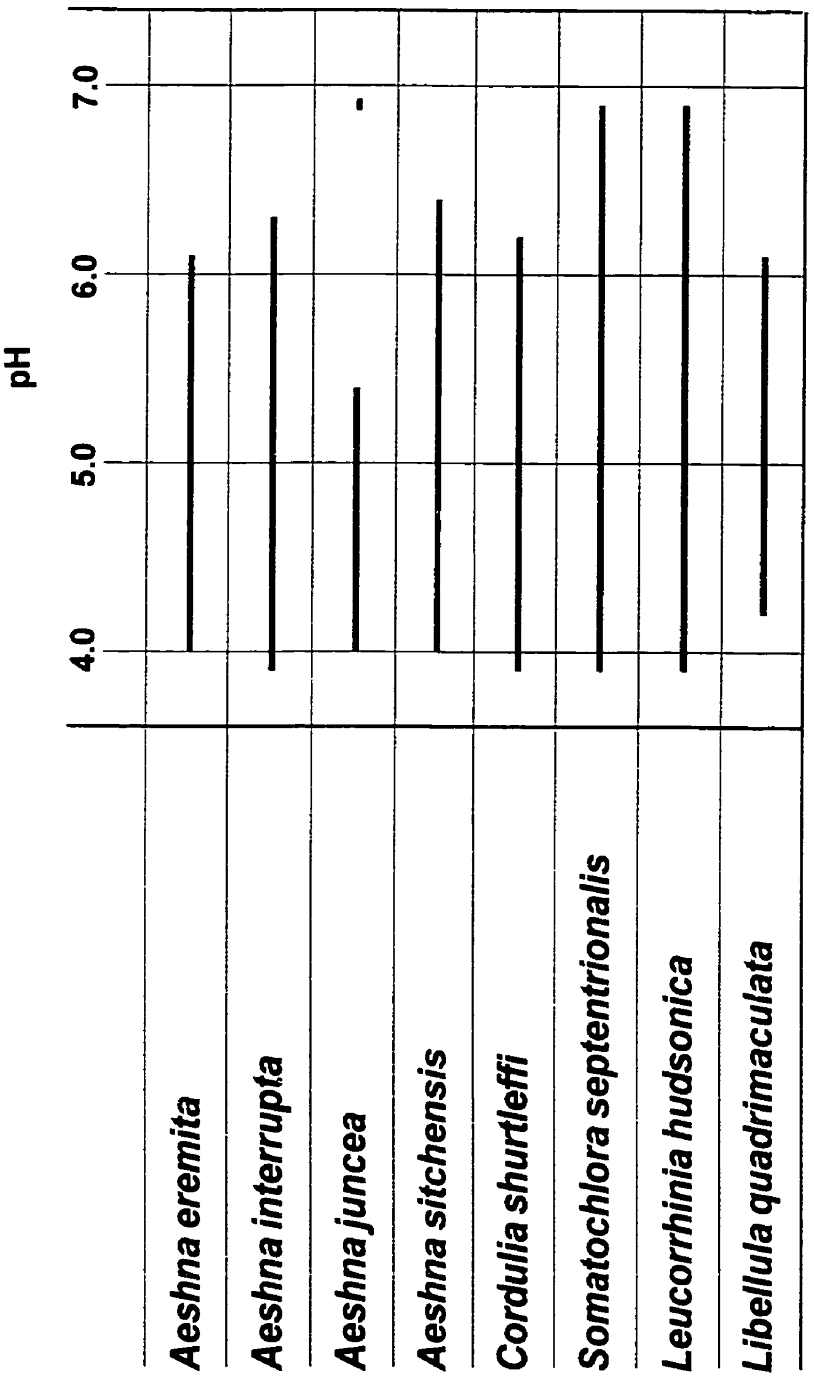

pH
4.0
5.0
6.0
7.0
Aeshna eremita
Aeshna interrupta
Aeshna juncea
Aeshna sitchensis
Cordulia shurtleffi
Somatochlora septentrionalis
Leucorrhinia hudsonica
Libellula quadrimaculata

Figure 1.4. Dendrogram illustrating associations between odonate species, based on Jaccard index of similarity. Higher values indicate greater similarity.

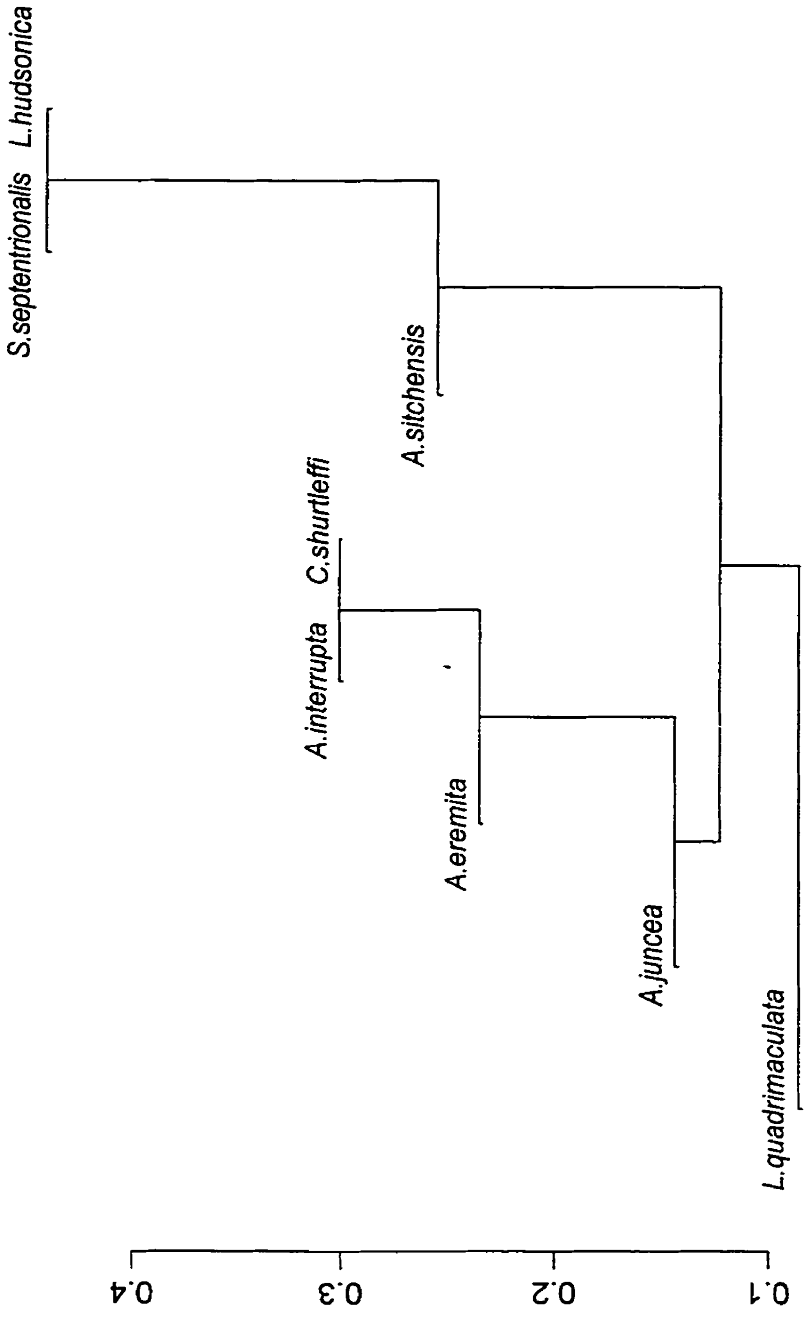

S.septentrionalis
L.hudsonica
A.sitchensis
A.interrupta
C.shurtleffi
A.eremita
A.juncea
L.quadrimaculata
0.4
0.3
0.2
0.1

Figure 1.5. Dendrogram illustrating associations between odonate species, based on "Manhattan" distance. Lower values indicate greater similarity.

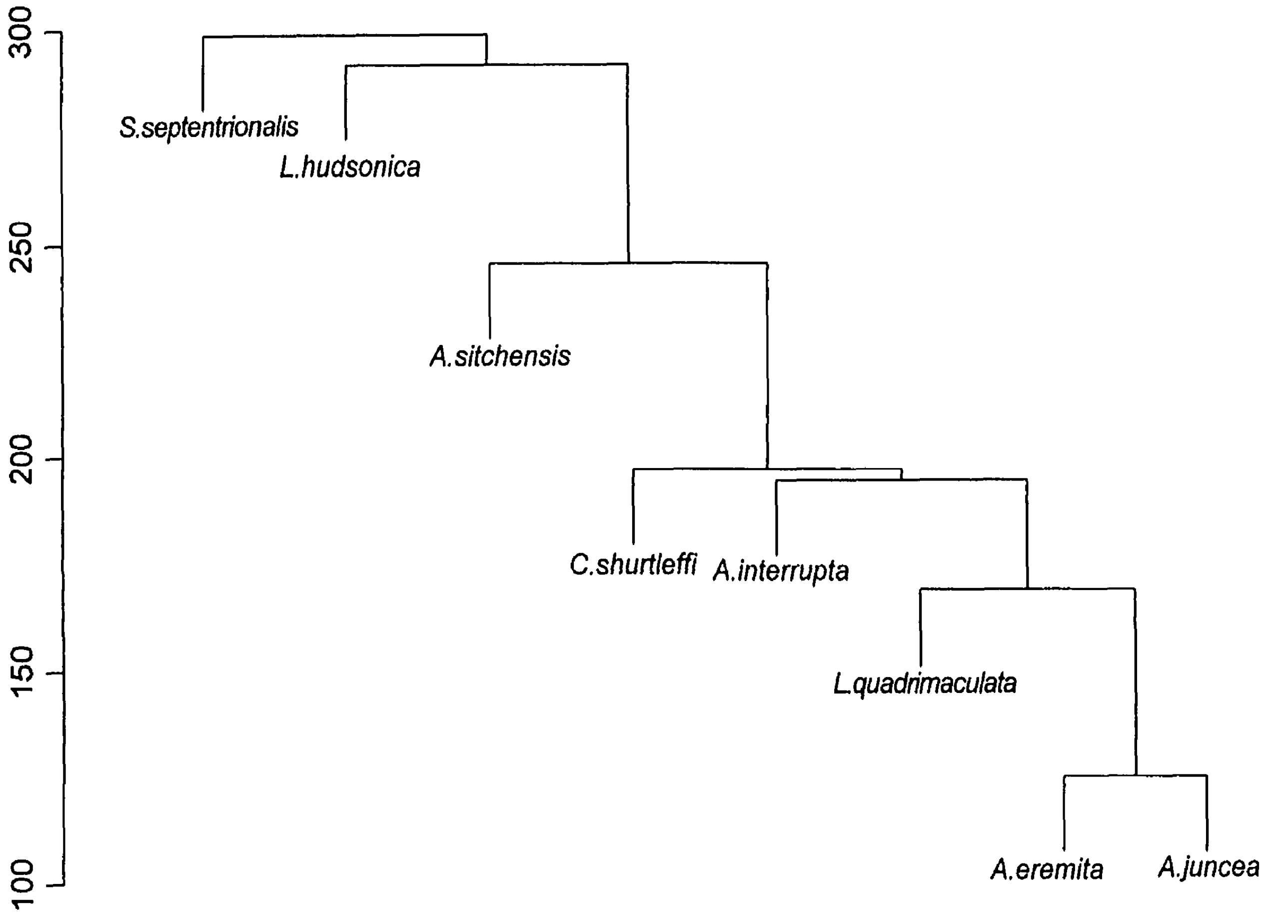

300
250
200
150
100
S.septentrionalis
L.hudsonica
A.sitchensis
C.shurtleffi
A.interrupta
L.quadrimaculata
A.eremita
A.juncea

Table 1.1. Coefficients of significant predictor contributions from generalized linear models of species incidence. Critical p=0.1. Non-significant values are not presented. No significant relationship was noted between the incidence of *Libellula quadrimaculata* and pool characteristics and is excluded from the table. Pool bottom substrate and the amount of emergent vegetation did not significantly contribute to the model of any species, and are omitted from the table. The coefficients for slope type are relative to the *gradual* level.

	Aeshna eremita	*Aeshna interrupta*	*Aeshna juncea*	*Aeshna sitchensis*	*Cordulia shurtleffi*	*Somatochlora septentrionalis*	*Leucorrhinia hudsonica*
Depth (10cm)		1.01		-0.697	0.583		
Mud (10%)				0.021	-0.038	0.026	-0.034
Pool size (10m²)	0.778					0.340	0.298
pH (0.5 units)							-1.18
Plant species richness		1.15			0.916		0.866
Pool Vegetation Submerged (10%)							-0.019
Slope type			0.978		0.456		0.383

Table 1.2. Comparison of species incidence in pool classes between the present study and results from Larson and House (1990). Values presented are gross number of occupied pools and (in parantheses) percentage of total pools within the size class. **Lestes disjunctus* values are from a subset of data and sample sizes accompany the number of occupied pools for that species.

	1-10m^2		10.1-100m^2		>100m^2	
	this study	Larson and House	this study	Larson and House	this study	Larson and House
Number of pools	161	*28*	157	*54*	27	*13*
*Lestes disjunctus**	0(/11) (0)	*1* *(4)*	12(/34) (35)	*16* *(29)*	13(/20) (65)	*3* *(23)*
Aeshna eremita	5 (3)	*0* *(0)*	22 (14)	*42* *(77)*	10 (37)	*9* *(69)*
Aeshna juncea	11 (7)	*1* *(4)*	9 (6)	*1* *(2)*	1 (4)	*0* *(0)*
Aeshna sitchensis	38 (24)	*16* *(56)*	32 (20)	*2* *(4)*	2 (7)	*1* *(8)*
Cordulia shurtleffi	25 (16)	*3* *(11)*	40 (25)	*45* *(84)*	5 (19)	*11* *(84)*
Somatochlora septentrionalis	62 (39)	*7* *(26)*	63 (40)	*42* *(77)*	7 (26)	*10* *(77)*
Leucorrhinia hudsonica	118 (73)	*10* *(37)*	122 (78)	*54* *(100)*	14 (52)	*12* *(92)*
Libellula quadrimaculata	17 (11)	*18* *(63)*	11 (7)	*14* *(25)*	2 (7)	*2* *(15)*

Chapter 2

The Effects of Landscape Structure on Peatland Dragonflies and Damselflies (Odonata) in the Gros Morne Greater Ecosystem

Chapter Abstract

I examined the effect of landscape composition on the incidence of peatland odonates in the Gros Morne Greater Ecosystem. I sampled exuviae and larvae from bogs within 15 2km x 2km landscapes to determine how the amount of peatland within a landscape (<20%, 25-45%, 50-70% of landscape area) and the type of habitat surrounding a sampled peatland influenced the incidence of five odonate taxa. Greater amounts of peatland within a landscape had positive effects on the incidence of *Aeshna sitchensis*, *Enallagma* spp. and *Cordulia shurtleffi*, but negative effects on *Leucorrhinia hudsonica* and *Somatochlora septentrionalis*. Peatlands surrounded by forest had a positive effect on *C. shurtleffi* incidence but negative effects on *L. hudsonica* and *Enallagma* spp. I explain these patterns using knowledge of the species' life histories and movement behaviours, and surmise how these are influenced by landscape structure.

Introduction

Habitat has a clear effect on the distribution and dynamics of animal populations, as has been illustrated for different taxa (Robinson and Holmes 1984, Fox and Cham 1994, Burke and Nol 1998, Lindenmayer et al. 1999, Sodhi et al. 1999, Reunanen et al. 2000). How individual organisms respond to habitat variables differs with the species and even within a species (e.g. Brown and Brown 1984, Zabel and Tscharatke 1998, Jonsell et al. 1999, With et al. 1999), and may be explained partly by how different organisms perceive their environment spatially, often at different spatial scales (Baker 1993, With 1994a). At least within functional groups, studies have shown relationships between response to habitat structure at different scales and body size (Roland and Taylor 1997, Sutherland et al. 2000), and is often linked to an organism's mobility (With 1994a, 1994b, With et al. 1999).

An individual's movement behaviour is strongly affected by the needs of the individual and the spatial structure of elements required to meet those needs. Depending upon the individual's immediate needs, movements may be done at a fine spatial scale (e.g., from one leaf to another) or at a large spatial scale (between trees or woodlots) to access spatially separated elements. Although the same individual may react to the environment at multiple spatial scales throughout its life (With et al. 1999), movement observed at the landscape scale may be considered the most important in influencing such things as population persistence and structure, and interspecific population dynamics (Taylor 1990, Stelter et al. 1997, With and King 1999). The structure of the landscape is very pertinent to understanding these large-scale processes.

Landscape Structure

Landscape structure may be considered the spatial relationship between habitats at a large scale (Turner 1989). Dunning et al. (1992) considered measures of landscape structure as falling into two main categories, namely *landscape physiognomy* and *landscape composition*. Essentially, physiognomy may be a measure of the arrangement of habitats, and composition may be a measure of the relative amounts of habitat types in a landscape. Dunning et al. (1992) illustrated how these two components of landscape structure were applicable in the examination of four ecological processes: landscape complementation, landscape supplementation, source/sink relationships and neighborhood effects. However, Taylor et al. (1993) argued that physiognomy and composition were not enough to fully understand these processes. Since the movement ability of an organism is so important to ecological processes, including the four presented by Dunning et al. (1992), a third component of landscape structure was suggested by Taylor et al. (1993) that they termed *landscape connectivity*, following Merriam (1984). Landscape connectivity is a measure of how the landscape obstructs or promotes organism movement between resources (Taylor et al. 1993). Since the publication of Taylor et al. (1993), the importance of determining landscape connectivity in understanding population dynamics and interpreting pattern of distribution has been recognised by landscape ecologists (reviewed by Tischendorf and Fahrig 2000).

Since its 1993 definition, the term *landscape connectivity* has had different meanings to ecologists. Often, connectivity has been taken to mean the extent of physical contact between habitat patches, such as through the use of habitat corridors (With et al. 1999, Tischendorf and Fahrig 2000). Although this *structural connectivity* may be readily measured in an objective fashion, it does not equate to the original definition of landscape connectivity. As Tischendorf and Fahrig (2000) point out, the presence of a habitat corridor does not necessarily mean that movement between patches is facilitated, neither does the absence of corridors mean movement is inhibited. *Functional connectivity* is a measure of the connection of habitat patches by organism movement, measuring the behavioral response of an organism to the physiognomy and composition of habitats in the landscape (With et al. 1999, Tischendorf and Fahrig 2000). This interpretation of landscape connectivity is more closely aligned to the original meaning of the term (Taylor et al. 1993).

Although determining how the landscape affects movement is very important to understanding ecological processes and population dynamics, it is a measure of a behavioral response to landscape structure rather than a component of it. Landscape connectivity is taxon-specific and cannot be measured independently from focus organisms (Taylor et al. 1993). Also, it may be strongly influenced by other factors, such as temporal effects (e.g. time of day, season), climate and weather, organism sex and age. However, a measure of landscape connectivity in a system would provide help in interpreting patterns and dynamics of populations.

To fully appreciate the relationship between the landscape and organisms one must attempt to build up knowledge on three things: how the landscape is arranged, the pattern of the organisms' distribution and how the organisms move through the landscape. The quantitative description of a landscape and knowledge of its arrangement is crucial to understanding how organisms respond to different landscapes. Determining how animals are distributed in particular landscapes is fundamental to studying the effects of habitat on organisms, and will aid in understanding how populations are influenced by the distribution of individual elements and combinations of elements. However, the picture is incomplete without some knowledge of how the animals move in the landscape and how their movements may be altered by the physiognomy and composition of landscape elements. Efforts should be made to address each of these components to elucidate the relationship between habitat and focus organisms.

One can examine the structure of the landscape by considering the arrangement and proportions of resource and non-resource habitat, as suggested by Dunning et al. (1992) and others (e.g. With and Crist 1995, Wiens et al. 1997). Certainly, it is vitally important to consider the distribution of resources when addressing how landscape structure affects organisms, but how does one define a resource? A patch of forest may be used for nesting by a songbird, but that forest patch is neither independent from its non-forest surroundings nor a comprehensive resource for the songbird throughout its life. Different elements in a landscape vary in utility over space and time, and may be regarded as a spatially dependent cost-benefit function (Wiens 1995). However, I argue that few taxa are known well enough to decide what are not resources to an organism, which may also differ with such things as organism sex, age and season. I suggest defining landscape structure in relation to different habitat types, differentiated by independent methods, not by making binary decisions of what are resources to an organism and what are not. The organism's response may be used to infer *a posteriori* what elements or combinations of elements positively or negatively affect the organism.

Finally, one must attempt to examine the structure of the landscape in such a way as to make it biologically meaningful to the focus organisms. The spatial scale at which measurements are taken and at which the landscape is defined is important to understanding the relationship between the focus organisms and habitat. This allows one to increase confidence in statements regarding the effect of landscape structure on the organism without fearing other more relevant effects are felt at different spatial scales. The appropriate scales may be defined or estimated through the use of experimentation and observation of movement behaviour of the focus organisms (Wiens and Milne 1989, May 1993, Tischendorf and Fahrig 2000). At a minimum, this requires knowledge of the life history of the organisms, if not explicit observations of movement. Only at the appropriate scale is it meaningful to study landscape structure effects on organisms.

In this study, I chose to examine the influence of landscape composition on a collection of related organisms. I sought to determine how these organisms are affected: a) by differences in availability of breeding habitat in the landscape, and b) by the types of habitat surrounding the breeding sites. To address these questions, I chose a group of mobile insects (Odonata) which inhabit peatland habitat in a boreal ecosystem, and compared the incidence of species in different landscapes, measured at an appropriate scale. Using knowledge of the species' life history, I attempted to interpret species responses in relation to the movement, behaviour and requirements of taxa.

Study System

The boreal forest dominating northern Canada is the largest terrestrial forest ecosystem in the world, covering almost two-thirds of Canada's landmass (Pilarski 1994). Without human influence, the boreal forest landscape is shaped by broad-scale changes induced by forest fire, wind and peaks in insect cycles (Carrow 1993). Anthropogenically, the dynamics and structure of this landscape is altered through the suppression of fire and the extraction of resources, such as through peat mining and forestry (e.g. Brumelis and Carleton 1989).

The effects of these human activities in the southern boreal forest have been illustrated in numerous studies, examining vegetation (e.g. Brumelis and Carleton 1988, 1989, Hamilton and Yearsley 1988, Machmer and Steeger 1995, Lauchtenschlager 1995), birds (e.g. Hutto 1995, Norton and Hannon 1997, Drolet and Desrochers 1999, Niemi et al. 1998, Harrison and Bruna 1999) and other vertebrates (e.g. Waldick et al. 1999). Relatively few studies have examined comparable anthropogenic effects on insects, but our knowledge is increasing (e.g. Hollifield and Dimmick 1995, Niemala et al. 1993, Roland and Taylor 1997, Pither and Taylor 1998, Sahlen 1999, Jonsen and Taylor 2000a, 2000b).

The relationships between human land use, its consequent alteration of landscape structure, and animal movement and distribution in the landscape have been examined experimentally in recent years. Much of this work has been directed toward how human land use reduces and fragments resources (Andren 1994, Collinge 1996, Fahrig 1997, Harrison and Bruna 1999), and how this fragmentation affects movement (e.g. Taylor and Merriam 1996, Pither and Taylor 1998, Jonsen and Taylor 2000a). Many studies are devoted to how forestry practices affect forest habitat, which in turn affect the forest's organisms (e.g. Yahner 1993), but fewer studies have examined the effects of logging on non-forest inhabitants (e.g. Dickson et al. 1983, France 1997). These latter studies were primarily interested in how logging creates suitable breeding habitat for animals, and do not delve into how logging affects other existing habitats in the landscape.

Open peatland is the focus habitat in this study. The surrounding habitat may have considerable influence on peatland animals, affecting populations directly and indirectly. Directly, non-peatland habitat may alter the movement and dispersal capabilities of animals, either by facilitating movement between peatlands or by presenting a barrier to dispersal. Surrounding habitat may also increase the health of peatland animals by harboring important resources, such as roost sites and prey populations (Watanabe 1986, Taylor and Merriam 1996). Indirectly, the landscape may alter the energy flow within and through a peatland, influencing such local effects as the nutrient loads within pools, water level fluctuations and pH (Van Wirdum 1993). Differences in plant incidence and growth (Van Wirdum 1993), and the incidence and abundance of prey, predator and competitor species, could result from these changes in the local environment. Examining how inhabitants of one apparently unaltered habitat are affected by changes in another habitat is an important but often neglected exercise (Anderson 1992, Stout et al. 1993, France 1997).

Since protected areas are not ecologically separated from their surroundings, and may be greatly influenced by processes occurring outside their boundaries, it is wise to consider systems that include both the protected areas and their surroundings (the "greater ecosystem" concept of Grumbine 1990). Learning how the alteration of surrounding habitat influences peatland odonates can have important implications with respect to conservation strategies used to preserve the ecological integrity of systems within the parks. The restriction of forestry practices within a park may not be enough to ensure the integrity or survival of protected systems near the park boundaries.

One of my objectives was to examine the effect of forestry, specifically clearcut logging, on a group of non-forest animals living in adjacent areas. This may provide useful information on how patterns of animal distribution observed in a natural landscape can be related to those expected in human-altered landscapes.

Study Taxa

Work examining the effect of habitat at coarse spatial scales on insects and other invertebrates has increased recently (e.g. Roland and Taylor 1997, Dubbert et al. 1998, Bommarco 1998, Holland and Fahrig 2000). Insects are a good group with which to work due to their ease of study, their broad ranges of mobility and the probable range of response insects may have to habitat structure, from a very fine spatial scale to the scale of the landscape.

Dragonflies and damselflies (Insecta: Odonata), hereafter referred to as odonates, are relatively large insects that may be separated into two clearcut groups. Damselflies (Odonata: Zygoptera) are generally small and are weak fliers, with the presumption of limited mobility (but see Taylor and Merriam 1996, Pither and Taylor 1998, Jonsen and Taylor 2000a), while the larger dragonflies are stronger fliers with greater mobility. Besides structural and behavioral differences, their life histories are similar and are described below.

For the first part of their lives, odonates live as larvae in various aquatic habitats, with some species living in lakes and rivers while others live in wetlands. Depending upon the species, odonates live this aquatic existence for a few months to a few years (especially in northern climates, e.g. Newfoundland) (Corbet 1999), as much as 99% or more of their total lifespan, gradually moving through discrete stadia as they grow (Corbet 1999). At the end of their immature stage, odonates crawl out of the water, break open their larval skins and slowly emerge as adults. The shed larval skins, or exuviae, are left behind when the odonates take their maiden flight.

The odonates leave the area to mature and forage for up to a week. Dispersal is believed to be greatest at this stage of life, although movement can occur just as regularly in mature individuals (Parr 1973, Michiels and Dhondt 1991, Taylor and Merriam 1996, Conrad et al. 1999). When sexually matured, the odonates return to breeding habitat, sometimes the natal water body, to reproduce. Site selection for oviposition is species specific, but may involve visual, sociological, tactile and even thermosensory cues, with common links to open water and the presence of suitable substrates, such as certain plant species (Corbet 1999). The primary cause for a larva's presence in a water body is the oviposition by its mother at that water body, although the survival of a larva is dependent upon abiotic influences (e.g. water chemistry, drought), prey populations, and the presence of other species (competitors and/ or predators) (Corbet 1999). At a discrete water body, one may be confident that odonate larvae found have been subject to the conditions within that water body for their lives, and that a female or females initially selected that water body at which to oviposit.

Odonate population dynamics may be affected by landscape structure (Samways 1993, Pither and Taylor 1998, Jonsen and Taylor 2000a, 2000b). Of the 38 odonate species currently known from Newfoundland, most are known to occur in peatland habitat, some as peatland obligates (Chapter 1). Peatland may be considered a required resource since it provides a habitat in which these odonates may live as larvae and mate and oviposit as adults. Habitat surrounding natal peatland may or may not be a resource used by peatland odonates, and could also hinder or facilitate movement around and between peatlands. By examining the relationship between the amount of peatland in a landscape and odonate populations, and by comparing odonate populations in peatlands surrounded by different habitats, I can determine if an effect of habitat structure at a landscape scale influences the dynamics of resident odonates.

Methods

Study Area

This study was conducted in the Main River area (49°45'N, 57°16'W), east of Gros Morne National Park, Newfoundland, Canada. The area is adjacent to the Long Range Mountains and Gros Morne National Park to the west and includes a significant portion of the Main River and Humber River watersheds. The region consists of open lakes and rivers within boreal forest dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), scrub (tuckamore) dominated by stunted balsam fir and other woody plants, and open peatland (hereafter, "bogs") dominated by sedge (Cyperaceae) and moss (*Sphagnum* sp.). Bogs are most often composed of solid peat interspersed with discrete water-filled pools, in which populations of dragonflies and damselflies exist as larvae.

The forests of the region are being harvested at present, with most logging activity concentrated in the south. Logging roads and smaller isolated clearcuts are widespread through the area. Bogs within these clearcuts remain intact and undisturbed by direct logging activity, but may be affected indirectly.

General Study Design

To examine the effects of landscape structure on peatland odonates, two questions were proposed. Firstly, does the type of habitat surrounding the peatland affect odonate populations in peatland habitat? Secondly, does the amount of peatland habitat in a landscape affect odonate populations?

For this study, LANDSCAPES[1] were considered to be 2 km x 2 km squares arbitrarily placed in the study region. This scale was thought to be reasonable after considering the distances normally traveled by non-migratory odonates is little more than a kilometre, and usually much less (Corbet 1999). LANDSCAPES were included in the study if they fit into one

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[1] *Factors included in models are presented in small caps font.*

of the TREATMENTS described below and if they were accessible by foot and/or truck within half a day's travel.

To address the first question, LANDSCAPES with different amounts of peatland habitat were compared. LANDSCAPES were chosen for comparison if they fell into one of three TREATMENTS: <20% of the area composed of peatland (*Little Bog*), 25-45% peatland (*Medium Bog*) or 50-70% peatland (*Big Bog*). To keep LANDSCAPES comparable, they were only chosen for this comparison if the surrounding habitat was dominated (>79%) by scrub, and no part of the LANDSCAPE included clearcut habitat.

To address the second question, LANDSCAPES surrounded by different types of habitat were compared. LANDSCAPES were chosen for comparison if 25-45% of the area was composed of peatland and placed in one of three TREATMENTS if they met the following criteria: surrounding habitat dominated (>79%) by balsam fir forest (*Forest*) or scrub (*Scrub*) and had no clearcut component, or the surrounding habitat was dominated by clearcut (*Clearcut*). To conserve effort, landscapes in the *Scrub* treatment were also included in the *Medium Bog* treatment of the first comparison.

Within each LANDSCAPE, BOGS were chosen, within which POOLS were randomly selected for sampling if they had an initial DEPTH of at least 10 cm and a minimum surface AREA of 2 m^2.

Pool Characteristics

At each sampled pool, nine covariates were measured or estimated. Maximum water depth was measured to the nearest centimetre using an incremented wooden stake; the maximum depth of three to five measurements was recorded.

The pH of each pool during every visit was measured in the field using a portable pH meter (Oakton pH Testr 2 with automatic temperature compensation). The meter was calibrated at regular intervals using three separate buffer solutions, and showed accuracy to within 0.1 units.

A discrete BANK, usually dominated by sedge and sphagnum, surrounded all pools. Many pools had perpendicular or overhanging banks, while others had more gradually sloping banks; all sampled pools were subsequently scored as belonging to one of two categories (*gradual, steep*). Most pool BOTTOMS were generally flat but differed in their dominant substrate material. Pools were categorised as having one of the following substrates, with classifications based on preliminary pool surveys: *mud, mud/moss, mud/detritus.*

Since I believed vegetation to be an important influence on the distribution of odonate adults and larvae, several scores were made with respect to a pool's plant community. The incidences of all vascular plant species observed growing within a pool or along a pool's immediate edge (<10 cm from pool) were noted, as was the incidence of sphagnum either within or alongside a pool. Values of plant species RICHNESS were calculated and incorporated into analyses. The amount of plant cover (all species pooled) was also estimated for the extent of EMERGENT and SUBMERGED vegetation across the area of the pool, and the amount of pool area with exposed MUD.

Measurements of PH and plant community were taken during each visit (two or three over the field season).

Each pool was georeferenced using real-time GPS accurate to within 0.5 m and was used to locate individual pools on aerial photos. The size of each sample pool was estimated by examining aerial photo coverage of the area taken at a scale of 1:12,500, scanned at 600 dpi. The resolution at this scale gave a ratio of 0.282 m^2 to each pixel, and by tallying the total number of pixels within each pool, I was able to arrive at an estimate of AREA.

Larval Odonate Sampling

At the beginning of the field season (5-17 June 1999), larvae were sampled from a subset of POOLS within the larger nested design. Five POOLS within each BOG were sampled for larvae. One BOG was sampled in each of two LANDSCAPES representing each TREATMENT. A random point on each pool was chosen and every two or four metres (depending on size of pool) an aquatic dip net ('D' shape, 12" x 8", 500 micron netting) was used to sweep submerged vegetation and mud from 0.5 m from the bank towards the sampler.

Larvae were sorted, identified and measured on site and returned to the study pool. Head width and body length were measured to the nearest 0.05 mm using vernier calipers. A set of voucher specimens, taken from pools other than those sampled within the study design, was retained.

Larval odonate sampling was performed prior to the main flight period of the local adult odonates, but some emergence was noted through the presence of exuviae and teneral adults at the pools. Since few odonates were found to emerge during this period, and since Ubukata (1981) found the overall efficiency of exuvial odonate sampling to be much higher than larval odonate sampling, I deemed the loss of larvae due to adult emergence during this period to be negligible.

For species with sufficient abundance, I attempted to compare the age structure of larval populations between treatments. Stadium size was thought to be consistent across environments for a population (Larson and House 1990), and assuming that members of each stadium are sampled with equal probability, a histogram of larval sizes pooled for each species may be produced to determine size classes; these were translated into approximate stadium classes. For the purpose of analysis, and because an individual cohort may be split between multiple stadia (Corbet 1999), frequency of individuals in different size classes were compared to determine a difference in size class ratios between TREATMENTS. For example, does the proportion of large larvae to small larvae differ between TREATMENTS.

Exuvial Odonate Sampling

Searches for exuviae at POOLS were made two times during June and July. Essentially, the design for exuvial odonate sampling was similar to the larval survey component, but replicates were increased. Within each TREATMENT, three replicate LANDSCAPES were chosen, in which two BOGS were chosen for each LANDSCAPE. Based on the location of peatlands in terrain, I classed each peatland *a posteriori* to be either an ombrogenous bog or a fen (soligenous or otherwise). From each landscape, one bog and one fen were chosen for sampling. Within each BOG, ten replicate POOLS were sampled. Pools were surveyed for exuviae visually and tactually, searching along the pool's perimeter within a band roughly 2 m wide, centred on the discrete pool edge. Only the perimeter along one half of the pool, as estimated by area in the field, was sampled. The section of pool to be sampled, either the northern, southern, eastern or western half, was chosen randomly, and the same perimeter was sampled during repeat visits. Exuviae were retained, then counted and identified to species, if possible, in the lab. Additionally, some living and dead adults associated with exuviae were collected for identification purposes.

Statistical Analysis

To determine if pool characteristics were confounded with the effect of TREATMENT, analyses on these data were performed for each comparison. For any observed difference between treatments that had less than a 10% probability of occurring by chance I took to indicate the variable was confounded with TREATMENT.

The frequencies of pool BOTTOM substrates and bank SLOPES were analysed using G-tests of independence for each comparison (Sokal and Rohlf 1981). For other pool characteristics, I used a nested ANOVA for each comparison using the **aov** procedure of S-Plus (Chambers and Hastie 1992) after suitably transforming the data to meet test assumptions. Within this design, I specified the error terms as POOL nested within BOG, nested within LANDSCAPE, nested within TREATMENT, to determine the effect of landscape type on each pool characteristic.

The relationships between TREATMENT and odonate populations were examined by fitting generalized linear models, or glms (McCullagh and Neldar 1989), using the **glm** procedure of S-plus (Chambers and Hastie 1992). Pool characteristic variables were fit first to control for their local effect, a conservative approach that ensures that an observed effect is due to TREATMENT rather than local (pool) habitat attributes. After fitting all necessary covariates, the nested design factors were then fitted: TREATMENT, LANDSCAPE and BOG. Any covariates regarded as confounded with TREATMENT were alternately fit both before and after TREATMENT to determine the magnitude of indirect and direct effect of TREATMENT. I fit Quasi-likelihood models to compensate for under- and over-dispersed data and tested for significance of predictor variables using an F-test (McCullagh and Neldar 1989).

For the significance of a TREATMENT effect in each model, I present actual probabilities of Type I error. Other statements of significance are based on a maximum error of $p<0.1$.

Results

Pool Characteristics

Only one pool characteristic, PH, was significantly confounded with TREATMENT, within the comparison of surrounding habitat (p=0.006). Forest landscapes had generally higher PH than scrub or clearcut landscapes (Figure 2.1). In comparing odonate response to different surrounding habitats, models were first fit including then excluding PH to determine the confounded effect on TREATMENT. The significant contributions of PH and other pool characteristic predictors are denoted in Tables 2.1-2.3, and the presence of a confounded effect of PH in individual models is noted below.

General Survey Results

Nine hundred sixty-seven larvae were sampled within the study bogs. The odonate fauna of the region was dominated by one species, *Leucorrhinia hudsonica*, which represented 72% of the total sample (see Appendix 1).

The relationship of the relative abundance (mean number of larvae found in each sample at each pool) to TREATMENT was examined by fitting models with Poisson errors where relative abundance was set as the response variable. This was performed for *L. hudsonica* only, and only for larger larvae (see below).

The abundance of *L. hudsonica* allowed for the study of larval age structure with respect to TREATMENT. A histogram of larval head width for *L. hudsonica* illustrated six discrete size classes (Figure 2.2)[2]. The assumption that stadia were sampled with equal probability was not true for smaller larvae (head width < 2.1 mm; Figure 2.2) so these were excluded from subsequent estimates of relative abundance. Abundance within each size class was examined between the treatments by modelling the ratio of F to F-1 and F-1 to F-2 within

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[2] *It is believed that head width is inconsistent within and between odonate stadia (Corbet 1999, T. Lawson, pers. comm.). However, for academic interest, I make the assumption in this cursory analysis that size class as measured by head width corresponds to larval age.*

the pools. Models were fit with binomial errors. Larval abundance and incidence of other species was low and uninformative, thus models were not fit for the other sampled species.

Five thousand two hundred sixty-eight exuviae were collected and I was able to model the effect of TREATMENT on the incidence of four species found in sufficient numbers: the large dragonfly *Aeshna sitchensis*, two medium-sized emerald dragonflies *Cordulia shurtleffi* and *Somatochlora septentrionalis,* and *L. hudsonica*. Incidence was modeled due to the large number of counts of zero. All models of incidence were fit with binomial errors since the response variables were binary (presence/absence). I was unable to differentiate the exuviae of two small *Enallagma* damselfly species (*E. cyathigerum* and *E. boreale*) although samples of exuviae belonging to the species pair were sufficiently numerous for modelling. Instead, I modelled the incidence of the genus. Eight other species were sampled as exuviae, but none were found with sufficient frequency to model.

The Effect of Surrounding Habitat

After fitting local habitat predictors, I found no residual effect of TREATMENT on either the relative abundance of *L. hudsonica* larvae or the incidence of exuviae in landscapes with different surrounding habitat. However, altering the order of the fit of PH uncovered confounded effects in both models (Tables 2.4 and 2.5). *L. hudsonica* larvae were in lower abundance and emerged from fewer pools than expected in landscapes dominated by forest compared to clearcut or scrub landscapes (Figure 2.3).

The frequency at which *L. hudsonica* exuviae was found enabled me to explore the effect of TREATMENT on the abundance of exuviae of this species. Models were fit with Poisson errors. Although a confounded effect of PH was found in a comparison of exuvial abundance also, there remained a residual effect of TREATMENT over and above the effect of PH (Table 2.5); *L. hudsonica* exuvial abundance was higher than expected in scrub landscapes, lower in forest landscapes (Figure 2.3).

Larvae belonging to the genus *Enallagma* were rarely sampled; only nine were sampled in total. However, exuviae were more numerous. *E. boreale* and *E. cyathigerum*, pooled together, were found to have emerged at pools more frequently in scrub landscapes than in forest or clearcut landscapes (Table 2.6, Figure 2.4). Conversely, *Cordulia shurtleffi* was found in scrub landscapes with lower frequency than expected (Table 2.6, Figure 2.4). Although larval data were too few to use in models, they supported this result, with larval abundance higher in forest and clearcut landscapes than in scrub landscapes (mean number/ pool - forest = 2.4, clearcut = 4.9, scrub = 0.7).

Evidence for a response to surrounding habitat by other species was not statistically significant (Table 2.6) and sampled larvae were too few to make statements regarding patterns of distribution between treatments.

The Effect of the Amount of Peatland

The proportion of peatland in a landscape did not appear to have an effect on relative abundance of *L. hudsonica* larvae, but the structure of larval populations showed a response (Table 2.7). Although no difference in F to F-1 ratios between treatments was noted, landscapes with little peatland habitat had a smaller ratio of F-1 to F-2 larvae than expected (Figure 2.5). The difference in ratios is reflected by both a decrease in abundance of F-1 larvae and an increase in abundance of F-2 larvae in landscapes with <20% peatland (Figure 2.6).

Although the incidence of *L. hudsonica* emergence did not appear to differ between treatments, the abundance of emerging individuals was influenced by the amount of peatland in the landscape (Table 2.8). Abundance was higher than expected in landscapes with <20% peatland compared to landscapes with more peatland (Figure 2.5).

Exhibiting a comparable response was *Somatochlora septentrionalis*, which emerged with greater than expected frequency as the amount of peatland decreased (Table 2.9, Figure

2.7). The closely related *C. shurtleffi* showed an opposite response, instead emerging with greater than expected frequency as the amount of peatland increased (Table 2.9, Figure 2.7).

The proportion of peatland in a landscape also influenced the incidence of emergence of both *Enallagma* spp. and the large dragonfly, *Aeshna sitchensis* (Table 2.9). The small *Enallagma* damselflies emerged from pools with greater than expected frequencies in landscapes where >25% is peatland habitat (Figure 2.8). *A. sitchensis*, a highly mobile species, was found with greater than expected frequency in landscapes with more peatland, at least 50% of the landscape (Figure 2.8).

Discussion

Odonates are mobile animals that use habitats in the landscape to varying degrees, with certain species having affinity to specific habitat types (Chapter 1). The odonate taxa included in this analysis breed in peatlands and are influenced by factors at a fine spatial scale within the breeding habitat, linked primarily to the larval stage of life (Chapter 1, Corbet 1999). However, habitat structure at a large spatial scale has been shown to affect odonate populations (Pither and Taylor 1998, Jonsen and Taylor 2000a), and one must expect that the amount of peatland in the landscape and the types of other habitat in the landscape may have an effect on peatland odonates.

In the present study, I chose five odonate taxa that breed sympatrically in the same habitat and presumably have different perceptions of the environment due to differences in mobility and life history. How the odonate fauna of a region responds to differences in landscape structure may relate to how the animals move in the landscape and can tell us what broad ecological processes may affect the fauna on the whole, and what differences may exist between taxa that relate to specific life history traits. Despite species differences, I believe landscape structure influences the dispersal behaviour of these odonates. However, each species must be looked at individually, with knowledge of the species' life history at hand, before general conclusions can be made.

The taxon I had presumed to have the lowest mobility and limited dispersal ability was *Enallagma*, based on personal experience and published studies of these and other damselfly species. McPeek (1989) found *E. boreale* and *E. cyathigerum* to travel very little from their natal water bodies with limited movement between lakes only 10 m apart, and Garrison (1978) found little movement by *E. cyathigerum* even within the same water body (along a stream). In Washington, daily movement between water bodies and roosting sites was restricted to within a couple of hundred metres, 90% of individuals moving no more than 50 m (Logan 1971). Conrad et al. (1999) examined dispersal of a European population of *E. cyathigerum* in pools within an agricultural landscape. Although most individuals remained at the pools where they were captured, considerable movement between ponds was discovered, with 11% of recaptured adults dispersing to a second pool at least once (Conrad et al. 1999). Despite the frequency, movement was still limited and restricted to within a few hundred metres in the open landscape, long distance movements occurring only rarely (Conrad et al. 1999).

However rare, small numbers of individuals can move considerable distances, have the potential to move at the population level more than traditionally believed and are able to colonize remote habitats (Parr 1976, Conrad et al. 1999, Simpkin et al. 2000). A driving force for long distance displacement is wind (Corbet 1999). Small coenagrionid damselflies have been sampled from aerial plankton several kilometres in altitude (Russell 1994), and despite the assumption that active migration is not occurring, have been able to travel to drilling platforms in the Gulf of Mexico (pers. obs.) and to isolated islands, such as the Azores (K.D.B.Dijkstra, pers. comm.) many kilometres from a potential source. Rising air currents have been observed to play a part in this displacement, including that of *Enallagma cyathigerum* (Lempert in Corbet 1999). Indeed, even at a smaller spatial scale, wind can influence the dispersal of *Enallagma* (McPeek 1989). Although active dispersal may be minimal, passive dispersal through wind transportation may be much more important.

In this study, *Enallagma* showed a response to landscape structure. *Enallagma* incidence was greater than expected in more open landscapes: in peatlands surrounded by scrub and in landscapes with greater amounts of peatland. Apparently, forest habitat may be a barrier to dispersal, either through inhibiting active movement or by decreasing wind (Miner 1999) that would potentially disperse individuals passively. Certainly clearcuts no longer provide the same physical barrier, but they have been in this state for a few years only and are not yet comparable to scrub landscapes. Long distance movements are rare, as illustrated in the above studies, and clearcut areas have had little time to be colonized.

Within scrub landscapes, those with little peatland hosted fewer than expected *Enallagma*. These landscapes may provide little barrier to dispersal, but they also have smaller source populations and successful colonization probably occurs more rarely. These results illustrate to me that despite little active dispersal, landscape scale ecological processes, such as wind, influence population structure in *Enallagma*.

Unlike the *Enallagma* spp., the response of *C. shurtleffi* to landscape structure is not likely due to wind but to direct effects on movement choice and resource availability. Both species within the genus *Cordulia* have highly mobile behaviours and appear to use large areas in which to forage, mate and roost. In *C. shurtleffi*'s Palearctic congener, *C. aenea*, males patrol an area encompassing 30 m^2 at a breeding site and will return to the same territory repeatedly during the flight period (Ubukata 1975), but generally lead a transient life through a landscape, spending little time at the breeding site at any one visit (Ubukata 1975, Corbet 1999). *C. shurtleffi* behaviour is less well known, but what is known suggests they exhibit similar behaviour to that reported for *C. aenea* (Hilton 1983). The ability of tenerals to disperse in the prereproductive period is unknown, but may exceed the movements of reproductive adults.

When in a landscape with a greater amount of peatland, the mobile *C. shurtleffi* can take advantage of the increase in breeding habitat (Figure 2.7). What is especially interesting is the effect of surrounding habitat to *C. shurtleffi* populations. Landscapes recently or presently dominated by forest had a greater than expected number of pools occupied by *C. shurtleffi* (Figure 2.4). In this case, the physical structure of the forest does not appear to provide a barrier to dispersal, but instead promotes incidence. The answer lies in the species' life history. Forest is a resource for *C. shurtleffi*, as a foraging site and potentially as a habitat in which to roost and mate (Hilton 1983, Appendix 1). Instead of presenting a barrier, forest may increase the value of a peatland by offering additional elements necessary for fit individuals. The same relationship with forest has been noted by Cham et al. (1995) for the related *C. aenea*. Determining the dispersal ability of teneral and reproductive adult *C. shurtleffi* would help interpret if landscape structure is influencing the local movements of adults or the potentially large-scale dispersal of tenerals. Whatever the case, it is apparent that landscape structure influences *C. shurtleffi* populations.

Little is known regarding the life history of the similar *S. septentrionalis*. Presently, it is believed to belong to the wide-ranging and species-rich *Somatochlora*, and with this diversity comes a varied collection of habits and life histories. Although *S. septentrionalis* is closely allied with *S. whitehousei* (Needham et al. 2000), another poorly known species, one cannot easily transfer knowledge of one species onto another within this diverse genus.

Anecdotal evidence suggests *S. septentrionalis* is a peatland obligate, breeding only in bog pools and spending much, if not all, of its time in peatland habitat (Walker and Corbet 1975, Dunkle 2000, Appendix 1). If this is true, effective edge permeability (Wiens et al. 1997, Jonsen and Taylor 2000b) will be reduced and the surrounding habitat would have little direct effect on individual *S. septentrionalis*.

Although no effect of surrounding habitat was detected, the amount of peatland in a landscape appears to affect the incidence of *S. septentrionalis*, with more than expected occupied pools occurring in landscapes with little peatland (Figure 2.7). If edge permeability is low, individuals would rarely disperse outside of peatland, thus minimizing emigration. After colonizing a peatland in a sparse landscape through a rare dispersal event, individuals would tend to disperse only within the peatland, occupying an increasing proportion of pools. If peatland is limited (e.g. <20% of the landscape), the proportion of occupied pools would increase at a greater rate. This may explain the greater than expected frequency at which we found pools occupied by *S. septentrionalis* in landscapes with <20% peatland. It appears peatland is the critical habitat in the landscape for *S. septentrionalis*, and surrounding habitat has little effect on this peatland obligate.

Another peatland obligate, *A. sitchensis* is a larger odonate with strong flight and a potentially great ability to disperse. *A. sitchensis* is a relatively uncommon species within the peatlands of the Main River area, generally emerging from only a few study pools in each peatland. This species showed no difference in response to the three surrounding habitat types, and individuals have been observed flying through and using other habitats (Cannings 1982), so dispersal may effectively join bogs within a landscape regardless of intervening habitat. However, other processes at the scale of the bog appear to influence local clusters of individuals differently. Incidence of this species was greater than expected when the landscape was dominated by peatland (i.e. 50-70%), and yet little difference in response was noted between the other two treatments, providing evidence that a critical threshold was present (Turner and Gardner 1991). When 50% or more of the landscape is composed of peatland, more pools are successfully colonized by this species. This may be due to one of two things, or a combination of both. Although *A. sitchensis* does not restrict movement to peatland habitat, when breeding habitat is offered in abundance the dragonfly may exhibit a preference to move only within this habitat (i.e., emigration is lowered). Movements within a peatland exceed movements elsewhere, with adults more likely to remain within peatland habitat and oviposit in a greater proportion of pools. Alternatively, when greater amounts of peatland are present, emigration could remain the same but immigration may increase, since more dragonflies would be successful in dispersing to breeding habitat. Successful colonization of pools within the peatlands would increase accordingly. Experiments directly measuring the movement of this species within and without peatland may clarify the interpretation.

L. hudsonica is the most abundant and prevalent odonate in the Gros Morne Greater Ecosystem, seemingly ubiquitous in its distribution in peatland habitat. Be that as it may, patterns related to landscape structure do exist. How landscape structure alters these patterns is dependent upon the variable examined.

Although I found no residual effect of surrounding habitat type on larval abundance or exuviae incidence for the abundant *L. hudsonica*, removing pH from the models revealed a confounded effect between this variable and treatment. *L. hudsonica* preferred more acidic pools, and significantly more of these were found in scrub or clearcut landscapes than in those dominated by forest (Figure 2.3). Possibly, these results indicate a response of *L. hudsonica* to landscape structure directly, clouded by a similar response of pH. However, considering the tendency of *L. hudsonica* to occur in pools with lower water pH levels (Chapter 1), it is more likely the animals are responding to water acidity that is, in turn, influenced by landscape structure.

L. hudsonica populations are also affected by the amount of peatland in the landscape. The structure of intrapool larval populations was different in landscapes with <20% peatland, composed of more F-2 larvae relative to F-1 larvae than populations surrounded by more peatland. This could indicate an interannual difference in initial cohort numbers, or it could be due to different mortality rates between landscapes, with overall greater mortality in pools surrounded by little peatland. Although the influence of important local pool characteristics were taken into account in the models, prey populations were not measured and there may be reduced populations of prey for larger larvae in landscapes with little peatland. Whatever the reason, it is apparent that the amount of peatland in a landscape has an influence on population dynamics, and further study is needed to determine the cause.

A factor that may have important implications on population dynamics in different landscapes is the dispersal of adults. Other species of *Leucorrhinia* have been shown to exhibit some degree of site fidelity (e.g. *L. intacta* {Wolf et al. 1997}), and there is circumstantial data suggesting *L. hudsonica* behaves similarly (Hilton 1984). Especially when resources are limited, site fidelity can reduce dispersal behaviour and effectively remove emigration, much as was postulated for *S. septentrionalis*. If this is the case and the animals react to reduced peatland in the landscape, incidence or abundance would be greater at pools in landscapes with little breeding habitat. Although incidence showed no difference between the treatments according to my models, abundance was higher than expected in landscapes with <20% peatland supporting the above hypothesis. At the very least, these results show *L. hudsonica* is influenced by local habitat characteristics but also responds to habitat structure at the scale of the landscape.

The exact processes involved with how different habitats affect each species is not known with certainty, and further research is warranted. But this study has clearly shown that these insects react to landscape structure. Surrounding habitat has an effect on peatland odonates, and a change in the surroundings may alter odonate population dynamics. One mechanism that creates some of the most dramatic changes to the landscape is clearcut logging. Its presence in the study system allowed an initial examination of how this anthropogenic change influences peatland odonates.

No species showed a specific response to clearcut landscapes in any of the models. In *L. hudsonica*, the response to clearcut landscapes approximated the response to scrub landscapes, while in *Enallagma* and *C. shurtleffi* responses were more alike between clearcut and forest. Although this may lead some to believe the clearcut logging of forest surrounding peatland has little effect on the resident odonates, I think it is too soon to draw that conclusion. Firstly, the clearcuts surrounding my study bogs were recent, and considering odonates have long larval lives, the response to these landscape-level changes may be delayed. Secondly, from personal qualitative observations, the clearing of trees surrounding a peatland, sometimes right up to the bog margin, can drastically alter the wind and hydrology of the wetland. Both changes can have drastic effects on all pool inhabitants. Finally, at least one of my study taxa, *C. shurtleffi*, appears to use forest habitat, and tree harvest may remove elements required by this and other species. I believe that a study examining the effect of clearcut logging on peatland odonates should continue in the area, focusing on the age of clearcuts and time of regeneration, and allowing a response from these relatively long-lived insects to manifest itself.

Also needed are further empirical studies, especially field experiments, explicitly examining the hypotheses and conjectures based on circumstantial evidence and natural history observations. Experiments concentrating on movement would be valuable, especially those concerned with edge permeability, site fidelity and dispersal in different landscapes. All five odonate taxa responded to diffeences in landscape structure, but the patterns of response and the mechanisms involved were dissimilar. However, I believe dispersal to be a major factor influencing the different responses in the varied taxa. I consider this a significant first step in understanding the dynamics of peatland odonates in relation to the structure of landscapes and should provide a foundation for research in this study system.

Figure 2.1. Box plot of pH values in landscapes differing in surrounding habitat type. Whiskers encompass 95% of data. Median is displayed as horizontal line within each box.

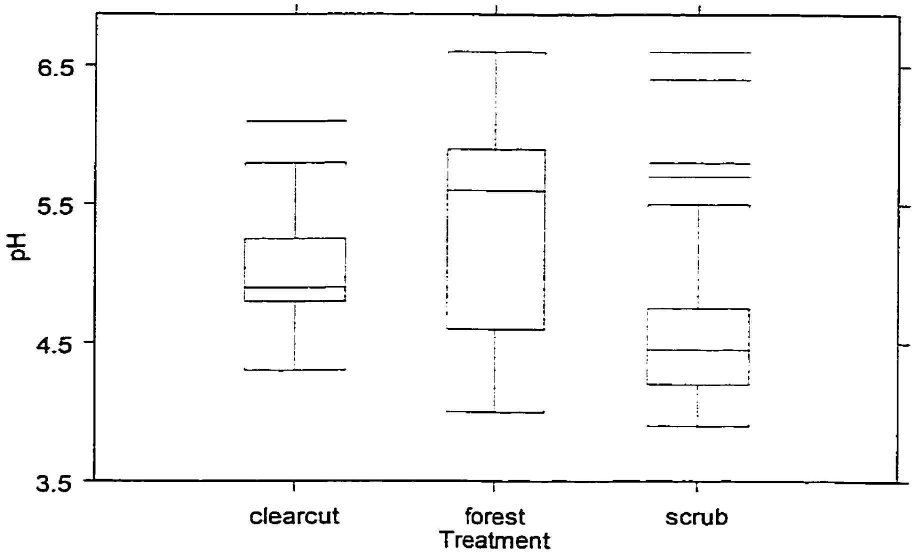

6.5
5.5
4.5
3.5
pH
clearcut
forest
scrub
Treatment

Figure 2.2. Histogram of head width of larval *Leucorrhinia hudsonica*. F, F-1, F-2... denote size classes I considered discrete for the purposes of analysis.

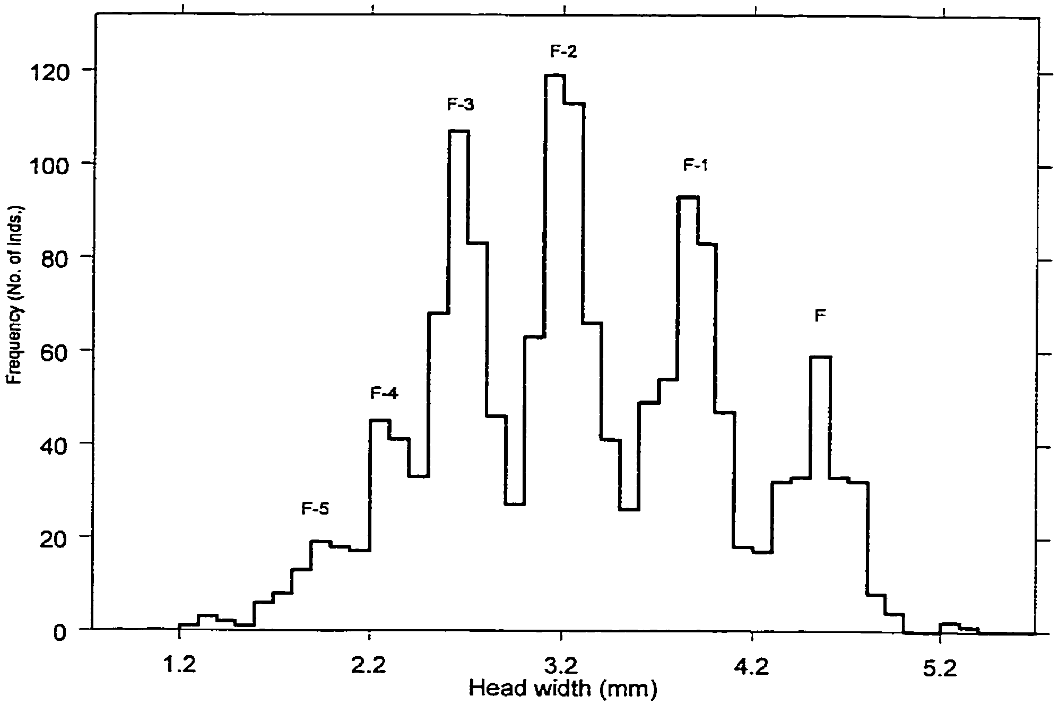

F-2
F-3
F-1
F
F-4
F-5
Frequency (No. of Inds.)
120
100
80
60
40
20
0
1.2
2.2
3.2
4.2
5.2
Head width (mm)

Figure 2.3. Partial residual plot from generalized linear models of the response of *Leucorrhinia hudsonica* to different habitat types surrounding the peatland. Squares= exuviae abundance, triangles = exuviae incidence, circles= larvae abundance.

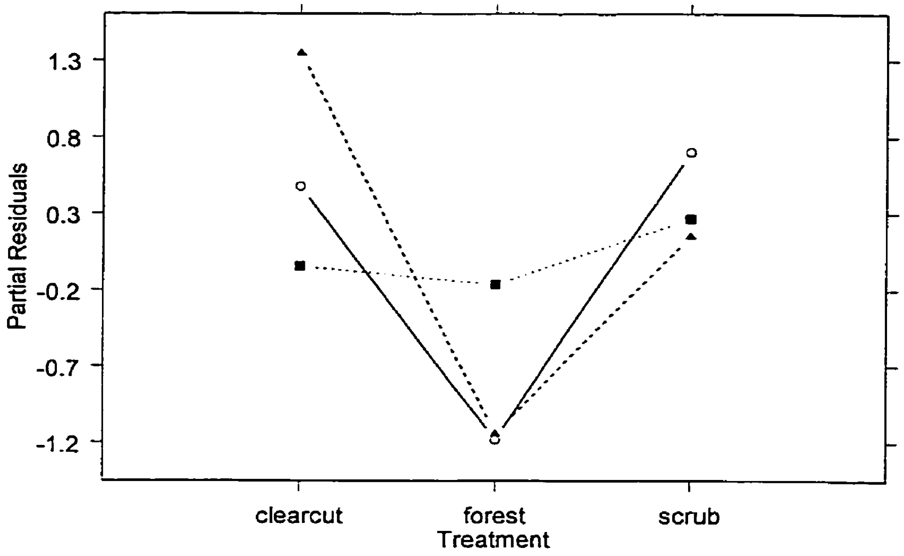

1.3
0.8
0.3
-0.2
-0.7
-1.2
Partial Residuals
clearcut
forest
scrub
Treatment

Figure 2.4. Partial residual plot from generalized linear models of the response of *Enallagma* spp. and *Cordulia shurtleffi* to different habitat types surrounding the peatland. Circles= *Enallagma* spp., triangles= *Cordulia shurtleffi*.

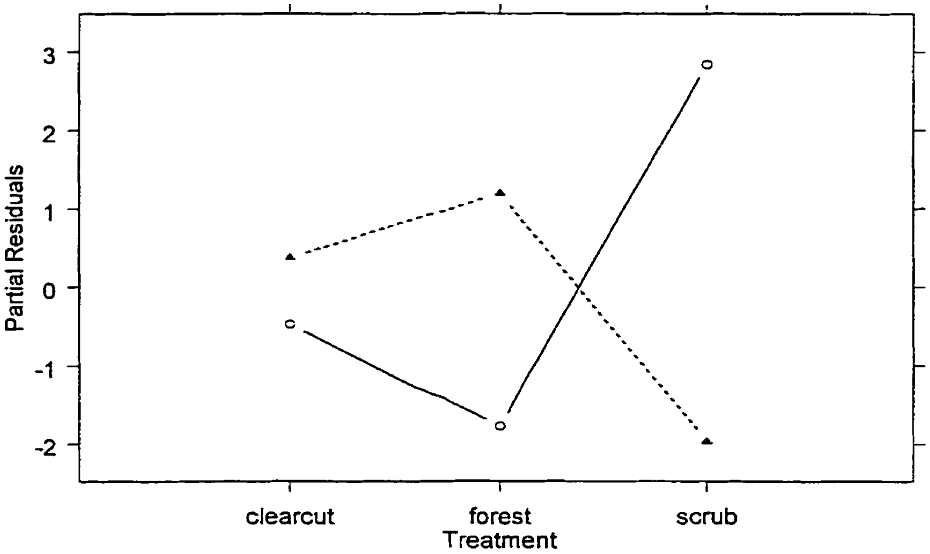

Partial Residuals
3
2
1
0
-1
-2
clearcut
forest
scrub
Treatment

Figure 2.5. Partial residual plot from generalized linear models of the response of *Leucorrhinia hudsonica* to different amounts of peatland. Triangles= exuviae abundance, circles= F-1: F-2 larval ratio.

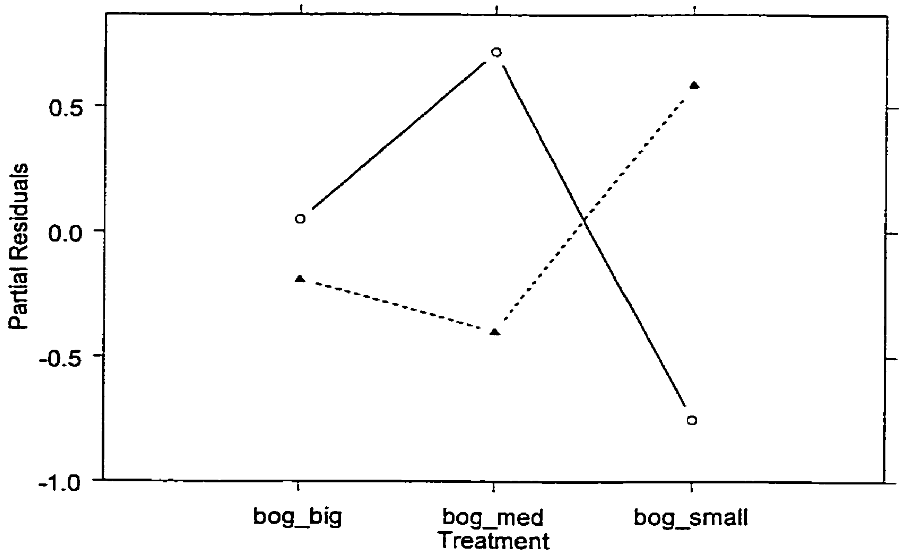
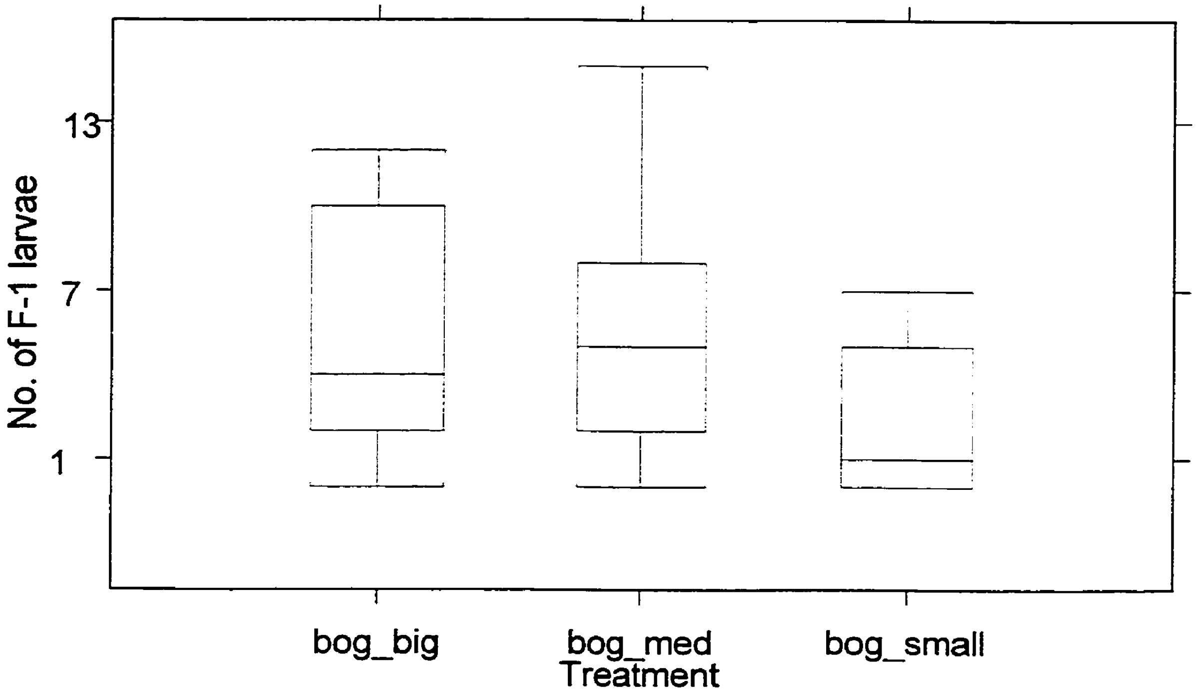

Partial Residuals
0.5
0.0
-0.5
-1.0
bog_big
bog_med
bog_small
Treatment

Figure 2.6. Box plots of abundance of F-1 and F-2 *Leucorrhinia hudsonica* larvae compared across landscapes differing in amount of peatland. Whiskers encompass 95% of data. Median is displayed as horizontal line within each box.


No. of F-1 larvae
13
7
1
bog_big
bog_med
bog_small
Treatment


No. of F-2 larvae
20
10
0
bog_big
bog_med
bog_small
Treatment

Figure 2.7. Partial residual plot from generalized linear models of the response of *Cordulia shurtleffi* and *Somatochlora septentrionalis* to different amounts of peatland. Circles= *Cordulia shurtleffi*, triangles= *Somatochlora septentrionalis*.

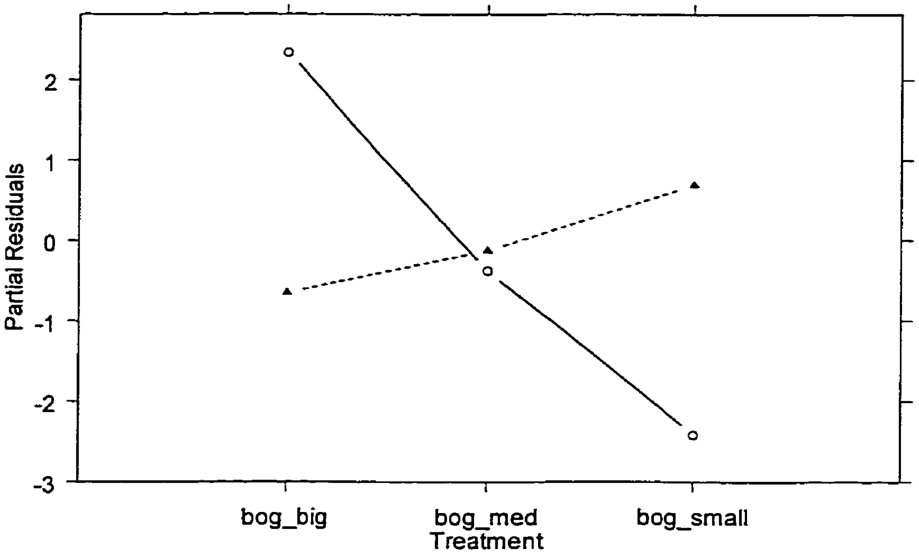

Partial Residuals
2
1
0
-1
-2
-3
bog_big
bog_med
bog_small
Treatment

Figure 2.8. Partial residual plot from generalized linear models of the response of *Enallagma* spp. and *Aeshna sitchensis* to different amounts of peatland. Circles= *Enallagma* spp., triangles= *Aeshna sitchensis.*

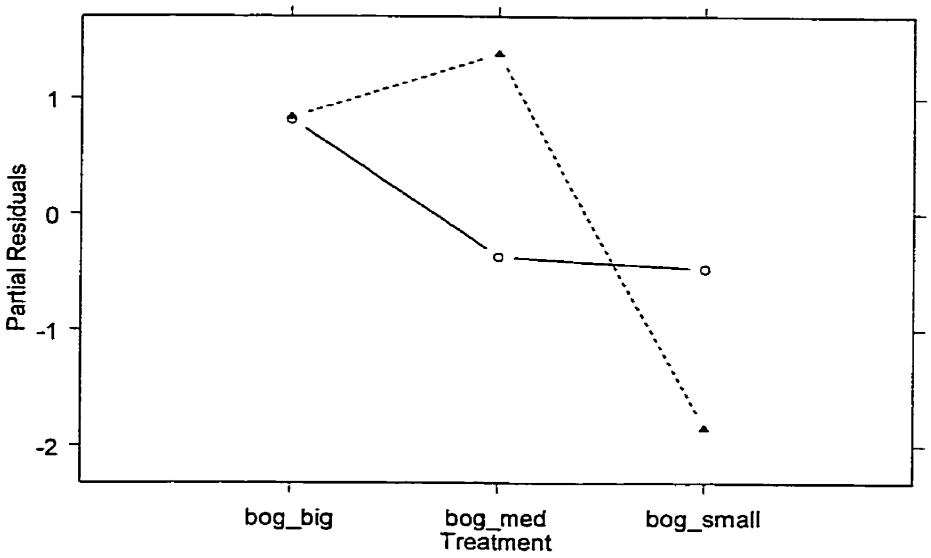

Partial Residuals
1
0
-1
-2
bog_big
bog_med
bog_small
Treatment

Table 2.1. Signs of coefficients of environmental covariates fit in generalized linear models of the incidence of *Enallagma* spp., *Leucorrhinia hudsonica*, *Aeshna sitchensis*, *Cordulia shurtleffi* and *Somatochlora septentrionalis*. Direction of coefficients are listed for only predictors that explain a significant ($p<0.1$) amount of variation. Parantheses indicate the estimate of the coefficient's value is poor (t-value <1.0). SUBMERGED did not significantly contribute to any model and is excluded. * Values listed for BOTTOM are relative to the factor *mud*. ** Values listed for SLOPE are relative to the factor *gradual*.

	Enallagma spp.		*A.sitchensis*		*C.shurtleffi*		*S.septentrionalis*		*L.hudsonica*	
	Matrix	Peatland	Matrix	Peatland	Matrix	Peatland	Matrix	Peatland	Matrix	Peatland
pH	(+)								-	-
log(DEPTH+1)	+	+	-		+	+			+	+
log(POOL SIZE)		+						+	+	
BOTTOM*										
mud/detritus	(+)	+					(+)			
mud/moss	(-)	(-)					(-)			
SLOPE** *steep*					(-)	+	-		(-)	
sqrt(PLANT RICHNESS)					+					
EMERGENT vegetation			(+)			-				
MUD	-	(-)			-		+		-	-

Table 2.2. Coefficient values of environmental covariates fit in generalized linear models of the larval ratios and larval abundance of *Leucorrhinia hudsonica*. Values are listed for only coefficients that explain a significant ($p<0.1$) amount of variation. Parantheses indicate the estimate of the coefficient's value is poor (t-value < 1.0). EMERGENT did not contribute significantly to any model and is excluded. * Values listed for BOTTOM are relative to the factor *mud*. ** Values listed for SLOPE are relative to the factor *gradual*.

	L. hudsonica					
	F: F-1 ratio		F-1: F-2 ratio		Abundance	
	Matrix	Peatland	Matrix	Peatland	Matrix	Peatland
pH					-1.86	
log(DEPTH+1)					(0.42)	
log(POOL SIZE)		(0.13)			0.98	
BOTTOM*						
mud/detritus		(-0.81)		(0.39)		
mud/moss		1.50		(-0.72)		
SLOPE** *steep*						0.51
sqrt(PLANT RICHNESS)		-4.44				
SUBMERGED vegetation			(-0.03)			
MUD			(-0.02)	-0.05	-0.06	

Table 2.3. Coefficient values of environmental covariates fit in generalized linear models of the abundance of *Leucorrhinia hudsonica* exuviae. Values are listed for only coefficients that explain a significant ($p<0.1$) amount of variation. Parantheses indicate the estimate of the coefficient's value is poor (t-value < 1.0). BOTTOM and EMERGENT did not significantly contribute to any model and is excluded. * Values listed for SLOPE are relative to the factor *gradual.*

	Abundance	
	Matrix	**Peatland**
PH	**-0.49**	**-0.29**
log(DEPTH+1)	**0.26**	**0.27**
log(POOL SIZE)	**0.12**	**(0.04)**
SLOPE* *steep*		**-0.08**
sqrt(PLANT RICHNESS)		**0.32**
SUBMERGED vegetation		**-0.01**
MUD	**-0.01**	**-0.02**

Table 2.4. Analysis of deviance tables. The response variables are the ratio and abundance of larval *Leucorrhinia hudsonica* in landscapes with differing matrix types. The models are Quasi-likelihood generalized linear models. The model of larval ratios was fit with binomial errors with an estimated dispersion parameters of 1.38. The model of larval abundance was fit with Poisson errors with an estimated dispersion parameter of 0.82.

		L.hudsonica Larvae					
		Abundance			**F-1: F-2 ratio**		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	29	54.84			32.79		
pH	1	20.2	20.31	<0.001	1.81	2.37	0.146
Environmental covariates	10	19.63	....	....	13.29	....	....
TREATMENT	2	1.37	0.69	0.518	3.65	2.40	0.127
LANDSCAPE	3	2.75	0.92	0.455	2.25	0.98	0.427
Residual	14	10.88			11.80		

Table 2.5. Analysis of deviance tables. The response variables are the incidence and abundance of *Leucorrhinia hudsonica* exuviae in landscapes with differing matrix types. The models are Quasi-likelihood generalized linear models. The model of incidence was fit with binomial errors with an estimated dispersion parameter of 0.80. The model of abundance was fit with Poisson errors with an estimated dispersion parameter of 0.68.

		L.hudsonica Exuviae					
		Incidence			**Abundance**		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	150	174.59			216.4		
pH	1	17.72	23.38	<0.001	19	25.31	<0.001
Environmental covariates	9	26.44	....	....	47.19	....	....
TREATMENT	2	0.66	0.44	0.647	6.5	4.33	0.015
LANDSCAPE	6	19.51	4.29	0.001	27.58	6.12	<0.001
BOG	7	15.53	2.93	0.007	9.18	1.75	0.104
Residual	125	94.73			106.95		

Table 2.6. Analysis of deviance tables. The response variables are the incidence of exuviae of *Enallagma* spp., *Aeshna sitchensis*, *Cordulia shurtleffi* and *Somatochlora septentrionalis* in landscapes with differing matrix types. The models are Quasi-likelihood generalized linear models fit with binomial errors. The estimated dispersion parameters, for the four models in order of presentation, are 0.83, 0.99, 1.49 and 1.22.

		Enallagma spp.			*A. sitchensis*			*C. shurtleffi*			*S. septentrionalis*		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	150	176.6			165.87			168.16			205.17		
pH	1	6.07	7.57	0.007	2.44	2.14	0.146	0.02	0.01	0.911	0.07	0.06	0.815
Environmental covariates	9	35.76	....	....	22.3	....	....	47.64	....	....	28.13	....	....
TREATMENT	2	4.72	2.94	0.057	4.67	2.04	0.134	10.48	3.01	0.053	0.18	0.07	0.932
LANDSCAPE	6	20.61	4.28	0.001	9.39	1.37	0.233	14.78	1.41	0.214	10.78	1.4	0.219
BOG	7	6.64	1.18	0.318	12.21	1.52	0.165	7.36	0.6	0.752	8.7	0.97	0.456
Residual	125	102.81			114.86			87.88			157.3		

Table 2.7. Analysis of deviance tables. The response variables are the ratios and the abundance of larval *Leucorrhinia hudsonica* in landscapes with different amounts of peatland. The models are Quasi-likelihood generalized linear models. The models of larval ratios were fit with binomial errors with estimated dispersion parameters of 1.38 and 1.42, respectively, while the model of abundance was fit with Poisson errors with an estimated dispersion parameter of 1.15.

		L.hudsonica Larvae								
		F: F-1 ratio			**F-1: F-2 ratio**			**Abundance**		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	29	66.66			78.88			44.27		
Environmental covariates	10	46.26	....	....	30.32	....	....	17.96	....	....
TREATMENT	2	1.06	0.38	0.688	29.35	10.34	0.056	3.38	1.86	0.192
LANDSCAPE	3	7.64	1.84	0.186	2.21	0.52	0.677	10.06	3.69	0.038
Residual	14	11.67			17.00			12.87		

Table 2.8. Analysis of deviance tables. The response variables are the incidence and the abundance of *Leucorrhinia hudsonica* exuviae in landscapes with different amounts of peatland. The models are Quasi-likelihood generalized linear models. The model of incidence was fit with binomial errors with an estimated dispersion parameter of 0.90, while the model of abundance was fit with Poisson errors with an estimated dispersion parameter of 0.73.

		L.hudsonica Exuviae					
		Incidence			**Abundance**		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	158	162.4			202.39		
Environmental covariates	10	28.07	....	....	54.48	....	....
TREATMENT	2	1.99	1	0.371	4.6	3.03	0.052
LANDSCAPE	6	8.25	1.38	0.228	4.96	1.09	0.372
BOG	8	15.52	1.94	0.058	11.75	1.94	0.059
Residual	132	108.57			126.6		

Table 2.9. Analysis of deviance tables. The response variables are the incidence of exuviae of *Enallagma* spp., *Aeshna sitchensis*, *Cordulia shurtleffi* and *Somatochlora septentrionalis* in landscapes with different amounts of peatland. The models are Quasi-likelihood generalized linear models fit with binomial errors. The estimated dispersion parameters, for the four models in order of presentation, are 0.93, 1.00, 1.01, and 1.09.

		Enallagma spp.			*A. sitchensis*			*C. shurtleffi*			*S. septentrionalis*		
Effect	**df**	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***	**Dev.**	***F***	***p(F)***
NULL	158	198			144.88			141.66			217.08		
Environmental covariates	10	41.33	....	....	6.01	....	....	24.86	....	....	26.4	....	....
TREATMENT	2	5.59	2.36	0.098	6.79	3.61	0.03	7.15	3.42	0.036	4.91	2.34	0.1
LANDSCAPE	6	24.01	3.38	0.004	18.03	3.2	0.006	8.78	1.4	0.219	5.06	0.81	0.566
BOG	8	10.76	1.14	0.342	7.16	0.95	0.476	7.27	0.87	0.544	23.3	2.78	0.007
Residual	132	116.31			106.89			93.6			157.42		

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Appendix 1

Natural History Observations of Gros Morne Greater Ecosystem Odonates

The following section contains written accounts for all species recorded within the Greater Ecosystem, detailing observations of natural history not previously discussed. Range maps (Figure A.1) show the distribution of records, to the nearest kilometre. Exact UTM coordinates for species recorded ten times or fewer are presented in Table A.1.

Lestidae

Only one member of this family was found during surveys, a widespread species found throughout Canada.

***Lestes disjunctus* (Common Spreadwing)**. This species was locally abundant in late summer, from early July onwards, flying commonly in peatland habitat. During exuvial surveys, adults were found captured by round-leaved sundew (*Drosera rotundifolia*) at the edge of bog pools. Most were mature adults, including a tandem pair captured together. Females oviposited in tandem with males, and were observed ovipositing in *Carex* spp. and *Juncus* spp. near the edge of bog pools.

Larvae were not captured during early June surveys, indicating that they were either too small to be detected at this time or they were absent from pool edges. No other species was noted to have such a relationship, including smaller coenagrionid damselflies. The first *L. disjunctus* larvae were found within study bog pools on June 29 (1999), just 16 days prior to the first emergence noted that year. They are considered to be univoltine in other parts of their range and have rapid growth (e.g. Duffy 1994), but it is difficult to believe that such a massive amount of growth, from an undetectable size to a size as large as other sympatric damselfly larvae, could occur in three weeks. Indeed, considering the size at which they were discovered in late June (length ~ 20 mm), and calculating their minimum size expected three weeks earlier based on Krishnaraj and Pritchard (1995) (length ~ 13 mm), they would certainly be detectable since smaller larvae (as small as 9 mm body length) from other damselfly species were detected using my methods. Furthermore, Larson and

House (1990) found *L. disjunctus* in their highest densities in pools greater than 10 m^2, and were absent from pools less than 1 m^2 in area. I believe *L. disjunctus* may pass the winter in the interior of the pools, avoiding detection earlier in the season, although they do use the emergent and submerged vegetation near the edge of pools during the summer. On July 20, 1999, a larva was observed at the edge of a bog pool using the submerged stem of a sedge (*Carex* sp.) to perch while it hunted for food. It sallied off its perch and captured prey swimming in free water approximately once every ten seconds during the two minutes of observation.

Coenagrionidae

Damselflies of this diverse family were in flight throughout the season, although abundance of particular species varied. Seven species were recorded within the Greater Ecosystem, six of which are taxa with northern distributions.

***Coenagrion interrogatum* (Subarctic Bluet).** This species has a northern distribution, having a known southern limit further north than any other damselfly in North America (Westfall and May 1996). In the peatlands of the Greater Ecosystem, it is common but localized. Although apparently absent from many bogs and fens visited, it appeared fairly abundant at others. Most *C. interrogatum* were observed close to bog pools in open bog, but one was collected in a small group of trees within an open peatland environment, after it had just captured a small spider.

No larvae or exuviae were identified, although adults were observed mating and ovipositing at or near bog pools during surveys over a period of about a month, with earliest emergence observed on June 15 (1998). On July 11, 1998, one pair was observed *in copu* in open bog greater than 20' from the nearest pool, perched on a tall sedge. Oviposition was generally done in tandem, as illustrated by Robert (1963), but I made one observation of underwater oviposition as described by Sawchyn and Gillot (1975), Fincke (1986) and Corbet (1999). During this occasion, after the pair was observed copulating, they perched in tandem on a sedge stem near the surface of a bog pool. As the female submerged below the surface, the male released his hold and remained stationary. Underwater, the female crawled around submerged woody material and green vegetation ovipositing repeatedly, for the six minutes of the observation.

***Coenagrion resolutum* (Taiga Bluet).** This species is a damselfly widespread throughout Canada, found further north than any other Zygoptera (Walker 1953, Westfall and May

1996). In the Greater Ecosystem, it is found in still water environments, including pools within bogs and fens and marshy bays of larger lakes. Perhaps due to it inhabiting a wider range of habitats, *C. resolutum* is more widespread throughout the Greater Ecosystem than its congener *C. interrogatum*. Its flight period lasts for about a month, with emergence starting in mid June, about a month later than that reported for southern Ontario (Walker 1953). Although adults were frequently observed in tandem around bog pools, no specific observations relating to mating behaviour were noted.

***Enallagma boreale* (Boreal Bluet).** The range of *E. boreale* extends across northern North America and is considered one of the most abundant *Enallagma* in northern Canada (Walker 1953, Westfall and May 1996). It is very similar to *E. cyathigerum* in size and pattern, but the two species are reproductively isolated through mechanical incompatibility (Paulson 1974). The two similar species may show differences in local distribution (Walker 1953, Garrison 1984). In the Greater Ecosystem, *E. boreale* was more common in the coastal region, inhabiting the same habitats as *Coenagrion resolutum*. Although present further east at higher elevations, the species was found infrequently and in lower numbers. Specific observations of reproductive behaviour were not noted.

***Enallagma cyathigerum* (Northern Bluet).** A Holarctic species found throughout Canada. This taxon is part of a complex in need of taxonomic revision (Westfall and May 1996). Individuals from Newfoundland are assigned to the nominate subspecies *E. c. cyathigerum* (Walker 1953, Westfall and May 1996), and some of my material from the Greater Ecosystem exhibit the characteristics of this race. However, other specimens, specifically males, display slightly smaller and hairier cerci than "typical" *E. c. cyathigerum*, although they resemble this taxon in other aspects of appearance and behaviour. These "aberrant" specimens may belong to an undescribed taxon, or be examples of either intrataxon variability or hybridization between *E. c. cyathigerum* and another recognized taxon (for further discussion, see Donnelly 1989, Donnelly 1998, McPeek 1998, May 1998, Tennessen 1998). Further sampling and analysis of these animals is needed to clarify the situation.

Our earliest observed emergence was on June 6 (1999), when a teneral male was collected as it emerged from a bog pool. This is four days earlier than that reported by Larson and House (1990). Flight of this species persisted through June and July, with flying adults seen as late as July 27 (1999), 12 days later than that reported by Larson and House (1990). *E. cyathigerum* is a common damselfly in the Greater Ecosystem, being more common away from the coast, different from that seen in *E. boreale*. With the two *Coenagrion*, it was abundant in peatland habitat in the Main River area, courting and mating near bog pools but spending some time (during maturation?) near the edge of the peatland habitat in tuckamore at the interface between open peatland and forest. Larvae were difficult to identify to species (see McPeek 1998), but Larson and House (1990) report *E. cyathigerum* as having its larval life extending three years in the bog pools of eastern Newfoundland, with a preference towards larger pools.

***Enallagma ebrium* (Marsh Bluet).** This damselfly generally prefers calcareous regions, found in abundance in marshes and eutrophic lake margins (Walker 1953). In the Greater Ecosystem, *E. ebrium* was found in this habitat type at one location within the coastal lowlands. However, adults were found in peatland habitat at two nearby locations, considered by Walker (1953) to be unusual but which may be more frequent (Holder and Kingsley 2000). At Berry Head Pond (coastal lake), males and females copulated in shrubby areas, perching on alder (*Alnus* sp.) within 20 m of the water, but oviposition was not noted.

***Ischnura verticalis* (Eastern Forktail).** One of the most abundant and ubiquitous odonates of southeastern Canada, *I. verticalis* is found from Manitoba through to Newfoundland inhabiting a wide range of wet habitats, from marshes to lakes to slow-moving streams. In the Greater Ecosystem, this damselfly is not as common as elsewhere in its range, but is instead infrequently seen in marshy bays of lakes and occasionally in bog pools within the coastal plain. My records are few in number, and observations are of few individuals at any one time. Two larvae were identified from collections in the Main River area, but no adults were seen during surveys away from coastal areas. Fully mature adults were observed in the coastal plain only in July, but based on these observations, and on their phenology in other parts of their range, emergence is earlier and probably occurs in June. Although both males and females were seen, no reproductive behaviour was observed.

Aeshnidae

This family of large dragonflies is represented by one genus, the diverse *Aeshna*, in the Gros Morne Greater Ecosystem. The seven species recorded were prevalent during the summer, from mid June through to the end of sampling. Only one other aeshnid species is known from Newfoundland, *A. canadensis* (Larson and Colbo 1983), and it may be expected to occur in the Greater Ecosystem based on its habitat preferences and known occurrence at nearby Spruce Brook (Walker 1958).

***Aeshna eremita* (Lake Darner)**. The largest and most widespread darner in the Greater Ecosystem, *A. eremita* is found across Canada in a variety of habitats, from large lakes to small bog pools. I most often observed this species in peatland habitat, but adults were also seen flying at the edges of lakes and along rivers, as well as along roads far from water. Earliest emergence was noted on June 20 (1999) and adults were flying until after surveys finished in August. Both homeochromatic and heterochromatic females were observed, and one female was noted ovipositing in *Carex* spp. and *Menyanthes trifoliata* along the borders of bog pools. No apparent habitat difference between heterochromatic and homeochromatic females, as presented by Brunelle (2000), was noted.

***Aeshna interrupta* (Variable Darner)**. A common darner found in the region in the same habitats as *A. eremita*. Although my material do not differ very much from a set of Ontario specimens with respect to physical measurements, such as hindwing length (Ontario: mean = 47.5 mm, n=8; Newfoundland: mean = 47.1, n=11), colour pattern was different. All observed and collected females and some males (e.g. three of seven collected male specimens) displayed convergent thoracic spots unlike the pattern shown by typical *A. i. interrupta* of eastern Canada (Figure A.2) and *A. i. lineata* of central Canada. However, specimens appearing to be of this colour form have been recorded once in each of New Brunswick, Prince Edward Island, Cape Breton Island and Maine (P.M. Brunelle, pers. comm.). This phenotype, also discussed by Walker (1958), may represent an undescribed taxon that more material and closer examination of specimens will clarify.

Copulation was observed only once, between a male and female that both showed the converging thoracic spots. They had just coupled in the air, flying low over the herb layer near a bog pool, when they were captured. Females oviposited alone at the edge of bog pools, although no specific observations were detailed in field notes.

***Aeshna juncea* (Sedge Darner).** This large darner is northern in distribution, found most often near peatland habitat, although some specimens were taken as they patrolled lakes and rivers. Along dirt roads running near open peatland, foraging males were seen flying linear circuits 2-3 m above the ground. However, individuals seen foraging along rivers and lakeshores flew much lower, rarely above 2 m and usually within a metre of the ground or water. Foraging was not noted in open peatland and no specific observations on mating and oviposition were made.

***Aeshna septentrionalis* (Azure Darner).** One of the two smallest darners in Newfoundland, *A. septentrionalis* was infrequently collected in parts of the Long Range and in the Main River area, most often associated with peatlands. Earliest emergence was noted on July 20 (1999), when an emerging adult was taken from the edge of a bog pool. In British Columbia, Whitehouse (1941) suggested *A. septentrionalis* emerged weeks earlier than *A. sitchensis* where the two species are sympatric, but my data, albeit poor for this species, do not support this argument (see Chapter 1). Oviposition was noted only once, with the female depositing eggs in the sphagnum at the edge of a pool apparently guarded by a hovering male. This non-contact guarding behaviour has not been previously noted for *A. septentrionalis*, although it is reported for other *Aeshna* (Utzeri and Raffi 1983).

Aeshna sitchensis **(Zigzag Darner).** *A. sitchensis* is the smallest and one of the commonest darners in the Greater Ecosystem. Exuviae were found as early as June 20 (1999), and the species was seen flying until the end of July. Unlike the similar *A. septentrionalis,* this species was found in peatlands at the coast as well as inland, sometimes the most abundant *Aeshna* in individual bogs and fens. Males and females were seen copulating while perched on low branches of tuckamore or on large rocks within open peatland. Females were always alone while they oviposited in saturated sphagnum near the pool edge, sometimes in pools that were <1 m^2 in area. The female would invariably perch on the bank of the pool facing outwards and probe her arching abdomen into the soft muck behind her, sometimes underwater. Contrary to the observations of Cannings (1982) in British Columbia, ovipositing females were always observed in open parts of the pool where the only vegetation was sphagnum, although other parts of the pool may have had stands of emergent plants. Males carefully patrolled bog pools but frequently rested on exposed mud and sphagnum within pools in much the same manner as ovipositing females, as has been reported by Cannings (1982).

Aeshna subarctica **(Subarctic Darner).** We infrequently found this species, always in peatlands and most records were of exuviae. Emergence from bog pools was observed twice, with the teneral males and exuviae collected as they clung to woody stems at the edge of the pool. No specific observations of reproduction or foraging were noted.

Aeshna umbrosa **(Shadow Darner).** This is another *Aeshna* found rarely during surveys. Adults were found foraging at scattered locations throughout the Greater Ecosystem along streams and lakes, and on forest roads. On July 21, 1998, a dead teneral adult male with exuviae was taken from an upland pool in the Long Range, surrounded by rock barren, ombrotrophic bog and tuckamore. Walker (1958) considered *A. umbrosa* to be found more typically in streams and small lakes near forest, but Brunelle (2000) observed them in abundance in a Cape Breton bog, including females ovipositing in the bog pools.

Gomphidae

Only one member of this family occurs in Newfoundland, and it is the gomphid with the northernmost distribution in North America. This species also occurs in the Greater Ecosystem.

***Ophiogomphus colubrinus* (Boreal Snaketail).** This attractive species was restricted to rivers in the Main River area. Adults were often seen during July and August patrolling along swift flowing streams and rivers with exposed rocks, but mature adults were observed on two occasions flying along forest roads over 500 m away from the nearest river. This species was seldom seen and exuviae were difficult to find because they were widely scattered on exposed rocks in the water and on the stream bank near the water's surface, usually underneath an overhang. I do not know if this is a result of the species choosing emergence sites that fit this description, or if it is due to these locations being more sheltered and thus protecting the exuviae from being washed or blown into the stream and carried away. Oviposition was not noted, but adults often perched near the surface of the water on exposed rocks within the river.

Corduliidae

This family is represented well in Newfoundland, but only by two genera. All eight Newfoundland species were recorded within the Greater Ecosystem. I expect two additional species of *Somatochlora* known for Labrador, *S. kennedyi* and *S. whitehousei* (Brunelle 1997), also occur on the island and could possibly occur in the Greater Ecosystem.

***Cordulia shurtleffi* (American Emerald).** A common species of peatlands in the Greater Ecosystem and much of Canada. The earliest emergence was recorded on June 6, 1999, ten days earlier than in 1998. Many times when a male intercepted a female at a bog pool they flew in tandem out of sight, presumably to copulate in the surrounding forest (Hilton 1983), but twice copulation was directly observed when it took place on tuckamore in open peatland. It is unknown how long copulation lasts since on both of these occasions copulation was discovered and interrupted in progress. Females oviposited by repeatedly dipping their abdomens in open water near the edges of bog pools, in the manner described by Hilton (1983). Individually marked adult males usually patrolled several pools in a circuit but would often disappear, only to return to the same circuit later during the same day. Hilton (1983) observed foraging only once, along a forest road, never at the bog pools themselves. On July 13, 1999, a female was captured in open forest between two bogs as it captured a deer fly (Tabanidae: *Chrysops* sp.) and perched on a spruce bough 3 m above the ground. Earlier observations I have made in other parts of their range suggest that foraging in this type of habitat is typical behaviour for *C. shurtleffi*.

***Somatochlora albicincta* (Ringed Emerald).** This species was recorded only five times, from locations near the coast and inland to the Main River area. Habitat was exclusively peatland, with larvae and exuviae found at bog pools. No observations of reproduction or foraging were made.

***Somatochlora cingulata* (Lake Emerald).** This species was recorded only five times, mostly from two locations in the Main River area. Larvae were found emerging on exposed rocky shorelines at one lake, but no mature adults were seen. At another lake, adults patrolled the shoreline and occasionally foraged over a shoreline clearing. No breeding behaviour was noted.

***Somatochlora forcipata* (Forcipate Emerald).** On only four occasions did I record this species. Walker and Corbet (1975) regarded *S. forcipata* as living its larval life in "small, spring-fed boggy streams," but Brunelle (1994) stated it is a species found in still waters, such as bogs, marshes and ponds in Atlantic Canada. My limited data agree with the latter. On July 4, 1998, I found adults emerging from very small puddles in an ombrotrophic bog, some puddles being much less than 1 m^2. My only other records are of adults flying along forest roads in the Main River area.

***Somatochlora franklini* (Delicate Emerald).** I observed this species only twice, both times in the Main River area. One individual was watched as it caught biting flies swarming around the observer in the middle of open peatland. The other observation was of an individual perched at the side of a forest road.

***Somatochlora minor* (Ocellated Emerald).** On July 13, 1999, a male was collected as it patrolled a small stream, about 1 m wide, flowing through open peatland. The male patrolled approximately 0.5 m above the stream's surface, below the profile of the surrounding peat, hovering for a few seconds at different locations before moving several metres and hovering again. Other males were seen along the same stream exhibiting the same behaviour, although their patrol routes never overlapped.

***Somatochlora septentrionalis* (Muskeg Emerald).** By far the commonest *Somatochlora*, found in peatland habitat throughout the Greater Ecosystem. Earliest emergence was recorded on June 16 (1999). Most adults emerged by crawling onto the bank and moved only a few centimetres from the water, but one individual on June 24, 1999, was watched for five minutes as it crawled approximately 65 cm from its natal pool, climbing up several different stems of *Scirpus* cf. *cespitosus* before choosing an "appropriate" one.

Adult males patrolled bog pools in much the same way as *C. shurtleffi*, but females oviposited more in the open, usually by quickly dipping their abdomen in the middle of open pools. Oviposition was noted at pools with steep banks and gradually sloping banks, supported by the presence of larvae in both types of pools, contrary to the statements of Whitehouse (1941).

***Somatochlora walshii* (Brush-tipped Emerald).** This species was seen only once. One male was collected on July 22, 1999, as it patrolled a slow stream bordered by tuckamore within a peatland, where the stream widened into a densely vegetated pool.

Libellulidae

Of this family, only eight species are known to occur in Newfoundland, five of which we collected in the Greater Ecosystem. One dragonfly was not identified to species, only to subgenus, and represented a sixth species for the Greater Ecosystem. *Sympetrum costiferum* was not recorded in the Greater Ecosystem but considering its preferred habitat of reedy marshes and bog, the species may occur at some locations near the coast in the Greater Ecosystem. *Pantala flavescens* is a wandering dragonfly that disperses long distances, and considering records from Cape Breton and other parts of Newfoundland, vagrants may be found in the Greater Ecosystem in the future.

***Leucorrhinia glacialis* (Crimson-ringed Whiteface).** Although this species is common in peatlands in the Maritimes, *L. glacialis* was rarely encountered in the Greater Ecosystem. Individual males were found at only three locations in peatlands near the coast during July, 1998. No behavioral observations were made.

***Leucorrhinia hudsonica* (Hudsonian Whiteface).** This small whiteface is the most common odonate in the Greater Ecosystem, occurring in greatest abundance in peatlands. Larvae were commonly found in the moss and mud at the bottom of bog pools, within a metre of the shore. One small larva was found within the water-filled of a *Sarracenia purpurea* near a bog pool (M.A. Krawchuk, pers. comm.), but it is unknown how the larva got into the leaf. During larval surveys in early June, larvae belonging to at least six discrete size classes were found (see Chapter 2), but it is unknown in what way they represent cohorts. However, the diversity of size classes indicates a number of cohorts coexist in these bog pools, with larvae growing for at least three or four years before maturation.

L. hudsonica was one of the earliest odonates to emerge, flying from June 6 onwards, peaking in numbers in late June and early July but quickly dropping off in numbers by the end of July. Adults emerged from bog pools near the shoreline, crawling only a few centimetres and emerging either on a plant or directly on the sphagnum mat or peat surrounding the pools, and exuviae were never found more than 10-20 cm from the pool edge.

Males were occasionally found resting on low plants in open peatland and resting or foraging near tuckamore at the edge of the peatland or along forest roads. However, they were most prevalent defending temporary territories along the edges of bog pools. General territorial behaviour was similar to the description of Hilton (1984), with males adopting the typical percher behaviour (see Corbet 1999) but territories were generally larger than 1 m^2, most often 100% larger or more. A typical 10 m^2 pool would have between one and four stationary males present in addition to transient males that would be chased away by the residents. On July 4, 1998, one isolated group of five bog pools chosen for observation had four individually marked resident males that took turns intercepting and chasing at least one transient male that repeatedly flew a circuit around each of the five pools, possibly indicating a second strategy for mate acquisition. At another set of pools, the same type of situation existed, but a transient male was successful in chasing away a marked resident male on one occasion and adopted his territory, only to lose it to the former resident when he returned a short while later.

Territorial males intercepted any other dragonfly that approached, including other species and even large *Aeshna*. Successful attempts to seize another dragonfly in tandem only involved conspecifics, although on one occasion a mature male was seen in tandem with a fresh teneral male several metres from the nearest pool. Intramale sperm transfer from the male's primary genitalia to his secondary genitalia was presumed to occur prior to seizing a female, as the only time it was seen to occur was during a July 19, 1999 observation of a male perched alone at the edge of a pool. The male brought the tip of his abdomen up to his secondary genitalia for a duration of 5-10 seconds, longer than the same behaviour described by Hilton (1984). Confirmation of sperm transfer was not made, but if the observed behaviour was accurately interpreted, *L. hudsonica* behaves differently from the congeneric *L. dubia* and *L. rubicunda* (Pajunen 1963). Soon after the presumed transfer, the male launched from his perch and chased a flying dragonfly (another male *L. hudsonica*).

Newly coupled *L. hudsonica* flew approximately 10 m and perched either on tuckamore or on open sphagnum mat within or at the edge of the peatland. After copulation, the pair separated and rested near each other until the female was ready to oviposit. The female dipped her abdomen to the surface of the pool about once per second, usually close to the shore, while the male hovered above and guarded her from molestation by other males. On some occasions, the guarding male left his place to intercept unattended females and begin copulatory proceedings with the newcomer.

I attempted to examine the movements of *L. hudsonica* by attaching tiny radar tags to the abdomens of captured males, using harmonic radar equipment similar to that reported by Roland et al. (1996). A radar tag was attached to the base of the abdomen with a minute amount of rubber cement, generally leaving the male unaffected, although excess glue occasionally spread onto the base of the hindwings affecting the insect's ability to fly; this was quickly corrected. Testing of the radar range showed a range of about 40 m, but effective range of the radar with tags mounted on dragonflies was only 10 m or less.

Attempts at tracking released individuals were met with limited success, as many dragonflies quickly flew across the release peatland and disappeared from sight, outside of the range of the harmonic radar. One release of 16 marked males with attached diodes was poorly timed because the release was made immediately prior to a lengthy cold and wet period. Individuals were relocated at the release site, and although most had not even moved from original perches three days later, others had moved several metres in the cold wet weather and were found using the harmonic radar. Others were flushed and tracked over a range of approximately 50 m, but were quickly lost. One individual was tracked for approximately 200 m and was lost for 15 minutes until careful hunting using the harmonic radar found it in tall grass approximately 75 m from where I last saw it. Despite my results, I believe harmonic radar may be useful in tracking *L. hudsonica*, especially for studies of short-range dispersal or territoriality.

***Leucorrhinia proxima* (Red-waisted Whiteface).** My records of this species in the Greater Ecosystem pertain to exuviae only, easily separated from the other two species by the presence of distinct dorsal spines and the lack of dark longitudinal stripes on the ventral surface of the abdomen. Although some larval *L. hudsonica* lacked these distinct stripes, they could be separated from *L. proxima* by the absence of distinct dorsal spines. *L. proxima* exuviae were found at bog pools in peatlands near the coast.

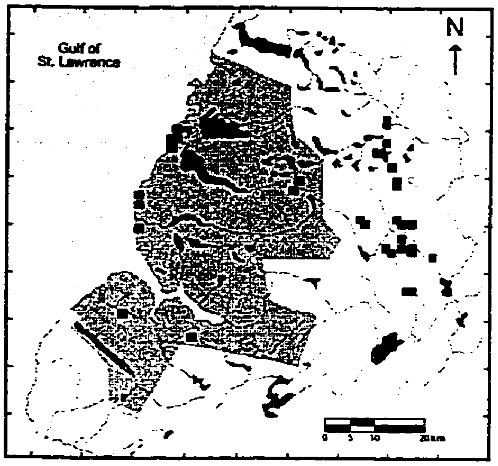
***Libellula quadrimaculata* (Four-spotted Skimmer).** A common and widespread dragonfly, it is considered by Walker and Corbet (1975) to be the commonest large skimmer in Canada and one of the earliest to emerge in the spring. My data support both statements. Our earliest date for flight was May 31 (1999), and adults were seen through to late July in peatlands. Exuviae found around bog pools were always close to the shore, never more than 20 cm away from the open water and usually clinging to the sphagnum mat rather than on erect vegetation.

Males were active and did not perch as much as *L. hudsonica*, but instead patrolled several nearby bog pools and were easily distracted by passing odonates. Males typically approached all large dragonflies that came near, especially *C. shurtleffi* and *S. septentrionalis* in addition to conspecifics, and would chase them sometimes out of sight. Copulation was brief and in the air, followed by the female ovipositing either alone or guarded by the male. On one occasion, a male guarded a female as she oviposited in five separate bog pools then unsuccessfully tried copulating with her a second time. Foraging was not noted.

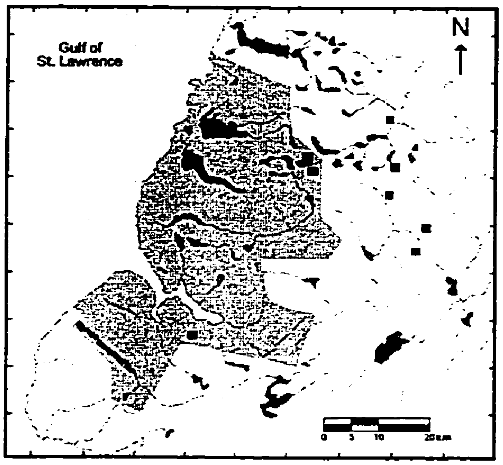
Sympetrum danae **(Black Meadowhawk).** This dark meadowhawk is probably more widespread in the Greater Ecosystem than our records indicate, as the bulk of its flight period (August) occurs after my surveys were completed. It is a denizen of peatlands, enduring its larval life in bog pools, with emergence occurring in early August. I found it mostly in coastal peatland but I have one record of a teneral female in the Main River area on August 5, 1999. This species was very wary and would readily fly high to escape from danger, including pairs in tandem. Females coupled with males were seen ovipositing in bog pools by tapping their abdomens to the pool surface at a rate faster than once per second. Preference was towards depositing eggs in patches of exposed mud within pools rather than in the open sections as suggested by Walker and Corbet (1975).

***Sympetrum* cf. *internum* (meadowhawk sp.).** A male *Sympetrum* was seen on August 2, 1998, that appeared to be predominantly red with a tan face. Attempts to capture it failed, and identification to species was impossible from just field observation. However, its coloration indicate it belonged to the subgenus *Kalosympetrum* (Carle 1993), of which only one species is known for Newfoundland, *S. internum*.

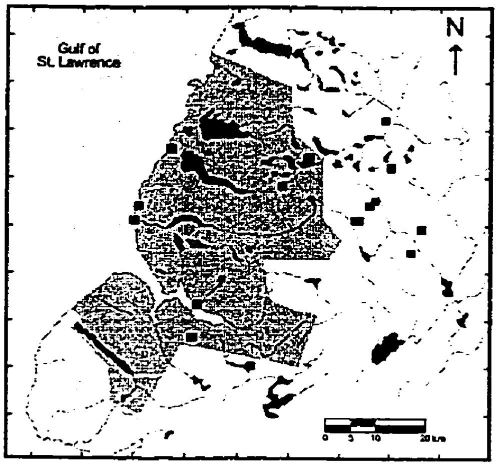
Figure A.1. Maps of distribution for all species recorded within the Gros Morne Greater Ecosystem during 1998 and 1999. All records are presented, including larvae, exuviae and adults. Location UTMs were rounded down to the nearest kilometre for mapping purposes. Exact UTMs for rare taxa (recorded fewer than ten times during the study) are presented in Table A.1. (5 pp.)



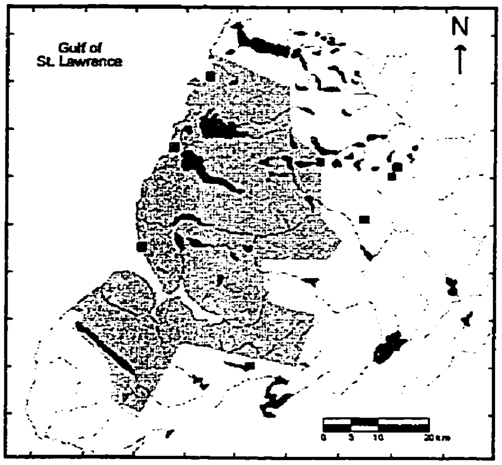
Lestes disjunctus



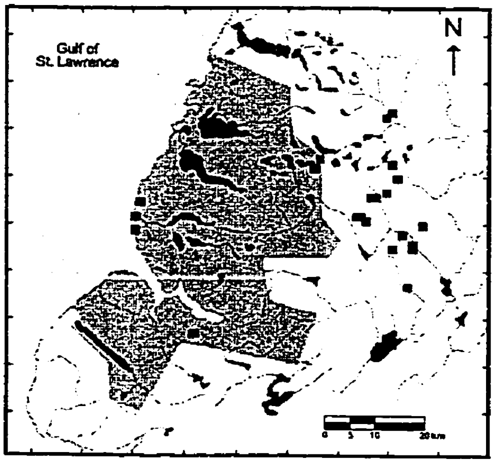
Coenagrion interrogatum



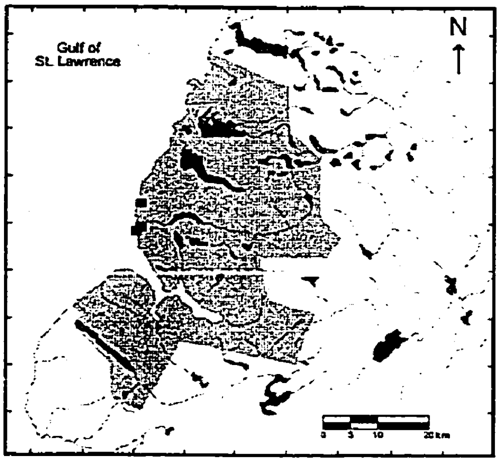
Coenagrion resolutum



Enallagma boreale

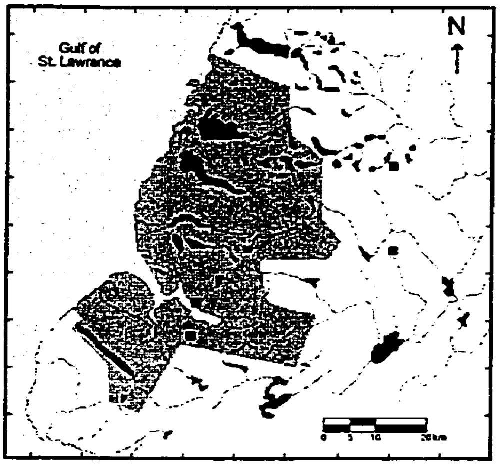


Enallagma cyathigerum

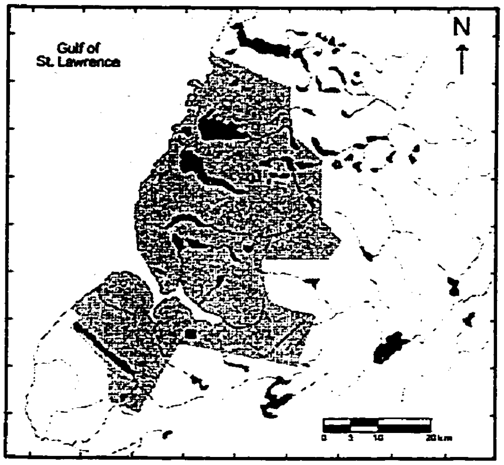


Enallagma ebrium

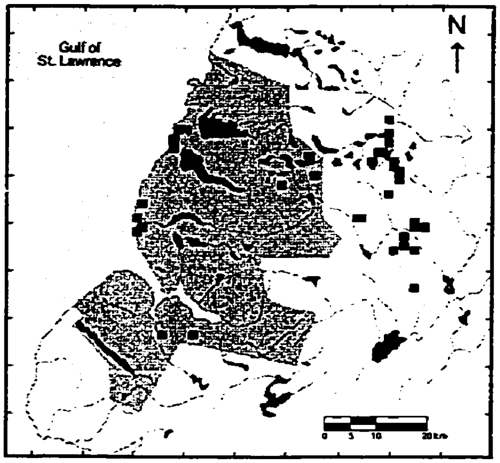
Figure A.1 cont'd.



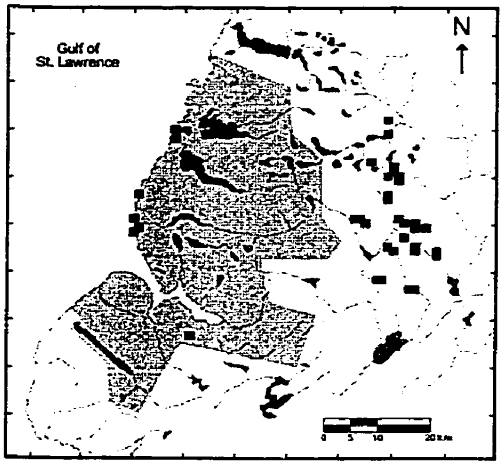
Ischnura verticalis



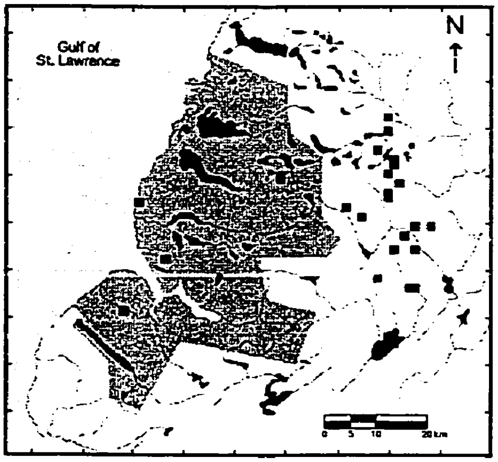
Nehalennia irene



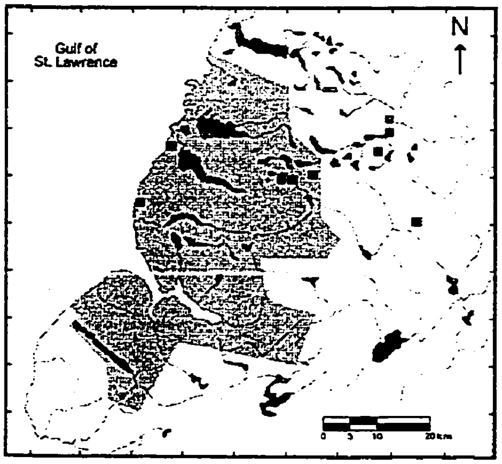
Aeshna eremita



Aeshna interrupta



Aeshna juncea



Aeshna septentrionalis

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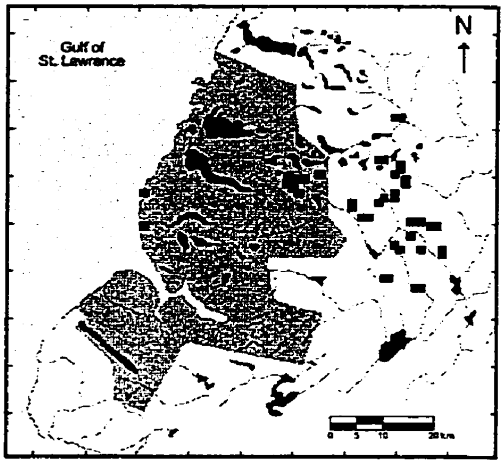
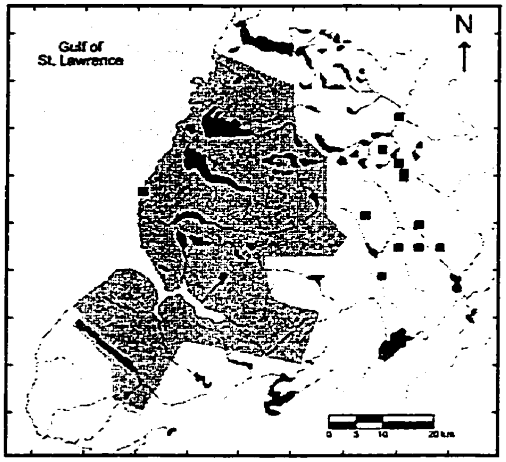
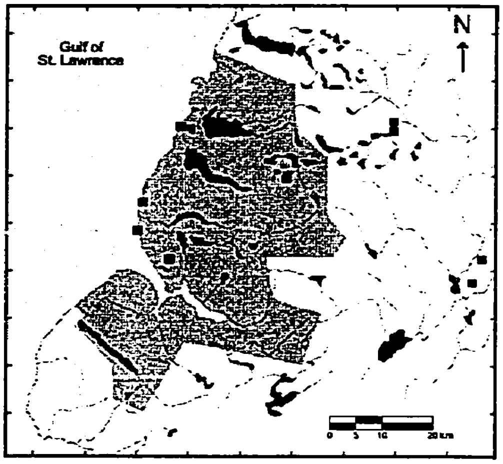


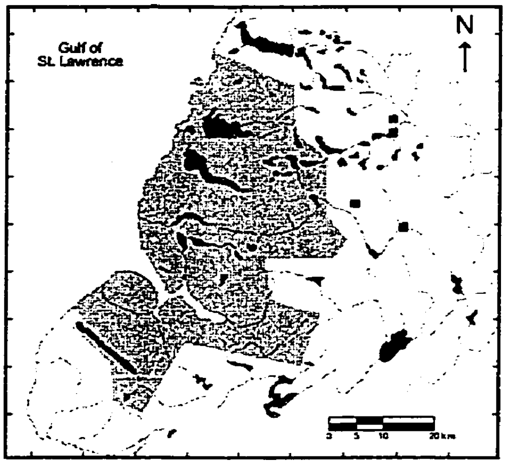
Aeshna sitchensis



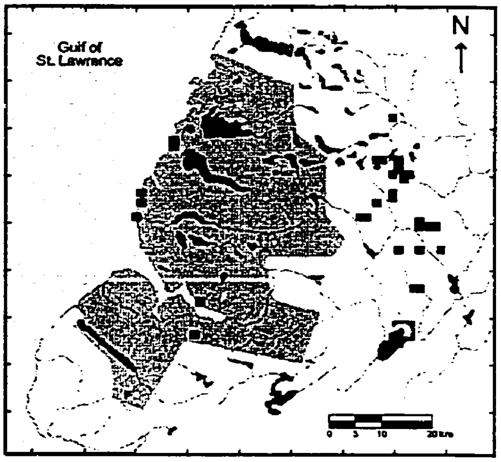
Aeshna subarctica



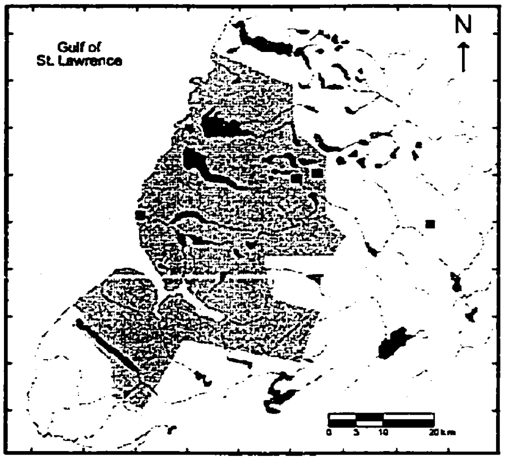
Aeshna umbrosa



Ophiogomphus colubrinus



Cordulia shurtleffi



Somatochlora albicincta

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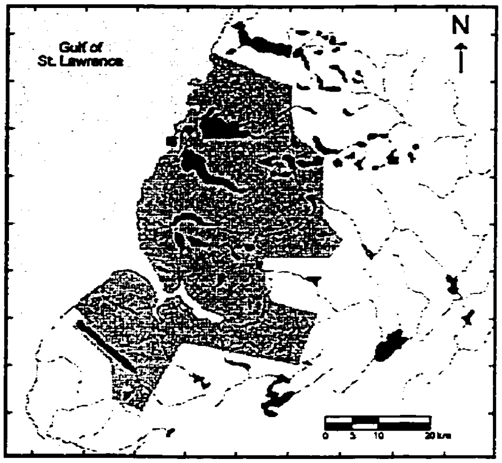
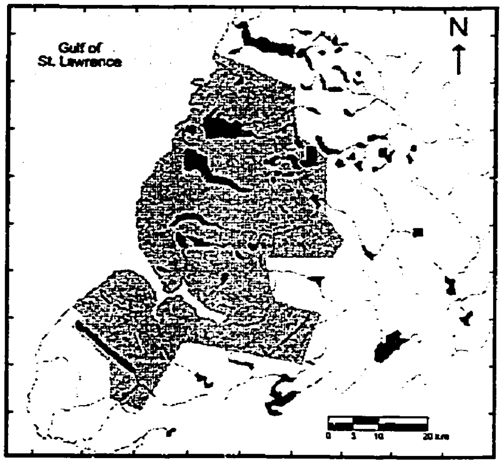
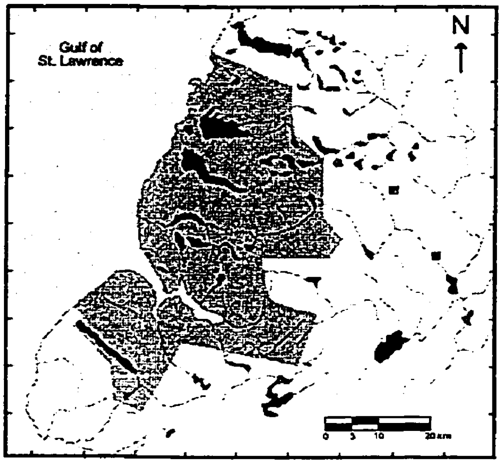


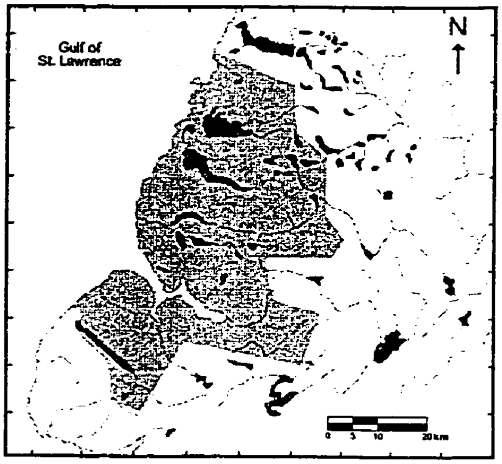
Somatochlora cingulata



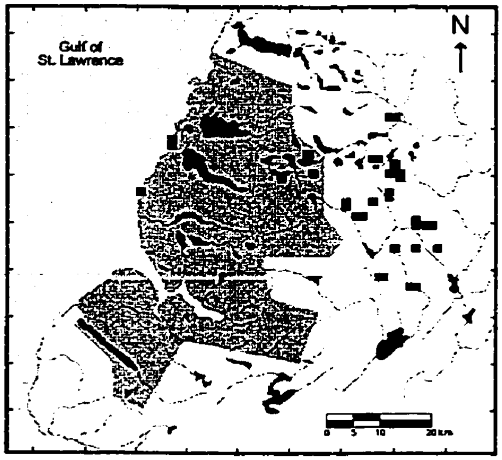
Somatochlora forcipata



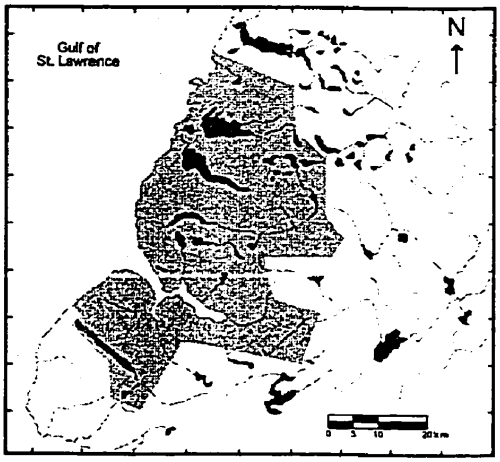
Somatochlora franklini



Somatochlora minor



Somatochlora septentrionalis



Somatochlora walshii

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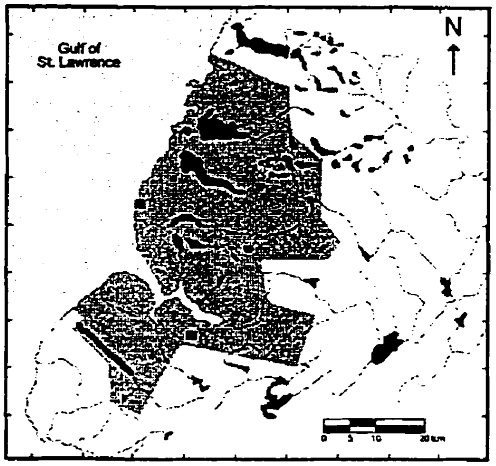
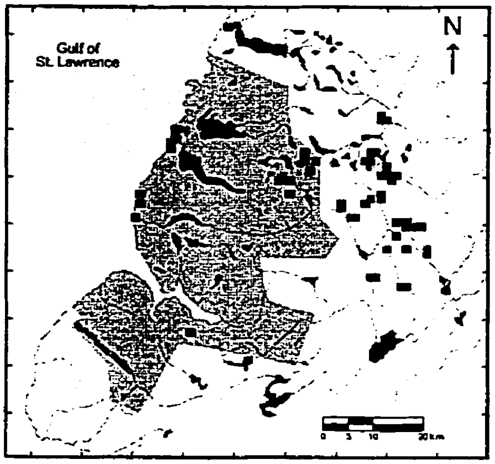
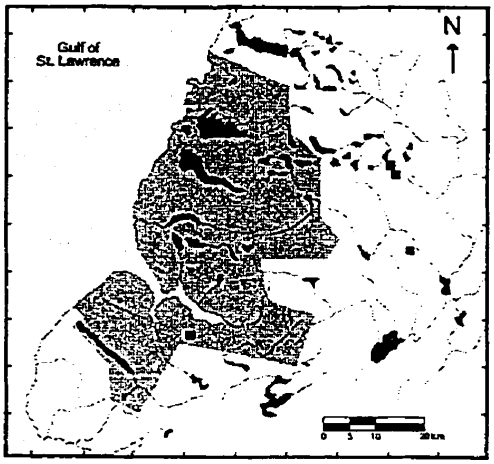


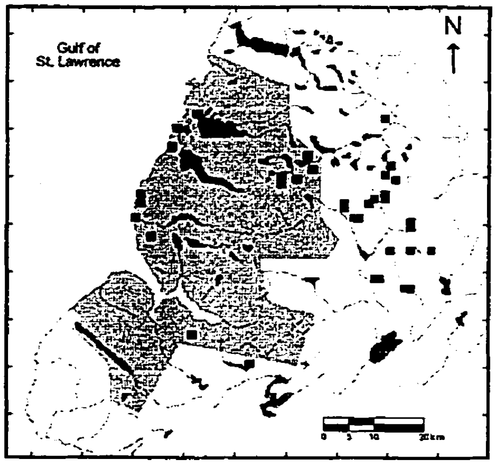
Leucorrhinia glacialis



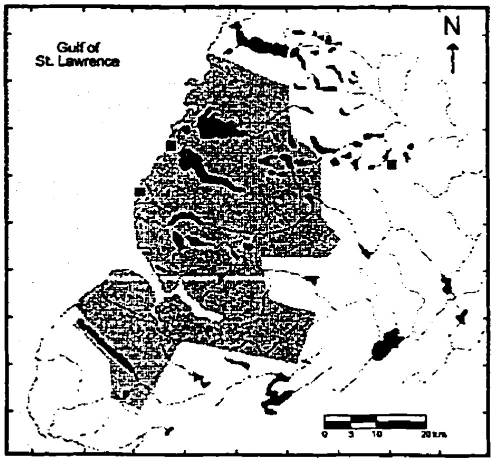
Leucorrhinia hudsonica



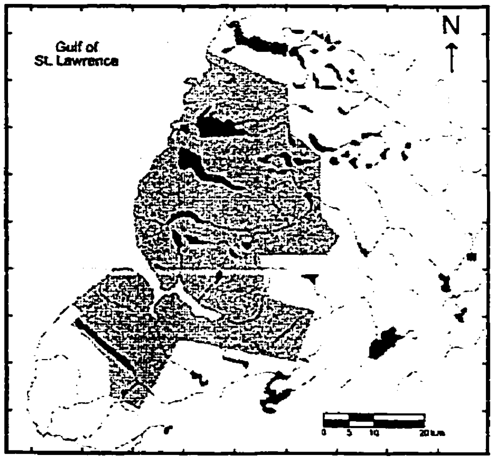
Leucorrhinia proxima



Libellula quadrimaculata



Sympetrum danae



Sympetrum cf. *internum*

Figure A.2. Scans of *Aeshna interrupta* specimens from the Main River area. a) Female exhibiting convergent thoracic spots, collected on 1999.07.22, at UTM 21,479300,5519100. b) Male exhibiting typical *A. i. interrupta* thoracic pattern, collected on 1999.07.22, at UTM 21,481600,5497200.

a)

b)

Table A.1. Collection data for odonate species found up to ten times. UTM coordinates are based on North American Datum 1927. Dates are in the format yyyy.mm.dd. Observation type is self explanatory. Other information may be acquired by directly contacting the author. (2 pp.)

Scientific Name	**Date**	**UTM**	**Observation Type**
Aeshna septentrionalis	1998.07.15	21,437800,5516200	exuviae
Aeshna septentrionalis	1998.07.19	21,459400,5508500	adult
Aeshna septentrionalis	1998.07.22	21,461000,5509000	adult
Aeshna septentrionalis	1998.07.27	21,465000,5510000	adult
Aeshna septentrionalis	1998.07.28	21,465000,5510000	adult
Aeshna septentrionalis	1998.07.29	21,431500,5503800	exuviae
Aeshna septentrionalis	1998.08.01	21,477256,5515171	adult
Aeshna septentrionalis	1998.08.05	21,479300,5519100	adult
Aeshna septentrionalis	1998.08.08	21,437800,5516200	adult
Aeshna septentrionalis	1999.07.20	21,484366,5500086	adult & exuviae
Aeshna septentrionalis	1999.07.26	21,479000,5522400	adult
Aeshna subarctica	1998.07.17	21,432000,5505700	exuviae
Aeshna subarctica	1998.07.17	21,432000,5506300	exuviae
Aeshna subarctica	1998.08.01	21,477256,5515171	adult
Aeshna subarctica	1999.06.10	21,479578,5522374	larva
Aeshna subarctica	1999.06.26	21,480088,5493996	exuviae
Aeshna subarctica	1999.06.27	21,483931,5494079	exuviae
Aeshna subarctica	1999.06.27	21,477011,5488060	exuviae
Aeshna subarctica	1999.06.27	21,477055,5487985	exuviae
Aeshna subarctica	1999.06.28	21,488250,5493834	exuviae
Aeshna subarctica	1999.06.29	21,480050,5512400	larva
Aeshna subarctica	1999.07.10	21,473821,5500953	exuviae
Aeshna subarctica	1999.07.11	21,481430,5509637	exuviae
Aeshna subarctica	1999.07.11	21,481083,5509302	adult & exuviae
Aeshna subarctica	1999.07.20	21,483660,5499451	exuviae
Aeshna umbrosa	1998.07.	21,431500,5503500	adult
Aeshna umbrosa	1998.07.16	21,438500,5520000	exuviae
Aeshna umbrosa	1998.07.21	21,459400,5508500	adult & exuviae
Aeshna umbrosa	1998.07.29	21,431500,5503800	exuviae
Aeshna umbrosa	1998.08.02	21,493500,5486500	adult
Aeshna umbrosa	1998.08.02	21,495500,5491800	adult
Aeshna umbrosa	1998.08.05	21,479300,5519100	adult
Aeshna umbrosa	1998.08.05	21,478500,5521000	adult
Aeshna umbrosa	1998.08.06	21,479300,5519100	adult
Aeshna umbrosa	1998.08.08	21,431000,5498400	adult
Aeshna umbrosa	1998.08.08	21,436600,5491500	adult
Enallagma ebrium	1998.07.	21,431000,5498400	adult
Enallagma ebrium	1998.07.20	21,431500,5498500	adult
Enallagma ebrium	1998.07.25	21,431000,5498400	adult
Enallagma ebrium	1998.07.25	21,431900,5504300	adult
Enallagma ebrium	1998.08.08	21,431000,5498400	adult
Ischnura verticalis	1998.07.11	21,441500,5475800	adult
Ischnura verticalis	1998.07.11	21,442800,5483400	adult
Ischnura verticalis	1998.07.13	21,441500,5475800	adult
Ischnura verticalis	1999.06.05	21,480050,5512400	larva
Ischnura verticalis	1999.06.06	21,480109,5494018	larva
Leucorrhinia glacialis	1998.06.27	21,441500,5475800	adult
Leucorrhinia glacialis	1998.07.05	21,431500,5503500	adult
Leucorrhinia glacialis	1998.07.13	21,441500,5475800	adult
Leucorrhinia proxima	1998.06.27	21,441500,5475800	exuviae
Leucorrhinia proxima	1999.06.04	21,480050,5512400	larva
Leucorrhinia proxima	1999.06.16	21,484091,5494067	larva
Leucorrhinia proxima	1999.06.23	21,481426,5509641	exuviae
Nehalennia irene	1998.06.27	21,441500,5475800	adult
Nehalennia irene	1998.07.13	21,441500,5475800	adult

Table A.1 cont'd.

Scientific Name	**Date**	**UTM**	**Observation Type**
Ophiogomphus colubrinus	1998.08.06	21,479300,5519100	adult & exuviae
Ophiogomphus colubrinus	1999.07.09	21,479300,5519100	exuviae
Ophiogomphus colubrinus	1999.07.10	21,472300,5503500	exuviae
Ophiogomphus colubrinus	1999.07.10	21,480800,5499200	exuviae
Ophiogomphus colubrinus	1999.07.26	21,479000,5522400	adult
Somatochlora albicincta	1998.07.22	21,461000,5509000	adult
Somatochlora albicincta	1998.07.27	21,465000,5510000	adult
Somatochlora albicincta	1998.07.28	21,465000,5510000	exuviae
Somatochlora albicincta	1999.05.23	21,430500,5501100	larva
Somatochlora albicincta	1999.07.15	21,486057,5498890	exuviae
Somatochlora cingulata	1998.07.01	21,465900,5512900	adult & exuviae
Somatochlora cingulata	1998.07.02	21,465900,5512900	adult & exuviae
Somatochlora cingulata	1998.08.08	21,437800,5516500	exuviae
Somatochlora cingulata	1999.07.17	21,479500,5513400	adult
Somatochlora cingulata	1999.07.24	21,479500,5513400	adult
Somatochlora forcipata	1998.07.04	21,464400,5514200	adult & exuviae
Somatochlora forcipata	1998.07.04	21,464178,5515015	adult & exuviae
Somatochlora forcipata	1998.08.01	21,477500,5515300	adult
Somatochlora forcipata	1999.07.15	21,485000,5498000	adult
Somatochlora franklini	1999.07.13	21,479900,5506800	adult
Somatochlora franklini	1999.08.02	21,488200,5493400	adult
Somatochlora minor	1999.07.13	21,479000,5506000	adult
Somatochlora walshii	1999.07.22	21,481700,5497200	adult
Sympetrum danae	1998.07.28	21,432000,5506000	adult
Sympetrum danae	1998.08.08	21,437800,5516200	adult & exuviae
Sympetrum danae	1998.08.08	21,432000,5506000	adult
Sympetrum danae	1999.08.05	21,480050,5512400	adult
Sympetrum internum	1998.08.02	21,495500,5491800	adult

Appendix 2

Raw data for study pools - Pool characteristics

Field Explanations

Trtmnt = Treatment (scrub a.k.a. bog_medium; forest; clearcut; bog_big; or bog_sml = bog_small)

Lndscpe = code letter unique within a treatment

Bog = code letter unique within a landscape

Pool = code number unique within a bog

landuniq = unique landscape code letter

pooluniq = unique pool code

Northing = UTM northing, NAD 1927

Easting = UTM easting, NAD 1927

Elev = elevation, in metres

pH = pH, to nearest 0.1 unit

Depth = depth, in centimetres

Pl.area = pool area, in square metres

Slope = bank slope (gradual or steep)

Bottom = bottom substrate (mud/det = mud/detritus; mud/mo = mud/moss; or mud)

plnt.rich = plant species richness at pool

Peri.em = percent cover of emergent vegetation at pool, as measured by perimeter occupied

Area.em = percent cover of emergent vegetation at pool, as measured by area occupied

Subm = percent cover of submerged vegetation at pool, as measured by area occupied

mud = percent cover of exposed mud at pool, as measured by area occupied

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
scrub	a	x	1	A	Ax1	5494064	484107	344	4.2	86	27.918	steep	mud/det	6	90	30	40	0
scrub	a	x	2	A	Ax2	5494067	484092	344	4	2	15.228	gradual	mud	9	90	30	40	0
scrub	a	x	3	A	Ax3	5494057	484095	345	4.1	34	7.896	steep	mud/mo	8	100	70	90	0
scrub	a	x	4	A	Ax4	5494069	484116	345	4	7	14.1	gradual	mud/mo	8	100	60	60	10
scrub	a	x	5	A	Ax5	5494071	484110	345	4	10	10.434	steep	mud/mo	10	100	70	70	10
scrub	a	x	6	A	Ax6	5494105	483944	341	4.1	14	8.178	gradual	mud/det	7	40	60	50	20
scrub	a	x	7	A	Ax7	5494080	483932	343	4	72	9.87	steep	mud/mo	7	100	60	100	0
scrub	a	x	8	A	Ax8	5494087	483932	343	4	69	19.458	steep	mud/mo	7	100	40	90	0
scrub	a	x	9	A	Ax9	5494098	483948	343	4	24	24.252	gradual	mud	7	40	40	40	20
scrub	a	x	10	A	Ax10	5494094	483947	343	3.9	29	5.076	steep	mud/mo	4	100	10	100	0
scrub	a	y	1	A	Ay1	5493684	483997	362	4.2	63	44.556	gradual	mud	9	90	70	50	20
scrub	a	y	2	A	Ay2	5493687	484010	362	4.5	79	32.148	steep	mud/det	8	80	10	60	0
scrub	a	y	3	A	Ay3	5493680	483976	361	4.3	94	76.422	gradual	mud	9	90	30	40	10
scrub	a	y	4	A	Ay4	5493683	484003	362	4.1	18	10.716	gradual	mud	7	90	70	40	50
scrub	a	y	5	A	Ay5	5493686	483989	362	4.2	10	13.536	gradual	mud	9	80	50	30	60
scrub	a	y	6	A	Ay6	5493744	483878	359	4.9	40	18.048	gradual	mud	8	60	50	30	40
scrub	a	y	7	A	Ay7	5493747	483925	360	4.1	82	37.506	steep	mud/det	9	90	20	30	0
scrub	a	y	8	A	Ay8	5493738	483908	360	4.3	59	28.764	steep	mud/det	10	90	40	40	0
scrub	a	y	9	A	Ay9	5493736	483919	360	3.9	21	33.558	gradual	mud/det	7	100	80	80	30
scrub	a	y	10	A	Ay10	5493755	483920	360	4.2	104	37.506	steep	mud	9	30	10	20	10
forest	a	x	1	B	Bx1	5493799	488289	244	5.6	0	67.962	steep	mud/det	8	60	30	40	30
forest	a	x	2	B	Bx2	5493795	488288	244	5.6	3	39.48	steep	mud	12	80	40	40	30
forest	a	x	3	B	Bx3	5493792	488288	244	6	0	13.818	gradual	mud/det	7	80	50	40	50
forest	a	x	4	B	Bx4	5493807	488284	244	4.5	0	22.842	gradual	mud	8	70	30	10	50
forest	a	x	5	B	Bx5	5493799	488282	243	5.9	1	16.356	steep	mud/det	11	80	50	50	40
forest	a	x	6	B	Bx6	5493845	488244	242	4.4	26	12.408	gradual	mud	10	80	60	40	50
forest	a	x	7	B	Bx7	5493835	488245	243	4.5	28	9.024	gradual	mud	10	80	60	20	40
forest	a	x	8	B	Bx8	5493847	488243	242	4	24	2.82	gradual	mud	11	90	40	30	70
forest	a	x	9	B	Bx9	5493834	488250	242	4.3	12	18.048	gradual	mud/det	8	80	30	80	90
forest	a	x	10	B	Bx10	5493828	488245	243	4.1	10	9.588	gradual	mud	9	100	20	10	90
forest	a	y	1	B	By1	5493503	488286	233	6.6	25	8.178	gradual	mud/mo	9	60	40	70	20
forest	a	y	2	B	By2	5493501	488289	233	6.4	19	4.794	gradual	mud/mo	9	70	50	60	40
forest	a	y	3	B	By3	5493501	488282	232	6.2	19	5.358	gradual	mud/mo	10	90	70	60	30
forest	a	y	4	B	By4	5493496	488288	232	6.3	34	2.538	gradual	mud/mo	9	70	40	60	10
forest	a	y	5	B	By5	5493502	488275	233	5.7	26	10.998	gradual	mud	10	80	40	60	20
forest	a	y	6	B	By6	5493488	488272	232	6.4	24	16.074	gradual	mud/det	7	70	40	70	20
forest	a	y	7	B	By7	5493488	488274	232	6	16	14.1	gradual	mud	11	80	80	70	20
forest	a	y	8	B	By8	5493493	488271	232	6.1	12	26.79	gradual	mud	9	70	50	60	20

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
forest	a	y	9	B	By9	5493492	488270	231	6	24	17.202	gradual	mud/det	8	100	70	80	10
forest	a	y	10	B	By10	5493495	488274	232	6.4	19	9.588	gradual	mud	10	100	60	70	20
clearcut	a	x	1	C	Cx1	5494019	480109	378	4.8	36	54.144	steep	mud/det	11	70	20	30	10
clearcut	a	x	2	C	Cx2	5494021	480122	378	4.8	18	43.992	steep	mud	8	40	10	20	30
clearcut	a	x	3	C	Cx3	5494019	480122	378	4.8	53	36.942	steep	mud	9	40	10	40	0
clearcut	a	x	4	C	Cx4	5494010	480115	378	4.9	100	5.64	steep	mud/mo	10	60	20	30	10
clearcut	a	x	5	C	Cx5	5494004	480109	378	5	96	15.792	steep	mud	11	60	20	40	10
clearcut	a	x	6	C	Cx6	5494004	480100	378	5	62	22.56	gradual	mud	9	90	50	50	10
clearcut	a	x	7	C	Cx7	5494010	480103	379	5.2	21	22.56	steep	mud	6	80	20	20	10
clearcut	a	x	8	C	Cx8	5493997	480093	379	5.1	38	30.456	gradual	mud	7	90	50	40	10
clearcut	a	x	9	C	Cx9	5493993	480088	378	4.7	13	15.228	gradual	mud/det	8	60	30	70	50
clearcut	a	x	10	C	Cx10	5493996	480089	379	5	72	23.97	steep	mud/det	8	100	40	60	10
clearcut	a	y	1	C	Cy1	5493896	480186	368	4.8	23	42.018	gradual	mud/det	6	90	70	50	30
clearcut	a	y	2	C	Cy2	5493886	480189	368	4.9	73	26.226	steep	mud	8	80	30	50	10
clearcut	a	y	3	C	Cy3	5493888	480188	368	4.7	29	11.562	gradual	mud	8	100	50	30	50
clearcut	a	y	4	C	Cy4	5493876	480194	368	5.1	66	33.276	steep	mud/det	7	60	20	60	0
clearcut	a	y	5	C	Cy5	5493889	480189	368	5.1	30	32.148	gradual	mud/det	6	90	70	60	30
clearcut	a	y	6	C	Cy6	5493878	480209	366	4.7	14	21.432	gradual	mud	8	90	80	30	60
clearcut	a	y	7	C	Cy7	5493879	480205	367	4.9	29	12.69	gradual	mud/det	8	70	40	70	10
clearcut	a	y	8	C	Cy8	5493891	480218	366	4.7	22	21.15	gradual	mud/det	6	90	70	50	10
clearcut	a	y	9	C	Cy9	5493885	480216	368	4.6	17	5.358	gradual	mud	8	70	70	60	40
clearcut	a	y	10	C	Cy10	5493888	480215	366	4.6	14	16.92	steep	mud	7	70	50	20	10
clearcut	b	x	1	D	Dx1	5500957	473829	432	5	75	19.458	steep	mud/det	9	70	10	40	10
clearcut	b	x	2	D	Dx2	5500960	473808	430	4.8	69	12.69	steep	mud/mo	7	70	30	50	10
clearcut	b	x	3	D	Dx3	5500955	473808	431	4.8	30	6.486	steep	mud/mo	8	70	20	50	0
clearcut	b	x	4	D	Dx4	5500954	473821	432	5	47	14.664	steep	mud/mo	8	60	30	50	10
clearcut	b	x	5	D	Dx5	5500955	473815	431	4.9	61	22.56	steep	mud/det	8	80	40	40	10
clearcut	b	x	6	D	Dx6	5500788	473858	428	4.9	51	5.358	steep	mud/mo	6	60	20	30	20
clearcut	b	x	7	D	Dx7	5500785	473857	428	5	85	14.664	steep	mud/mo	10	70	30	30	0
clearcut	b	x	8	D	Dx8	5500780	473857	428	5.5	69	13.536	steep	mud	11	70	20	50	0
clearcut	b	x	9	D	Dx9	5500781	473863	428	4.7	13	43.992	steep	mud/mo	8	70	50	40	0
clearcut	b	x	10	D	Dx10	5500777	473848	428	4.9	45	101.802	steep	mud	8	70	50	50	0
clearcut	b	y	1	D	Dy1	5500771	473463	421	4.4	14	51.606	gradual	mud	6	50	40	10	30
clearcut	b	y	2	D	Dy2	5500778	473446	420	4.3	40	75.576	gradual	mud/mo	9	100	90	90	0
clearcut	b	y	3	D	Dy3	5500788	473462	421	4.5	51	20.868	steep	mud/mo	10	50	20	30	10
clearcut	b	y	4	D	Dy4	5500786	473457	421	4.3	19	6.768	gradual	mud	6	60	30	20	10
clearcut	b	y	5	D	Dy5	5500782	473471	421	4.7	83	20.022	steep	mud/det	10	60	10	10	0
clearcut	b	y	6	D	Dy6	5500720	473379	418	5	15	10.998	steep	mud	9	80	50	30	90

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
clearcut	b	y	7	D	Dy7	5500720	473374	418	5	45	54.99	steep	mud/mo	14	90	30	80	0
clearcut	b	y	8	D	Dy8	5500710	473393	419	5.5	29	36.096	steep	mud	8	80	60	50	10
clearcut	b	y	9	D	Dy9	5500723	473384	419	4.6	14	8.742	gradual	mud	9	90	80	20	50
clearcut	b	y	10	D	Dy10	5500713	473390	419	5.8	23	20.868	steep	mud	10	90	70	50	10
forest	b	x	1	E	Ex1	5499353	483663	337	4.8	30	13.254	steep	mud	9	70	50	10	90
forest	b	x	2	E	Ex2	5499356	483667	336	4.8	57	16.356	steep	mud	2	80	20	40	0
forest	b	x	3	E	Ex3	5499350	483661	337	4.6	77	38.07	steep	mud	9	30	10	30	20
forest	b	x	4	E	Ex4	5499344	483642	337	4.5	72	14.664	gradual	mud	9	80	50	20	10
forest	b	x	5	E	Ex5	5499363	483682	337	4.6	79	22.56	steep	mud	5	50	30	30	10
forest	b	x	6	E	Ex6	5499471	483658	339	4.7	137	25.662	steep	mud	6	100	50	50	10
forest	b	x	7	E	Ex7	5499457	483662	338	4.6	38	25.662	steep	mud/det	8	70	60	60	10
forest	b	x	8	E	Ex8	5499451	483676	338	4.5	23	58.938	gradual	mud/det	10	60	40	40	10
forest	b	x	9	E	Ex9	5499446	483672	338	4.3	34	16.074	gradual	mud	8	70	30	30	30
forest	b	x	10	E	Ex10	5499451	483660	338	4.7	108	71.064	steep	mud	9	90	20	20	0
forest	b	y	1	E	Ey1	5500114	484368	287	5.8	97	47.094	gradual	mud	8	90	30	30	20
forest	b	y	2	E	Ey2	5500097	484369	284	5.7	25	39.198	gradual	mud	8	80	20	40	10
forest	b	y	3	E	Ey3	5500093	484400	287	5.6	49	39.198	steep	mud	11	30	10	30	10
forest	b	y	4	E	Ey4	5500097	484359	284	6.1	15	5.358	gradual	mud	5	80	40	20	30
forest	b	y	5	E	Ey5	5500086	484366	285	5.8	26	7.896	steep	mud/det	9	80	30	50	10
forest	b	y	6	E	Ey6	5500088	484368	287	5.8	16	4.794	steep	mud	7	40	10	20	10
forest	b	y	7	E	Ey7	5500096	484369	287	5.6	34	7.614	steep	mud/det	7	50	20	50	20
forest	b	y	8	E	Ey8	5500092	484350	285	5.9	101	48.786	steep	mud	8	90	10	20	10
forest	b	y	9	E	Ey9	5500098	484367	284	6.1	23	11.844	gradual	mud	8	90	70	70	30
forest	b	y	10	E	Ey10	5500092	484364	287	5.6	23	7.896	steep	mud/det	8	70	20	60	10
bog_big	a	x	1	F	Fx1	5504185	476020	368	4.4	17	21.996	steep	mud	5	80	50	10	40
bog_big	a	x	2	F	Fx2	5504179	476025	368	4.6	12	9.024	steep	mud	4	70	40	20	20
bog_big	a	x	3	F	Fx3	5504197	476042	369	4.5	14	1.128	steep	mud	7	80	40	40	30
bog_big	a	x	4	F	Fx4	5504194	476041	366	4.6	5	1.692	steep	mud	6	70	30	20	40
bog_big	a	x	5	F	Fx5	5504191	476052	366	4.5	8	2.256	steep	mud	5	80	40	30	20
bog_big	a	x	6	F	Fx6	5504159	475792	371	5	12	7.05	gradual	mud	8	80	70	20	40
bog_big	a	x	7	F	Fx7	5504165	475799	370	5.1	16	11.844	gradual	mud/det	6	90	70	30	40
bog_big	a	x	8	F	Fx8	5504154	475787	370	5.4	28	9.306	gradual	mud	5	50	20	20	20
bog_big	a	x	9	F	Fx9	5504172	475806	370	5.2	19	7.05	gradual	mud/det	7	80	60	70	20
bog_big	a	x	10	F	Fx10	5504155	475791	369	5.1	19	33.84	gradual	mud	6	80	70	60	50
bog_big	a	y	1	F	Fy1	5504360	475691	373	4.4	23	6.768	gradual	mud	5	80	40	50	10
bog_big	a	y	2	F	Fy2	5504364	475695	374	4.6	25	5.64	gradual	mud	8	80	60	50	20
bog_big	a	y	3	F	Fy3	5504368	475706	373	4.7	27	8.742	gradual	mud/det	4	90	80	60	10
bog_big	a	y	4	F	Fy4	5504368	475694	373	4.6	14	9.87	gradual	mud	6	80	40	40	20

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
bog_big	a	y	5	F	Fy5	5504366	475701	373	4.7	31	5.358	gradual	mud/det	7	70	40	60	10
bog_big	a	y	6	F	Fy6	5504365	475675	374	4.6	16	5.076	gradual	mud	4	90	20	20	10
bog_big	a	y	7	F	Fy7	5504375	475686	373	4.5	19	4.512	gradual	mud/det	6	70	50	50	10
bog_big	a	y	8	F	Fy8	5504368	475682	373	4.6	12	5.922	gradual	mud	4	70	40	20	10
bog_big	a	y	9	F	Fy9	5504366	475680	374	4.6	20	11.562	gradual	mud	5	70	30	20	10
bog_big	a	y	10	F	Fy10	5504373	475679	374	4.6	22	6.768	gradual	mud	4	80	30	30	20
bog_big	b	x	1	G	Gx1	5505417	478799	354	4.4	11	13.254	gradual	mud/mo	14	70	10	20	10
bog_big	b	x	2	G	Gx2	5505405	478761	354	4.3	22	25.38	steep	mud	14	90	10	10	0
bog_big	b	x	3	G	Gx3	5505401	478755	355	4.3	32	15.792	steep	mud	14	90	10	20	0
bog_big	b	x	4	G	Gx4	5505397	478759	354	4.3	39	18.048	gradual	mud	14	90	30	70	0
bog_big	b	x	5	G	Gx5	5505432	478797	354	4.3	7	12.408	gradual	mud	14	50	20	10	30
bog_big	b	x	6	G	Gx6	5505590	478788	357	4.2	26	NA	steep	mud/det	6	100	70	60	0
bog_big	b	x	7	G	Gx7	5505577	478774	356	4.5	32	NA	gradual	mud/det	5	90	30	40	20
bog_big	b	x	8	G	Gx8	5505605	478762	354	4.3	10	NA	gradual	mud/mo	7	100	80	90	10
bog_big	b	x	9	G	Gx9	5505569	478769	355	4.4	23	NA	gradual	mud	5	90	80	80	0
bog_big	b	x	10	G	Gx10	5505583	478770	355	4.4	20	NA	gradual	mud/det	4	70	60	80	30
bog_big	b	y	1	G	Gy1	5506057	479081	355	4.7	15	18.048	gradual	mud/det	9	50	30	50	20
bog_big	b	y	2	G	Gy2	5506111	479110	356	6.1	39	156.228	gradual	mud	12	70	60	60	10
bog_big	b	y	3	G	Gy3	5506116	479125	355	5.5	77	40.608	steep	mud	6	80	20	40	10
bog_big	b	y	4	G	Gy4	5506125	479102	354	6.1	39	60.066	gradual	mud/det	9	80	50	70	10
bog_big	b	y	5	G	Gy5	5506054	479094	354	4.6	15	12.126	steep	mud/det	8	30	30	40	20
bog_big	b	y	6	G	Gy6	5505795	478942	354	4.7	101	138.18	steep	mud	14	70	20	10	0
bog_big	b	y	7	G	Gy7	5505800	478979	355	4.6	62	33.276	steep	mud/mo	14	50	30	40	10
bog_big	b	y	8	G	Gy8	5505795	478970	353	4.5	54	29.046	steep	mud/mo	14	90	40	40	10
bog_big	b	y	9	G	Gy9	5505770	478931	356	4.5	84	174.84	steep	mud/det	14	100	40	80	10
bog_big	b	y	10	G	Gy10	5505802	478987	353	4.6	53	33.84	steep	mud	14	70	30	20	20
bog_big	c	x	1	H	Hx1	5513113	476798	556	4.8	74	95.88	gradual	mud/det	6	100	40	40	0
bog_big	c	x	2	H	Hx2	5513098	476775	556	4.6	38	5.64	gradual	mud/mo	6	80	60	60	0
bog_big	c	x	3	H	Hx3	5513125	476787	557	4.7	45	55.272	gradual	mud/det	6	100	60	60	0
bog_big	c	x	4	H	Hx4	5513110	476777	556	4.5	54	6.204	gradual	mud/mo	5	80	30	50	0
bog_big	c	x	5	H	Hx5	5513103	476774	556	4.7	46	1.692	gradual	mud/mo	7	60	60	80	10
bog_big	c	x	6	H	Hx6	5512699	476856	556	4.4	29	12.126	gradual	mud	8	80	50	90	0
bog_big	c	x	7	H	Hx7	5512724	476870	554	4.6	25	12.408	gradual	mud/mo	6	80	50	60	10
bog_big	c	x	8	H	Hx8	5512718	476867	554	4.7	50	7.614	steep	mud	9	80	40	30	0
bog_big	c	x	9	H	Hx9	5512710	476851	555	4.7	41	23.688	gradual	mud/det	7	60	40	30	10
bog_big	c	x	10	H	Hx10	5512718	476864	554	4.6	35	15.792	steep	mud/det	6	70	30	40	0
bog_big	c	y	1	H	Hy1	5513276	476098	562	4.4	14	89.112	gradual	mud	9	70	70	30	20
bog_big	c	y	2	H	Hy2	5513268	476104	563	4.7	46	184.992	gradual	mud/det	10	90	40	40	10

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
bog_big	c	y	3	H	Hy3	5513304	476218	561	4.7	26	33.84	gradual	mud/det	5	100	40	60	0
bog_big	c	y	4	H	Hy4	5513323	476256	561	4.4	23	20.022	gradual	mud	7	100	40	40	10
bog_big	c	y	5	H	Hy5	5513391	476283	560	4.6	35	20.586	steep	mud	8	100	10	10	0
bog_big	c	y	6	H	Hy6	5513414	476242	560	4.6	24	5.076	gradual	mud	7	80	20	50	10
bog_big	c	y	7	H	Hy7	5513404	476299	559	4.5	61	12.408	steep	mud/det	5	70	30	30	0
bog_big	c	y	8	H	Hy8	5513414	476250	560	4.5	15	8.46	steep	mud	9	90	30	10	10
bog_big	c	y	9	H	Hy9	5513414	476290	559	4.3	40	12.126	steep	mud	7	100	10	20	0
bog_big	c	y	10	H	Hy10	5513384	476277	560	4.5	66	26.79	gradual	mud	5	100	40	50	10
bog_sml	a	x	1	I	Ix1	5522450	479603	445	4.1	5	1.128	gradual	mud	2	90	20	10	40
bog_sml	a	x	2	I	Ix2	5522375	479579	446	4.5	26	22.278	gradual	mud/mo	6	80	30	30	0
bog_sml	a	x	3	I	Ix3	5522370	479576	445	4.4	13	18.33	gradual	mud	2	80	30	40	10
bog_sml	a	x	4	I	Ix4	5522466	479588	445	4.3	19	9.588	steep	mud/mo	5	80	20	40	0
bog_sml	a	x	5	I	Ix5	5522471	479587	445	4.3	16	13.254	gradual	mud/mo	4	90	10	20	0
bog_sml	a	x	6	I	Ix6	5522411	479685	443	4.4	18	12.126	gradual	mud	4	60	10	10	10
bog_sml	a	x	7	I	Ix7	5522427	479674	443	4.2	10	9.87	steep	mud/mo	5	60	40	50	0
bog_sml	a	x	8	I	Ix8	5522416	479684	443	4.3	14	10.716	gradual	mud	5	30	40	10	10
bog_sml	a	x	9	I	Ix9	5522426	479681	443	4.5	19	10.152	gradual	mud/mo	6	50	40	50	0
bog_sml	a	x	10	I	Ix10	5522409	479667	445	4.5	47	12.126	steep	mud	6	70	10	10	0
bog_sml	a	y	1	I	Iy1	5522347	478944	456	4.5	12	11.28	gradual	mud/det	6	80	50	50	20
bog_sml	a	y	2	I	Iy2	NA	NA	455	4.6	15	NA	gradual	mud/det	5	90	40	50	10
bog_sml	a	y	3	I	Iy3	5522343	478940	455	4.4	10	10.152	gradual	mud/det	6	70	70	30	10
bog_sml	a	y	4	I	Iy4	5522340	478928	456	4.6	15	11.28	gradual	mud/det	5	60	30	40	20
bog_sml	a	y	5	I	Iy5	5522355	478926	454	4.7	22	20.304	gradual	mud/det	4	60	10	60	10
bog_sml	a	y	6	I	Iy6	5522386	479030	455	4.5	84	34.968	steep	mud/mo	9	100	10	30	0
bog_sml	a	y	7	I	Iy7	5522379	479029	455	4.5	95	20.022	steep	mud	6	100	20	40	0
bog_sml	a	y	8	I	Iy8	5522378	479020	455	4.4	73	69.372	steep	mud	5	90	30	40	0
bog_sml	a	y	9	I	Iy9	5522394	479023	455	4.4	65	19.458	steep	mud/mo	9	90	10	40	0
bog_sml	a	y	10	I	Iy10	5522395	479015	453	4.3	29	25.38	steep	mud	7	90	20	10	0
forest	c	x	1	J	Jx1	5509742	481608	389	4.6	58	5.076	steep	mud/mo	9	80	30	70	0
forest	c	x	2	J	Jx2	5509736	481613	390	4.7	45	8.178	steep	mud	9	70	10	10	10
forest	c	x	3	J	Jx3	5509743	481612	389	4.6	36	21.714	steep	mud	10	50	20	20	20
forest	c	x	4	J	Jx4	5509746	481616	389	6.5	30	60.348	gradual	mud	9	90	30	20	10
forest	c	x	5	J	Jx5	5509747	481607	389	4.6	50	3.666	gradual	mud/mo	9	70	50	60	10
forest	c	x	6	J	Jx6	5509635	481435	390	5.6	20	5.358	gradual	mud/det	9	40	40	70	20
forest	c	x	7	J	Jx7	5509635	481431	391	5.9	24	16.356	gradual	mud/det	8	40	10	60	10
forest	c	x	8	J	Jx8	5509641	481426	390	6	89	20.304	gradual	mud/det	11	80	20	40	10
forest	c	x	9	J	Jx9	5509634	481431	390	5.7	40	12.972	steep	mud/det	9	60	20	80	0
forest	c	x	10	J	Jx10	5509637	481431	391	5.8	38	8.742	gradual	mud/det	9	60	40	30	30

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
forest	c	y	1	J	Jy1	5509479	481224	388	4.5	42	7.05	steep	mud	8	80	50	60	30
forest	c	y	2	J	Jy2	5509487	481226	388	5.4	46	7.05	steep	mud/det	7	50	20	40	10
forest	c	y	3	J	Jy3	5509494	481229	388	5.6	88	9.588	steep	mud	5	40	20	20	0
forest	c	y	4	J	Jy4	5509425	481187	388	5.7	91	23.97	steep	mud	9	50	30	30	0
forest	c	y	5	J	Jy5	5509466	481224	388	4.6	39	11.844	gradual	mud	7	40	30	30	30
forest	c	y	6	J	Jy6	5509300	481083	390	4.8	14	61.758	steep	mud/det	6	60	30	40	10
forest	c	y	7	J	Jy7	5509305	481095	392	4.7	34	9.306	gradual	mud	7	20	20	40	10
forest	c	y	8	J	Jy8	5509295	481081	391	4.8	32	332.478	gradual	mud/det	7	60	20	20	10
forest	c	y	9	J	Jy9	5509310	481103	390	4.8	36	13.536	steep	mud/det	8	40	20	40	10
forest	c	y	10	J	Jy10	5509303	481084	390	4.8	49	58.092	steep	mud/det	7	60	30	40	0
clearcut	c	x	1	K	Kx1	5503352	471404	412	5.1	27	NA	steep	mud/mo	6	100	80	80	10
clearcut	c	x	2	K	Kx2	5503354	471404	412	5.4	16	NA	gradual	mud	7	100	70	70	0
clearcut	c	x	3	K	Kx3	5503347	471396	412	5.3	37	NA	steep	mud/det	5	90	40	70	10
clearcut	c	x	4	K	Kx4	5503352	471396	412	5.3	32	NA	steep	mud	5	100	70	50	10
clearcut	c	x	5	K	Kx5	5503343	471399	412	5.2	22	NA	gradual	mud	5	100	70	50	0
clearcut	c	x	6	K	Kx6	5503383	471326	414	4.8	19	NA	gradual	mud/det	6	60	50	50	20
clearcut	c	x	7	K	Kx7	5503382	471321	414	4.8	15	NA	gradual	mud/mo	6	90	80	70	10
clearcut	c	x	8	K	Kx8	5503392	471308	415	4.9	25	NA	gradual	mud/det	5	80	80	50	20
clearcut	c	x	9	K	Kx9	5503388	471326	415	4.7	17	NA	gradual	mud/det	6	40	40	60	10
clearcut	c	x	10	K	Kx10	5503391	471303	415	4.8	24	NA	gradual	mud/det	8	100	70	60	10
clearcut	c	y	1	K	Ky1	5503700	470941	451	6.1	17	NA	steep	mud/det	8	90	30	40	0
clearcut	c	y	2	K	Ky2	5503703	470940	452	5.3	27	NA	steep	mud/det	8	20	20	40	20
clearcut	c	y	3	K	Ky3	5503703	470936	452	5.5	21	NA	gradual	mud/det	9	70	30	30	30
clearcut	c	y	4	K	Ky4	5503714	470936	453	5.3	28	29.328	gradual	mud/det	8	30	20	40	10
clearcut	c	y	5	K	Ky5	5503712	470937	453	5.3	22	NA	gradual	mud/det	7	70	30	50	20
clearcut	c	y	6	K	Ky6	5503752	470914	458	5.3	23	8.46	gradual	mud	7	80	60	60	40
clearcut	c	y	7	K	Ky7	5503753	470927	459	5.5	40	20.022	steep	mud	8	90	60	60	20
clearcut	c	y	8	K	Ky8	5503753	470906	458	4.9	39	8.46	gradual	mud	7	100	80	80	30
clearcut	c	y	9	K	Ky9	5503761	470922	457	5.6	23	22.56	gradual	mud	7	90	50	30	30
clearcut	c	y	10	K	Ky10	5503755	470913	458	5.5	44	5.358	steep	mud	7	90	30	40	10
scrub	b	x	1	L	Lx1	5510183	479447	489	4.5	14	20.868	steep	mud	8	40	10	10	0
scrub	b	x	2	L	Lx2	5510168	479469	489	4.6	24	33.558	steep	mud	7	60	20	20	10
scrub	b	x	3	L	Lx3	5510173	479488	489	4.3	6	58.092	gradual	mud/mo	10	80	40	40	30
scrub	b	x	4	L	Lx4	5510177	479498	489	4.6	16	44.556	gradual	mud/mo	10	70	50	40	10
scrub	b	x	5	L	Lx5	5510183	479466	489	4.1	2	10.434	steep	mud	8	90	70	30	30
scrub	b	x	6	L	Lx6	5510099	479387	489	4.7	23	NA	gradual	mud/det	5	50	40	30	20
scrub	b	x	7	L	Lx7	5510116	479410	490	4.5	13	NA	gradual	mud	7	80	60	30	40
scrub	b	x	8	L	Lx8	5510115	479390	489	4.6	20	NA	gradual	mud/det	8	70	50	40	60

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
scrub	b	x	9	L	Lx9	5510122	479414	489	4.6	29	NA	gradual	mud	6	60	40	40	20
scrub	b	x	10	L	Lx10	5510109	479382	491	4.8	55	NA	gradual	mud/det	8	70	10	20	20
scrub	b	y	1	L	Ly1	5510494	479856	472	4.8	25	NA	gradual	mud	7	70	50	10	10
scrub	b	y	2	L	Ly2	5510488	479861	473	4.8	13	NA	gradual	mud/mo	7	80	60	40	0
scrub	b	y	3	L	Ly3	5510477	479868	473	5.2	17	NA	gradual	mud/mo	8	50	40	40	0
scrub	b	y	4	L	Ly4	NA	NA	473	5.7	36	NA	gradual	mud/mo	4	80	50	30	0
scrub	b	y	5	L	Ly5	5510482	479858	473	4.9	50	NA	steep	mud/det	8	90	50	40	10
scrub	b	y	6	L	Ly6	5510561	479841	465	4.9	55	NA	steep	mud	5	100	20	30	0
scrub	b	y	7	L	Ly7	5510576	479818	467	4.5	23	NA	gradual	mud/det	5	90	50	40	10
scrub	b	y	8	L	Ly8	5510564	479830	467	4.6	20	NA	steep	mud	7	90	20	20	0
scrub	b	y	9	L	Ly9	5510566	479842	466	4.7	10	NA	gradual	mud/det	7	90	40	60	30
scrub	b	y	10	L	Ly10	5510572	479842	465	4.7	13	NA	steep	mud/mo	5	70	30	30	10
scrub	c	x	1	M	Mx1	5487892	477186	357	5.8	55	5.922	gradual	mud	12	70	50	10	40
scrub	c	x	2	M	Mx2	5487898	477183	357	5.5	25	58.374	gradual	mud	8	60	20	20	10
scrub	c	x	3	M	Mx3	5487902	477181	356	6.6	34	10.152	steep	mud/mo	5	50	20	20	10
scrub	c	x	4	M	Mx4	5487898	477180	357	6.4	67	12.972	gradual	mud	6	50	10	10	10
scrub	c	x	5	M	Mx5	5487893	477181	357	5.7	17	6.204	steep	mud	9	80	30	10	50
scrub	c	x	6	M	Mx6	5487996	477053	352	4.5	10	4.23	steep	mud	6	100	90	80	0
scrub	c	x	7	M	Mx7	5488060	477011	357	4.4	51	43.992	gradual	mud/det	5	90	70	80	10
scrub	c	x	8	M	Mx8	5487992	477054	355	4.7	18	5.076	steep	mud/mo	5	70	20	50	10
scrub	c	x	9	M	Mx9	5487985	477055	354	4.8	18	5.922	steep	mud/mo	4	90	60	80	10
scrub	c	x	10	M	Mx10	5487979	477056	354	4.8	18	7.614	steep	mud/mo	6	90	30	70	0
scrub	c	y	1	M	My1	5487638	477542	369	4.4	37	7.614	gradual	mud	10	70	60	30	40
scrub	c	y	2	M	My2	5487631	477543	369	4.2	14	46.53	gradual	mud	7	40	40	20	50
scrub	c	y	3	M	My3	5487629	477540	370	4.2	23	29.046	gradual	mud	11	40	70	30	40
scrub	c	y	4	M	My4	5487615	477539	370	4.5	12	6.768	steep	mud	7	40	40	20	50
scrub	c	y	5	M	My5	5487611	477549	369	4.2	18	9.024	gradual	mud	7	40	30	20	50
scrub	c	y	6	M	My6	5487603	477554	371	4.2	33	25.38	gradual	mud/det	7	80	70	60	20
scrub	c	y	7	M	My7	5487608	477577	371	4.3	54	75.012	gradual	mud	12	70	70	50	30
scrub	c	y	8	M	My8	5487610	477545	370	4.4	31	7.896	gradual	mud	9	90	70	40	40
scrub	c	y	9	M	My9	5487595	477549	370	4.4	89	10.998	steep	mud	7	30	10	20	10
scrub	c	y	10	M	My10	5487615	477549	370	4.1	46	84.036	gradual	mud	12	80	70	30	30
bog_sml	b	x	1	N	Nx1	5485888	483073	278	4.5	18	11.844	steep	mud	10	40	30	20	20
bog_sml	b	x	2	N	Nx2	5485884	483060	278	4.5	6	20.586	steep	mud	9	80	40	30	20
bog_sml	b	x	3	N	Nx3	5485886	483072	278	4.5	11	2.538	steep	mud	9	50	50	30	50
bog_sml	b	x	4	N	Nx4	5485888	483062	277	4.5	49	14.664	steep	mud	8	30	10	20	20
bog_sml	b	x	5	N	Nx5	5485889	483065	277	4.4	13	20.022	steep	mud	9	50	40	20	10
bog_sml	b	x	6	N	Nx6	5485899	483078	277	4.5	68	60.348	steep	mud/det	10	80	40	40	10

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Northing	Easting	Elev	pH	Depth	Pl.area	Slope	Bottom	plnt.rich	Peri.em	Area.em	Subm	Mud
bog_sml	b	x	7	N	Nx7	5485902	483061	277	4.3	15	16.638	steep	mud	7	50	50	50	20
bog_sml	b	x	8	N	Nx8	5485893	483055	278	4.5	67	40.608	gradual	mud	8	70	30	10	20
bog_sml	b	x	9	N	Nx9	5485904	483054	278	4.3	25	18.048	gradual	mud	6	90	80	60	50
bog_sml	b	x	10	N	Nx10	5485895	483079	277	4.4	60	10.998	gradual	mud	8	70	30	30	10
bog_sml	b	y	1	N	Ny1	5485837	483564	274	4.5	26	7.332	gradual	mud	7	80	50	30	40
bog_sml	b	y	2	N	Ny2	5485840	483557	275	4.8	54	21.15	gradual	mud	11	70	30	50	20
bog_sml	b	y	3	N	Ny3	5485846	483562	274	4.7	64	3.948	steep	mud	5	80	40	50	10
bog_sml	b	y	4	N	Ny4	5485841	483554	275	4.7	64	72.756	gradual	mud	11	80	30	60	10
bog_sml	b	y	5	N	Ny5	5485832	483579	274	4.5	26	16.074	gradual	mud	8	60	30	40	10
bog_sml	b	y	6	N	Ny6	5485837	483601	273	4.4	16	4.794	gradual	mud	9	100	70	80	10
bog_sml	b	y	7	N	Ny7	5485824	483629	272	4.5	24	8.178	gradual	mud	9	70	40	40	10
bog_sml	b	y	8	N	Ny8	5485843	483598	274	4.5	22	6.486	gradual	mud/mo	6	100	70	80	10
bog_sml	b	y	9	N	Ny9	5485821	483626	273	4.6	59	27.354	gradual	mud	9	100	60	70	20
bog_sml	b	y	10	N	Ny10	5485851	483613	271	4.7	84	21.714	steep	mud/det	8	90	40	40	10
bog_sml	c	x	1	O	Ox1	5498858	486066	266	5.6	37	5.423	steep	mud	6	70	30	20	10
bog_sml	c	x	2	O	Ox2	5498868	486075	263	6.1	38	15.936	gradual	mud	11	70	40	40	20
bog_sml	c	x	3	O	Ox3	5498887	486066	263	6.1	44	31.983	steep	mud/mo	12	60	10	40	10
bog_sml	c	x	4	O	Ox4	5498891	486058	263	6.1	45	24.900	steep	mud	9	80	30	40	10
bog_sml	c	x	5	O	Ox5	5498894	486062	264	6.3	45	35.856	steep	mud	12	70	30	30	10
bog_sml	c	x	6	O	Ox6	5498902	486200	260	6.4	35	13.391	steep	mud/det	8	90	20	30	10
bog_sml	c	x	7	O	Ox7	5498895	486202	260	6.6	27	21.691	gradual	mud/det	4	100	20	20	10
bog_sml	c	x	8	O	Ox8	5498898	486202	259	6.5	23	31.983	gradual	mud/det	9	100	50	50	20
bog_sml	c	x	9	O	Ox9	5498891	486201	259	6.4	23	28.331	gradual	mud/mo	7	100	20	50	10
bog_sml	c	x	10	O	Ox10	5498895	486196	259	6.2	10	5.4227	gradual	mud	4	100	60	20	10
bog_sml	c	y	1	O	Oy1	5498889	486792	290	6.2	36	21.691	steep	mud	6	80	20	30	10
bog_sml	c	y	2	O	Oy2	5498894	486794	290	6.9	15	159.804	gradual	mud	12	100	60	50	10
bog_sml	c	y	3	O	Oy3	5498881	486789	290	6.4	25	21.691	gradual	mud	10	60	20	10	10
bog_sml	c	y	4	O	Oy4	5498890	486784	289	5.9	23	3.984	steep	mud/det	7	100	10	90	0
bog_sml	c	y	5	O	Oy5	5498894	486767	289	5.7	19	3.984	gradual	mud	7	60	20	40	10
bog_sml	c	y	6	O	Oy6	5498898	486753	290	5.9	20	13.391	gradual	mud/det	5	40	20	40	40
bog_sml	c	y	7	O	Oy7	5498898	486748	290	5.3	22	113.324	gradual	mud	12	90	60	40	50
bog_sml	c	y	8	O	Oy8	5498982	486712	288	6.4	35	80.677	gradual	mud	8	100	40	40	40
bog_sml	c	y	9	O	Oy9	5498928	486739	290	6.5	19	28.331	gradual	mud	8	60	50	30	30
bog_sml	c	y	10	O	Oy10	5498912	486777	290	5.5	19	11.067	gradual	mud	6	60	20	20	20

Appendix 3

Raw data for study pools - exuvial and larval odonate data

Field Explanations

Trtmnt = Treatment (scrub a.k.a. bog_medium; forest; clearcut; bog_big; or bog_sml = bog_small)

Lndscpe = code letter unique within a treatment

Bog = code letter unique within a landscape

Pool = code number unique within a bog

landuniq = unique landscape code letter

pooluniq = unique pool code

Lh_F = number of *Leucorrhinia hudsonica* larvae assigned to size class F

Lh_F-1 = number of *Leucorrhinia hudsonica* larvae assigned to size class F-1

Lh_F-2 = number of *Leucorrhinia hudsonica* larvae assigned to size class F-2

Enal_ex = number of *Enallagma* spp. exuviae

Asit_ex = number of *Aeshna sitchensis* exuviae

Cshu_ex = number of *Cordulia shurtleffi* exuviae

Ssep_ex = number of *Somatochlora septentrionalis* exuviae

Lhud_ex = number of *Leucorrhinia hudsonica* exuviae

Total_ex = total number of exuviae of all species combined

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
scrub	a	x	1	A	Ax1	3	7	6	14	0	0	0	7	25
scrub	a	x	2	A	Ax2	5	10	6	2	0	0	1	11	14
scrub	a	x	3	A	Ax3	0	0	3	0	0	0	0	0	0
scrub	a	x	4	A	Ax4	2	2	12	0	1	0	0	1	2
scrub	a	x	5	A	Ax5	0	8	11	0	0	0	0	1	2
scrub	a	x	6	A	Ax6	NA	NA	NA	0	0	0	0	11	11
scrub	a	x	7	A	Ax7	NA	NA	NA	0	0	0	0	1	2
scrub	a	x	8	A	Ax8	NA	NA	NA	4	0	0	0	1	5
scrub	a	x	9	A	Ax9	NA	NA	NA	2	1	0	0	20	23
scrub	a	x	10	A	Ax10	NA	NA	NA	0	0	0	0	1	1
scrub	a	y	1	A	Ay1	NA	NA	NA	0	0	0	1	11	12
scrub	a	y	2	A	Ay2	NA	NA	NA	46	0	0	0	55	101
scrub	a	y	3	A	Ay3	NA	NA	NA	61	0	0	0	48	119
scrub	a	y	4	A	Ay4	NA	NA	NA	0	0	0	4	7	12
scrub	a	y	5	A	Ay5	NA	NA	NA	0	0	0	1	1	2
scrub	a	y	6	A	Ay6	NA	NA	NA	1	2	0	0	5	9
scrub	a	y	7	A	Ay7	NA	NA	NA	18	0	2	0	37	59
scrub	a	y	8	A	Ay8	NA	NA	NA	11	0	0	0	28	39
scrub	a	y	9	A	Ay9	NA	NA	NA	1	0	1	1	20	24
scrub	a	y	10	A	Ay10	NA	NA	NA	30	0	1	0	4	37
forest	a	x	1	B	Bx1	0	0	0	0	1	0	0	0	1
forest	a	x	2	B	Bx2	0	1	0	0	0	0	0	0	0
forest	a	x	3	B	Bx3	0	0	0	0	0	0	0	0	0
forest	a	x	4	B	Bx4	1	0	2	0	0	0	0	1	1
forest	a	x	5	B	Bx5	0	1	0	0	3	0	0	0	3
forest	a	x	6	B	Bx6	NA	NA	NA	0	0	0	1	0	2
forest	a	x	7	B	Bx7	NA	NA	NA	0	0	1	1	6	8
forest	a	x	8	B	Bx8	NA	NA	NA	0	5	0	6	5	16
forest	a	x	9	B	Bx9	NA	NA	NA	0	1	0	1	0	12
forest	a	x	10	B	Bx10	NA	NA	NA	0	0	0	5	1	8
forest	a	y	1	B	By1	NA	NA	NA	0	0	0	1	0	1
forest	a	y	2	B	By2	NA	NA	NA	0	0	0	1	0	1
forest	a	y	3	B	By3	NA	NA	NA	0	1	0	0	0	1
forest	a	y	4	B	By4	NA	NA	NA	0	0	0	0	0	0
forest	a	y	5	B	By5	NA	NA	NA	0	2	0	3	1	8
forest	a	y	6	B	By6	NA	NA	NA	0	2	0	0	0	2
forest	a	y	7	B	By7	NA	NA	NA	0	1	0	0	0	2
forest	a	y	8	B	By8	NA	NA	NA	0	1	0	0	0	1

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
forest	a	y	9	B	By9	NA	NA	NA	0	0	0	0	0	0
forest	a	y	10	B	By10	NA	NA	NA	0	0	0	0	1	1
clearcut	a	x	1	C	Cx1	7	2	5	0	0	0	0	30	30
clearcut	a	x	2	C	Cx2	2	1	2	0	0	0	1	10	11
clearcut	a	x	3	C	Cx3	8	5	7	0	0	3	0	31	34
clearcut	a	x	4	C	Cx4	10	5	8	12	0	2	2	45	65
clearcut	a	x	5	C	Cx5	4	3	1	3	0	4	0	19	33
clearcut	a	x	6	C	Cx6	NA	NA	NA	1	2	0	1	27	32
clearcut	a	x	7	C	Cx7	NA	NA	NA	0	0	0	3	11	16
clearcut	a	x	8	C	Cx8	NA	NA	NA	0	0	0	1	20	21
clearcut	a	x	9	C	Cx9	NA	NA	NA	0	0	0	0	8	9
clearcut	a	x	10	C	Cx10	NA	NA	NA	0	0	0	1	48	52
clearcut	a	y	1	C	Cy1	NA	NA	NA	5	3	0	5	7	20
clearcut	a	y	2	C	Cy2	NA	NA	NA	17	0	0	0	45	63
clearcut	a	y	3	C	Cy3	NA	NA	NA	0	0	0	0	5	5
clearcut	a	y	4	C	Cy4	NA	NA	NA	30	0	2	0	65	97
clearcut	a	y	5	C	Cy5	NA	NA	NA	0	2	0	3	12	21
clearcut	a	y	6	C	Cy6	NA	NA	NA	0	2	0	1	29	32
clearcut	a	y	7	C	Cy7	NA	NA	NA	1	0	1	0	67	70
clearcut	a	y	8	C	Cy8	NA	NA	NA	0	0	0	0	14	14
clearcut	a	y	9	C	Cy9	NA	NA	NA	0	3	0	0	26	29
clearcut	a	y	10	C	Cy10	NA	NA	NA	0	2	1	0	27	30
clearcut	b	x	1	D	Dx1	0	0	0	0	0	10	0	0	11
clearcut	b	x	2	D	Dx2	0	5	8	1	0	11	0	0	12
clearcut	b	x	3	D	Dx3	2	0	0	6	1	0	0	4	11
clearcut	b	x	4	D	Dx4	1	0	3	3	0	10	0	1	15
clearcut	b	x	5	D	Dx5	1	4	4	7	0	9	0	4	21
clearcut	b	x	6	D	Dx6	NA	NA	NA	4	0	4	3	52	65
clearcut	b	x	7	D	Dx7	NA	NA	NA	0	0	3	0	1	6
clearcut	b	x	8	D	Dx8	NA	NA	NA	2	0	1	0	0	4
clearcut	b	x	9	D	Dx9	NA	NA	NA	0	0	0	0	4	4
clearcut	b	x	10	D	Dx10	NA	NA	NA	0	0	6	0	6	12
clearcut	b	y	1	D	Dy1	NA	NA	NA	0	1	0	1	5	7
clearcut	b	y	2	D	Dy2	NA	NA	NA	7	0	0	0	12	19
clearcut	b	y	3	D	Dy3	NA	NA	NA	48	0	9	3	39	100
clearcut	b	y	4	D	Dy4	NA	NA	NA	0	0	1	0	0	1
clearcut	b	y	5	D	Dy5	NA	NA	NA	9	0	8	0	9	26
clearcut	b	y	6	D	Dy6	NA	NA	NA	0	1	0	3	0	4

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
clearcut	b	y	7	D	Dy7	NA	NA	NA	79	0	5	0	23	111
clearcut	b	y	8	D	Dy8	NA	NA	NA	1	0	0	0	21	25
clearcut	b	y	9	D	Dy9	NA	NA	NA	0	0	0	2	0	2
clearcut	b	y	10	D	Dy10	NA	NA	NA	0	0	2	2	3	7
forest	b	x	1	E	Ex1	NA	NA	NA	0	0	0	0	0	0
forest	b	x	2	E	Ex2	NA	NA	NA	0	0	0	0	0	3
forest	b	x	3	E	Ex3	NA	NA	NA	5	0	0	0	11	17
forest	b	x	4	E	Ex4	NA	NA	NA	2	0	2	0	31	37
forest	b	x	5	E	Ex5	NA	NA	NA	0	0	0	1	1	2
forest	b	x	6	E	Ex6	NA	NA	NA	2	0	0	2	31	35
forest	b	x	7	E	Ex7	NA	NA	NA	1	0	2	2	22	28
forest	b	x	8	E	Ex8	NA	NA	NA	0	0	1	2	18	21
forest	b	x	9	E	Ex9	NA	NA	NA	0	0	0	3	4	7
forest	b	x	10	E	Ex10	NA	NA	NA	41	0	4	1	52	110
forest	b	y	1	E	Ey1	NA	NA	NA	0	0	1	0	4	8
forest	b	y	2	E	Ey2	NA	NA	NA	0	1	0	1	1	3
forest	b	y	3	E	Ey3	NA	NA	NA	0	0	4	0	8	13
forest	b	y	4	E	Ey4	NA	NA	NA	0	0	0	0	2	2
forest	b	y	5	E	Ey5	NA	NA	NA	1	1	0	1	0	5
forest	b	y	6	E	Ey6	NA	NA	NA	0	0	0	2	0	3
forest	b	y	7	E	Ey7	NA	NA	NA	0	0	0	0	4	5
forest	b	y	8	E	Ey8	NA	NA	NA	0	0	5	4	12	27
forest	b	y	9	E	Ey9	NA	NA	NA	2	1	0	2	2	7
forest	b	y	10	E	Ey10	NA	NA	NA	0	0	1	2	1	6
bog_big	a	x	1	F	Fx1	0	10	9	1	0	0	0	1	2
bog_big	a	x	2	F	Fx2	2	12	4	1	1	0	1	5	9
bog_big	a	x	3	F	Fx3	1	10	3	0	0	0	0	3	3
bog_big	a	x	4	F	Fx4	2	2	1	0	0	0	0	0	0
bog_big	a	x	5	F	Fx5	2	2	1	0	0	0	0	5	5
bog_big	a	x	6	F	Fx6	NA	NA	NA	0	0	0	0	2	2
bog_big	a	x	7	F	Fx7	NA	NA	NA	0	0	0	0	0	1
bog_big	a	x	8	F	Fx8	NA	NA	NA	0	0	2	1	9	13
bog_big	a	x	9	F	Fx9	NA	NA	NA	1	0	0	1	2	4
bog_big	a	x	10	F	Fx10	NA	NA	NA	0	0	0	0	0	2
bog_big	a	y	1	F	Fy1	NA	NA	NA	0	0	0	0	0	0
bog_big	a	y	2	F	Fy2	NA	NA	NA	3	0	0	0	1	4
bog_big	a	y	3	F	Fy3	NA	NA	NA	2	3	0	2	15	22
bog_big	a	y	4	F	Fy4	NA	NA	NA	15	1	0	1	4	21

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
bog_big	a	y	5	F	Fy5	NA	NA	NA	3	0	0	1	8	12
bog_big	a	y	6	F	Fy6	NA	NA	NA	0	0	0	0	0	0
bog_big	a	y	7	F	Fy7	NA	NA	NA	0	0	1	0	5	6
bog_big	a	y	8	F	Fy8	NA	NA	NA	1	0	0	0	3	5
bog_big	a	y	9	F	Fy9	NA	NA	NA	2	0	0	0	0	2
bog_big	a	y	10	F	Fy10	NA	NA	NA	0	0	0	0	1	2
bog_big	b	x	1	G	Gx1	0	0	2	0	0	0	0	7	7
bog_big	b	x	2	G	Gx2	14	2	5	0	1	2	7	128	138
bog_big	b	x	3	G	Gx3	9	7	2	0	0	0	0	77	77
bog_big	b	x	4	G	Gx4	2	6	8	0	0	0	0	9	9
bog_big	b	x	5	G	Gx5	1	1	1	0	0	0	0	1	3
bog_big	b	x	6	G	Gx6	NA	NA	NA	2	0	0	0	6	8
bog_big	b	x	7	G	Gx7	NA	NA	NA	0	0	0	1	12	13
bog_big	b	x	8	G	Gx8	NA	NA	NA	0	0	0	0	0	0
bog_big	b	x	9	G	Gx9	NA	NA	NA	0	1	0	3	29	33
bog_big	b	x	10	G	Gx10	NA	NA	NA	0	0	2	0	7	9
bog_big	b	y	1	G	Gy1	NA	NA	NA	0	0	8	3	0	11
bog_big	b	y	2	G	Gy2	NA	NA	NA	3	0	2	0	0	6
bog_big	b	y	3	G	Gy3	NA	NA	NA	9	0	1	0	1	13
bog_big	b	y	4	G	Gy4	NA	NA	NA	2	0	0	0	2	6
bog_big	b	y	5	G	Gy5	NA	NA	NA	0	1	3	4	5	15
bog_big	b	y	6	G	Gy6	NA	NA	NA	7	0	17	0	42	69
bog_big	b	y	7	G	Gy7	NA	NA	NA	0	0	0	1	29	30
bog_big	b	y	8	G	Gy8	NA	NA	NA	0	0	0	0	96	96
bog_big	b	y	9	G	Gy9	NA	NA	NA	0	1	0	1	1	5
bog_big	b	y	10	G	Gy10	NA	NA	NA	0	0	1	1	8	11
bog_big	c	x	1	H	Hx1	NA	NA	NA	42	0	0	1	68	111
bog_big	c	x	2	H	Hx2	NA	NA	NA	0	0	0	0	14	14
bog_big	c	x	3	H	Hx3	NA	NA	NA	11	0	0	3	149	163
bog_big	c	x	4	H	Hx4	NA	NA	NA	20	0	0	0	2	22
bog_big	c	x	5	H	Hx5	NA	NA	NA	0	0	0	0	5	5
bog_big	c	x	6	H	Hx6	NA	NA	NA	0	0	0	0	0	0
bog_big	c	x	7	H	Hx7	NA	NA	NA	0	0	1	0	0	1
bog_big	c	x	8	H	Hx8	NA	NA	NA	3	0	0	0	2	5
bog_big	c	x	9	H	Hx9	NA	NA	NA	4	0	0	0	0	4
bog_big	c	x	10	H	Hx10	NA	NA	NA	1	0	0	1	3	5
bog_big	c	y	1	H	Hy1	NA	NA	NA	1	0	0	1	0	2
bog_big	c	y	2	H	Hy2	NA	NA	NA	5	2	13	4	70	96

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
bog_big	c	y	3	H	Hy3	NA	NA	NA	3	0	1	0	9	13
bog_big	c	y	4	H	Hy4	NA	NA	NA	0	0	0	0	0	0
bog_big	c	y	5	H	Hy5	NA	NA	NA	0	0	2	0	7	9
bog_big	c	y	6	H	Hy6	NA	NA	NA	0	0	0	0	1	1
bog_big	c	y	7	H	Hy7	NA	NA	NA	1	0	0	0	2	3
bog_big	c	y	8	H	Hy8	NA	NA	NA	0	0	0	0	7	7
bog_big	c	y	9	H	Hy9	NA	NA	NA	1	0	1	0	6	9
bog_big	c	y	10	H	Hy10	NA	NA	NA	0	0	0	3	6	9
bog_sml	a	x	1	I	Ix1	0	0	0	0	0	0	0	0	0
bog_sml	a	x	2	I	Ix2	1	1	15	0	0	0	4	11	15
bog_sml	a	x	3	I	Ix3	0	0	0	0	0	0	2	0	2
bog_sml	a	x	4	I	Ix4	0	0	11	0	0	0	1	0	1
bog_sml	a	x	5	I	Ix5	0	1	3	0	0	0	2	3	5
bog_sml	a	x	6	I	Ix6	NA	NA	NA	0	0	0	1	4	5
bog_sml	a	x	7	I	Ix7	NA	NA	NA	0	0	0	1	0	1
bog_sml	a	x	8	I	Ix8	NA	NA	NA	0	0	0	1	18	19
bog_sml	a	x	9	I	Ix9	NA	NA	NA	0	0	0	1	17	18
bog_sml	a	x	10	I	Ix10	NA	NA	NA	0	0	0	0	6	6
bog_sml	a	y	1	I	Iy1	NA	NA	NA	2	0	0	2	9	13
bog_sml	a	y	2	I	Iy2	NA	NA	NA	1	0	0	1	5	7
bog_sml	a	y	3	I	Iy3	NA	NA	NA	0	0	0	0	1	1
bog_sml	a	y	4	I	Iy4	NA	NA	NA	0	0	0	0	5	6
bog_sml	a	y	5	I	Iy5	NA	NA	NA	0	0	0	0	5	5
bog_sml	a	y	6	I	Iy6	NA	NA	NA	11	0	0	0	4	15
bog_sml	a	y	7	I	Iy7	NA	NA	NA	11	0	2	0	3	16
bog_sml	a	y	8	I	Iy8	NA	NA	NA	0	0	0	0	3	3
bog_sml	a	y	9	I	Iy9	NA	NA	NA	10	0	1	0	13	26
bog_sml	a	y	10	I	Iy10	NA	NA	NA	0	0	0	0	11	12
forest	c	x	1	J	Jx1	NA	NA	NA	0	0	0	0	14	14
forest	c	x	2	J	Jx2	NA	NA	NA	0	0	0	0	24	24
forest	c	x	3	J	Jx3	NA	NA	NA	0	0	1	0	2	3
forest	c	x	4	J	Jx4	NA	NA	NA	0	0	0	0	19	19
forest	c	x	5	J	Jx5	NA	NA	NA	0	0	0	0	6	6
forest	c	x	6	J	Jx6	NA	NA	NA	0	0	0	1	1	2
forest	c	x	7	J	Jx7	NA	NA	NA	2	0	4	1	3	12
forest	c	x	8	J	Jx8	NA	NA	NA	0	0	0	1	5	11
forest	c	x	9	J	Jx9	NA	NA	NA	0	0	1	0	7	13
forest	c	x	10	J	Jx10	NA	NA	NA	0	0	0	2	4	7

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
forest	c	y	1	J	Jy1	0	0	1	0	0	0	0	0	0
forest	c	y	2	J	Jy2	0	0	0	0	1	0	0	0	1
forest	c	y	3	J	Jy3	0	3	1	0	0	2	0	0	2
forest	c	y	4	J	Jy4	0	1	1	0	0	3	0	0	3
forest	c	y	5	J	Jy5	0	0	0	0	0	0	0	0	0
forest	c	y	6	J	Jy6	NA	NA	NA	0	0	0	0	8	9
forest	c	y	7	J	Jy7	NA	NA	NA	2	0	0	0	9	11
forest	c	y	8	J	Jy8	NA	NA	NA	0	0	0	1	3	6
forest	c	y	9	J	Jy9	NA	NA	NA	0	0	0	0	15	15
forest	c	y	10	J	Jy10	NA	NA	NA	0	0	0	0	17	19
clearcut	c	x	1	K	Kx1	NA	NA	NA	0	0	0	0	5	5
clearcut	c	x	2	K	Kx2	NA	NA	NA	0	1	0	0	0	2
clearcut	c	x	3	K	Kx3	NA	NA	NA	0	0	0	0	1	1
clearcut	c	x	4	K	Kx4	NA	NA	NA	0	0	0	0	4	4
clearcut	c	x	5	K	Kx5	NA	NA	NA	0	0	0	0	5	7
clearcut	c	x	6	K	Kx6	NA	NA	NA	0	0	0	0	1	1
clearcut	c	x	7	K	Kx7	NA	NA	NA	0	0	0	1	8	9
clearcut	c	x	8	K	Kx8	NA	NA	NA	0	0	0	0	5	5
clearcut	c	x	9	K	Kx9	NA	NA	NA	0	0	0	2	4	6
clearcut	c	x	10	K	Kx10	NA	NA	NA	0	0	0	0	1	1
clearcut	c	y	1	K	Ky1	NA	NA	NA	0	0	0	1	0	2
clearcut	c	y	2	K	Ky2	NA	NA	NA	0	0	0	1	0	1
clearcut	c	y	3	K	Ky3	NA	NA	NA	0	1	0	0	0	1
clearcut	c	y	4	K	Ky4	NA	NA	NA	0	0	0	0	0	0
clearcut	c	y	5	K	Ky5	NA	NA	NA	0	0	0	0	1	1
clearcut	c	y	6	K	Ky6	NA	NA	NA	0	0	0	1	0	1
clearcut	c	y	7	K	Ky7	NA	NA	NA	0	1	0	4	0	5
clearcut	c	y	8	K	Ky8	NA	NA	NA	0	0	0	1	1	2
clearcut	c	y	9	K	Ky9	NA	NA	NA	0	0	0	0	0	0
clearcut	c	y	10	K	Ky10	NA	NA	NA	0	0	0	1	3	4
scrub	b	x	1	L	Lx1	12	5	3	0	0	0	6	66	73
scrub	b	x	2	L	Lx2	8	5	4	0	0	2	1	60	63
scrub	b	x	3	L	Lx3	1	2	7	0	0	0	0	2	2
scrub	b	x	4	L	Lx4	2	15	9	1	0	0	1	16	18
scrub	b	x	5	L	Lx5	0	0	0	0	0	0	0	0	0
scrub	b	x	6	L	Lx6	NA	NA	NA	1	0	0	2	6	9
scrub	b	x	7	L	Lx7	NA	NA	NA	0	1	0	5	3	10
scrub	b	x	8	L	Lx8	NA	NA	NA	0	0	0	5	21	26

Trtmnt	Lndscpe	Bog	Pool	landuniq	poolunic	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
scrub	b	x	9	L	Lx9	NA	NA	NA	0	0	0	3	32	35
scrub	b	x	10	L	Lx10	NA	NA	NA	10	0	0	5	12	27
scrub	b	y	1	L	Ly1	NA	NA	NA	0	0	0	0	21	21
scrub	b	y	2	L	Ly2	NA	NA	NA	0	0	0	0	3	3
scrub	b	y	3	L	Ly3	NA	NA	NA	0	0	0	2	2	4
scrub	b	y	4	L	Ly4	NA	NA	NA	1	0	0	1	19	21
scrub	b	y	5	L	Ly5	NA	NA	NA	2	0	0	6	2	10
scrub	b	y	6	L	Ly6	NA	NA	NA	3	0	1	0	12	20
scrub	b	y	7	L	Ly7	NA	NA	NA	10	0	0	3	14	27
scrub	b	y	8	L	Ly8	NA	NA	NA	0	1	0	2	22	25
scrub	b	y	9	L	Ly9	NA	NA	NA	0	0	0	6	1	7
scrub	b	y	10	L	Ly10	NA	NA	NA	0	0	0	0	11	11
scrub	c	x	1	M	Mx1	NA	NA	NA	0	2	0	11	22	37
scrub	c	x	2	M	Mx2	NA	NA	NA	0	1	0	1	1	5
scrub	c	x	3	M	Mx3	NA	NA	NA	0	0	0	0	3	3
scrub	c	x	4	M	Mx4	NA	NA	NA	0	1	0	0	0	1
scrub	c	x	5	M	Mx5	NA	NA	NA	0	0	0	1	0	1
scrub	c	x	6	M	Mx6	NA	NA	NA	0	2	0	0	2	5
scrub	c	x	7	M	Mx7	NA	NA	NA	1	2	0	0	146	159
scrub	c	x	8	M	Mx8	NA	NA	NA	0	0	0	0	5	5
scrub	c	x	9	M	Mx9	NA	NA	NA	0	2	0	0	1	5
scrub	c	x	10	M	Mx10	NA	NA	NA	0	1	0	0	0	1
scrub	c	y	1	M	My1	NA	NA	NA	1	0	0	18	11	30
scrub	c	y	2	M	My2	NA	NA	NA	0	1	0	10	4	16
scrub	c	y	3	M	My3	NA	NA	NA	0	0	0	20	9	30
scrub	c	y	4	M	My4	NA	NA	NA	0	1	0	5	0	6
scrub	c	y	5	M	My5	NA	NA	NA	0	0	0	5	1	6
scrub	c	y	6	M	My6	NA	NA	NA	0	0	0	14	13	27
scrub	c	y	7	M	My7	NA	NA	NA	0	1	0	25	9	39
scrub	c	y	8	M	My8	NA	NA	NA	0	0	0	0	0	0
scrub	c	y	9	M	My9	NA	NA	NA	0	0	0	0	24	24
scrub	c	y	10	M	My10	NA	NA	NA	0	0	0	12	8	21
bog_sml	b	x	1	N	Nx1	7	7	6	0	1	0	2	37	41
bog_sml	b	x	2	N	Nx2	4	5	24	0	0	0	1	14	15
bog_sml	b	x	3	N	Nx3	3	2	3	0	0	0	0	8	8
bog_sml	b	x	4	N	Nx4	16	0	4	1	0	2	1	79	88
bog_sml	b	x	5	N	Nx5	9	5	6	0	0	0	0	33	33
bog_sml	b	x	6	N	Nx6	NA	NA	NA	1	0	0	5	167	176

Trtmnt	Lndscpe	Bog	Pool	landuniq	pooluniq	Lh_F	Lh_F-1	Lh_F-2	Enal_ex	Asit_ex	Cshu_ex	Ssep_ex	Lhud_ex	Total_ex
bog_sml	b	x	7	N	Nx7	NA	NA	NA	0	1	0	8	6	15
bog_sml	b	x	8	N	Nx8	NA	NA	NA	0	0	0	3	92	99
bog_sml	b	x	9	N	Nx9	NA	NA	NA	0	0	0	2	2	4
bog_sml	b	x	10	N	Nx10	NA	NA	NA	0	0	1	0	59	64
bog_sml	b	y	1	N	Ny1	NA	NA	NA	0	2	0	0	0	2
bog_sml	b	y	2	N	Ny2	NA	NA	NA	0	0	0	1	1	5
bog_sml	b	y	3	N	Ny3	NA	NA	NA	0	0	2	0	5	9
bog_sml	b	y	4	N	Ny4	NA	NA	NA	16	0	0	0	1	25
bog_sml	b	y	5	N	Ny5	NA	NA	NA	0	0	0	0	3	3
bog_sml	b	y	6	N	Ny6	NA	NA	NA	0	0	0	0	7	7
bog_sml	b	y	7	N	Ny7	NA	NA	NA	0	1	0	3	3	9
bog_sml	b	y	8	N	Ny8	NA	NA	NA	0	0	0	0	1	1
bog_sml	b	y	9	N	Ny9	NA	NA	NA	0	0	0	9	3	14
bog_sml	b	y	10	N	Ny10	NA	NA	NA	3	0	2	0	11	20
bog_sml	c	x	1	O	Ox1	NA	NA	NA	0	0	0	0	9	9
bog_sml	c	x	2	O	Ox2	NA	NA	NA	3	0	0	1	0	4
bog_sml	c	x	3	O	Ox3	NA	NA	NA	5	0	2	0	11	19
bog_sml	c	x	4	O	Ox4	NA	NA	NA	4	1	0	4	42	57
bog_sml	c	x	5	O	Ox5	NA	NA	NA	4	0	0	0	4	9
bog_sml	c	x	6	O	Ox6	NA	NA	NA	0	0	0	0	4	4
bog_sml	c	x	7	O	Ox7	NA	NA	NA	0	0	0	1	0	1
bog_sml	c	x	8	O	Ox8	NA	NA	NA	0	0	0	2	4	6
bog_sml	c	x	9	O	Ox9	NA	NA	NA	0	1	0	1	12	14
bog_sml	c	x	10	O	Ox10	NA	NA	NA	0	0	0	1	2	3
bog_sml	c	y	1	O	Oy1	NA	NA	NA	0	0	2	0	8	10
bog_sml	c	y	2	O	Oy2	NA	NA	NA	0	0	0	7	12	20
bog_sml	c	y	3	O	Oy3	NA	NA	NA	0	0	0	2	6	8
bog_sml	c	y	4	O	Oy4	NA	NA	NA	0	1	0	1	0	2
bog_sml	c	y	5	O	Oy5	NA	NA	NA	0	0	0	2	0	2
bog_sml	c	y	6	O	Oy6	NA	NA	NA	0	0	0	0	0	0
bog_sml	c	y	7	O	Oy7	NA	NA	NA	0	0	0	2	0	2
bog_sml	c	y	8	O	Oy8	NA	NA	NA	0	0	0	3	7	10
bog_sml	c	y	9	O	Oy9	NA	NA	NA	0	0	0	0	0	0
bog_sml	c	y	10	O	Oy10	NA	NA	NA	0	0	0	0	0	0