

THE POTENTIAL FOR REPLACEMENT OF AQUATIC ARTHROPODS BY TAXA PERFORMING EQUIVALENT ECOLOGICAL FUNCTIONS

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of

Graduate Studies

by

Dwight Alvin Williamson

In Partial Fulfillment of the

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of

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DWIGHT ALVIN WILLIAMSON

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

MASTER OF SCIENCE

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ABSTRACT

Three models were developed to describe the mechanisms by which the ecological roles of species lost as a result of environmental perturbation may be assumed by other, more tolerant taxa. Model I (re-colonization) follows from literature on classic succession. Model II (niche width expansion) and Model III (redundant species) are derived as the inverse of species packing theory. Species interactions and community attributes may affect the type of operative model and therefore, may have predictive value. Information was obtained from over 100 studies on niche overlap and resource partitioning regarding how widespread potential replacement might be, based upon the predictive tools associated with each model. The potential for replacement does not appear widespread, and would be limited to ~ 20% of guild-forming organisms. Replacement by Model II would be most probable, followed by Model III and Model I.

The aquatic arthropod community was examined in six small boreal forest ponds located in Sandilands Provincial Forest, Manitoba, Canada, in order to experimentally assess hypotheses concerning potential replacement. Of the original 108 taxa, 36 (33.3%) had potential replacements that could perform an equivalent ecological function without altering the size spectrum of the replacement community.

The six ponds were similar in size, uniform in morphology, located in the same area, and had been colonized for the same period of time, but the aquatic arthropod community differed substantially among ponds. Canonical Correspondence Analysis (CCA) was used to relate the distribution and abundance of aquatic arthropods in the six study ponds to 91 measured or derived environmental variables. Environmental variables included in the final CCA model that best explained the observed variability were pond

pH, area covered by macrophytes, and percent substrate comprising silt (overall model fit: $p = 0.005$; first canonical axis: $p = 0.004$). This model explained 88.8% of the variability in species distribution and abundance and 71.7% of the variability in the key 36 species with replacement potential.

A method was derived to calculate niche overlap in canonical space in order to predict which of the 36 candidate replacement species had the potential to colonize available pond habitat and to achieve similar abundance as hypothetically lost taxa. Replacement by Model I was limited to ~ 10% of the total available "opportunities" for replacement. Replacement by Model II or Model III was more likely in ~ 25% of the total available "opportunities". Replacement by both Model I and Model II or III mechanisms appeared more likely for species located in ponds of average environmental conditions relative to those located near the lower or upper ends of a gradient.

FORWARD

This thesis is arranged in paper-style. The Literature Review, normally presented as a single chapter in traditional theses, appears in Chapters II and III. These chapters, entitled "Development of Replacement Models" and "Evidence for Potential Replacement", respectively, also include a re-interpretation of existing studies in the context of functional replacement potential. Presentation of the information in this manner better sets the framework for the remaining work in Chapters IV, V and VI.

All data are listed in Williamson (1994) and are available on disk in Excel Version 3.0. Voucher specimens were deposited in the J.B. Wallis Museum of Entomology, University of Manitoba.

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CHAPTER I

GENERAL INTRODUCTION

Ecological integrity, *sensu* Regier (1990) and Kay and Schneider (1994), is thought to result when systems are: (1) energetic, with natural ecosystemic processes being strong and not severely constrained; (2) self-organizing in an evolving manner; (3) self-defending against invasions by exotic organisms; (4) robust with the ability to survive and recover from occasional crises; (5) attractive to informed humans; and (6) productive of goods and opportunities valued by humans. Toxic substances in the aquatic environment may compromise the integrity of ecosystems by inducing a number of effects, depending upon the nature of the material, the duration and magnitude of exposure, and the sensitivity of the exposed community. For example, examination of community composition above and below an effluent outfall may reveal one of three possible outcomes (Cairns 1974, Stauffer and Hocutt 1980). First, the community composition may be exactly the same, indicating that all functional niches have been preserved, thus implying little or no impact. Second, some lost species may have been replaced by others performing the same function, thus implying that community change has occurred but that the function of the system has been conserved. Third, loss of species may have occurred without replacement, indicating that both community structure and system function have been altered. Courtemanch and Davies (1987) defined the second outcome as change--species loss in a community with replacement, and the third outcome as harm--species loss in a community without replacement.

The phenomenon of stress-induced succession is shown conceptually in Figure 1 (Odum *et al.* 1979). Increasing perturbation causes differing output responses from the affected community. Relatively low levels of perturbation result in ecosystem

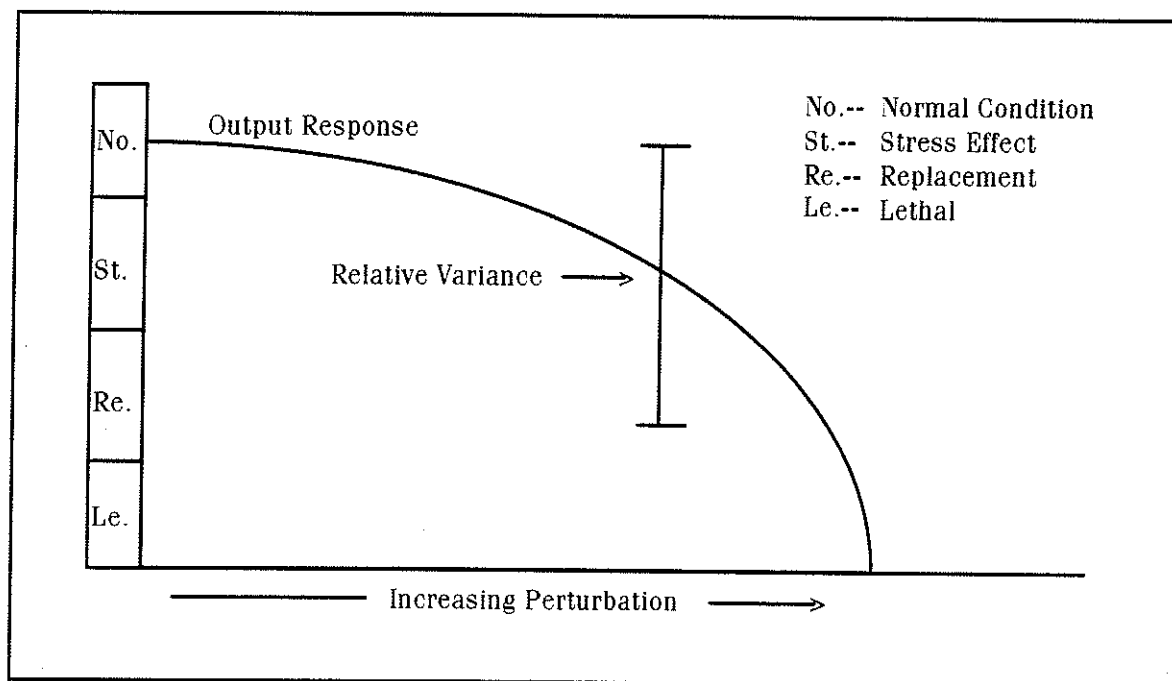


Figure 1. Conceptual response of aquatic communities to toxicant-induced stress (modified from Odum *et al.* 1979). The relative variance represents theoretical differences in output responses between species.

stress, as measured by some function of individual or community performance. As perturbations increase in magnitude, organism replacement may occur, followed finally by loss of taxa from the system.

Cairns and Dickson (1976) suggested that complex systems, advanced in successional stage, likely have a high degree of structural and functional redundancy; the function of a single species lost from complex systems may be replaced by other remaining members of the community. Further, Minns *et al.* (1990) estimated the number of lakes that may be affected by acid precipitation in eastern Canada. Criteria for damage was a 20% decrease in species richness in 20% of lakes within each area. Minns *et al.* (1990) recognized that the 20% decrease in species could occur initially, but that re-colonization by acid-tolerant forms might later increase species richness, although not to the extent that all acid-related species losses could be replaced. Thus, environmental harm is thought to be mitigated, in some cases (Schindler *et al.* 1985), by the maintenance of ecosystem function in the presence of stress through the replacement of sensitive species by more tolerant taxa performing a similar ecological function.

Stephan *et al.* (1985) developed water quality criteria to protect aquatic communities, based in part upon the recognition that sensitive species lost because of toxicant stress may be replaced by more tolerant taxa capable of performing the same ecological function. By their method, not all species are afforded protection and not all communities are protected at all times and in all places, since it is assumed that aquatic communities can withstand some stress and can recover. Stephan *et al.*'s (1985) resulting criteria are intended to protect all but 5% of the genera at any site from unacceptable effects. Unacceptable effects are difficult to define (Stephan 1986), but acknowledged in

the concept is the notion that the mere presence of human activity may cause some community change.

The phenomenon of functional replacement may be more prevalent in less complex forms of life such as fungi, bacteria, Protozoa and microalgae (Stephan 1985), but the method applies equally to all forms of aquatic life. Modifications however, can be made at specific sites to provide more complete protection to sensitive, important species. This method has been used to develop national water quality criteria in the United States and has been adopted for use in two Canadian jurisdictions (Williamson 1988, Ministère de L'Environnement du Québec 1991).

The potential for stress-induced replacement of lost species by other more tolerant species performing the same ecological function has not been rigorously examined. Examination of this hypothesis is the focus of this thesis. Within this thesis, I will:

- i) discuss elements of evolutionary and ecological theory that explain how one species can perform a similar ecological role in the absence of another taxon (Chapter II);
- ii) develop models describing potential functional replacement (Chapter II);
- iii) estimate how widespread the phenomenon might be within aquatic communities, through evidence from niche overlap studies (Chapter III);
- iv) assess a data set consisting of aquatic arthropod fauna and related environmental variables from six boreal forest study ponds in the following two ways:

- a) estimate similarity between potential replacement species and hypothetically lost species based upon generalized resource partitioning attributes of each (Chapter IV);
- b) estimate niche overlap in canonical space along environmental gradients among the six ponds (Chapter V). Assuming that the species assemblage in all six ponds represents the available colonizing pool, predictions can be made regarding which species may be able to replace taxa in other study ponds based upon habitat preferences or physical and chemical factors that may influence colonization and subsequent population success;

Combining the outcomes from (a) and (b) will result in the identification of potential replacement species for each hypothetically lost taxon following environmental perturbation (Chapter VI); and,

- v) summarize information relative to the new perspective presented in this thesis and discuss further studies that will be required to more convincingly demonstrate functional replacement (Chapter VI).

CHAPTER II

DEVELOPMENT OF REPLACEMENT MODELS

ABSTRACT

Three hypotheses were developed to describe possible mechanisms by which the ecological function of one species lost from a habitat as a result of environmental perturbation could be replaced by another taxon. Model I assumes re-colonization of the habitat by a second and similar species. Under conditions of Model I, the hypothetically lost taxon and the potential replacement species do not co-exist. The potential replacement species: (1) are probably poor competitors relative to the hypothetically lost taxon; (2) probably have inflexible niche widths; and (3) must have good dispersal abilities. It is predicted that replacement by Model I would most likely occur in stable habitats that are resource limited. *A priori* evidence to predict the potential for Model I replacement would be significant niche overlap in allopatric populations and competitive exclusion.

In Model II (niche width expansion), developed principally from species packing theory, co-existing species expand their niche width to utilize unused resources left by removal of the original species. Species would co-exist through resource partitioning prior to removal and would likely be present as part of a functional guild. Species capable of replacement by Model II must have the flexibility to alter niche widths through behavioural or short-term phenotypical mechanisms. *A priori* predictive evidence for potential replacement by Model II would include significant niche overlap in allopatric populations, and wider niche width in allopatric populations relative to sympatric populations.

Model III (redundant species) replacement, also derived from species packing theory, would occur in cases where co-existing species, as part of a functional guild, do not partition resources. Rather, resources are not limiting such that a number of species co-exist while performing a similar ecological function. The co-existing species would have large niche overlap. Following loss of one species, the remainder would increase their rate of resource processing, but would not increase niche widths (*i.e.*, utilize more of the same resources left unused by the lost species). *A priori* predictive evidence for the potential replacement by Model III would be significant niche overlap in sympatric populations.

Under Model I replacement, species diversity would not change. However, species diversity would decline under both Model II and Model III. Although system function would not change through Model II and Model III replacement hypotheses, there may be residual effects on system stability or on other community variables. These residual effects have not been considered.

INTRODUCTION

The niche is a useful concept for understanding relationships of species within and among communities (Whittaker 1965, 1975). Niche width and overlap have been used in a number of ways: (1) to evaluate competitive relationships within assemblages of species (Hutchinson 1957, Abrams 1980); (2) to gain a better understanding of how organisms co-exist (Molles 1978, Kovalak 1980, Cross 1981, Crowder 1981, Crowley and Johnson 1982, Hildrew *et al.* 1984, Nummelin *et al.* 1984, Gorman 1988); (3) to determine whether or not an organism has the potential to displace a pest vector, thus function as a biological control organism (Cedeno-Leon and Thomas 1982); (4) to determine whether or not a community has been affected by environmental disturbance (Rader and Ward 1989); and (5) to examine similarities between species in different communities or different environments (Fuentes 1976, Race 1982). Niche overlap may also prove useful for determining the extent of functional similarity between species and hence, evaluate whether or not one species may be able to replace the function of another species.

The objectives of this chapter are:

- i) to describe the niche of an organism and discuss how the niche concept can be used to assess functional similarity of two species;
- ii) to develop models that describe potential functional replacement.

The Niche

Schoener (1989) gave a thoughtful account of the development of ecological niche theory. The niche was originally defined by Grinnell (1917) as the place of an animal in its environment, then by Elton (1927) as an animal's relationship with its prey and predators. Schoener (1989) contended that both Grinnell's (1917) and Elton's (1927) concepts of the niche were essentially similar. Hutchinson (1957) formalized the definition of the niche as the relationship of an animal to all the factors or dimensions of its biotic and abiotic environment with which the animal has adapted. Thus, the niche can be envisaged as an abstract multidimensional hypervolume or space with each axis representing one abiotic or biotic factor. Hutchinson (1957) called this the fundamental niche of the species. Each species is adapted to tolerate a certain range of each factor or variable. This range is defined as the niche width and the combination of all upper and lower limits for all variables then describes the niche space that each species is able to occupy (Figure 1). Each species will have an optimal point on each resource axis where long-term survival and proportional utilization of resources are optimal (Schoener 1989), and this will diminish to sub-optimal conditions near the upper or lower limit of the axis (Hutchinson 1957).

Niche width is often used as the inverse of ecological specialization (Colwell and Futuyma 1971). Organisms with small niche width along any one resource dimension are ecologically specialized. Facultative feeding mechanisms may allow organisms to occupy wider niche widths than obligate or specialized feeding mechanisms (Cummins and Klug 1979). Two species in a community may share part or all of one or more abiotic or biotic axes. The extent of axes sharing or that part of an organism's niche that is simultaneously

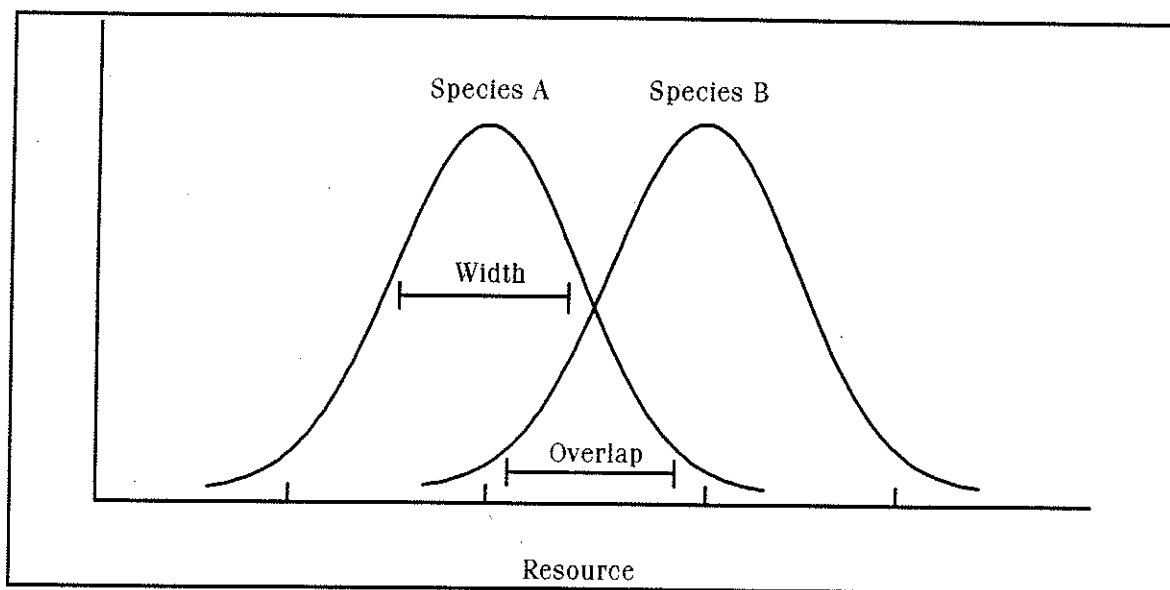


Figure 1. Description of simplified niche metrics for two co-existing species (from Hale 1981).

occupied by other organisms (Johnson 1977) has been defined as niche overlap (*e.g.*, Griffiths 1986).

DISCUSSION

Mathematical Description of Community Function

MacArthur (1972) derived an equation to describe the relationship in the undisturbed community shown in Figure 1. This equation, with modification, can be used to understand and subsequently test hypotheses concerning the replacement of one species' function by another within an altered community. The equation, following re-arrangement of terms, is as follows:

$$D_r = D_u \left[\frac{D_s}{\lambda} \right], \text{ where} \quad (\text{Eq. 1})$$

D_r = diversity of resources used by the entire community;

D_u = diversity of resources used by an average species;

D_s = species diversity;

λ = Rayleigh ratio.

The Rayleigh ratio is defined as follows:

$$\lambda = \frac{\sum_{i,k} \alpha_{ik} X_i X_k}{\sum X_i^2}, \text{ where} \quad (\text{Eq. 2})$$

α = niche overlap between species i and k (MacArthur and Levins (1967) niche overlap index);

X = abundance of species i and k ;

$$\alpha = \frac{\sum_j u_{ij} u_{kj}}{\sum_j u_{ij}^2}, \text{ where} \quad (\text{Eq. 3})$$

$$u_{ij} = a_{ij} \sqrt{\frac{K_j w_j}{r_j}}, \text{ and} \quad (\text{Eq. 4})$$

$$u_{kj} = a_{kj} \sqrt{\frac{K_j w_j}{r_j}}, \text{ where} \quad (\text{Eq. 5})$$

u_{ij} and u_{kj} = utilization of resource j by species i and k , respectively;

a_{ij} and a_{kj} = probability that during a unit of time an individual of species i and k encounters and eats a given individual of resource j ;

K_j = asymptote of j when both species i and k are present;

w_j = weight per unit of quantity of resource j ;

r_j = intrinsic rate of growth.

In a simplified community, where it is assumed that the abundance of all species is equal, the following relationship holds:

$$\lambda \approx 1 + C\bar{\alpha}, \text{ where} \quad (\text{Eq. 6})$$

C = number of neighbours in niche space;

$\bar{\alpha}$ = niche overlap between an average pair of species.

It is unlikely that species abundance will be equal in most real communities. Therefore, this simplification of the Rayleigh relationship is normally not applicable.

MacArthur (1972) advocated the use of the inverse of Simpson's index to represent diversity in his equation. Simpson's diversity index is as follows:

$$D = \frac{1}{\sum_i p_i^2}, \text{ where} \quad (\text{Eq. 7})$$

D = diversity of species, diversity of resources used by the entire community, or diversity of resources used by individual species;

p_i = proportion of all individuals belonging to the i species, proportion of resources along a specific axis, and proportion of species' utilization of resources along this axis.

Resource utilization is expressed as a proportion within MacArthur's (1972) equation when Simpson's diversity index is used. In the particular case of one species being replaced by another, the absolute processing of resources by the entire community must be maintained, regardless of how the proportion of resources is shared by individual species. Thus, in this special case an additional constraint must be imposed. The sum of

resources processed by individual species (Eq. 8), must be held constant between the original community and the replacement community.

$$\sum_j u_{ij} u_{lj} = \sum_j u_{ij} u_{rj}, \text{ where} \quad (\text{Eq. 8})$$

u_{ij} and u_{lj} = species i and lost species l in the original community
(species k from Eq. 3 now becomes lost species l);
 u_{ij} and u_{rj} = species i and replacement species r in the altered
community.

D_r is a broad measure of community function, since it incorporates both information on community structure and information on resources processed by the community. Following species replacement, D_r must remain unchanged. Thus,

$$D_{ul} \left[\frac{D_{sl}}{\lambda_l} \right] = D_{ur} \left[\frac{D_{sr}}{\lambda_r} \right], \text{ where} \quad (\text{Eq. 9})$$

the equation on either side of equality represents a measure of the function of the community prior to species loss and the function of the replacement community, denoted by the subscript l and r , respectively.

MacArthur's (1972) equation can be applied to two or more species using resources along any one resource axis or can be expanded to the multivariate case of a community of organisms using resources along several resource axes. Harner and Whitmore (1977) extended the MacArthur and Levins (1967) measure of niche overlap α to the multivariate case. Some properties of α were explored by Maurer (1982) and Smith (1982), allowing statistical inference. In the multivariate case, it is expected that the

overall abundance of all organisms in the community would remain relatively constant following replacement. When applied to one or more taxa replacing the function of a lost species, abundance of an individual taxon may well change (*e.g.*, see later development of replacement Models II or III); a change in abundance may be necessary to allow the community to process the same amount of resources with fewer species. In these cases, the term $1 + C_{\bar{a}}$ should be replaced by the Rayleigh ratio λ .

The MacArthur - Levins (1967) measure of niche overlap has been criticized for several reasons. Hurlbert (1978) identified three concerns. First, it is really an estimate of the Lotka - Volterra competition coefficient and therefore is not synonymous with niche overlap even though MacArthur and Levins (1967) referred to it as a niche overlap measure. Second, it is affected by the distribution of non-shared resources. Third, it does not account for the abundance or availability of resources being shared. The first criticism is one of semantics and not of substance; it matters less what a measure is called than what it actually measures. The third criticism is not valid in the present application since, by Eq. 8, resources are held constant between the original and unperturbed communities, thus explicitly accounting for abundance of resources being shared. The second criticism remains unanswered and in further work, it may be necessary to substitute a more appropriate measure.

MacArthur (1972) reported that the equation to describe species packing is mathematical and does not assume any underlying biological structure. MacArthur (1972) developed the equation simply to represent what must happen when additional species are added to a system: overlap increases, niche width decreases, or additional resources are exploited. The equation takes on biological meaning when resource axes and units of measurement are correctly chosen for any given community.

Functional Replacement Models

MODEL I: RE-COLONIZATION

Model I (re-colonization) is based on the tenet that lost or removed taxa in one aquatic system will be replaced through colonization by another, functionally equivalent species. Colonization would occur through classic succession (Krebs 1985) whereby a new species exploits resources in an unoccupied niche. Model I is shown conceptually in Figure 2. Invasion by species "D" follows loss of species "B". Species "B" and "D" have similar niche widths and interact with other members of the community in similar manner.

According to Model I replacement, all variables in the modified MacArthur (1972) equation remain unchanged following loss of species "B" and re-colonization by species "D". Function of the ecosystem will be conserved by replacement species "D" having a similar utilization function (D_{ui}) as lost species "B". Diversity and amount of resources processed by the community (D_r) is maintained although community composition is altered.

Model I, to a large extent, depends upon the presence of two or more ecologically similar species. The evolution of two ecologically similar species has been described in past studies. Mayr's (1969) biological species concept includes the dimensional evolution of each species in space and time (Burma 1949, Dunbar 1950). Evolution is the process of change within populations following speciation. Depending upon the time scale and the nature of the evolutionary and ecological forces, two species occurring in either sympatry or allopatry may have retained or developed many similar features. This has been referred

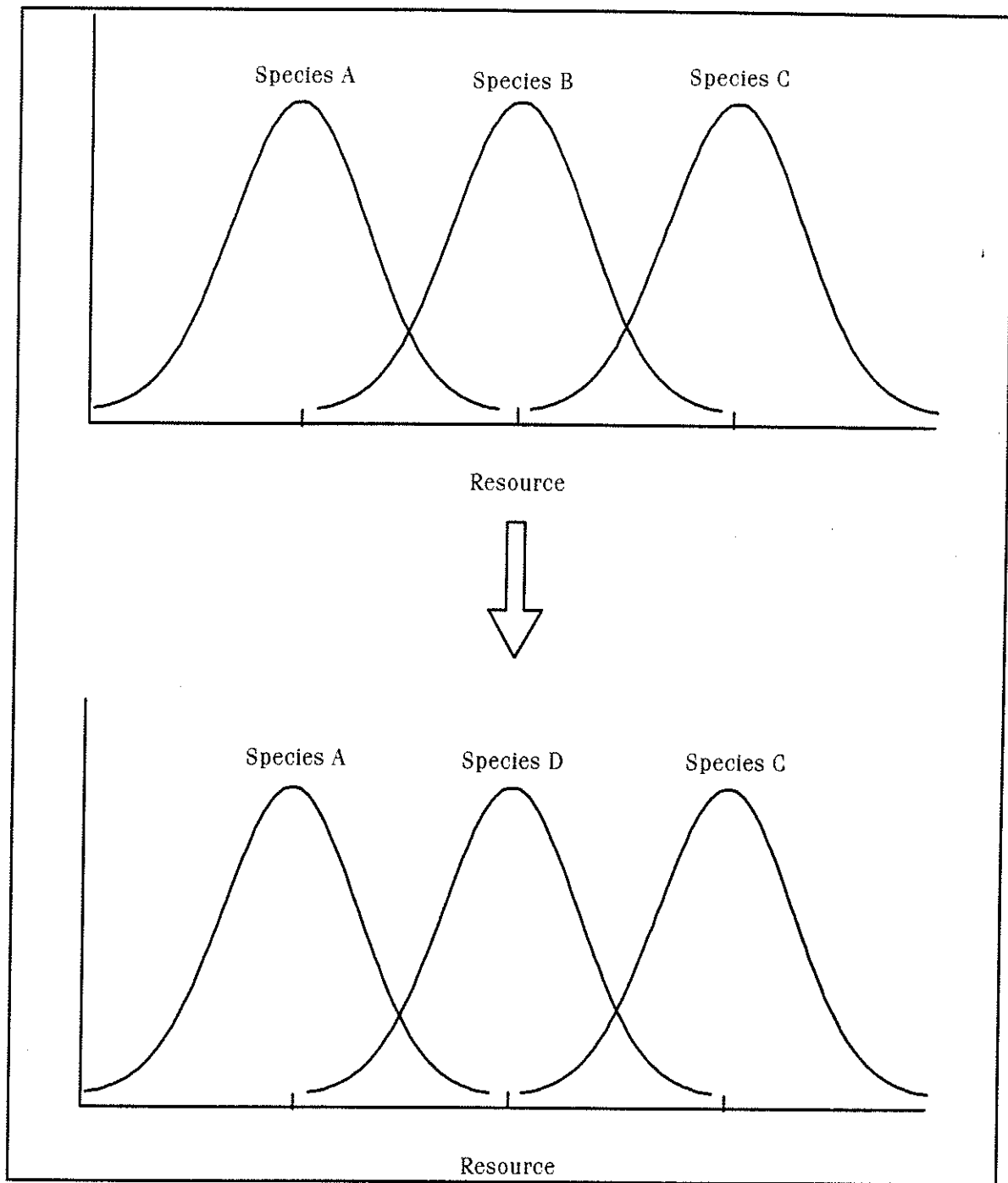


Figure 2. Model I - functionally equivalent replacement by re-colonization.

to as parallel or convergent evolution (Griffiths 1986) and occurs when the same characters are retained or developed in different species within common ancestral lineages in response to similar evolutionary pressures (MacArthur and Levins 1967, Mayr 1969, Giller and McNeill 1981, Ghilarov 1984). Two species, having evolved in similar environments may, therefore, share important attributes that allow them to perform the same ecological function. Merritt and Cummins (1984) described the convergent evolution of similar scraper mandibles in four species of aquatic insects, representing four families and two orders (Trichoptera: Glossosomatidae, Helicopsychidae, Limnephilidae and Coleoptera: Psephenidae).

In the absence of experimental studies, it is hypothesized that evidence supporting the potential extent of Model I replacement in natural systems may be found in studies concerning competitive exclusion. According to the Principle of Gause (Whittaker 1975), also referred to as the Principle of Gause-Volterra (Hutchinson 1957) or the Principle of Competitive Exclusion (Hardin 1960), no two species can occupy the same niche in a stable environment. That is, n species cannot co-exist on less than n resources, or in less than n niches or when limited by less than n factors (Armstrong and McGehee 1980). The species that is at a competitive disadvantage will be excluded from the habitat (*e.g.*, Ayala 1970, Gause 1970, Southwood 1977, Subra and Dransfield 1984). For example, species "B" and species "D", are sufficiently similar that species "D" is excluded because of its competitive disadvantage. Should loss of species "B" occur through anthropogenic stress, species "D" may suddenly gain the competitive advantage and re-colonize. The second re-colonizing species may overlap in a number of other resource axes such that it is able to continue the same ecological function as the lost species.

MODEL II: NICHE WIDTH EXPANSION

The second model follows from Roughgarden (1972) in which niche width is hypothesized to increase following removal of competing phenotypes. Model II (niche width expansion) is also consistent with the inverse of a species packing hypothesis of MacArthur (1972). In Model II, one (or more) remaining species within the stressed community increase resource utilization to compensate for the function of the lost taxon, in part, through expanding niche width (D_w). Model II is shown conceptually in Figure 3. Species "A" increases niche width in order to continue the ecological function of the lost taxon, species "B". There is nothing in the relationship between species "A" and species "B" to imply the potential for symmetrical replacement. That is, although species "A" replaces the ecological function of species "B", the reverse is not suggested. Following Model II replacement, niche overlap ($\bar{\alpha}$) is unchanged. Species diversity (D_s) and number of neighbours (C) are reduced and diversity and resources used by average species (D_u) are increased. System function is therefore conserved since D_r remains unchanged.

According to Model II, functionally equivalent species co-exist through partitioning of resources. In the absence of actual experimental studies on Model II replacement, evidence for its potential in natural systems may be found by reviewing resource partitioning studies. A number of researchers have been intrigued by the co-existence of species with apparent ecological similarities. This has prompted the generation of a large body of literature concerning the mechanisms evolved by these ecologically similar organisms to partition resources. Such studies have often involved the use of niche overlap metrics and therefore, may yield useful information concerning the probability of Model II replacement.

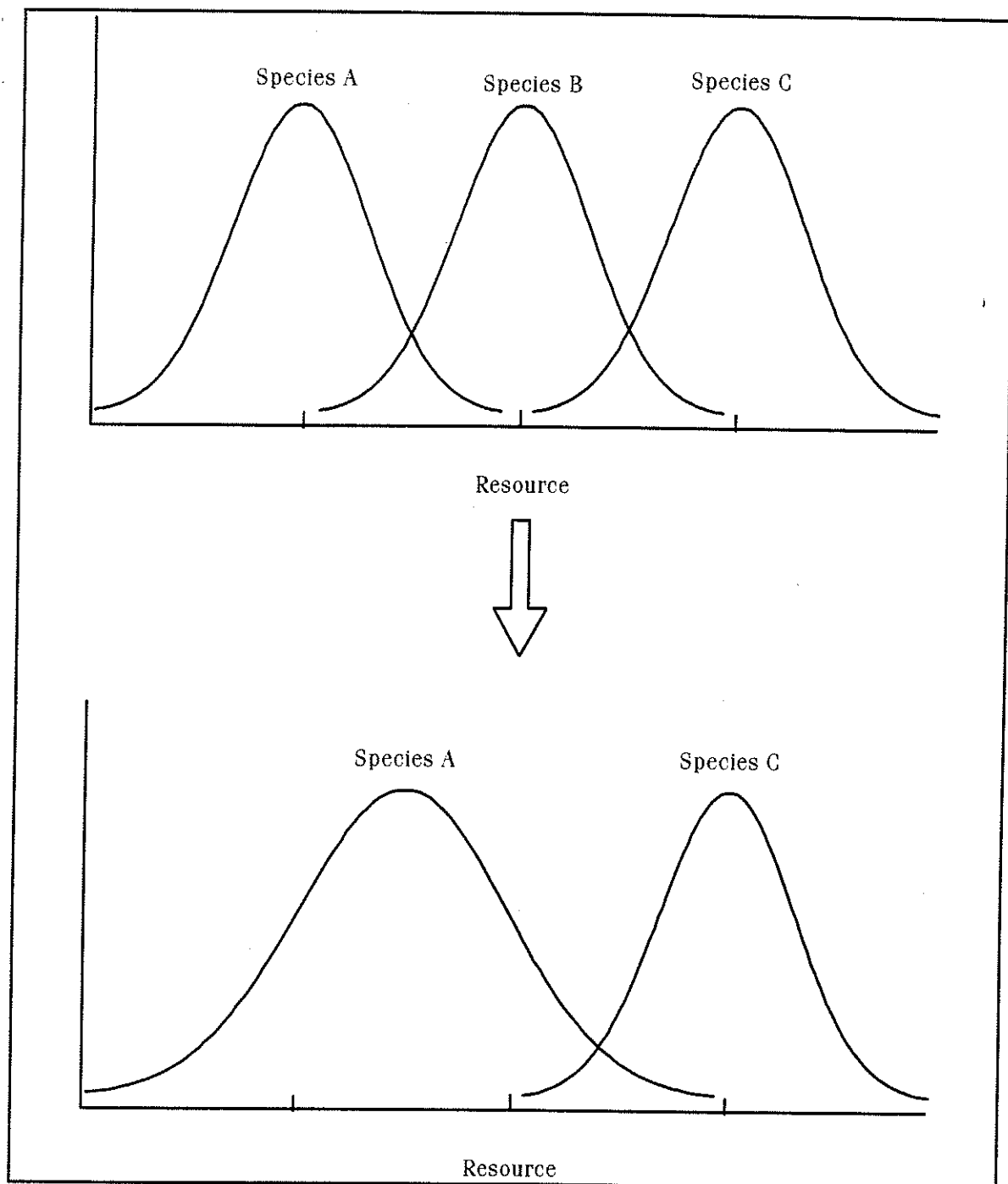


Figure 3. Model II - functionally equivalent replacement by remaining species increasing niche width to compensate for lost taxon.

Niche width expansion in co-existing odonates may have been observed by Benke and Benke (1975). Standing stock of an assemblage of odonates within an abandoned small farm pond in South Carolina, including congeneric species of *Epithea* and *Celithemis*, appeared to be buffered at the community level (Benke and Benke 1975). A number of species had complementary life histories such that during years when one species was reduced in numbers through apparently normal variability, another would be present in higher numbers. This resulted in relatively consistent odonate density and biomass from one year to another.

MacArthur (1972) developed several hypotheses to account for the pattern of resource partitioning between competing species and the number of species that could exist within a community. The hypothesis from which Model II replacement was derived is a prediction that species can be added to a community by reducing average niche width (*i.e.*, species become more specialized). Should species packing occur by existing taxa reducing niche widths, the alternate may occur following loss of species.

Mechanisms to reduce niche overlap by partitioning resources will be favoured in species that are in direct competition for limiting resources (Schoener 1974, Whittaker 1975). Thus, the total fitness of a species will increase if its exploitation of resources is not limited or restricted by a competing species. MacArthur and Levins (1967) and MacArthur (1972) have referred to this as the concept of limiting similarity. The mechanisms utilized by individuals to limit competition are variable, and range from short-term or phenotypical changes to long-term evolutionary changes (Moermond 1979).

Short-term or phenotypical changes operate at the individual level, and may include altered facultative behavioural activities, growth, and reproduction (Moermond

1979). Examples include: (1) the altered behavioural expansion of the niche width of the salamander, *Desmognathus fuscus* (Rafinesque), in the presence of two other congeneric *Desmognathus* competitors (Southerland 1986); (2) the temporal reproductive activity alterations in sympatric leopard frogs in Mexico (Frost 1983); (3) the flexible and dynamic habitat partitioning or niche shifts (Sale 1979) in a guild of stream minnows (Angermeier 1987, Gorman 1988); (4) niche shifts in sympatric versus allopatric populations of brook trout and creek chub (Magnan and FitzGerald 1982); and (5) niche shifts in three species of competing sunfishes (Werner and Hall 1979). Anholt (1990) also reported that most damselflies are generalist feeders and may switch behavioural feeding methods should a change in prey species occur (see also Crowley and Johnson 1982). Similar switching in feeding behaviour has been reported for herbivorous branchipods grazing on diatoms (Glasser 1978) and for limnetic and littoral cladocerans (Meyers 1984). Williamson (1984) and Krylov (1988) reported that many predators have wide niche widths for prey, with varying functional responses depending upon available prey species. Phenotypical changes in response to competition may be expressed differently even within the same population. Basset and Rossi (1987) demonstrated that individuals of the isopod *Proasellus coxalis* Dollfus, when offered a variety of food sources, selected one of two possibilities. Some individuals specialized on a small range of fungi, resulting in small brood sizes but high reproductive efficiencies, whereas the generalists had large brood sizes but low reproductive efficiencies. Although thought to be relatively rare, this appears to be a compensating mechanism adopted by this organism to maintain fitness under different trophic conditions. It therefore may be possible that short-term, individual phenotypical responses aimed at reducing competition, are reversible once the competing species are lost from the system following environmental stress.

Long-term genetic or evolutionary changes occur at the population level and may include character displacement (Moermond 1979). Character displacement has been reported by Klopfer and MacArthur (1961) for the culmen lengths in male sympatric bird species in Panama and Costa Rica and by Fjeldsa (1983) for bill morphology in sympatric grebes. However, there was evidence in this latter case that some evolutionary changes had occurred within the last century. Further, Tokeshi (1986) noted that chironomids appeared to have maximized temporal population dynamics in response to the period of greatest production in the epiphytic algal community. Two types of adaptation were involved. The first type, likely controlled by long-term evolutionary processes, involved the adjustment of the life-cycle to coincide with the period of greatest algal production. The second type, likely because of the resilience of the chironomid community, involved larvae of multivoltine species reaching maximum growth and population size during the spring period. Should long-term changes have occurred at the population level, it is unlikely that such changes would be reversible once the competing organism is lost or removed from the system.

MODEL III: REDUNDANT SPECIES

The third and final replacement model is derived from an inverse of one of MacArthur's (1972) species packing hypotheses. MacArthur (1972) predicted that species can be added to a community by increasing average niche overlap. As new species are added to a community, niche overlap increases to the extent that similar or redundant species co-exist without resource partitioning (Figure 4).

Large niche overlap in the unaltered original community results in the presence of redundant species. Following Model III (redundant species) replacement, species diversity

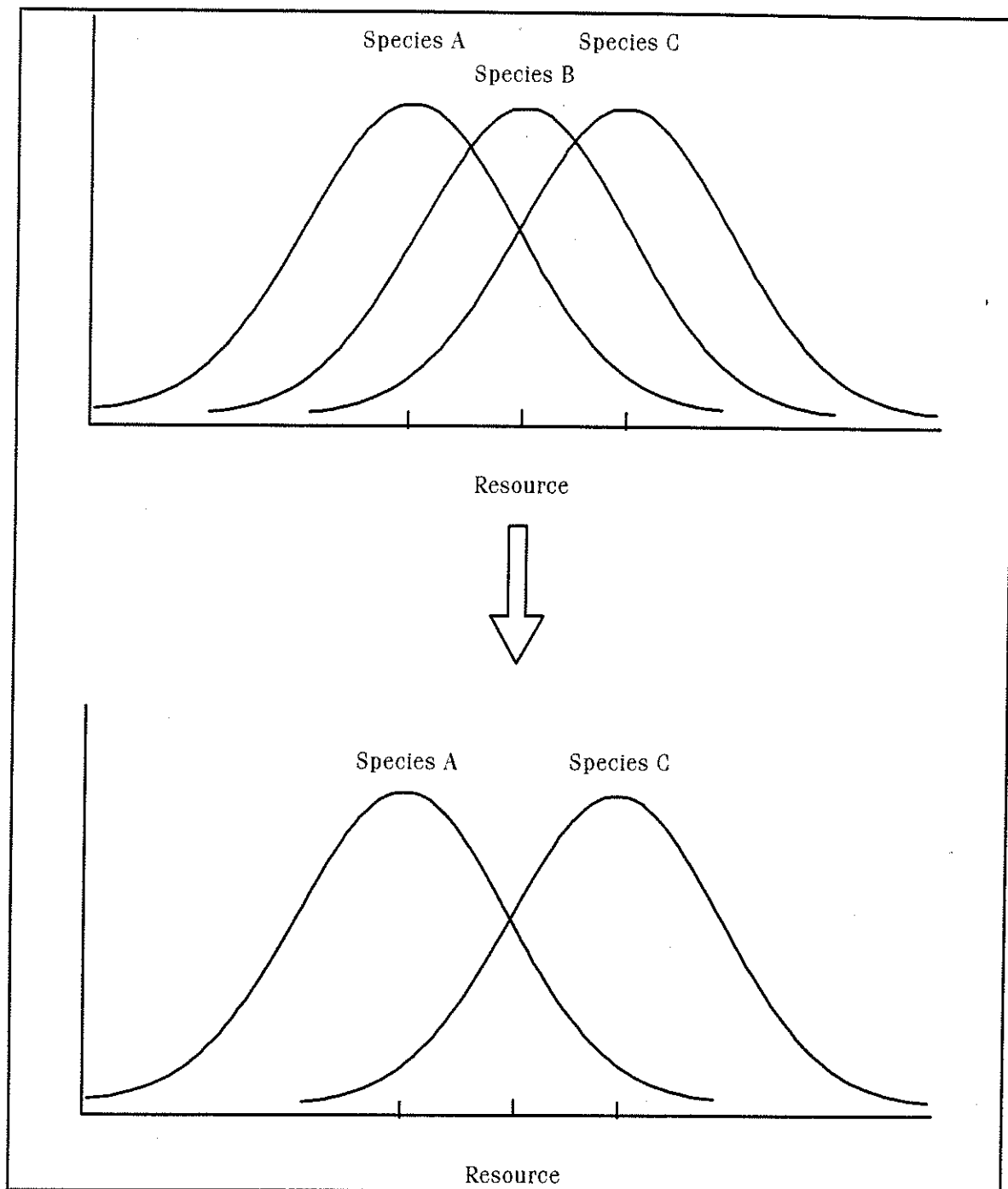


Figure 4. Model III - functionally equivalent replacement by reduction of niche overlap following species removal.

(D_s), number of neighbours (C), and average niche overlap ($\bar{\alpha}$) are reduced while diversity and amount of resources processed by an average species (D_u) are increased. Community function (D_r) is conserved. The increase in D_u is caused by compensation in the resource utilization functions of the remaining species. Abundance of the remaining species must increase in order to satisfy the constraint imposed by Eq. 8. Competition of some type must be operative, otherwise there would be no reason to expect replacement species to increase in abundance following loss of taxa from original community. Diversity of resources used by individual species (D_{ui}) does not change since niche width is not altered.

Model III relies to a large extent upon the co-existence of species in some communities without resource partitioning. Bruns (1981) found no evidence that resource partitioning occurred as similar species were added to a guild of predaceous aquatic insects in a stream in Montana during some times of the year (Model III) although reduction in niche width was apparent during other times (Model II). Bruns (1981) attributed this to the possibility that resources were not limiting in this aquatic system at some times or that other stochastic processes were operating, therefore reducing the need for species to partition resources. A similar finding was reported by Bohnsack and Talbot (1980) and Grossman (1981) for reef and stream fish, respectively. Bruns (1981) reported that species diversity was significantly correlated with average niche overlap in a negative relationship, implying that diffuse competition (Pianka 1974) was operative. Diffuse competition differs from classic competition between two species in that it operates between groups of species.

Hale (1981) examined the relationship between several niche parameters and morphological types within a guild of predatory aquatic insects in a riffle habitat in order

to test MacArthur's (1972) predictions. Hale (1981) randomly constructed 50 communities from a pool of 271 insect types, and then compared these random communities to actual riffle communities (see also Gatz 1981, Douglas 1987 and Strauss 1987 for a similar assessment of co-existing stream fishes). Almost all measures of community description did not differ significantly between the random and actual communities, implying that similar organisms may co-exist without substantial resource partitioning. However, the random communities had a greater proportion of shorter interspecies distances relative to actual riffle communities. This suggested to Hale (1981) that there was some limit to the extent of similarity in co-existing communities, but through the mechanism of diffuse competition. Similarly, Crowley and Johnson (1982) found that co-occurrence of 37 species of odonates at 201 sites clustered according to habitat type was not significantly different than expected from random assembly.

Hutchinson (1957), Gilpin and Justice (1972), May (1974), Tilman (1977, 1981), and Armstrong and McGehee (1980) reported a number of cases where apparently competing organisms co-existed without resource partitioning. Co-existence is apparent when the environment is stochastic, the relationship between the growth rate of the competing species and the limiting resource is non-linear, the population density is variable, or the species do not differ significantly in their use of the limiting resource. These conditions may be common in aquatic environments, allowing for the co-existence of a large number of similar species. Such cases have been discussed by Hutchinson (1961) with regard to phytoplankton, by Ghilarov (1984) with regard to zooplankton and other species, and by Grossman (1981), Angermeier (1987), and Gorman (1988) with regard to stream fishes.

Istock (1973) used the term species "ensemble" to refer to groups of co-occurring, ecologically similar organisms with the potential to co-adapt. Istock (1973) suggested that a model involving "errors of exploitation" allowed a large number of similar corixids to co-exist. The "errors of exploitation" model essentially assumes that food resources are not limiting, a situation which may occur frequently in stochastic environments. Should one of these co-existing species be removed, it may be possible for the other species to maintain the cycling of material and flow of energy as if both species were present.

A summary of the major features of each replacement model is shown in TABLE 1. Model II and III are similar in many ways and therefore, it may not be possible in most systems to determine which of the two might be operative. However, they differ conceptually and therefore should be regarded as different mechanisms. It is likely that each may operate in different types of communities or in different groups of species.

TABLE 1. Major features of the three models describing mechanisms by which potential species replacement may occur following environmental perturbation.

Model	Mode of Replacement	Number of Species (Diversity)	Characteristics of Replacement Species	Characteristics of Habitat	Evidence for Predicting Potential Replacement
Model I	• re-colonization	• unchanged	<ul style="list-style-type: none"> • poor competitor relative to the lost species • does not co-exist with lost species prior to perturbation • inflexible niche width • good dispersal ability 	<ul style="list-style-type: none"> • stable • resources limited 	<ul style="list-style-type: none"> • significant niche overlap in allopatric populations • competitive exclusion
Model II	• niche expansion	• declines	<ul style="list-style-type: none"> • ability to alter niche width through behavioural or short-term phenotypical traits in response to competition • may be present as part of a functional guild • co-exist through resource partitioning with lost species prior to perturbation 	<ul style="list-style-type: none"> • stable • resources limited 	<ul style="list-style-type: none"> • significant niche overlap in allopatric populations • niche width is wider in allopatric populations relative to sympatric populations
Model III	• redundant species	• declines	<ul style="list-style-type: none"> • may be present as part of a functional guild • co-exist without resource partitioning with lost species prior to perturbation 	<ul style="list-style-type: none"> • unstable • resources may not be limited but competition must be present 	<ul style="list-style-type: none"> • significant niche overlap in sympatric populations

CHAPTER III

EVIDENCE FOR POTENTIAL REPLACEMENT

ABSTRACT

Over 200 studies involving resource partitioning by apparently competing organisms were reviewed; ~ 120 of these provided sufficient detail to judge the potential for replacement without alteration of community function. These studies involved 11 phyla and over 2000 species-pairs. Functional replacement likely could not occur in more than ~ 20% of guild-forming congeneric organisms. Patterns were not evident within any single phylum, class, family, genus, or within similar functional guilds.

Replacement by Model I (re-colonization) appears to be least common. Evidence from competitive exclusion studies suggests that when replacement is possible, it would occur by Model I in ~ 10% of cases. Replacement by Model II (niche width expansion) appears to be more common. Model II replacement could potentially occur in ~ 70% of cases, with the remainder being Model III (redundant species). There appears to be greater potential for Model III replacement among aquatic insects than among other groups. The presence of ecological equivalents cannot be demonstrated unequivocally in most resource partitioning studies because symmetrical niche overlap metrics were used, only one resource axis was examined, or resource overlap was examined within a single community of apparently competing organisms.

INTRODUCTION

It is important to gain an understanding of how widespread the phenomenon of potential functional replacement might be within aquatic communities to make judgments on the extent to which communities might naturally compensate for environmental perturbation. One of the features that all three replacement models have in common (Chapter II, TABLE 1) is the use of niche overlap to predict whether replacement is likely. A large body of literature exists on niche overlap among species in various communities. This literature was generated over the past 20 years as researchers attempted to understand mechanisms that controlled communities or led to structure within communities. In this chapter, studies on niche overlap in aquatic communities are reviewed; data are re-analyzed relative to the potential for one species to replace the function of another following hypothetical loss as a result of environmental disturbance. The objectives of this chapter are to describe various measures of niche overlap, to discuss their utility for predicting the likelihood that one species may be able to replace the ecological function of another, and to present new information concerning the potential for functional replacement.

Measures of Niche Overlap

Methods to measure niche overlap have been developed by a number of workers to yield information principally concerning the similarity between organisms and hence, the potential for competition (*e.g.*, Schoener 1970, Colwell and Futuyma 1971, Green 1971, Pielou 1972, Pianka 1973, Hurlbert 1978, Petraitis 1979, Lawlor 1980). Niche overlap metrics have been divided into four general groups (Petraitis 1979), namely: (1) distance measures (Levins 1968, Schoener 1968, MacArthur 1972); (2) association indices (Cody

1974); (3) correlation coefficients (Levins 1968, Pianka 1973); and (4) information measures (Horn 1966). Petraitis (1979) subsequently developed a metric based upon likelihood theory and later showed that niche overlap could be related to the consumption vectors in a resource utilization model (Petraitis 1989). Hurlbert (1978) developed a metric that was weighted in accordance with the amount of resource present. This metric was used to determine the probability of encounter of one organism with another.

Multivariate niche overlap methods, mainly involving multivariate discriminant analysis, have been used by Green (1971, 1974), Rossi *et al.* (1984), Macdonald and Green (1986), and McNeely (1987). Niche width has been estimated in canonical correspondence analysis by the standard deviation or tolerance of the distribution of a species along a gradient (ter Braak and Barendregt 1986, ter Braak and Looman 1986, ter Braak and van Dam 1989). ter Braak (1991) reported that Green's (1971) estimation of niche width using multivariate discriminant analysis is equivalent to canonical correspondence analysis applied to presence-absence data (Chessel *et al.* 1982, 1987; Lebreton *et al.* 1988). Niche metrics in canonical space have been discussed by Dueser and Shugart (1978, 1979, 1982), Carnes and Slade (1982), and Van Horne and Ford (1982). Dueser and Shugart (1979) estimated overlap in canonical space following discriminant analysis by calculating the proportion of planar overlap of the 95% confidence ellipses. Green (1974) suggested that niche width in multivariate space can be estimated by the 50% confidence ellipse and that niche overlap can be visually estimated from plots of the 50% confidence ellipses.

A number of the niche overlap measures are symmetrical (*e.g.*, Pianka 1973) and are intended to yield the same value regardless of niche width, while others, such as that developed by Levins (1968), are asymmetrical. That is, with the use of symmetrical

measures, overlap of species "a" on species "b" results in the same overlap coefficient as the reciprocal comparison. For the purpose of determining the potential for one species to replace another, symmetrical measures are not appropriate, since it is important that information on the niche width of the two organisms be retained within the overlap metric. Most univariate overlap metrics result in coefficients ranging from 0.0 to 1.0 with 1.0 implying complete overlap (*e.g.*, Levins 1968). Overlap values > 0.70 may be considered significant and values < 0.30 may be considered insignificant (Macdonald 1983), although most often, values > 0.60 are interpreted as being significant (Fuller and Hynes 1987).

Most measures of niche overlap, with the exception of multivariate discriminant analysis, involve estimating resource overlap along one dimension or one type of resource, such as food. When more than one axis is considered, the individual overlap measures must be either summed or multiplied, depending upon whether or not the resource axes are dependent or independent, respectively (May 1975). The decision regarding dependence or independence of axes is rather arbitrary (Rossi *et al.* 1984).

The most appropriate measure of niche overlap is uncertain, since a number of existing metrics have been criticized (Hurlbert 1978, 1982; Abrams 1980, 1982) and the reliability of the resulting information has been questioned (Wallace and Ramsey 1983, Zaret and Smith 1984, Smith 1985). Further, some methods used to measure niche overlap may not be useful for determining the potential for functional replacement. Slobodchikoff and Schulz (1980) cautioned that Petraitis' (1979) likelihood measure, should not be used to determine overlap between organisms that occur in two separate habitats. Niche width and overlap may be reduced in sympatric populations (Davies *et al.* 1982, Thorman 1982) in order to allow co-existence (MacArthur 1972). Contrary to Slobodchikoff and Schulz (1980), this feature of Petraitis' (1979) likelihood measure

makes it ideal for predicting the potential for Model II replacement where niche width is expected to be wider in allopatric populations relative to sympatric populations.

Functional Similarity

The sum of all individual processes involved in the movement, transportation, or cycling of materials and in the flow of energy between trophic levels can be referred to as the function of a system (Lindeman 1942; see also the review by Hecky 1984). The functional integrity of an aquatic system can therefore be assured by the maintenance of these individual processes (Regier 1990, U.S. EPA 1990). Individual species within any community play a role in the movement of materials and in the flow of energy. This role, as defined by Hutchinson (1957), is the fundamental niche of an organism. The number of resource axes in the fundamental niche of any organism is relatively large, representing all abiotic and biotic factors. Because not all resource axes can be measured (Green 1971) and because some resource axes are more important than others in describing the role of an organism (Giller and McNeill 1981), some simplification is required in order to realistically describe the niche of each organism. The resource axes can be grouped into temporal, spatial, and trophic axes (Pianka 1973), based upon the major categories of methods used by organisms to partition resources. These axes can be further subdivided into macrohabitat, microhabitat, food type, food size, diel time, and seasonal time (Schoener 1974). It is assumed that when significant differences exist between two organisms in any of the three major categories, the two organisms probably function differently in contributing to the movement of materials or to the flow of energy within a system.

Assessment of functional similarity may be confounded by a number of factors. For example, aquatic insects may change the spatial and trophic resources exploited from one life stage to another. An early larval instar may be a generalist feeder, whereas a later nymphal instar may become a more specialized feeder because of development or maturation of the feeding apparatus (Titmus and Badcock 1981). Ontogenetic morphological and behavioural changes have similarly been reported for other organisms during maturation (Werner 1979, Tallman and Gee 1982, Marrin 1983, Griffiths 1986, Ross 1986, Mark *et al.* 1987, Walls 1990). Moreover, some aquatic insect larvae switch behavioural feeding habits depending upon the density and the type of available prey species (Murdoch 1969, Moore 1988), whereas others do not (Cothran and Thorp 1985, Spitze 1985).

METHODS

Pertinent literature was examined for evidence of: (1) competitive exclusion (Model I - re-colonization); (2) cases of short-term, phenotypical mechanisms used to partition resources (Model II - niche width expansion); and (3) similar species co-existing without resource partitioning (Model III - redundant species). Judgments were made on the probability that one species might be replaced by another similar species, without disruption of ecological function, based upon the extent of fundamental or realized niche overlap. In almost all cases, the judgment of the original author was used concerning whether niche overlap was significant or not. In cases where such judgments were not made but sufficient information was presented, overlap was considered significant according to the criteria of Fuller and Hynes (1987). Sufficient detail was provided in ~ 120 resource partitioning studies, representing 11 phyla and 2127 combinations of aquatic

or semi-aquatic species. Approximately 100 other studies did not contain sufficient detail to allow judgments to be made concerning replacement potential.

RESULTS AND DISCUSSION

Examples of potential replacement from four studies are described below. These examples are typical of the ~ 120 studies that contained sufficient detail to allow judgments regarding potential for functional replacement.

Case Studies

EXAMPLE STUDY 1: TROPHIC RESOURCE AXIS PARTITIONING

Blois (1985) examined trophic resource partitioning in a small man-made pond in France in order to understand the mechanisms that allowed co-existence among the Anisoptera larvae *Anax imperator* Leach, *Aeshna cyanea* Müller and *Libellula depressa* Leach. Niche overlap was measured with Pianka's (1973) index for diet, life cycle, and microhabitat or spatial distribution. *Aeshna cyanea* and *A. imperator* occupied the same ecological niche, had similar life cycles, and had identical diets. Diets were composed of microcrustacea, Zygoptera, and Ephemeroptera larvae. Large differences were evident between *Ae. cyanea* - *L. depressa* and *A. imperator* - *L. depressa*, especially in diet. This was attributed to a combination of morphological and ethological characteristics such as differences in the shape of the prementum and labial palps, which allowed the aeshnids to capture and manipulate larger prey items than the libellulids. On the basis of this information, it would appear that the two aeshnids could replace the function of each

other should either be lost or removed, whereas neither could replace the function of *L. depressa*.

EXAMPLE STUDY 2: TROPHIC RESOURCE AXIS PARTITIONING WITH EVIDENCE OF COMPETITIVE EXCLUSION

Reynolds and Scudder (1987a) determined the fundamental feeding niches of *Cenocorixa bifida hungerfordi* Lansbury and *Cenocorixa expleta* (Uhler). These two species co-exist in some saline lakes but not in others, with *C. expleta* being able to successfully breed in lakes of higher salinity than *C. bifida hungerfordi*. A large range of prey taxa, similar to those found in the littoral zone of most lakes, were provided in controlled feeding experiments. Both species had a common range of acceptable food items, as evidenced during single prey feeding experiments. There was some evidence that *C. bifida hungerfordi* preferred dead food rather than live food, whereas there was no such preference exhibited by *C. expleta*. The two species may differ in their ability or efficiency to detect, capture, or handle live prey. Both species accepted 16 of the 17 prey items presented during the feeding experiments. Although the proportions of each item selected were slightly different between species, such differences were not statistically significant. Reynolds and Scudder (1987a) noted that in moderately saline lakes, both species co-existed even though they were ecologically similar in terms of breeding and feeding patterns, and were closely related sympatric species. It was speculated that large environmental fluctuations within the study region prevented one species from eliminating the other as a result of competition. However, *C. expleta* was absent from lakes of low salinity. Reynolds and Scudder (1987a) thought that competition for food in such lakes might result in the exclusion of *C. expleta*.

Reynolds and Scudder (1987b) attempted to differentiate between the fundamental and realized feeding niches of *C. expleta* and *C. bifida hungerfordi* in both sympatry and allopatry. Since these species overlap considerably in terms of the fundamental niche, it was expected that this should create competition such that the realized feeding niche should overlap more in allopatry than in sympatry. Although not definitive, there was considerable overlap in the realized feeding niches of these two species in both sympatry and allopatry. Other factors may be present that operate to exclude *C. expleta* from lakes with low salinity. Thus, *C. expleta* and *C. bifida* may be able to replace the function of each other in ponds with low salinity, but not in waters of moderate salinity.

EXAMPLE STUDY 3: ASYMMETRIC PARTITIONING OF HABITAT

Co-existence of two notonectid predators, *Notonecta undulata* Say and *N. insulata* Kirby, was examined in a small man-made pond in Connecticut (Streams 1987). *Notonecta undulata* was one of the most common notonectids in the study area, thereby providing sufficient sources for re-colonization should exclusion occur due to adverse conditions. *N. insulata* was less common. Both populations exhibited significant spatial separation during most times of the year, except when pond volume was significantly reduced late in the summer season. Most *N. undulata* were found near the pond edge in water < 0.3 m deep, while most *N. insulata* were found in the central area of the pond in water > 0.5 m. Spatial separation was thought to occur earlier in the life stages, either by an ovipositing female or by behaviour of an early instar. In experiments conducted to determine water temperature tolerances, *N. insulata* could not tolerate higher water temperatures, therefore possibly restricting this species to deeper and cooler water habitat. *Notonecta undulata* was slightly larger than *N. insulata*, which may have conferred a slight competitive advantage. Recruitment of *N. undulata* occurred continuously during

the early part of the summer, but only occurred during a short period of time for *N. insulata*. This pattern may be one of the reasons explaining the larger numbers of *N. undulata*. In cage experiments, *N. undulata* was not affected by water depth alone, whereas survival of *N. insulata* was affected by water depth. *Notonecta undulata* may be able to replace the function of *N. insulata* in deeper water should *N. insulata* be lost or removed but reciprocal replacement in shallow water by *N. insulata* is unlikely.

EXAMPLE STUDY 4: NO APPARENT RESOURCE AXIS PARTITIONING

Johnson *et al.* (1984), using *in situ* enclosures, attempted to determine the role played by interspecific and intraspecific competition to allow *Enallagma divagans* Selys and *E. traviatum* Selys to co-exist. There was little evidence of resource partitioning between the two species, although food limitation was not apparent within the enclosures. Exploitation competition was not considered to be a major factor in the experiment. However, the average condition of *E. divagans* larvae appeared to be density-dependent. The authors attributed this density-dependent relationship to aggressive behaviour among the larvae or other forms of interference competition. Even though the presence of density-dependent effects on condition were statistically significant, Johnson *et al.* (1984) thought that their influence on population dynamics was not large. Survival and biomass production were significantly greater for *E. divagans* than for *E. traviatum*; however, neither effect was dependent upon density. From examination of fecal pellets, considerable overlap in diet was evident. Given the high dietary overlap between these *Enallagma* and their ability to co-exist without apparent obligate factors to partition resources, one species may be able to replace the function of the other, should either be lost or removed from the system.

An overview of the results is shown in TABLE 1. Detailed information is presented in Williamson (1994). Ecological function of ~ 17% of the total number of species could potentially be replaced by other taxa. The range of potential replacements varied considerably among major taxonomic groups. Within the Holothuroidea, potential replacements were identified for 4.5% of the species examined in resource partitioning studies, whereas 100% of Spermatophyta and Turbellaria had potential replacements. However, few resource partitioning studies were available for several groups, including the Spermatophyta and Turbellaria. The largest data set was available for Mollusca, Crustacea, Insecta, and Osteichthyes; generalizations drawn from studies on these latter groups may provide a more realistic insight into replacement patterns relative to less-studied taxa.

Competitive exclusion was not a major outcome of interaction between hypothetically lost and potential replacement taxa. Therefore, little evidence for the Model I replacement is available. Overall, competitive exclusion was evident in ~ 10% of the total potential replacement taxa. For Mollusca, Crustacea, Insecta, and Osteichthyes, competitive exclusion was evident in 17%, 14%, 3.4%, and 5.4%, respectively (Figure 1).

Potential replacement and hypothetically lost taxa tended to partition habitat or space more often than food or time. Overall, habitat was partitioned by slightly over 50% of the potential replacement and hypothetically lost taxa (Figure 2). Within the most studied groups, potential replacement and hypothetically lost taxa partitioned habitat 96%, 75%, 36%, and 54% for Mollusca, Crustacea, Insecta, and Osteichthyes, respectively. Interestingly, 47% of the potential replacement and hypothetically lost insect taxa apparently did not partition resources. This may provide some evidence for Model III replacement in aquatic insect communities.

TABLE 1. Overview of the resource partitioning studies listed in Williamson (1994).

Group	Summary of Studies						Resource Partitioning Among Potential Replacement Taxa				Taxonomic Level of Replacement		
	Number of Studies Reviewed	Number of Higher Taxonomic Groups	Number of Species-Pairs	Number of Species With Replacement Potential	Percentage Replacement Potential	Competitive Exclusion Among Potential Replacement Taxa (Model I)	Temporal Resource (Model II)	Spatial Resource (Model II)	Trophic Resource (Model II)	No Apparent Partitioning (Model III)	Congeneric Replacement	Confamilial Replacement	Other
Thallophyta	4	2 Classes	20	9 (9) ^a	45% ^a	66%		22%	78%			100%	
Spermatophyta	1	1 Family	2	2 (0)	100%	100%		100%			100%		
Protozoa	1	1 Class	2	1 (1)	50%	0%			100%		100%		
Turbellaria	1	1 Family	2	2 (2)	100%	100%			100%		100%		
Mollusca	15	2 Classes	60	24 (11)	40%	17%		96%	4%		33.3%	58.4%	8.3%
Annelida	4	2 Classes	81	10 (0)	12%	— ^b		60%	40%		20%	80%	
Acariformes	1	1 Order	12	4 (0)	33%	— ^b		100%			100%		
Crustacea	17	6 Orders	327	60 (17)	18%	14%		75%	3.3%	21.7%	26.7%	66.7%	6.6%
Insecta	25	18 Families	652	87 (38)	13%	3.4%	7%	36%	10%	47%	54%	46% ^c	
Holothuroidea	2	1 Class	133	6 (0)	4.5%	— ^b			100%				100%
Osteichthyes	40	25 Families	744	149 (101)	20%	5.4%		54%	27%	19%	57%	34%	9%
Amphibia	6	2 Families	16	12 (4)	75%	25%	33.3%	16.7%	16.7%	33.3%	100%		
Reptilia	1	1 Family	6	2 (2)	33%	0%		100%				100%	
Aves	1	1 Subfamily	72	4 (0)	5.5%	0%		100%			50%	50%	
Total	119	11 Phyla	2129	372 (185)	17.3%	10%	3%	54%	20%	23%	49%	44%	7%

^a Numbers in parentheses are potential replacements associated with considerable uncertainty.

^b Zero or unknown.

^c Twenty-eight of these were identified only to genus.

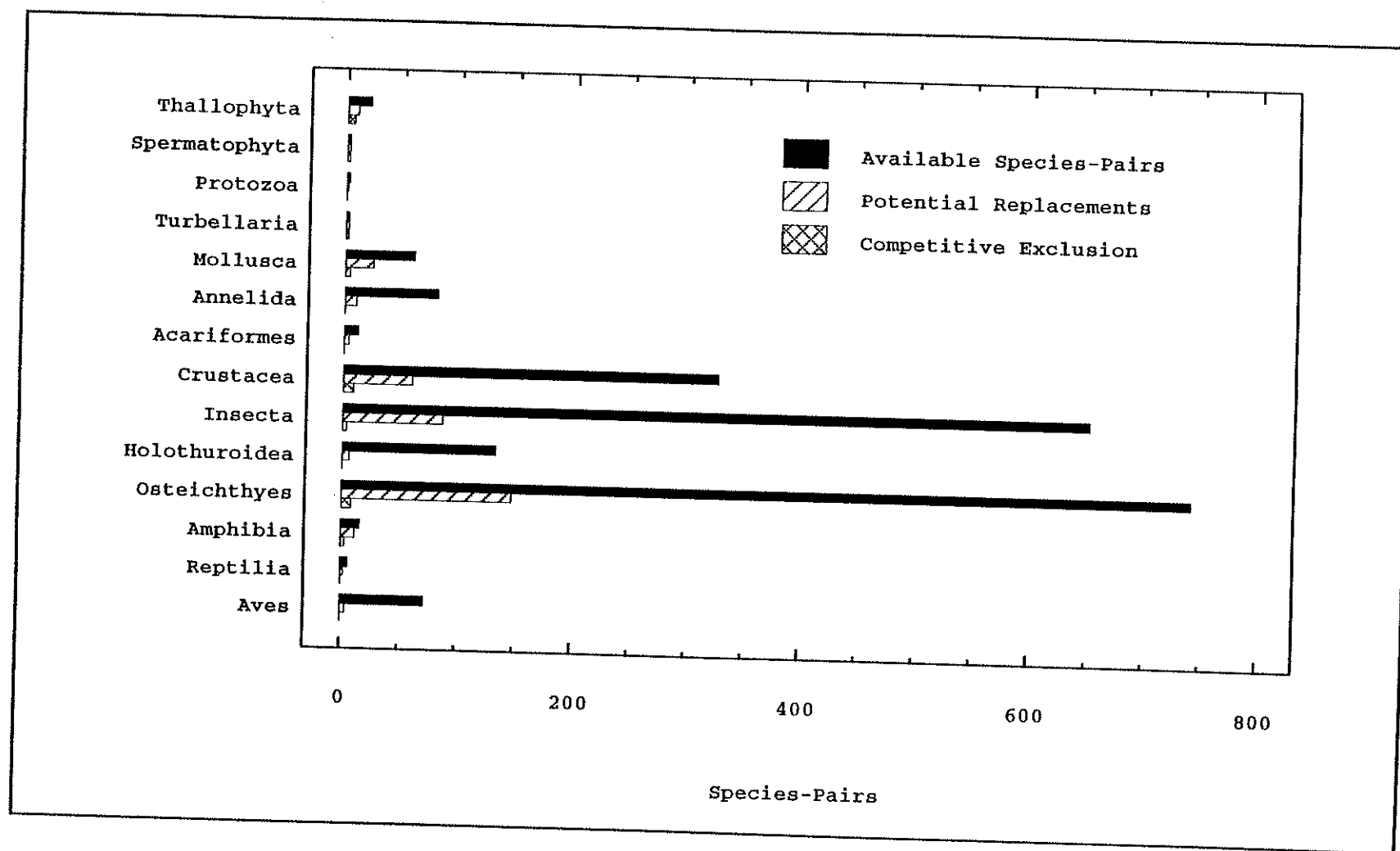


Figure 1. Clustered bar graph showing the number of potential replacements identified in relation to the number of species-pairs available from the literature. When potential replacement taxa were located, the number of cases of competitive exclusion is shown.

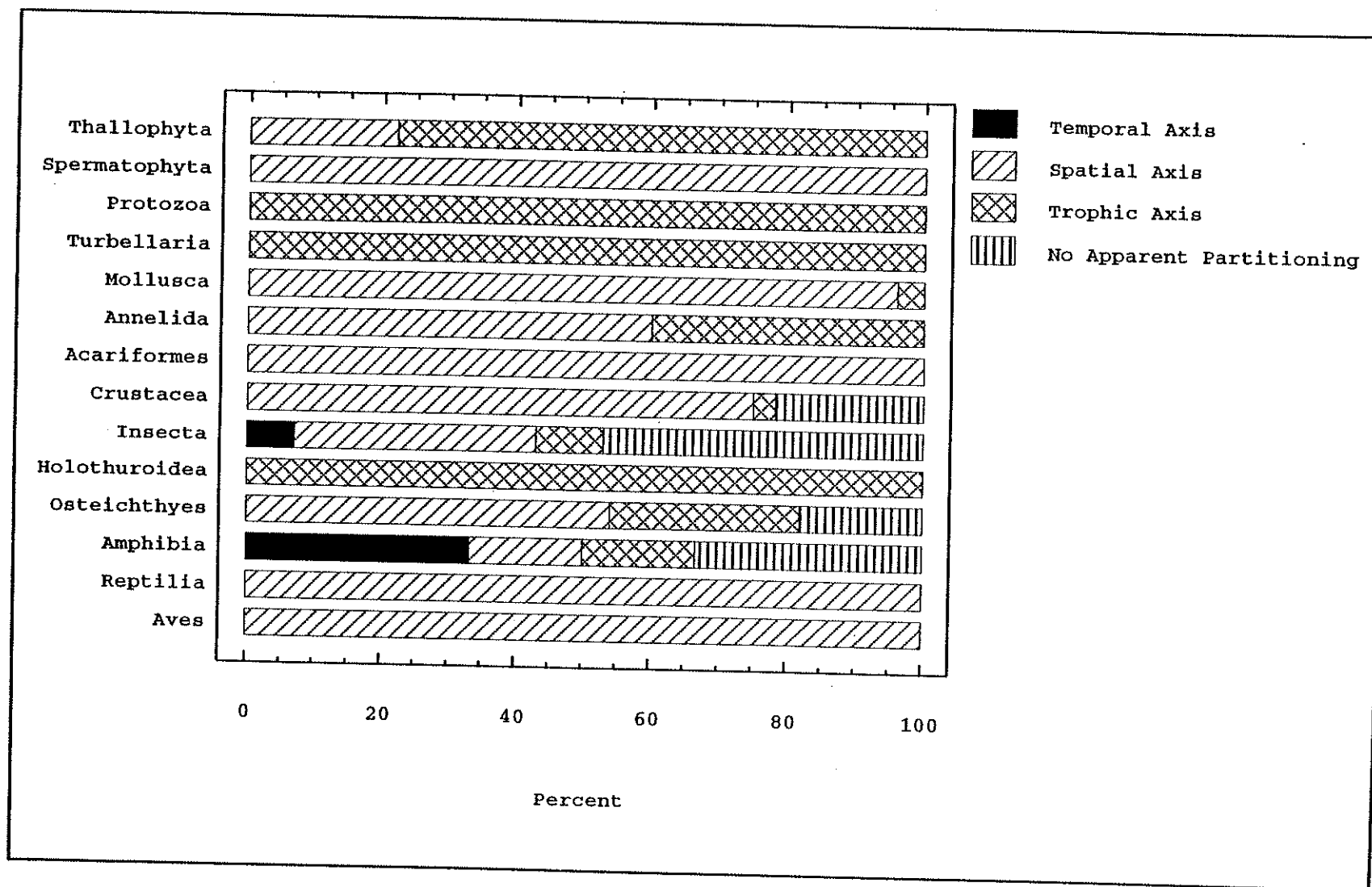


Figure 2. Stacked bar graph showing the percentage of potential replacement species that partitioned various resource axes.

There were slightly more potential replacement taxa in the same genus as hypothetically lost taxa, with overall replacement at the congeneric level of nearly 50% (Figure 3). The majority of the remaining potential replacements were from the same family as hypothetically lost taxa. Within the most studied groups, replacement potential at the congeneric level was 33.3%, 26.7%, 54%, and 57% for Mollusca, Crustacea, Insecta, and Osteichthyes, respectively.

Similar to the observation of May (1986), there is no simple dichotomy of pattern evident. There does not appear to be any consistent trend in the potential for ecological replacement within any single phylum, class, family, genus, or within similar functional guilds. The majority of studies involved aquatic insects or fish. The overall percentage of potential replacement taxa from these groups was similar. Potential for replacement within other groups was highly variable, but only a limited number of studies were available.

There is potential for the replacement of ecological function following loss of some taxa. However, this potential is not widespread and may be limited to a number of closely related organisms within functional guilds. The majority of the identified potential replacement organisms belonged to the same genus as the hypothetically lost taxa. This is consistent with the findings of Ross (1986) who demonstrated for fish that the ecological separation within co-existing congeners was much less than within confamilial or conordinal assemblages. However, there was some evidence to support potential replacement at the family level.

Competitive exclusion was evident in only a small percentage of interactions. Thus, either Model I replacement is uncommon or the utility of competitive exclusion for

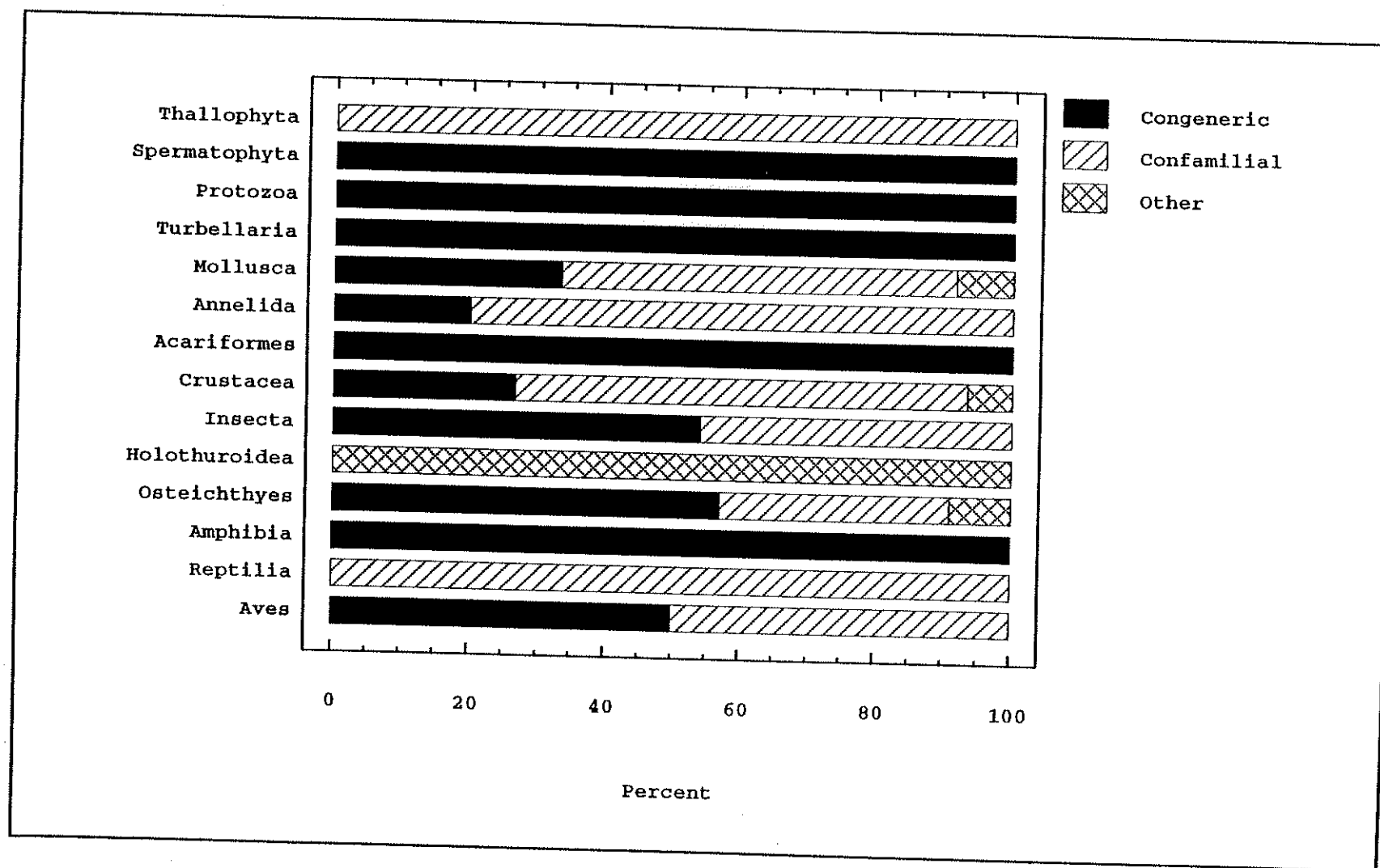


Figure 3. Stacked bar graph showing the systematic relationship between hypothetically lost taxa and potential replacement species.

detecting this type of potential replacement is limited. Competitive exclusion could have limited utility for two reasons, at least in aquatic systems. First, competitive exclusion may not be common in aquatic communities that are structured by stochastic processes as suggested by Grossman (1981). Schlosser (1982) reported that exclusion is probably not a common response to competition in shallow, unstable habitats. In such habitats, rates of re-colonization are normally high, thus reducing the length of time organisms are competing. When re-colonization rates are low, gradual changes in physical condition because of competitive interaction or temporal variation in reproductive success may be the most common responses (see also Hutchinson 1961, Kullberg 1982, and Sommer 1983, regarding lack of exclusion in algal communities). The lack of competitive exclusion was demonstrated in models developed by Smith *et al.* (1975) and Powell and Richerson (1985), although a number of outcomes are possible in coral reef fishes as demonstrated by Abrams (1984), and in phytoplankton as demonstrated by Sommer (1983) and Lange (1974). Second, exclusion may occur only when one species has a tremendous competitive advantage. Therefore, when competitive exclusion does occur, it may be between two species that differ greatly, such as the exclusion of the rotifers *Brachionus calyciflorus* Pallas and *Keratella cochlearis* (Gosse) by *Daphnia pulex* Richard when they were in competition for the same size of phytoplankton (Gilbert 1985) or the exclusion of the gastropod *Biomphalaria glabrata* (Say) by the introduction of a larger prosobranch snail (Pointier *et al.* 1988). In this latter case, the prosobranch destroyed the vegetation beds that *B. glabrata* also depended upon. In the former case, the rotifers could not be expected to replace the function of the cladoceran even though they compete along one resource axis. Competitive displacement or niche shifts as opposed to complete exclusion is probably the most likely outcome of competitive interactions within most aquatic systems. This has been reported in a number of cases where the displaced organism did

not appear to be at a great competitive disadvantage (Capelli and Munjal 1982, Capelli and Magnuson 1983).

A pattern that emerged was the relatively high percentage of potential replacement and hypothetically lost taxa that partitioned habitat in order to co-exist. This finding may not be surprising since habitat is most often partitioned by communities of co-existing species (Schoener 1974, Cudney and Wallace 1980, Toft 1985), with the exception of fish (Ross 1986). This may have significant implications since potential replacement taxa, in the absence of lost or removed taxa, may be able to more easily shift microhabitat selection than changing food consumption or altering life cycle. Niche shifts following release of competition may support the potential for Model II replacement. Alternatively, this pattern may be an artifact of the types of studies that were available for assessment. For example, co-existing species that partitioned resources on the basis of food, likely would have been judged incapable of potential replacement unless evidence of abilities to shift feeding patterns following removal of one of the taxa was presented.

The use of niche overlap between co-existing organisms to identify patterns concerning the existence of ecological equivalents has a number of disadvantages. Most studies were conducted to determine the role of competition in structuring communities and how community members responded to this competition by partitioning resources. These studies usually involved closely-related taxa within functional guilds. Differences between organisms that could be used to develop an explanation of co-existence were sought and in most cases, differences were found. However, very few studies were conducted to determine similarities as opposed to differences. Further, should the limiting similarity hypothesis (MacArthur and Levins 1967) be operative, there is a limit to the

degree of similarity between two competing organisms, so that when organisms that are apparently in competition are selected for study, differences will inevitably be found.

Perhaps the best studies to determine the potential for Model II replacement are those in which resource use of species in both sympatry and allopatry were examined, such as the study conducted by Rossi *et al.* (1983) for two isopods. Niche width differs between the two populations; therefore, information on intraspecific resource use flexibility is provided. In sympatric populations, niche width and overlap is often: (1) reduced, probably to allow co-existence (*e.g.*, Thorman 1982); or (2) variable, as described by Davies *et al.* (1982) for two Hirundinea (leeches) when niche width changed depending upon which species was numerically dominant. Liem (1984) also noted that fish are quite versatile since any one fish, regardless of mouth orientation, can harvest food from any location merely by re-orienting the body. This can therefore result in niche expansion, niche shifts, and extensive niche overlap. Niche overlap studies then must be focused upon attempting to describe the potential (fundamental) versus the realized niche (Hutchinson 1957, Rorslett 1987). The ability of an organism to actually occupy its potential niche then can be described by a probability function (Rorslett 1987). Similarly, the most suitable niche overlap metrics are those in which overlap is asymmetrical (*e.g.*, Levins 1968), or those in which overlap can be simultaneously assessed along multiple resource axes [*e.g.*, multivariate techniques such as discriminant analysis (Green 1971)]. For example, as previously mentioned, because of the asymmetrical nature of niche overlap, one species may be able to replace another in certain circumstances, but not in others [*e.g.*, Reynoldson *et al.* (1981) for *Polycelis nigra* (Müller) and *P. tenuis* Ijima].

CHAPTER IV **REPLACEMENT POTENTIAL OF ARTHROPODS IN SIX BOREAL FOREST STUDY PONDS BASED UPON GENERALIZED ECOLOGICAL FUNCTION**

ABSTRACT

Functional group classification and size spectrum analysis were used to identify potential replacements for taxa inhabiting six study ponds in Sandilands Provincial Forest, Manitoba, Canada. Out of 108 species of aquatic arthropods, 36 species (33.3%) had at least one potential replacement. Potential replacement taxa processed similar food materials, in the same microhabitat, at the same time, using the same feeding method, and were similar in size as the original or hypothetically lost species.

INTRODUCTION

The potential for one species to replace the ecological role of another depends to a large extent, upon the replacement species processing similar food materials, in the same microhabitat, at the same time, and using the same feeding method as the original species. In turn, the replacement species must cycle matter and transfer energy to other trophic levels in a manner similar to the original species.

Classification of aquatic insects according to ecological function, independent of taxonomic classification, has developed since the early 1950's (see discussion by Merritt and Cummins 1984). Functional group classification has been used to advance and modify concepts related to longitudinal zonation in stream systems (Vannote *et al.* 1980, Culp and Davies 1982, Minshall *et al.* 1983, Bruns and Minshall 1985, Minshall *et al.* 1985, Statzner and Higler 1985). Functional group classification has been used in recent years to relate aquatic community census data to environmental disturbance (Karr and Dudley 1981, Karr *et al.* 1986, U.S. EPA 1990, Karr 1991). Classification of aquatic arthropods into functional groups may provide the first step in broadly determining the pool of available potential replacement taxa for any given species.

The hypothetically removed or lost species and the available pool of potential replacement species must be similar in size for two reasons. First, there is a direct relationship between the size of the consumer and the size of prey species or food particles processed. The importance of size differences between predators and prey has been described in feeding strategy theory (Schoener 1971), shown mathematically for zooplankton (Vanderploeg and Scavia 1979) and other species, and demonstrated in field studies for a number of aquatic insect species. Kovalak (1980) found that size of prey

varied with plecopteran predator size in a stream community. Relationships between predator size and prey size have been shown by Sheldon (1969), Werner and Hall (1974), Wilson (1975), Siegfried and Knight (1976), Kovalak (1978), Schroder (1986), and Warren and Lawton (1987).

Second and not completely independent of the first, the biomass size spectrum of the altered community must remain similar to the original community, even though the species complement has changed. Biomass size spectrum is the distribution of biomass in a system across the range of organism size (Sprules *et al.* 1991) and biomass flow is the movement of biomass from one size to another (Borgmann 1987). The potential replacement species must be capable of moving biomass up the size spectrum in a similar manner as the original species. Sprules and Munawar (1986) suggested that residual variation around the normalized biomass size spectrum may be an indication of system perturbation, and thus a reflection of altered energy flow from small to large organisms or shifts in matter cycling. Biomass flow up the size spectrum can be directly related to diversity and amount of resources processed by the community (*e.g.*, D_r from Eq. 1 and Eq. 9, Chapter II).

Size spectrum analysis has become commonplace in recent years, leading to the development of theory of particle-size distribution patterns related to ecological and physiological processes (Borgmann 1987, Gaedke 1993). This theory was principally developed from study of planktonic communities and may not completely hold for zoobenthic biomass size spectra. Rodríguez and Magnan (1993) found biomass size spectra to differ significantly in macrobenthos communities relative to planktonic communities. Nevertheless, the only assumption being made in the present study is that

the size spectrum of the community should remain unchanged after species replacement, regardless of the underlying form of the original community's size spectrum.

The objective of this chapter is to assess the aquatic arthropod community structure in six small boreal forest ponds and to develop hypotheses concerning the availability of potential replacement taxa. The data set was assessed as follows:

- 1) by determining the generalized ecological function of each species from published literature;
- 2) by identifying for each species, other taxa that are members of the same functional feeding group, process food by the same method, normally consume a similar type of food, occupy the same preferred microhabitat, and forage for food, avoid predators, etc., using the same behavioural traits;
- 3) by statistically comparing each species with its respective group of potential replacement taxa and rejecting as potential replacements those that differ significantly in size.

MATERIALS AND METHODS

Study Area

During the mid-1950's, a large number of relatively small, uniformly shaped ponds were excavated along access roads throughout Sandilands Provincial Forest. Sandilands Provincial Forest is located ~ 60 km southeast of Winnipeg, Manitoba, Canada (Figure 1).

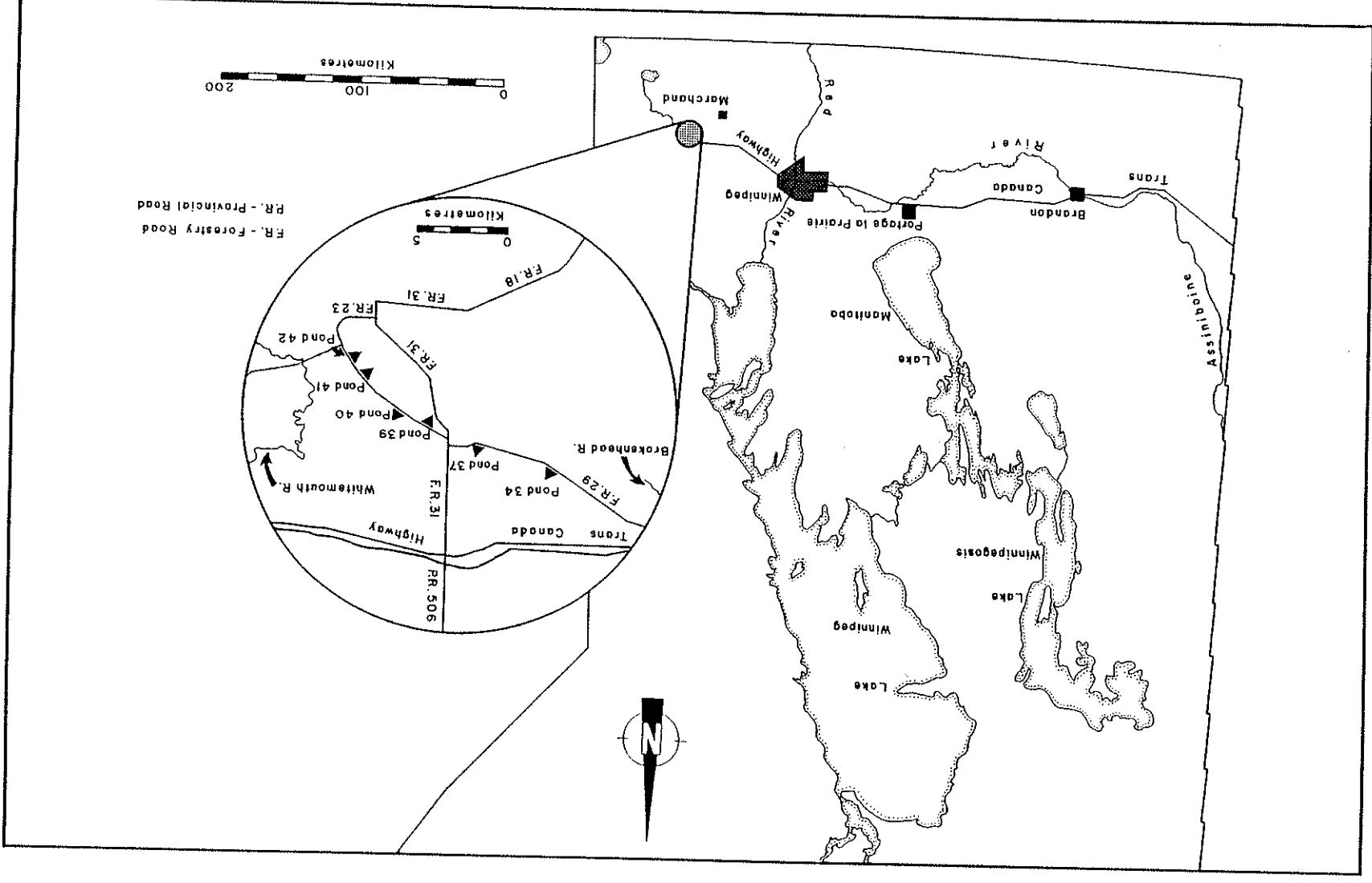


Figure 1. Study area showing the location of the six Sandilands Provincial Forest ponds.

The ponds were intended to retain water for fire suppression by the Manitoba Department of Natural Resources. Most ponds were never used for this purpose and have therefore remained relatively undisturbed. Colonization and succession have occurred over a period of ~ 35 years. The ponds more closely resemble fens than other wetland types (Zoltai 1987) except that banks are steep and uniform. The structure of the aquatic insect community in six of these ponds was studied during a two-year period, beginning in the autumn of 1988 and continuing until the autumn of 1990. Information was also collected on descriptors of pond environment or habitat. These included water chemistry variables, physical attributes of bottom sediments, structure and composition of the macrophyte community, pond morphology, and hydrology.

Approximately 100 such ponds were examined during the initial phase of this study. Six ponds were selected for intensive study based upon a number of criteria: (1) uniformity in morphology; (2) good development of macrophyte community; (3) close proximity to each other; (4) minimal surface inflow or outflow; and (5) resistance to drought. In addition, all of the ponds were located in a relatively isolated area, thus providing some degree of protection against vandalism or other disturbance during the study. During the initial pond selection and data collection phase, all ponds were numbered sequentially. This identification system was retained throughout the study even though only ponds numbered 34, 37, 39, 40, 41, and 42 were selected. Geo-reference information (Trimble Navigation Ensign Global Positioning System using Canada mv (NAS-E) mapping datum, with 3-dimensional solution from a minimum of 5 satellites) is listed in Williamson (1994).

Climate within the study area is continental, with average annual rainfall of 508 mm (Weir 1983). The ponds are located in Temperature Zone 2, with 2600 to 3000

degree days above 5.6°C (Weir 1983). Surface deposits in the area are composed of marsh, fen, swamp, and bog deposits up to 6 m thick. Glaciofluvial deposits, consisting of gravel, sand and silt, are located throughout the area. Moraines can also be found within glaciofluvial deposition areas. Prominent beach ridges exist throughout some areas of Sandilands Provincial Forest. Remnants of glacial deposits consist of highly calcareous till, derived from Paleozoic carbonate rock. In addition, small bedrock outcrops are located in some areas. Predominant soils consist of Gray Luvisol, Eutric Brunisol, with organic Fibrisol and Mesisols located to the east. Soils are coarse and well drained and the terrain is level to undulating. Vegetation, typical of boreal forest, is mainly mixed stands of spruce and aspen (Weir 1983).

Arthropod Community

A modified Ekman dredge (0.052 m²) was used to sample the pond insect community quantitatively. A 1.83 m pole was attached to the topmost structure of the dredge. Two levers each 1.83 m in length were attached to the two jaws and connected to the central pole near its distal end with 0.76 m arms. Downward pressure could be exerted on these levers, thus assisting the springs to completely close the sampling jaws. Nitex[®] nylon screen (400 µm aperture) was placed across the top opening of the dredge to minimize insects escaping while the Ekman was being lowered into place. Because of the extensive macrophyte growth at most sampling locations, a 19.7 cm wide cutting blade placed perpendicular on the end of a pole, was used to sever all vegetative growth around the margins of the dredge. A large net, also constructed of 400 µm aperture Nitex[®] nylon net, was placed around the dredge before it was completely removed from the water to trap any escaping animals and the contents were emptied into this net. All samples were collected while wading in the ponds. The samples were sieved and preserved by adding ~

500 mL of 10% formalin solution (Edmondson and Winberg 1971). Rose bengal was added to the formalin solution at a concentration of 100 mg L⁻¹ (Mason and Yevich 1967).

Three dredge samples were randomly collected from each pond four times during the open-water period (normally during April, June, August and October). Sampling locations were determined with the use of a grid and the generation of random numbers. Two line transects were located on the ponds. The first transect was placed across the width of the pond near the approximate pond centre. The second transect was placed perpendicular to the first across the length of the pond, also near the approximate pond center. The transects were marked off in 0.5 m intervals. Thus, the transects served as the abscissa and ordinate to divide the ponds into four quadrats. Random numbers were generated from a normal distribution with various minimum and maximum values that corresponded to the pond widths and lengths. Hence, every location within each pond had equal probability of being sampled each time. In order to maintain a consistent approach, the abscissa was always located parallel to the adjacent access road.

Additionally, one qualitative sweep sample using a standard D-frame net with 400 × 800 µm mesh was collected from each pond on each sampling occasion. The sweep samples were collected to ensure that specimens present in low abundance were enumerated and to verify that all dominant taxa were being sampled by the Ekman dredge. One continuous sweep with the net was made within one randomly selected pond quadrat.

Arthropods were separated from the substrate with the use of sugar flotation (Lackey and May 1971). An initial specific gravity of 1.130 to 1.135 was effective. An aliquot of ~ 500 mL sediment was thoroughly mixed with 2 L of sugar solution. Masses

of stems, leaves, roots and other plant material were thoroughly pulled apart and examined carefully for invertebrates through a magnifying lens and fluorescent light assembly. The surface of the flotation solution was systematically scanned also through the magnifying lens. Once all visible organisms were removed, the sediment and flotation solution were again thoroughly mixed. This continued until no additional organisms were located after three such iterations. Invertebrates were preserved in 70% ethanol.

Arthropods were identified to species, where possible, using available taxonomic information. Specimens from several families, especially Chironomidae and Chaoboridae, were not enumerated and identified. Total body length, excluding antennae and abdominal appendages (after Hale 1981), maximum body width and head capsule width measurements were made on all individuals with an ocular micrometer. In cases where both adults and immatures within the same genus were present and where immatures could not be identified to the species level, the immatures were treated as separate species for all calculations and statistical analyses.

Data Analysis

Information on functional feeding group, habit, preferred microhabitat, dominant food and feeding mechanism was assembled for all taxa. Similarity among arthropods was calculated using the following formula (Johnson and Wichern 1988):

$$\text{Similarity} = \frac{\sum (X_{ir})}{\sum (X_r)}, \quad (\text{Eq. 1})$$

expressed as a proportion, where:

X_{lr} = resource state X shared by lost species l and replacement species r ;

X_r = resource state X of replacement species r .

A matrix was constructed of similarity proportions. Only species with similarities of 1.00 were retained for additional analysis, since similarity less than 1.00 meant that differences existed in at least one major ecological function. Taxa were then grouped with respective potential replacement species (*i.e.*, those potential replacement taxa with similarity of 1.00).

Within the present study, head capsule width was used as an analog of size spectra. Head capsule width is related to the size of feeding structures, at least in predatory aquatic insects. Measurements assembled by Hale (1981) for 271 morphological types were re-analyzed. In Hale's (1981) study, total body length represented factors affecting site selection and site accessibility and mandible gape represented factors affecting selected prey sizes. A good relationship was found between total body length and mandible gape ($p < 0.00001$, $r = 0.55836$, $n = 271$). This relationship improved when several outliers were removed ($p < 0.00001$, $r = 0.70196$, $n = 261$). Eight of the outliers were dipteran piercers, engulfers or gatherers, one was a corixid piercer and one was a trichopteran grazer/scrapper. This relationship probably holds across many orders; as body size increases, size of feeding structures also increases, allowing larger predators to manipulate larger prey items.

Total body length and maximum body width measurements were also made on all specimens collected from the six study ponds, but both were highly correlated with head capsule width ($p < 0.00001$, $r = 0.8714$; $p < 0.00001$, $r = 0.7137$, respectively). Biomass

was not measured, but it is assumed that biomass is directly related to measurements of body size although the relationship will vary among species (Sprules *et al.* 1991). Hence, head capsule width was thought to adequately characterize the size spectrum of the arthropod species within the study ponds.

Head capsule widths of hypothetically lost taxa and potential replacement taxa were compared using Student's *t* mean difference test ($\alpha = 0.05$). Normality was tested with χ^2 goodness-of-fit ($\alpha = 0.05$), following distribution fitting procedures [STATGRAPHICS *PLUS* version 7 (Manugistics 1993)]. Most data were normally distributed and did not require transformation. Potential replacement taxa that differed significantly in head capsule width relative to hypothetically lost taxa, pooled over all sampling intervals, were then removed from further consideration. The remaining potential replacement taxa and hypothetically lost taxa were partitioned according to sampling interval. Head capsule widths were then compared using ANOVA ($\alpha = 0.05$). Partitioning according to sampling interval accounted for temporal variations in size development between species, thus indicating resource partitioning through life-cycle displacement.

A number of taxa were rejected from further analysis for several reasons. Transient species were rejected since the colonizing pool was either too small to sustain a population or the pond habitat was not favourable for continual occupancy. Taxa were considered transient when only one individual was collected in one pond on one sampling occasion. Coleoptera larvae were included in the early part of the analysis but were later excluded. Coleoptera larvae could only be identified to genus; several species of adults within the same genus were often present. Coleoptera larvae differed substantially in ecological function relative to adults and often had wider niche widths. In many cases,

Coleoptera larvae were identified as potential replacements for a number of species of coleopteran adults, even when adults of the same genera were rejected as possible replacement taxa. It seemed unreasonable that the larvae but not the adult of one genus would be able to replace the ecological function of an adult of another genus. Taxa were also rejected when information was not available for functional feeding group, habit, dominant food, or feeding mechanism (e.g., Chironomidae, Chaoboridae, and most Hydrophilidae).

RESULTS AND DISCUSSION

Arthropod taxa found in each pond are listed in TABLE 1. A total of 108 species were identified. Ecological function attributes for each taxon are shown in TABLE 2 with associated codes listed in TABLE 3. The matrix of similarity proportions is presented in Williamson (1994). Mean head capsule widths are shown in TABLE 4. Functionally similar species are grouped in TABLE 5 along with probabilities of significant head capsule differences between hypothetically lost taxa and potential replacement taxa. Probabilities that functionally similar species differ significantly in head capsule size following partitioning by time are shown in TABLE 6.

Hyalella azteca (Saussure), the only Amphipoda present, did not share major ecological function with other species. *Hyalella azteca* was the only burrowing periphyton scraper present.

Four Ephemeroptera species were present, although only *Callibaetis* sp. was found in most ponds. *Caenis diminuta* Walker and *Caenis youngi* Roemhild shared all major ecological functions and were similar in size. The *Caenis* species appeared able to

TABLE 1. Arthropods collected from the six Sandilands Provincial Forest study ponds. Species presence is indicated by "1", and absence is indicated by "0".

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Amphipoda	Talitridae	<i>Hyalella azteca</i> (Saussure)	adult	Hya azt	1	1	1	1	1	1
Emphemeroptera	Siphonuridae	<i>Siphonurus alternata</i> (Say) (probably)	larvae	Sip alt	0	0	0	0	0	1
Emphemeroptera	Baetidae	<i>Callibaetis</i> sp. Eaton	larvae	Cal sp.	0	1	1	1	1	1
Emphemeroptera	Caenidae	<i>Caenis diminuta</i> Walker	larvae	Cae dim	0	0	1	0	0	1
Emphemeroptera	Caenidae	<i>Caenis youngi</i> Roemhild	larvae	Cae you	0	0	1	1	1	0
Anisoptera	Aeshnidae	<i>Aeshna canadensis</i> Walker	nymph	Aes can	1	0	0	0	1	0
Anisoptera	Aeshnidae	<i>Aeshna interrupta</i> Walker	nymph	Aes int	1	1	1	1	1	0
Anisoptera	Aeshnidae	<i>Anax junius</i> Drury	nymph	Anx jun	1	0	0	0	0	0
Anisoptera	Corduliidae	<i>Cordulia shurtleffi</i> Scudder	nymph	Cor shu	1	0	0	0	0	1
Anisoptera	Corduliidae	<i>Somatochlora williamsoni</i> Walker	nymph	Som wil	1	1	1	1	1	1
Anisoptera	Libellulidae	<i>Leucorrhinia frigida</i> Hagen	nymph	Leu fri	1	0	0	0	0	0
Anisoptera	Libellulidae	<i>Leucorrhinia hudsonica</i> (Selys)	nymph	Leu hud	1	0	0	0	0	0
Anisoptera	Libellulidae	<i>Leucorrhinia intacta</i> Hagen	nymph	Leu int	1	1	1	1	1	1
Anisoptera	Libellulidae	<i>Leucorrhinia proxima</i> Calvert	nymph	Leu pro	1	0	0	0	1	1
Anisoptera	Libellulidae	<i>Libellula quadrimaculata</i> Linne	nymph	Lib qua	1	0	1	1	1	1
Anisoptera	Libellulidae	<i>Sympetrum danae</i> Sulzer	nymph	Sym dan	0	0	0	0	0	1
Anisoptera	Libellulidae	<i>Sympetrum obtrusum</i> (Hagen)	nymph	Sym obt	0	1	1	0	0	0
Zygoptera	Lestidae	<i>Lestes congener</i> Hagen	nymph	Les con	1	0	1	1	1	1
Zygoptera	Lestidae	<i>Lestes disjunctus disjunctus</i> Selys	nymph	Les dis	0	0	1	0	1	1
Zygoptera	Lestidae	<i>Lestes dryas</i> Kirby	nymph	Les dry	0	0	0	1	0	0
Zygoptera	Lestidae	<i>Lestes unguiculatus</i> Hagen	nymph	Les ung	1	0	1	0	0	1
Zygoptera	Coenagrionidae	<i>Coenagrion angulatum</i> Hagen	nymph	Coe ang	0	0	0	1	1	1
Zygoptera	Coenagrionidae	<i>Coenagrion resolutum</i> (Hagen)	nymph	Coe res	1	0	0	1	1	1
Zygoptera	Coenagrionidae	<i>Enallagma cyathigerum</i> (Charpentier)	nymph	Ena cya	1	1	1	1	1	1
Hemiptera	Veliidae	<i>Microvelia pulchella</i> Westwood (probably)	immature	Mic pul	0	0	0	0	0	1
Hemiptera	Gerridae	<i>Gerris buenoi</i> Kirkaldy	adult	Ger bue	1	0	1	1	1	1
Hemiptera	Gerridae	<i>Gerris dissortis</i> Drake and Harris	adult	Ger dis	1	1	1	0	0	0
Hemiptera	Belostomatidae	<i>Lethocerus americanus</i> (Leidy)	adult	Let ame	0	0	0	1	0	0
Hemiptera	Nepidae	<i>Ranatra fusca</i> Palisot de Beauvois	adult	Ran fus	0	0	1	0	0	0
Hemiptera	Corixidae	<i>Callicorixa audeni</i> Hungerford	adult	Cal aud	0	0	0	1	1	1
Hemiptera	Corixidae	<i>Hesperocorixa atopodonta</i> (Hungerford)	adult	Hes ato	0	1	1	1	1	1
Hemiptera	Corixidae	<i>Hesperocorixa minorella</i> (Hungerford)	adult	Hes min	0	0	0	0	0	1
Hemiptera	Corixidae	<i>Hesperocorixa vulgaris</i> (Hungerford)	adult	Hes vul	0	1	1	1	1	1
Hemiptera	Corixidae	<i>Sigara (Vermicorixa) alternata</i> (Say)	adult	Sig alt	1	1	1	1	1	1
Hemiptera	Corixidae	<i>Sigara (Arctosigara) conocephala</i> (Hungerford)	adult	Sig con	0	0	0	1	0	0
Hemiptera	Corixidae	<i>Sigara (Arctosigara) decoratella</i> (Hungerford)	adult	Sig dec	0	0	0	0	0	1
Hemiptera	Corixidae	<i>Sigara (Vermicorixa) grossolineata</i> Hungerford	adult	Sig gro	0	0	1	0	1	1

TABLE 1. Continued.

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Hemiptera	Notonectidae	<i>Notonecta borealis</i> Bueno and Hussey	adult	Not bor	1	0	0	0	0	0
Hemiptera	Notonectidae	<i>Notonecta irrorata</i> Uhler	adult	Not irr	1	0	0	0	1	0
Hemiptera	Notonectidae	<i>Notonecta kirbyi</i> Hungerford	adult	Not kir	0	0	1	1	0	0
Hemiptera	Notonectidae	<i>Notonecta undulata</i> Say	adult	Not und	0	1	1	1	1	1
Trichoptera	Phryganeidae	<i>Banksiola crotchii</i> Banks	larvae	Ban cro	1	1	0	1	1	1
Trichoptera	Phryganeidae	<i>Ptilostomis</i> sp. Kolenati	larvae	Pti sp.	0	0	1	1	0	0
Trichoptera	Limnephilidae	<i>Anabolia</i> sp. Stephens	larvae	Ana sp.	0	0	1	0	0	0
Trichoptera	Limnephilidae	<i>Limnephilus</i> sp. 1 Leach	larvae	Lim sp1	0	0	1	0	0	0
Trichoptera	Limnephilidae	<i>Limnephilus</i> sp. 2 Leach	larvae	Lim sp2	0	0	1	0	0	0
Trichoptera	Limnephilidae	<i>Nemotaulius hostilis</i> (Hagen)	larvae	Nem hos	0	0	1	0	0	0
Trichoptera	Leptoceridae	<i>Oecetis inconspicua</i> (Walker) Complex	larvae	Oec inc	0	1	1	1	1	1
Coleoptera	Gyrinidae	<i>Gyrinus aquiris</i> LeConte	adult	Gyr aqu	0	1	0	0	0	0
Coleoptera	Haliplidae	<i>Haliplus canadensis</i> Wallis	adult	Hal can	1	1	1	0	0	0
Coleoptera	Haliplidae	<i>Haliplus connexus</i> Matheson	adult	Hal con	1	0	0	0	0	0
Coleoptera	Haliplidae	<i>Haliplus immaculicollis</i> Harris	adult	Hal imm	1	1	1	1	1	1
Coleoptera	Haliplidae	<i>Haliplus longulus</i> LeConte	adult	Hal lon	0	0	0	0	1	0
Coleoptera	Haliplidae	<i>Haliplus salinarius</i> Wallis	adult	Hal sal	0	0	0	0	1	0
Coleoptera	Haliplidae	<i>Haliplus</i> sp. Latreille	larvae	Hal sp.	1	1	1	1	1	1
Coleoptera	Haliplidae	<i>Haliplus strigatus</i> Roberts	adult	Hal str	0	0	1	0	0	0
Coleoptera	Haliplidae	<i>Haliplus subgutatus</i> Crotch	adult	Hal sub	0	0	1	1	0	0
Coleoptera	Haliplidae	<i>Peltodytes edentulus</i> (LeConte)	adult	Pel ede	0	0	0	1	0	0
Coleoptera	Haliplidae	<i>Peltodytes</i> sp. Regimbart	larvae	Pel sp.	0	0	0	1	0	0
Coleoptera	Haliplidae	<i>Peltodytes tortulosus</i> Roberts	adult	Pel tor	0	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Acilius semisulcatus</i> Aube	adult	Aci sem	1	0	0	1	1	1
Coleoptera	Dytiscidae	<i>Acilius</i> sp. Leach	larvae	Aci sp.	0	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Agabus anthracinus</i> Mannerheim	adult	Aga ant	0	1	0	0	0	0
Coleoptera	Dytiscidae	<i>Agabus</i> sp. Leach	larvae	Aga sp.	0	0	0	1	1	1
Coleoptera	Dytiscidae	<i>Colymbetes longulus</i> LeConte	adult	Col lon	1	0	0	0	0	0
Coleoptera	Dytiscidae	<i>Colymbetes sculpilis</i> Harris	adult	Col scu	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Coptotomus longulus</i> LeConte	adult	Cop lon	0	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Desmopachria convexa</i> (Aube)	adult	Des con	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Dytiscus dauricus</i> Gebler	adult	Dyt dau	0	1	1	0	0	0
Coleoptera	Dytiscidae	<i>Dytiscus</i> sp. Linnaeus	larvae	Dyt sp.	0	1	0	1	0	1
Coleoptera	Dytiscidae	<i>Graphoderus liberus</i> (Say)	adult	Grp lib	0	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Graphoderus perplexus</i> Sharp	adult	Grp per	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Graphoderus</i> sp. Dejean	larvae	Grp sp.	0	0	0	0	1	1
Coleoptera	Dytiscidae	<i>Hydaticus aruspex</i> Clark	adult	Hda aru	1	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Hydaticus</i> sp. Leach	larvae	Hda sp.	0	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Hydroporus paugus</i> Fall	adult	Hdp pau	0	1	0	0	0	0

TABLE 1. Continued.

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Coleoptera	Dytiscidae	<i>Hydroporus rubyi</i> Larson	adult	Hdp rub	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Hydroporus rufinasus</i> Mannerheim	adult	Hdp ruf	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Hydroporus</i> sp. Clairville	larvae	Hdp sp.	0	1	0	1	0	0
Coleoptera	Dytiscidae	<i>Hydroporus</i> sp. 1 Clairville	adult	Hdp sp1	1	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Hygrotus putruelis</i> (LeConte)	adult	Hyg pat	0	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Hygrotus salinarius</i> (Wallis)	adult	Hyg sal	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Hygrotus sayi</i> Balfour-Browne	adult	Hyg say	0	1	1	1	1	1
Coleoptera	Dytiscidae	<i>Hygrotus</i> sp. 1 Stephens	adult	Hyg sp1	0	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Hygrotus</i> sp. 2 Stephens	adult	Hyg sp2	0	0	0	0	1	1
Coleoptera	Dytiscidae	<i>Laccophilus biguttatus</i> Kirby	adult	Lac big	0	0	0	0	1	0
Coleoptera	Dytiscidae	<i>Laccophilus maculosus</i> Say	adult	Lac mac	0	0	1	1	1	1
Coleoptera	Dytiscidae	<i>Laccophilus</i> sp. Leach	larvae	Lac sp.	0	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Liodessa affinis</i> (Say)	adult	Lio aff	0	1	1	1	1	1
Coleoptera	Dytiscidae	<i>Rhantus binotatus</i> (Harris)	adult	Rha bin	1	1	1	1	0	1
Coleoptera	Dytiscidae	<i>Rhantus frontalis</i> (Marshall)	adult	Rha fro	1	0	0	0	0	0
Coleoptera	Dytiscidae	<i>Rhantus</i> sp. Dejean	larvae	Rha sp.	0	0	1	0	0	0
Coleoptera	Dytiscidae	<i>Rhantus suturellus</i> (Harris)	adult	Rha sut	1	0	1	0	0	0
Coleoptera	Hydrophilidae	<i>Anacaena limbata</i> (Fabricius)	adult	Anc lim	1	0	0	0	0	1
Coleoptera	Hydrophilidae	<i>Berosus striatus</i> (Say)	adult	Ber str	0	0	0	0	0	1
Coleoptera	Hydrophilidae	<i>Cymbiodyta minima</i> Notman	adult	Cym min	0	0	0	1	0	0
Coleoptera	Hydrophilidae	<i>Cymbiodyta vindicata</i> Fall	adult	Cym vin	0	0	0	0	0	1
Coleoptera	Hydrophilidae	<i>Enochrus (Lumetus) hamiltoni</i> (Horn)	adult	Eno ham	1	0	0	0	0	0
Coleoptera	Hydrophilidae	<i>Enochrus (Methyrus) ochraceus</i> (Melsheimer)	adult	Eno och	0	0	0	0	1	0
Coleoptera	Hydrophilidae	<i>Helophorus (Rhopaleophorus) angusticollis</i> d'Orchymont	adult	Hel ang	0	0	0	0	0	1
Coleoptera	Hydrophilidae	<i>Helophorus (Rhopaleophorus) lacustris</i> LeConte	adult	Hel lac	0	1	0	0	0	0
Coleoptera	Hydrophilidae	<i>Hydrobius fuscipes</i> (Linne)	adult	Hdb fus	0	1	0	0	0	0
Coleoptera	Hydrophilidae	<i>Hydrochara obtusata</i> (Say)	adult	Hdc obt	1	0	0	0	0	0
Coleoptera	Hydrophilidae	<i>Hydrochus pseudosquamifer</i> D.C. Miller	adult	Hdu pse	0	0	1	0	1	0
Coleoptera	Hydrophilidae	<i>Tropisternus lateralis nimbatus</i> (Say)	adult	Tro lat	1	0	0	0	1	0
Coleoptera	Hydrophilidae	<i>Tropisternus</i> sp. Solier	larvae	Tro sp.	0	0	0	0	0	1
Coleoptera	Hydraenidae	<i>Hydraena angulicollis</i> Notman	adult	Hdr ang	1	0	0	0	1	1
Coleoptera	Scirtidae	<i>Cyphon</i> sp. Paykull	adult	Cyp sp.	0	0	0	0	1	0

TABLE 2. Functional attributes of arthropod taxa collected from the six Sandilands Provincial Forest study ponds. Attribute codes are located in TABLE 3. "1" indicates the presence of an attribute, while "0" indicates the absence of an attribute.

	Functional Feeding Group					Habit											Microhabitat					Dominant Food								Feeding Mechanism											Reference																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																
	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																	
<i>Hyalella azteca</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. Continued.

	Functional Feeding Group					Habit											Microhabitat					Dominant Food								Feeding Mechanism											Reference
	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11	
<i>Notonecta irrorata</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Notonecta kirbyi</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Notonecta undulata</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Banksiola crotchii</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Ptilostomis sp.</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Anabolia sp.</i>	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Limnephilus sp. 1</i>	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	Merritt and Cummins (1984)	
<i>Limnephilus sp. 2</i>	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Nemotaulius hostilis</i>	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	Merritt and Cummins (1984)	
<i>Oecetis inconspicua</i> Complex	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)	
<i>Gyrinus aquiris</i>	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Haliphus canadensis</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Haliphus connexus</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus immaculicollis</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus longulus</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus salinarius</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus sp.</i>	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus strigatus</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Haliphus subguttatus</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Peltodytes edentulus</i>	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	Merritt and Cummins (1984)	
<i>Peltodytes sp.</i>	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	Merritt and Cummins (1984)	
<i>Peltodytes tortulosus</i>	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	Merritt and Cummins (1984)	
<i>Acilius semisulcatus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	Merritt and Cummins (1984)	
<i>Acilius sp.</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Agabus anthracinus</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Agabus sp.</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Colymbetes longulus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Colymbetes sculpitilis</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Coptotomus longulus</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Desmopachria convexa</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Dytiscus dauricus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Dytiscus sp.</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Graphoderus liberus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Graphoderus perplexus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Graphoderus sp.</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydaticus aruspex</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydaticus sp.</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydroporus paugus</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydroporus rubyi</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydroporus rufinatus</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hydroporus sp.</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	

TABLE 2. Continued.

	Functional Feeding Group					Habit											Microhabitat					Dominant Food								Feeding Mechanism											Reference
																		Code																							
	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11	
<i>Hydroporus</i> sp. 1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Hygrotus patruelis</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hygrotus salinarius</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)	
<i>Hygrotus sayi</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Hygrotus</i> sp. 1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Hygrotus</i> sp. 2	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Laccophilus biguttatus</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Laccophilus maculosus</i>	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Laccophilus</i> sp.	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Liodessa affinis</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Rhantus binotatus</i>	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Rhantus frontalis</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Rhantus</i> sp.	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Rhantus suturellus</i>	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Anacaena limbata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	Merritt and Cummins (1984)
<i>Berosus striatus</i>	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Cymbiodyta minima</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Cymbiodyta vindicata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Enochrus (Lumetus) hamiltoni</i>	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Enochrus (Methyrus) ochraceus</i>	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Helophorus (Rhoptelephorus) angusticollis</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Helophorus (Rhoptelephorus) lacustris</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Hydrobius fuscipes</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Hydrochara obtusata</i>	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Hydrochus pseudosquamifer</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Tropisternus lateralis nimbatus</i>	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Tropisternus</i> sp.	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Hydraena angulicollis</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)
<i>Cyphon</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Merritt and Cummins (1984)

TABLE 3. Functional attributes of arthropod taxa collected from the six Sandilands Provincial Forest study ponds and associated codes used in similarity analysis.

Habit	Code
Skaters	1
Planktonic	2
Divers	3
Swimmers	4
Clingers	5
Sprawlers	6
Climbers	7
Burrowers	8
Climbers (poor swimmers)	9
Burrowers (sand and gravel)	10
Burrowers (silt)	11
Microhabitat	Code
Sediments	1
Vascular hydrophytes	2
Detritus	3
Silt	4
Surface	5

TABLE 3. Continued.

Functional Feeding Group	Code	Dominant Food	Code	Feeding Mechanism	Code
Shredders	1	Living Vascular Tissue	1	Herbivores-chewers and miners of live macrophytes	1
		Decomposing Vascular Tissue (CPOM)	2	Detritivores-chewers of CPOM	2
		Wood	3	Gougers	3
Collectors	2	Decomposing Fine Particulate Organic Matter (FPOM)	4	Detritivores-filterers or suspension feeders	4
				Detritivores-gatherers or deposit (sediment) feeders	5
		Neuston scavengers	5		
Scrapers	3	Periphyton	6	Herbivores-grazing scrapers of mineral and organic surfaces	6
Macrophyte Piercers	4	Living Vascular Hydrophyte Cell and Tissue Fluids or Filamentous Algal Cell Fluids	7	Herbivores-pierce tissues or cells and suck fluids	7
Predators	5	Living Animal Tissue	8	Engulfers-carnivores attack prey and ingest whole animals or parts	8
				Piercers-carnivores attack prey pierce tissues and cells and suck fluids	9
				Engulfers-carnivores stalk and attack prey ingest whole animals or parts	10
				Engulfers-carnivores scavengers ingest whole animals or parts	11

TABLE 4. Mean head capsule width of arthropods collected from the six Sandilands Provincial Forest study ponds.

Species	Number of Specimens	Mean Head Capsule Width (mm)	Standard Deviation
<i>Hyalella azteca</i>	a	—	—
<i>Siphonurus alternata</i>	2	2.37	0.22
<i>Callibaetis</i> sp.	90	1.13	0.40
<i>Caenis diminuta</i>	2	0.81	0.19
<i>Caenis youngi</i>	86	0.71	0.29
<i>Aeshna canadensis</i>	14	5.18	1.82
<i>Aeshna interrupta</i>	15	4.29	2.50
<i>Anax junius</i>	2	5.21	0.22
<i>Cordulia shurtleffi</i>	11	3.16	1.24
<i>Somatochlora williamsoni</i>	11	3.33	1.58
<i>Leucorrhinia frigida</i>	1	3.48	—
<i>Leucorrhinia hudsonica</i>	3	4.48	0.09
<i>Leucorrhinia intacta</i>	1133	3.49	1.17
<i>Leucorrhinia proxima</i>	3	3.27	1.82
<i>Libellula quadrimaculata</i>	25	4.51	1.76
<i>Sympetrum danae</i>	3	3.48	2.20
<i>Sympetrum obtrusum</i>	4	2.13	0.46
<i>Lestes congener</i>	37	2.57	0.80
<i>Lestes disjunctus disjunctus</i>	3	2.81	0.81
<i>Lestes dryas</i>	2	2.59	0.00
<i>Lestes unguiculatus</i>	10	3.38	0.68
<i>Coenagrion angulatum</i>	26	2.16	0.38
<i>Coenagrion resolutum</i>	86	1.85	0.55
<i>Enallagma cyathigerum</i>	1564	2.19	0.65
<i>Microvelia pulchella</i>	a	—	—
<i>Gerris buenoi</i>	3	1.34	0.08
<i>Gerris dissortis</i>	7	1.86	0.06
<i>Lethocerus americanus</i>	1	18.50	—
<i>Ranatra fusca</i>	1	2.05	—
<i>Callicorixa audeni</i>	7	2.16	0.19
<i>Hesperocorixa atopodonta</i>	36	2.80	0.16
<i>Hesperocorixa minorella</i>	3	2.11	0.09
<i>Hesperocorixa vulgaris</i>	22	3.02	0.19
<i>Sigara (Vermicorixa) alternata</i>	87	1.90	0.13
<i>Sigara (Arctosigara) conocephala</i>	1	2.37	—
<i>Sigara (Arctosigara) decoratella</i>	1	2.21	—
<i>Sigara (Vermicorixa) grossolineata</i>	3	1.69	0.05
<i>Notonecta borealis</i>	2	3.24	0.11
<i>Notonecta irrorata</i>	3	2.95	0.78
<i>Notonecta kirbyi</i>	2	2.73	0.61
<i>Notonecta undulata</i>	24	2.51	0.38
<i>Banksiola crotchii</i>	11	2.15	2.71
<i>Ptilostomis</i> sp.	2	1.82	0.78
<i>Anabolia</i> sp.	1	2.05	—
<i>Limnephilus</i> sp. 1	2	0.87	0.11
<i>Limnephilus</i> sp. 2	1	0.95	—
<i>Nemotaulius hostilis</i>	1	2.21	—
<i>Oecetis inconspicua</i> Complex	46	0.76	0.11
<i>Gyrinus aquiris</i>	1	1.74	—
<i>Haliphus canadensis</i>	10	0.93	0.07
<i>Haliphus connexus</i>	1	0.80	—
<i>Haliphus immaculicollis</i>	20	0.63	0.09
<i>Haliphus longulus</i>	1	0.62	—
<i>Haliphus salinarius</i>	1	0.86	—
<i>Haliphus</i> sp.	93	0.42	0.15
<i>Haliphus strigatus</i>	1	0.62	—
<i>Haliphus subguttatus</i>	2	0.80	0.09
<i>Peltodytes edentulus</i>	1	0.74	—
<i>Peltodytes</i> sp.	2	0.34	0.04

TABLE 4. Continued.

Species	Number of Specimens	Mean Head Capsule Width (mm)	Standard Deviation
<i>Peltodytes tortulosus</i>	6	0.80	0.00
<i>Acilius semisulcatus</i>	16	3.19	0.09
<i>Acilius</i> sp.	2	1.90	0.00
<i>Agabus anthracinus</i>	1	1.90	—
<i>Agabus</i> sp.	27	1.36	0.41
<i>Colymbetes longulus</i>	1	3.95	—
<i>Colymbetes sculptilis</i>	1	3.48	—
<i>Coptotomus longulus</i>	1	2.37	—
<i>Desmopachria convexa</i>	1	0.74	—
<i>Dytiscus dauricus</i>	2	8.50	0.71
<i>Dytiscus</i> sp.	5	2.79	1.67
<i>Graphoderus liberus</i>	2	2.92	0.11
<i>Graphoderus perplexus</i>	1	3.79	—
<i>Graphoderus</i> sp.	3	1.52	0.88
<i>Hydaticus aruspex</i>	5	3.38	0.18
<i>Hydaticus</i> sp.	4	1.40	0.89
<i>Hydroporus paugus</i>	1	1.11	—
<i>Hydroporus rubyi</i>	1	0.86	—
<i>Hydroporus rufinasus</i>	1	0.92	—
<i>Hydroporus</i> sp.	4	0.57	0.11
<i>Hydroporus</i> sp. 1	2	1.39	0.39
<i>Hygrotus patruelis</i>	1	0.99	—
<i>Hygrotus salinarius</i>	1	1.48	—
<i>Hygrotus sayi</i>	22	0.94	0.13
<i>Hygrotus</i> sp. 1	1	0.86	—
<i>Hygrotus</i> sp. 2	3	1.25	0.13
<i>Laccophilus biguttatus</i>	1	1.29	—
<i>Laccophilus maculosus</i>	4	1.76	0.10
<i>Laccophilus</i> sp.	7	0.99	0.26
<i>Liodessa affinis</i>	23	0.62	0.03
<i>Rhantus binotatus</i>	6	2.58	0.08
<i>Rhantus frontalis</i>	2	2.45	0.11
<i>Rhantus</i> sp.	1	0.92	—
<i>Rhantus suturellus</i>	2	2.61	0.11
<i>Anacaena limbata</i>	8	0.79	0.05
<i>Berosus striatus</i>	1	1.36	—
<i>Cymbiodyta minima</i>	1	0.74	—
<i>Cymbiodyta vindicata</i>	2	1.23	0.09
<i>Enochrus (Lumetus) hamiltoni</i>	1	1.58	—
<i>Enochrus (Methyrus) ochraceus</i>	1	0.86	—
<i>Helophorus (Rhopaleophorus) angusticollis</i>	1	0.80	—
<i>Helophorus (Rhopaleophorus) lacustris</i>	1	0.92	—
<i>Hydrobius fuscipes</i>	1	3.32	—
<i>Hydrochara obtusata</i>	6	5.97	2.24
<i>Hydrochus pseudosquamifer</i>	2	0.68	0.09
<i>Tropisternus lateralis nimbatus</i>	2	2.37	0.00
<i>Tropisternus</i> sp.	2	1.08	0.04
<i>Hydraena angulicollis</i>	26	0.45	0.15
<i>Cyphon</i> sp.	1	0.99	—

^a Head capsule width not measured on *Hyaella azteca* or *Microvelia pulchella*.

TABLE 5. Functionally similar taxa showing probability of mean head capsule width difference between hypothetically lost taxa (first column) and potential replacement taxa (subsequent columns).

Lost Taxa		Potential Replacement Taxa											
Hya azt	No functionally similar taxon available.												
Sip alt	No functionally similar taxon available.												
Cal sp.	No functionally similar taxon available.												
Cae dim	Cae you (not sig.)												
Cae you	Cae dim (not sig.)												
Aes can	Anx jun (not sig.)	Aes int (not sig.)											
Aes int	Anx jun (not sig.)	Aes can (not sig.)											
Anx jun	Aes int (not sig.)	Aes can (not sig.)											
Cor shu	Sym obt (not sig.)	Sym dan (not sig.)	Lib qua (<0.05)										
Som wil	Sym obt (not sig.)	Sym dan (not sig.)	Oec inc (<0.0001)	Lib qua (not sig.)									
Leu fri	Single specimen collected in only one pond.												
Leu hud	Sym obt (<0.001)	Sym dan (not sig.)	Pti sp. (<0.01)	Leu pro (not sig.)	Leu int (not sig.)	Les ung (<0.05)	Les dry (<0.001)	Les dis (<0.05)	Les con (<0.001)	Ena cya (<0.0001)	Coe res (<0.0001)	Coe ang (<0.0001)	Ban cro (not sig.)
Leu int	Sym obt (<0.05)	Sym dan (not sig.)	Pti sp. (<0.05)	Leu pro (not sig.)	Leu hud (not sig.)	Les ung (not sig.)	Les dry (not sig.)	Les dis (not sig.)	Les con (<0.0001)	Ena cya (<0.0001)	Coe res (<0.0001)	Coe ang (<0.0001)	Ban cro (<0.001)
Leu pro	Sym obt (not sig.)	Sym dan (not sig.)	Pti sp. (not sig.)	Leu int (not sig.)	Leu hud (not sig.)	Les ung (not sig.)	Les dry (not sig.)	Les dis (not sig.)	Les con (not sig.)	Ena cya (<0.01)	Coe res (<0.001)	Coe ang (<0.01)	Ban cro (not sig.)
Lib qua	Som wil (not sig.)	Cor shu (<0.05)											
Sym dan	Sym obt (not sig.)	Som wil (not sig.)	Leu pro (not sig.)	Leu int (not sig.)	Leu hud (not sig.)	Cor shu (not sig.)							

TABLE 5. Continued.

Lost Taxa			Potential Replacement Taxa																						
Sym obt	Sym dan (not sig.)	Som wil (not sig.)	Leu pro (not sig.)	Leu int (<0.05)	Leu hud (<0.001)	Cor shu (not sig.)																			
Les con	Leu pro (not sig.)	Leu int (<0.0001)	Leu hud (<0.001)	Les ung (<0.01)	Les dry (not sig.)	Les dis (not sig.)																			
Les dis	Leu pro (not sig.)	Leu int (not sig.)	Leu hud (<0.05)	Les ung (not sig.)	Les dry (not sig.)	Les con (not sig.)																			
Les dry	Leu pro (not sig.)	Leu int (not sig.)	Leu hud (<0.001)	Les ung (not sig.)	Les dis (not sig.)	Les con (not sig.)																			
Les ung	Leu pro (not sig.)	Leu int (not sig.)	Leu hud (<0.05)	Les dry (not sig.)	Les dis (not sig.)	Les con (<0.01)																			
Coe ang	Pti sp. (not sig.)	Leu pro (<0.01)	Leu int (<0.0001)	Leu hud (<0.0001)	Ena cya (not sig.)	Coe res (<0.01)	Ban cro (not sig.)																		
Coe res	Pti sp. (not sig.)	Leu pro (<0.001)	Leu int (<0.0001)	Leu hud (<0.0001)	Ena cya (<0.0001)	Coe ang (<0.01)	Ban cro (not sig.)																		
Ena cya	Pti sp. (not sig.)	Leu pro (<0.01)	Leu int (<0.0001)	Leu hud (<0.0001)	Coe res (<0.0001)	Coe ang (not sig.)	Ban cro (not sig.)																		
Mic pul	Ger dis (<0.0001)	Ger buc (<0.0001)																							
Ger buc	Mic pul (<0.0001)	Ger dis (<0.0001)																							
Ger dis	Mic pul (<0.0001)	Ger buc (<0.0001)																							
Let ame	Single specimen collected in only one pond.																								
Ran fus	Single specimen collected in only one pond.																								
Cal aod	Rha sut (<0.05)	Rha sp. (i.d.) ^A (not sig.)	Rha fro (not sig.)	Rha bin (<0.001)	Not und (<0.05)	Not kir (<0.05)	Not irr (<0.05)	Not bor (<0.001)	Lio aff (<0.0001)	Lac sp. (<0.0001)	Lac mac (<0.01)	Hyg sp2 (<0.001)	Hyg say (<0.0001)	Hdp spl (<0.01)	Hdp sp. (<0.0001)	Hda sp. (not sig.)	Hda aru (<0.0001)	Grp sp. (not sig.)	Grp lib (<0.01)	Dyt sp. (not sig.)	Dyt dau (<0.0001)	Aga sp. (<0.0001)	Aci sp. (not sig.)	Aci sem (<0.0001)	
Hes ato	Tro lat (<0.01)	Sig gro (<0.0001)	Sig alt (<0.0001)	Pel tor (<0.0001)	Hes vul (<0.0001)	Hes min (<0.0001)	Hal sub (<0.0001)	Hal imm (<0.0001)	Hal can (<0.0001)																
Hes min	Tro lat (<0.05)	Pel tor (<0.0001)	Hes vul (<0.0001)	Hes ato (<0.0001)	Hal sub (<0.01)	Hal imm (<0.0001)	Hal can (<0.0001)	Sig gro (<0.01)	Sig alt (<0.01)																
Hes vul	Tro lat (<0.001)	Sig gro (<0.0001)	Sig alt (<0.0001)	Pel tor (<0.0001)	Hes min (<0.0001)	Hes ato (<0.0001)	Hal sub (<0.0001)	Hal imm (<0.0001)	Hal can (<0.0001)																

TABLE 5. Continued.

Lost Taxa						Potential Replacement Taxa												
Sig alt	Tro lat (<0.0001)	Sig gro (<0.01)	Hes vul (<0.0001)	Hes ato (<0.0001)	Hes min (<0.01)													
Sig con	Single specimen collected in only one pond.																	
Sig dec	Single specimen collected in only one pond.																	
Sig gro	Tro lat (<0.0001)	Sig alt (<0.01)	Hes vul (<0.0001)	Hes ato (<0.0001)	Hes min (<0.01)													
Not bor	Rha sp. (i.d.)	Not und (<0.05)	Not kir (not sig.)	Not irr (not sig.)	Lio aff (<0.0001)	Lac sp. (<0.0001)	Lac mac (<0.001)	Hyg sp2 (<0.001)	Hyg say (<0.0001)	Hdp sp1 (<0.05)	Hdp sp. (<0.0001)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.001)	Aga sp. (<0.0001)	Aci sp. (<0.01)
Not irr	Rha sp. (i.d.)	Not und (not sig.)	Not kir (not sig.)	Not bor (not sig.)	Lio aff (<0.0001)	Lac sp. (<0.001)	Lac mac (<0.05)	Hyg sp2 (<0.05)	Hyg say (<0.0001)	Hdp sp1 (not sig.)	Hdp sp. (<0.01)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.05)	Aga sp. (<0.0001)	Aci sp. (not sig.)
Not kir	Rha sp. (i.d.)	Not und (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lio aff (<0.0001)	Lac sp. (<0.001)	Lac mac (<0.05)	Hyg sp2 (<0.05)	Hyg say (<0.0001)	Hdp sp1 (not sig.)	Hdp sp. (<0.01)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.05)	Aga sp. (<0.001)	Aci sp. (not sig.)
Not und	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Not bor (<0.05)	Lio aff (<0.0001)	Lac sp. (<0.0001)	Lac mac (<0.01)	Hyg sp2 (<0.0001)	Hyg say (<0.0001)	Hdp sp1 (<0.001)	Hdp sp. (<0.0001)	Hda sp. (<0.001)	Hda aru (<0.0001)	Grp sp. (<0.01)	Dyt sp. (not sig.)	Cal aud (<0.05)	Aga sp. (<0.0001)	Aci sp. (<0.05)
Ban ero	Pti sp. (not sig.)	Leu pro (not sig.)	Leu int (<0.001)	Leu hud (not sig.)	Ena cya (not sig.)	Coe res (not sig.)	Coe ang (not sig.)											
Pti sp.	Leu pro (not sig.)	Leu int (<0.05)	Leu hud (<0.01)	Ena cya (not sig.)	Coe res (not sig.)	Coe ang (not sig.)	Ban ero (not sig.)											
Ana sp.	Single specimen collected in only one pond.																	
Lim sp1	No functionally similar taxon available.																	
Lim sp2	Single specimen collected in only one pond.																	
Nem hos	Single specimen collected in only one pond.																	
Oec inc	Som wil (<0.0001)																	
Gyr aqu	Single specimen collected in only one pond.																	
Hal can	Pel tor (<0.001)	Hes vul (<0.0001)	Hes min (<0.0001)	Hes ato (<0.0001)	Hal sub (<0.05)	Hal inm (<0.0001)												

TABLE 5. Continued.

Lost Taxa		Potential Replacement Taxa																
Hal con	Single specimen collected in only one pond.																	
Hal imm	Pel tor	Hes vul	Hes min	Hes ato	Hal sub	Hal can												
	(<0.0001)	(<0.0001)	(<0.0001)	(<0.0001)	(<0.05)	(<0.0001)												
Hal lon	Single specimen collected in only one pond.																	
Hal sal	Single specimen collected in only one pond.																	
Hal sp.	Pel tor	Pel sp.	Hal sub															
	(<0.0001)	(not sig.)	(<0.01)															
Hal stri	Single specimen collected in only one pond.																	
Hal sub	Pel tor	Hes vul	Hes min	Hes ato	Hal imm	Hal can												
	(not sig.)	(<0.0001)	(<0.01)	(<0.0001)	(<0.05)	(<0.05)												
Pel edc	Single specimen collected in only one pond.																	
Pel sp.	Pel tor	Hal sp.																
	(<0.0001)	(not sig.)																
Pel tor	Hes vul	Hes min	Hes ato	Hal sub	Hal sp.	Hal imm	Hal can											
	(<0.0001)	(<0.0001)	(<0.0001)	(not sig.)	(<0.0001)	(<0.001)	(<0.001)											
Aci sem	Rha sut	Rha fro	Rha bin	Lac mac	Hda aru	Grp lib	Dyt dau	Cal aud										
	(<0.0001)	(<0.0001)	(<0.0001)	(<0.0001)	(<0.01)	(<0.01)	(<0.0001)	(<0.0001)										
Aci sp.	Cal aud	Rha sp.	Not und	Not kir	Not irr	Not bor	Lio aff	Lac sp.	Lac mac	Hyg sp2	Hyg say	Hdp spl	Hdp sp.	Hda sp.	Hda aru	Grp sp.	Dyt sp.	Aga sp.
	(not sig.)	(i.d.)	(<0.05)	(not sig.)	(not sig.)	(not sig.)	(<0.01)	(<0.0001)	(<0.01)	(not sig.)	(<0.01)	(<0.0001)	(not sig.)	(<0.001)	(not sig.)	(<0.001)	(not sig.)	(not sig.)
Aga ant	Single specimen collected in only one pond.																	
Aga sp.	Rha sp.	Not und	Not kir	Not irr	Not bor	Lio aff	Lac sp.	Lac mac	Hyg sp2	Hyg say	Hdp spl	Hdp sp.	Hda sp.	Hda aru	Grp sp.	Dyt sp.	Cal aud	Aci sp.
	(i.d.)	(<0.0001)	(<0.0001)	(<0.0001)	(<0.0001)	(<0.0001)	(<0.05)	(not sig.)	(not sig.)	(<0.0001)	(not sig.)	(<0.01)	(not sig.)	(<0.0001)	(not sig.)	(<0.001)	(<0.0001)	(not sig.)
Col lon	Single specimen collected in only one pond.																	
Col scu	Single specimen collected in only one pond.																	
Cop lon	Single specimen collected in only one pond.																	
Des con	Single specimen collected in only one pond.																	

TABLE 5. Continued.

Lost Taxa									Potential Replacement Taxa									
Dyt dau	Rha sut (<0.01)	Rha fro (<0.01)	Rha bin (<0.0001)	Lac mac (<0.0001)	Hda aru (<0.0001)	Grp lib (<0.01)	Cal aud (<0.0001)	Aci sem (<0.0001)										
Dyt sp.	Rha sp. (i.d.)	Not und (not sig.)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lio aff (<0.0001)	Lac sp. (<0.05)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hyg say (<0.0001)	Hdp sp1 (not sig.)	Hdp sp. (<0.05)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Cal aud (not sig.)	Aga sp. (<0.001)	Aci sp. (not sig.)
Grp lib	Rha sut (not sig.)	Rha fro (not sig.)	Rha bin (<0.01)	Lac mac (<0.001)	Hda aru (<0.05)	Dyt dau (<0.01)	Cal aud (<0.01)	Aci sem (<0.01)										
Gra per	Single specimen collected in only one pond.																	
Grp sp.	Rha sp. (i.d.)	Not und (<0.01)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lio aff (<0.0001)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hyg say (<0.01)	Hdp sp1 (not sig.)	Hdp sp. (not sig.)	Hda sp. (not sig.)	Hda aru (<0.01)	Dyt sp. (not sig.)	Cal aud (not sig.)	Aga sp. (not sig.)	Aci sp. (not sig.)
Hda aru	Not und (<0.0001)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lac mac (<0.0001)	Grp sp. (<0.01)	Grp lib (<0.05)	Dyt sp. (not sig.)	Dyt dau (not sig.)	Cal aud (<0.0001)	Aga sp. (<0.0001)	Aci sp. (<0.001)	Aci sem (<0.01)					
Hda sp.	Rha sp. (i.d.)	Not und (<0.001)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lio aff (<0.001)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hyg say (<0.05)	Hdp sp1 (not sig.)	Hdp sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (not sig.)	Aga sp. (not sig.)	Aci sp. (not sig.)	
Hdp pau	Single specimen collected in only one pond.																	
Hdp rub	Single specimen collected in only one pond.																	
Hdp ruf	Single specimen collected in only one pond.																	
Hdp sp.	Rha sp. (i.d.)	Not und (<0.0001)	Not kir (<0.01)	Not irr (<0.01)	Not bor (<0.0001)	Lio aff (not sig.)	Lac sp. (<0.05)	Lac mac (<0.0001)	Hyg sp2 (<0.01)	Hyg say (<0.0001)	Hdp sp1 (<0.05)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (<0.05)	Cal aud (<0.0001)	Aga sp. (<0.01)	Aci sp. (<0.001)	
Hdp sp1	Rha sp. (i.d.)	Not und (<0.001)	Not kir (not sig.)	Not irr (not sig.)	Not bor (<0.05)	Lio aff (<0.0001)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hyg say (<0.01)	Hdp sp. (<0.05)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.01)	Aga sp. (not sig.)	Aci sp. (not sig.)	
Hyg put	Single specimen collected in only one pond.																	
Hyg sal	Single specimen collected in only one pond.																	
Hyg say	Rha sp. (i.d.)	Not und (<0.0001)	Not kir (<0.0001)	Not irr (<0.0001)	Not bor (<0.0001)	Lio aff (<0.0001)	Lac sp. (not sig.)	Lac mac (<0.0001)	Hyg sp2 (<0.01)	Hdp sp1 (<0.01)	Hdp sp. (<0.0001)	Hda sp. (<0.05)	Grp sp. (<0.01)	Dyt sp. (<0.0001)	Cal aud (<0.0001)	Aga sp. (<0.0001)	Aci sp. (<0.0001)	
Hyg sp1	Single specimen collected in only one pond.																	
Hyg sp2	Rha sp. (i.d.)	Not und (<0.0001)	Not kir (<0.05)	Not irr (<0.05)	Not bor (<0.001)	Lio aff (<0.0001)	Lac sp. (not sig.)	Lac mac (<0.01)	Hyg say (<0.01)	Hdp sp1 (not sig.)	Hdp sp. (<0.01)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.001)	Aga sp. (not sig.)	Aci sp. (<0.01)	

TABLE 5. Continued.

Lost Taxa		Potential Replacement Taxa																
Lac big	Single specimen collected in only one pond.																	
Lac mac	Not und (<0.01)	Not kir (<0.05)	Not irr (<0.05)	Not bor (<0.001)	Hyg sp2 (<0.01)	Hyg say (<0.0001)	Hdp sp1 (not sig.)	Hdp sp. (<0.0001)	Hda sp. (not sig.)	Hda acu (<0.0001)	Grp sp. (not sig.)	Grp lib (<0.001)	Dyt sp. (not sig.)	Dyt dau (<0.0001)	Cal aud (<0.01)	Aga sp. (not sig.)	Aci sp. (not sig.)	Aci sem (<0.0001)
Lac sp.	Rha sp. (i.d.)	Not und (<0.0001)	Not kir (<0.001)	Not irr (<0.001)	Not bor (<0.0001)	Lio aff (<0.0001)	Hyg sp2 (not sig.)	Hyg say (not sig.)	Hdp sp1 (not sig.)	Hdp sp. (<0.05)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (<0.05)	Cal aud (<0.0001)	Aga sp. (<0.05)	Aci sp. (<0.01)		
Lio aff	Rha sp. (i.d.)	Not und (<0.0001)	Not kir (<0.0001)	Not irr (<0.0001)	Not bor (<0.0001)	Lac sp. (<0.0001)	Hyg sp2 (<0.0001)	Hyg say (<0.0001)	Hdp sp1 (<0.0001)	Hdp sp. (not sig.)	Hda sp. (<0.001)	Grp sp. (<0.0001)	Dyt sp. (<0.0001)	Cal aud (<0.0001)	Aga sp. (<0.0001)	Aci sp. (<0.0001)		
Rha bin	Rha sut (not sig.)	Rha fro (not sig.)	Grp lib (<0.01)	Dyt dau (<0.0001)	Cal aud (<0.001)	Aci sem (<0.0001)												
Rha fro	Rha sut (not sig.)	Rha bin (not sig.)	Grp lib (not sig.)	Dyt dau (<0.01)	Cal aud (not sig.)	Aci sem (<0.0001)												
Rha sp.	Not und (i.d.)	Not kir (i.d.)	Not irr (i.d.)	Not bor (i.d.)	Lio aff (i.d.)	Lac sp. (i.d.)	Hyg sp2 (i.d.)	Hyg say (i.d.)	Hdp sp1 (i.d.)	Hdp sp. (i.d.)	Hda sp. (i.d.)	Grp sp. (i.d.)	Dyt sp. (i.d.)	Cal aud (i.d.)	Aga sp. (i.d.)	Aci sp. (i.d.)		
Rha sut	Rha fro (not sig.)	Rha bin (not sig.)	Grp lib (not sig.)	Dyt dau (<0.01)	Cal aud (<0.05)	Aci sem (<0.0001)												
Ane lim	No functionally similar taxon available.																	
Ber stri	Single specimen collected in only one pond.																	
Cym min	Single specimen collected in only one pond; Insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.																	
Cym vin	No functionally similar taxon available.																	
Eno ham	Single specimen collected in only one pond.																	
Eno och	Single specimen collected in only one pond.																	
Hel ang	Single specimen collected in only one pond.																	
Hel lac	Single specimen collected in only one pond.																	
Hdb fus	Single specimen collected in only one pond; Insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.																	

TABLE 5. Continued.

Lost Taxa		Potential Replacement Taxa					
Hdc obt	Tro lat (not sig.)						
Hdu pse	No functionally similar taxon available.						
Tro lat	Sig gro (<0.001)	Sig alt (<0.0001)	Hes val (<0.001)	Hes min (<0.05)	Hes ato (<0.01)	Hdc obt (not sig.)	
Tro sp.	No functionally similar taxon available.						
Tro sp.	Single specimen collected in only one pond.						
Hdr ang	No functionally similar taxon available.						
Cyp sp.	Single specimen collected in only one pond; insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.						
^a insufficient data to compute significance of mean difference.							

TABLE 6. Functionally similar taxa showing probability of mean head capsule width difference between hypothetically lost taxa (first column) and potential replacement taxa (subsequent columns) following partitioning of data by sampling interval (species with significant head capsule width differences, as demonstrated by Student's *t* mean difference test, have been excluded).

Lost Taxa		Potential Replacement Taxa			
Hya azi	No functionally similar taxon available.				
Sip alti	No functionally similar taxon available.				
Cal sp.	No functionally similar taxon available.				
Cae dim	Cae you (not sig.)				
Cae you	Cae dim (not sig.)				
Aes can	Anx jun (not sig.)	Aes int (<0.05)			
Aes int	Anx jun (not sig.)	Aes can (<0.05)			
Anx jun	Aes int (not sig.)	Aes can (not sig.)			
Cor shu	Sym obt (<0.05)	Sym dan (not sig.)			
Som wil	Sym obt (not sig.)	Sym dan (not sig.)	Lib qua (<0.05)		
Leu fri	Single specimen collected in only one pond.				
Leu hud	Sym dan (<0.001)	Leu pro (not sig.)	Leu int (not sig.)	Ban cro (not sig.)	

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa								
Leu int	Sym dan (not sig.)	Leu pro (not sig.)	Leu hud (not sig.)	Les ung (not sig.)	Les dry (not sig.)	Les dis (not sig.)				
Leu pro	Sym obt (<0.05)	Sym dan (not sig.)	Pti sp. (not sig.)	Leu int (not sig.)	Leu hud (not sig.)	Les ung (not sig.)	Les dry (not sig.)	Les dis (not sig.)	Les con (not sig.)	Ban cro (not sig.)
Lib qua	Som wil (not sig.)									
Sym dan	Sym obt (not sig.)	Som wil (not sig.)	Leu pro (not sig.)	Leu int (not sig.)	Leu hud (<0.001)	Cor shu (not sig.)				
Sym obt	Sym dan (<0.05)	Som wil (not sig.)	Leu pro (<0.05)	Cor shu (<0.05)						
Les con	Leu pro (not sig.)	Les dry (not sig.)	Les dis (not sig.)							
Les dis	Leu pro (not sig.)	Leu int (not sig.)	Les ung (not sig.)	Les dry (not sig.)	Les con (not sig.)					
Les dry	Leu pro (not sig.)	Leu int (not sig.)	Les ung (not sig.)	Les dis (not sig.)	Les con (not sig.)					
Les ung	Leu pro (not sig.)	Leu int (not sig.)	Les dry (not sig.)	Les dis (not sig.)						
Coe ang	Pti sp. (not sig.)	Ena cya (not sig.)	Ban cro (not sig.)							
Coe res	Pti sp. (not sig.)	Ban cro (not sig.)								
Ena cya	Pti sp. (not sig.)	Coe ang (not sig.)	Ban cro (not sig.)							
Mic pul	All potential replacement taxa excluded because of significant size differences.									

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa					
Ger hue	All potential replacement taxa excluded because of significant size differences.						
Ger dis	All potential replacement taxa excluded because of significant size differences.						
Let ame	Single specimen collected in only one pond.						
Ran fus	Single specimen collected in only one pond.						
Cal aud	Rha sp. (i.d.) ^a	Rha fro (not sig.)	Hda sp. (<0.05)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aci sp. (not sig.)	
Hes ato	All potential replacement taxa excluded because of significant size differences.						
Hes min	All potential replacement taxa excluded because of significant size differences.						
Hes vul	All potential replacement taxa excluded because of significant size differences.						
Sig alt	All potential replacement taxa excluded because of significant size differences.						
Sig con	Single specimen collected in only one pond.						
Sig dec	Single specimen collected in only one pond.						
Sig gro	All potential replacement taxa excluded because of significant size differences.						
Not bor	Rha sp. (i.d.)	Not kir (<0.01)	Not irr (not sig.)	Hda sp. (<0.05)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa								
Not irr	Rha sp. (i.d.)	Not und (not sig.)	Not kir (not sig.)	Not bor (not sig.)	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aci sp. (not sig.)
Not kir	Rha sp. (i.d.)	Not und (not sig.)	Not irr (not sig.)	Not bor (<0.01)	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aci sp. (<0.0001)
Not und	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Dyt sp. (not sig.)						
Ban cro	Pti sp. (not sig.)	Leu pro (not sig.)	Leu hud (not sig.)	Ena cya (not sig.)	Coe res (not sig.)	Coe ang (not sig.)				
Pti sp.	Leu pro (not sig.)	Ena cya (not sig.)	Coe res (not sig.)	Coe ang (not sig.)	Ban cro (not sig.)					
Ana sp.	Single specimen collected in only one pond.									
Lim sp1	No functionally similar taxon available.									
Lim sp2	Single specimen collected in only one pond.									
Nem hos	Single specimen collected in only one pond.									
Oec inc	All potential replacement taxa excluded because of significant size differences.									
Gyr aqu	Single specimen collected in only one pond.									
Hal can	All potential replacement taxa excluded because of significant size differences.									
Hal con	Single specimen collected in only one pond.									

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa									
Hal imm	All potential replacement taxa excluded because of significant size differences.										
Hal lon	Single specimen collected in only one pond.										
Hal sal	Single specimen collected in only one pond.										
Hal sp.	Pel sp. (not sig.)										
Hal stri	Single specimen collected in only one pond.										
Hal sub	Pel tor (not sig.)										
Pel ede	Single specimen collected in only one pond.										
Pel sp.	Hal sp. (not sig.)										
Pel tor	Hal sub (not sig.)										
Aci sem	All potential replacement taxa excluded because of significant size differences.										
Aci sp.	Cal aud (not sig.)	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Lac mac (not sig.)	Hdp spl (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aga sp. (not sig.)	
Aga ant	Single specimen collected in only one pond.										
Aga sp.	Rha sp. (i.d.)	Lac mac (not sig.)	Hyg sp2 (<0.01)	Hdp spl (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)	Aci sp. (not sig.)				

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa												
Col lon	Single specimen collected in only one pond.													
Col scu	Single specimen collected in only one pond.													
Cop lon	Single specimen collected in only one pond.													
Des con	Single specimen collected in only one pond.													
Dyt dau	All potential replacement taxa excluded because of significant size differences.													
Dyt sp.	Rha sp. (i.d.)	Not und (not sig.)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Hda aru (not sig.)	Grp sp. (not sig.)	Cal aud (not sig.)	Aci sp. (not sig.)	
Grp lib	Rha sut (not sig.)	Rha fro (not sig.)												
Gra per	Single specimen collected in only one pond.													
Grp sp.	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hdp sp1 (not sig.)	Hdp sp. (not sig.)	Hda sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (not sig.)	Aga sp. (not sig.)	Aci sp. (not sig.)
Hda aru	Not kir (not sig.)	Not irr (not sig.)	Not bor (not sig.)	Dyt sp. (not sig.)										
Hda sp.	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Not bor (<0.05)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hdp sp1 (not sig.)	Hdp sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Cal aud (<0.05)	Aga sp. (not sig.)	Aci sp. (not sig.)
Hdp pau	Single specimen collected in only one pond.													
Hdp rub	Single specimen collected in only one pond.													

TABLE 6. Continued.

Lost Taxa		Potential Replacement Taxa									
Hdp ruf	Single specimen collected in only one pond.										
Hdp sp.	Rha sp. (i.d.)	Lio aff (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)							
Hdp sp1	Rha sp. (i.d.)	Not kir (not sig.)	Not irr (not sig.)	Lac sp. (not sig.)	Lac mac (not sig.)	Hyg sp2 (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aga sp. (not sig.)	Aci sp. (not sig.)
Hyg pat	Single specimen collected in only one pond.										
Hyg sal	Single specimen collected in only one pond.										
Hyg say	Rha sp. (i.d.)	Lac sp. (not sig.)									
Hyg sp1	Single specimen collected in only one pond.										
Hyg sp2	Rha sp. (i.d.)	Lac sp. (not sig.)	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aga sp. (not sig.)				
Lac big	Single specimen collected in only one pond.										
Lac mac	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)	Dyt sp. (not sig.)	Aga sp. (not sig.)	Aci sp. (not sig.)					
Lac sp.	Rha sp. (i.d.)	Hyg sp2 (not sig.)	Hyg say (not sig.)	Hdp sp1 (not sig.)	Hda sp. (not sig.)	Grp sp. (not sig.)					
Lio aff	Rha sp. (i.d.)	Hdp sp. (not sig.)									
Rha bin	Rha sut (not sig.)	Rha fro (not sig.)									

TABLE 6. Continued.

Lost Taxa					Potential Replacement Taxa											
Rha fro	Rha sut (not sig.)	Rha bin (not sig.)	Grp lib (not sig.)	Cal aud (not sig.)												
Rha sp.	Not und (i.d.)	Not kir (i.d.)	Not irr (i.d.)	Not bor (i.d.)	Lio aff (i.d.)	Lac sp. (i.d.)	Hyg sp2 (i.d.)	Hyg say (i.d.)	Hdp spl (i.d.)	Hdp sp. (i.d.)	Hda sp. (i.d.)	Grp sp. (i.d.)	Dyt sp. (i.d.)	Cal aud (i.d.)	Aga sp. (i.d.)	Aci sp. (i.d.)
Rha sut	Rha fro (not sig.)	Rha bin (not sig.)	Grp lib (not sig.)													
Anc lim	No functionally similar taxon available.															
Ber stri	Single specimen collected in only one pond.															
Cym min	Single specimen collected in only one pond; Insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.															
Cym vin	No functionally similar taxon available.															
Eno ham	Single specimen collected in only one pond.															
Eno och	Single specimen collected in only one pond.															
Hel ang	Single specimen collected in only one pond.															
Hel lac	Single specimen collected in only one pond.															
Hdb fus	Single specimen collected in only one pond; Insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.															
Hdc obt	Tro lat (not sig.)															

TABLE 6. Continued.

Lost Taxa	Potential Replacement Taxa
Hdu pse	No functionally similar taxon available.
Tro lat	Hdc obt (not sig.)
Tro sp.	No functionally similar taxon available.
Tro sp.	Single specimen collected in only one pond.
Hdr ang	No functionally similar taxon available.
Cyp sp.	Single specimen collected in only one pond; Insufficient information concerning functional feeding group, habit, dominant food, or feeding mechanism.

^a insufficient data to compute significance of mean difference.

replace the ecological function of each other. *Callibaetis* sp. and *Siphonurus alternata* (Say) were without potential replacements.

Nineteen Odonata were identified, including 12 anisopterans and seven zygopterans. All 19 species shared many ecological functions; separation was not distinct between the two sub-orders. All are predators, although only *Aeshna canadensis* Walker, *Aeshna interrupta* Walker, and *Anax junius* Drury capture prey by active stalking. Most odonate species are climbers with the exception of the sprawlers *Cordulia shurtleffi* Scudder, *Somatochlora williamsoni* Walker, and *Libellula quadrimaculata* L.. *Sympetrum* spp. are both climbers and sprawlers (Merritt and Cummins 1984), thus may have a wider niche breadth in this regard than other odonates. *Lestes* spp. may be both climbers and swimmers, thus may also have a wider niche breadth than odonates restricted to climbing or swimming.

All odonates had at least one potential replacement species; nine potential replacements were identified for the libellulid, *Leucorrhinia proxima* Calvert. All potential replacement species were odonates, except for *Banksiola crotchii* Banks and *Ptilostomis* sp.. *Banksiola crotchii* and *Ptilostomis* sp. were identified as potential replacements for five odonates since they shared ecological function and had similar head capsule widths.

Aeshna canadensis and *A. interrupta* did not differ significantly in head capsule width when all individuals were pooled. However, when individuals were partitioned by time, *A. canadensis* was significantly larger than *A. interrupta* (cf. TABLE 5 and TABLE 6; cf. Figure 2 and Figure 3). Walker (1958) observed elsewhere that *A. canadensis* emerged earlier than *A. interrupta*. These two aeshnid species developed at different

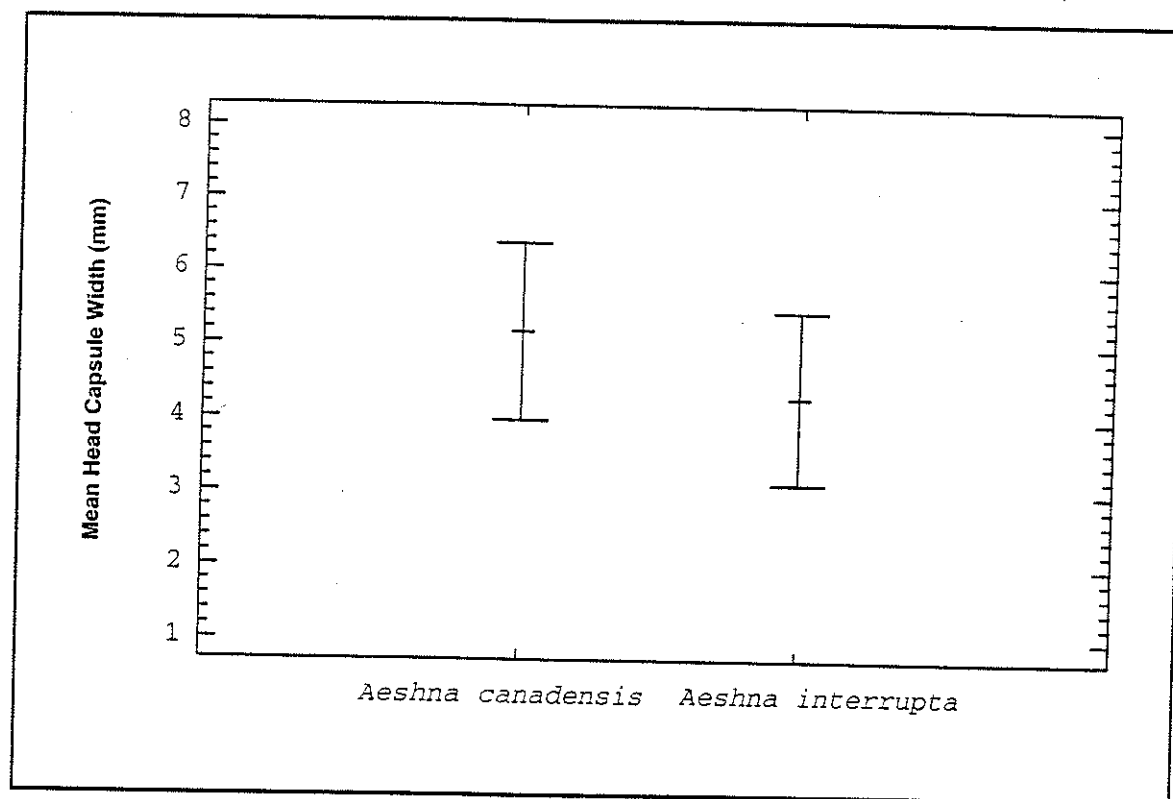


Figure 2. 95% confidence intervals for mean head capsule widths of *Aeshna canadensis* and *A. interrupta*.

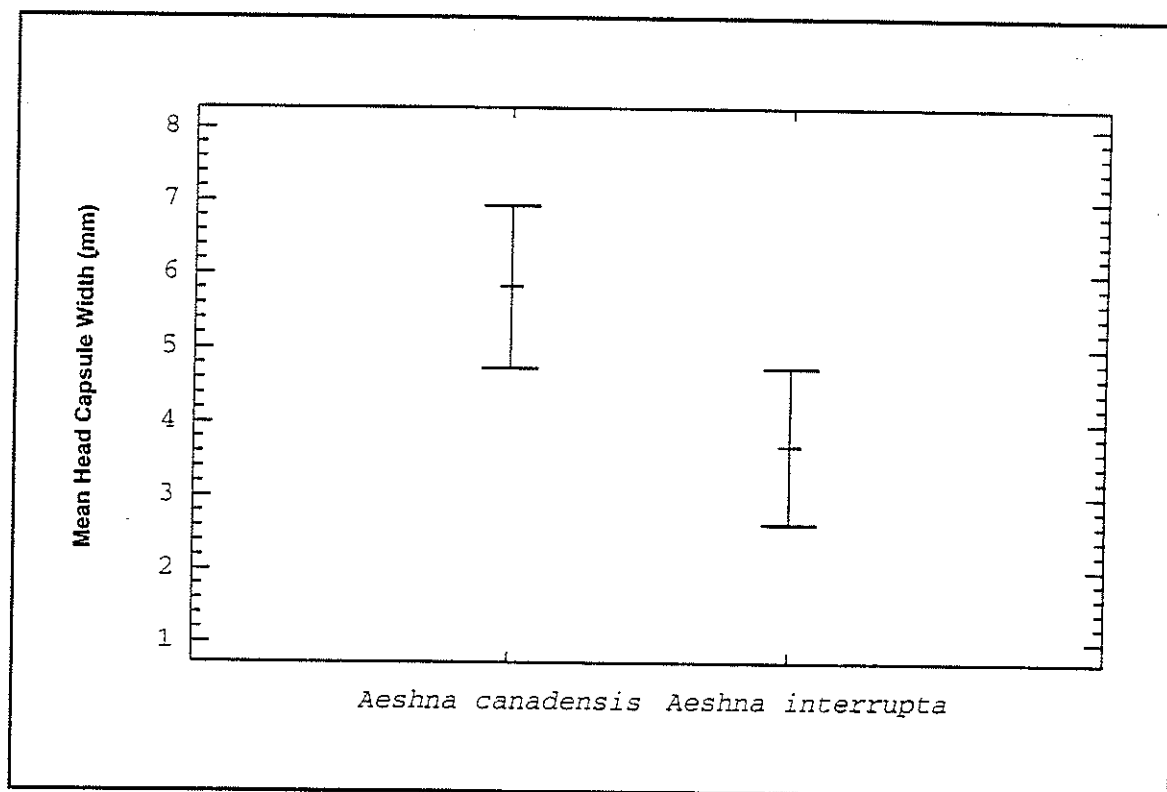


Figure 3. 95% confidence intervals for mean head capsule widths of *Aeshna canadensis* and *A. interrupta*, following partitioning by time.

rates, suggesting that resources may be partitioned by time. Several other similar-sized odonates may also partition time in order to co-exist.

Seventeen aquatic or semi-aquatic hemipterans were found in the ponds. These 17 were composed of one veliid, belostomatid, and nepid species, two gerrid species, eight corixid species and four notonectid species. Only *Sigara (Vermicorixa) alternata* Say was common to all six ponds. Potential replacement species were identified only for the four notonectids. Based upon generalized ecological function, all notonectid species would be able to replace each other's function except for those species that differed significantly in size. Two species of Coleoptera, *Hydroporus* sp. 1 and *Hydaticus aruspex* Clark, were identified as potential replacements for *Notonecta irrorata* Uhler and *N. kirbyi* Hungerford. *Notonecta*, *Hydroporus*, and *Hydaticus* are all piercing predators that capture prey by swimming and climbing in microhabitat dominated by macrophytes. These genera do not differ significantly in size in the pond habitat.

Notonecta kirbyi and *N. borealis* were not significantly different in size when all individuals were pooled, but did differ when partitioned by sampling interval (cf. TABLE 5 and TABLE 6). These two notonectids may partition time in order to co-exist.

Seven species of Trichoptera were present in the ponds; three species were transient, and potential replacements were present for two of the remaining four species. *Banksiola crotchii* Banks and *Ptilostomis* sp. shared ecological function with each other as well as with a number of odonates. *Banksiola* and *Ptilostomis* have wide niche breadths along several resource axes. Both genera are predominantly shredders, eating living and decomposing vascular tissue by chewing and mining. However, both genera are opportunistic and may become predatory engulfers, thus overlapping with many odonates.

Of the taxa identified, Coleoptera were the most diverse group inhabiting the ponds; there were 28 genera and at least 49 species. Twenty-six species were transient. Larvae were identified for 11 of the 28 genera. Two haliplids, *Haliplus subguttatus* Crotch and *Peltodytes tortulosus* Roberts, could potentially replace each other's ecological function, should either be lost from the habitat. A large number of dytiscids occurred in the pond habitat although only a few had potential replacements. Many dytiscids shared ecological function but often differed significantly in size. *Graphoderus liberus* (Say) could be potentially replaced by either *Rhantus suturellus* (Harris) or *R. frontalis* (Marsham). A third species, *R. binotatus* (Harris), although similar in functional attributes, differed significantly in size from *G. liberus*. Like other dytiscids, *Graphoderus* and *Rhantus* feed by attacking prey, piercing tissues, and removing fluids. *Hydaticus aruspex* Clark could potentially be replaced by three species of *Notonecta*: *N. kirbyi*, *N. irrorata*, and *N. borealis*. All have similar ecological function and are similar in size. An unknown species of *Hydroporus* had four potential replacements. Two of the potential replacements were other dytiscids (*Laccophilus maculosus* Say and *Hygrotus* sp. 2), while the remaining two were the notonectids *N. irrorata* and *N. kirbyi*. Mean head capsule width of the two notonectids was substantially larger than that of *Hygrotus*, but because of the small sample size, could not be statistically rejected. Like dytiscids, the notonectids are piercing predators. Most dytiscids prefer microhabitat with large numbers of macrophytes. The notonectids do well in both open water and in microhabitat containing macrophytes, so they may have an overall larger niche width in this regard. *Hydroporus* sp. 1 could potentially replace the general ecological function of both *Hygrotus* sp. 2 and *L. maculosus*.

Twelve species of Hydrophilidae occurred in the pond habitat but most were transient species. Only *Anacaena limbata* (Fabricius) and *Hydrochara obtusata* (Say) were collected in large numbers, but insufficient information on ecological function precluded further analysis.

One species of hydraenid and one species of scirtid were found in the ponds. The hydraenid, *Hydraena angulicollis* Notman, was relatively abundant. There were no species present that shared ecological function with *H. angulicollis*. Only a single specimen of the scirtid *Cyphon* sp. was collected, thus it was considered transient.

Of the original 108 taxa, 50 species were rejected from further consideration: 36 species were transient, insufficient ecological information was available for four species, and 10 species were unknown Coleoptera larvae with adults of the same genus present. Potential replacement species were not present for 22 taxa, because of either an absence of species with shared ecological function or a significant difference in size spectra. The 22 taxa without potential replacements included a single amphipod species, two species of Ephemeroptera and Trichoptera, eight species of Hemiptera, and nine species of Coleoptera. Thus, 36 of the original 108 taxa (33.3%) had potential replacements in the pond habitat based upon major ecological function and size. TABLE 7 contains a summary list of all potential replacement taxa.

TABLE 7. List of hypothetically lost taxa (first column) and potential replacement taxa (subsequent columns) collected from the six Sandilands Provincial Forest study ponds remaining after similarity analysis and size spectrum comparison.

Lost Species		Potential Replacement Species							
<i>Caenis diminuta</i>	<i>Caenis youngi</i>								
<i>Caenis youngi</i>	<i>Caenis diminuta</i>								
<i>Aeshna canadensis</i>	<i>Anax junius</i>								
<i>Aeshna interrupta</i>	<i>Anax junius</i>								
<i>Anax junius</i>	<i>Aeshna interrupta</i>	<i>Aeshna canadensis</i>							
<i>Cordulia shurtleffi</i>	<i>Sympetrum danae</i>								
<i>Somatochlora williamsoni</i>	<i>Sympetrum obtrusum</i>	<i>Sympetrum danae</i>							
<i>Leucorrhinia hudsonica</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Banksiola crotchii</i>						
<i>Leucorrhinia intacta</i>	<i>Sympetrum danae</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia hudsonica</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>			
<i>Leucorrhinia proxima</i>	<i>Sympetrum danae</i>	<i>Ptilostomis</i> sp.	<i>Leucorrhinia intacta</i>	<i>Leucorrhinia hudsonica</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>	<i>Lestes congener</i>	<i>Banksiola crotchii</i>
<i>Libellula quadrimaculata</i>	<i>Somatochlora williamsoni</i>								
<i>Sympetrum danae</i>	<i>Somatochlora williamsoni</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Cordulia shurtleffi</i>					
<i>Sympetrum obtrusum</i>	<i>Somatochlora williamsoni</i>								
<i>Lestes congener</i>	<i>Leucorrhinia proxima</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>						

TABLE 7. Continued.

Lost Species	Potential Replacement Species					
<i>Lestes disjunctus disjunctus</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes congener</i>	
<i>Lestes dryas</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes disjunctus disjunctus</i>	<i>Lestes congener</i>	
<i>Lestes unguiculatus</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>		
<i>Coenagrion angulatum</i>	<i>Ptilostomis</i> sp.	<i>Enallagma cyathigerum</i>	<i>Banksiola crotchii</i>			
<i>Coenagrion resolutum</i>	<i>Ptilostomis</i> sp.	<i>Banksiola crotchii</i>				
<i>Enallagma cyathigerum</i>	<i>Ptilostomis</i> sp.	<i>Coenagrion angulatum</i>	<i>Banksiola crotchii</i>			
<i>Notonecta borealis</i>	<i>Notonecta irrorata</i>	<i>Hydaticus aruspex</i>				
<i>Notonecta irrorata</i>	<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta borealis</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>	
<i>Notonecta kirbyi</i>	<i>Notonecta undulata</i>	<i>Notonecta irrorata</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>		
<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>				
<i>Banksiola crotchii</i>	<i>Ptilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia hudsonica</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>
<i>Ptilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>	<i>Banksiola crotchii</i>	
<i>Haliplus subguttatus</i>	<i>Peltodytes tortulosus</i>					

TABLE 7. Continued.

Lost Species		Potential Replacement Species			
<i>Peltodytes tortulosus</i>	<i>Halipplus subguttatus</i>				
<i>Graphoderus liberus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>			
<i>Hydaticus aruspex</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Notonecta borealis</i>		
<i>Hydroporus</i> sp. 1	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Laccophilus maculosus</i>	<i>Hygrotus</i> sp. 2	
<i>Hygrotus</i> sp. 2	<i>Hydroporus</i> sp. 1				
<i>Laccophilus maculosus</i>	<i>Hydroporus</i> sp. 1				
<i>Rhantus binotatus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>			
<i>Rhantus frontalis</i>	<i>Rhantus suturellus</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>		
<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>		

CHAPTER V

NICHE OVERLAP IN CANONICAL SPACE AMONG ARTHROPODS ALONG AN ENVIRONMENTAL GRADIENT IN SIX BOREAL FOREST STUDY PONDS

ABSTRACT

The aquatic arthropod community in six permanent, man-made ponds was studied during a two-year period from 1988 through 1990. Pond maximum depths were from 0.95 to 1.70 m, pond volumes were ~ 19 to 68 m³, and surface areas ranged from ~ 40 to 80 m². Well developed but variable macrophyte communities were present in all ponds.

A total of 108 arthropod taxa were identified; each pond contained a unique assemblage, with only seven species being common to all six ponds. *Leucorrhinia intacta* Hagen and *Enallagma cyathigerum* (Charpentier) were abundant in four of the six study ponds. *Hyaletta azteca* (Saussure) was present in all ponds but was abundant in only three. Shannon-Wiener diversity ranged from 1.022 to 4.690. Variation in observed distribution and abundance of taxa was related to measured or derived environmental factors with the use of Canonical Correspondence Analysis (CCA).

Variation in species distribution and abundance was related to pH, area of pond covered with macrophyte beds, and percent silt in bottom substrate. *Hyaletta azteca* was limited by the area of macrophyte species in association with *Sphagnum* sp.. Dominant odonates were more abundant in ponds with less coloured, mineralized water relative to ponds with highly coloured, acidic water from adjacent bog areas.

Inter-species and species-environment niche overlap were calculated in canonical space. Replacement by Model I (re-colonization) was predicted to be limited to ~ 10% of the total available cases. Replacement by Model II (niche width expansion) or Model III (redundant species), could not be ruled out in any of the available cases, but was estimated to be probable ~ 25% of the time. There was reasonable agreement between these results and the probability of functional replacement estimated from studies reported in the literature on niche overlap. Replacement by either Model I or Models II and III was more likely for species located in ponds of average environmental conditions relative to ponds located at the distal ends of an environmental gradient.

INTRODUCTION

Three models were developed (Chapter II) to describe the potential mechanisms by which the ecological function of one species could be replaced by another. The replacement species should process material and transfer energy in a similar manner as the lost species, but the models differ in how the lost and replacement species relate to their environment. For Model I (re-colonization), the lost species and their replacements do not co-exist. Replacement species must first, be able to colonize the habitat vacated by the lost species and second, be able to reach similar abundance as the lost species. For Model II (niche width expansion) and Model III (redundant species) the lost species and their replacements co-exist. Among other things, it is necessary that the replacement species be able to increase in abundance to compensate for the loss of material processing and energy flow caused by the removal of the original species (*i.e.*, to satisfy the constraint imposed by Eq. 8, Chapter II).

For each hypothetically lost taxon within a region, there may be a relatively large pool of potentially available replacement species, based upon generalized ecological function and size spectrum analysis (see Chapter IV). However, not all potentially available replacement species can colonize specific habitats or reach similar or greater abundance as the hypothetically lost taxa. Assessment of community structure in relation to environmental factors can yield information on the tolerance of individual species along the major environmental gradients affecting distribution and abundance.

Canonical Correspondence Analysis (CCA) is a non-linear, eigenvector ordination method recently developed for detecting relationships between environmental gradients and species distribution and abundance. It has been used in the following ways: (1) to

demonstrate the relationship between the distribution of hunting spiders and environmental data; (2) to link the occurrence of a number of species of macrophytes with water chemistry and soil types; (3) to show the change in algae community structure along a pollution gradient (ter Braak 1986); (4) to demonstrate the link between diatoms and water chemistry in acidified lakes (Dixit *et al.* 1989); (5) to reconstruct lake pH based upon diatoms in sediment cores (Stevenson *et al.* 1989); and (6) to yield insights into the relationship between a lacustrine macrobenthos community and its environment (Rodríguez and Magnan 1993). Canonical Correspondence Analysis has proven more effective for certain applications than methods such as canonical correlation or principal components analysis (ter Braak 1986) because CCA can detect uni-modal relationships rather than linear relationships. Most relationships between species composition and environmental gradients are uni-modal rather than linear (ter Braak 1986, 1989).

Canonical Correspondence Analysis can also relate species composition directly to measured environmental variables. The dominant gradients are extracted, given the constraint that they must be orthogonal linear combinations of the environmental variables (ter Braak 1986). Conventional methods (*e.g.*, principal components) extract linear relationships from the species data, which then must be indirectly related to environmental data. The theoretical basis for CCA is described by ter Braak (1985, 1986). A species response along an environmental gradient follows a Gaussian bell-shaped curve (Figure 1). This response can be related to environmental factors by correlation analysis. Canonical Correspondence Analysis solves a Gaussian response equation to fit species abundance and distribution to an environmental axis by ordination, while simultaneously solving an equation to fit the site or sample scores to the same environmental axis. The Gaussian response model for species is shown in Eq. 1.

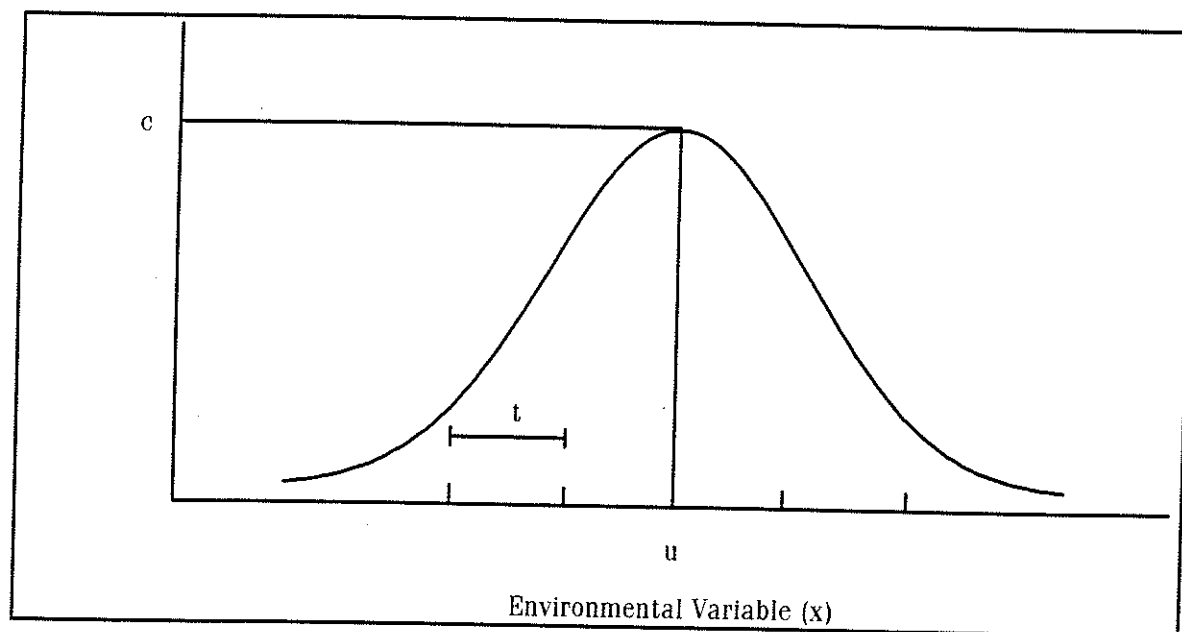


Figure 1. Description of the unimodal response of a species to its environment (from ter Braak 1987a). "c" is the maximum of the response curve, "u" is the mode or optimum, and "t" is the species tolerance, as estimated by the standard deviation, along an environmental gradient represented by some variable "x".

$$E(y_{ik}) = C_k \left[\frac{(x_i - u_k)^2}{t_k^2} \right], \text{ where} \quad (\text{Eq. 1})$$

$E(y_{ik})$ = expected (average) value of y_{ik} at site i that has score x_i

on the ordination axis;

C_k = the maximum of the response curve for species k ;

u_k = the mode or optimum for species k (the value of x for which the maximum C_k is obtained);

t_k = the tolerance of species k (an estimation of ecological amplitude of species k as represented by its standard deviation).

Canonical Correspondence Analysis correlates site scores with environmental data by solving the following equation:

$$x_i = b_o + \sum_{j=1}^q b_j z_{ij}, \text{ where} \quad (\text{Eq. 2})$$

x_i = score x at site i on the ordination axis;

b_o = intercept;

b_j = regression coefficient for environmental variable j ;

z_{ij} = $n \times (q+1)$ matrix containing environmental data.

Transition formulae enable Eq. 1 and Eq. 2 to be solved simultaneously.

The objectives of this chapter are as follows:

- i) to assess the community structure of six study ponds located in Sandilands Provincial Forest in relation to measured environmental variables;
- ii) to estimate niche widths along canonical axes for hypothetically lost taxa and potential replacement taxa identified in Chapter IV relative to the pond environment;
- iii) to estimate niche overlap in canonical space between hypothetically lost taxa and potential replacement taxa, and to estimate niche overlap in canonical space between potential replacement taxa and specific pond habitats; and
- iv) to refine predictions concerning the potential for replacement among aquatic insects in the six study ponds by using information generated from niche overlap in canonical space. Niche overlap in canonical space can assist to predict those species able to successfully colonize new pond habitat according to Model I, and to predict which co-existing species may successfully reach similar or greater replacement abundance according to Model II or Model III hypotheses.

MATERIALS AND METHODS

Study Area

A description of the study area is given in Chapter IV.

Arthropod Community

The methods used to sample the arthropod community are provided in Chapter IV.

Arthropod Community Structure

Species counts were converted to mean densities (organisms m^{-2}) for each pond for the entire study period. Geometric means were calculated from individual counts since the data were approximately log-normally distributed. Even with this transformation, some skewness remained because of the large number of zero counts. Because a number of rare species were collected in the sweep net samples but not in the Ekman dredge samples, it was thought important to convert this qualitative information into approximate densities. Conversions were made by multiplying insect abundances in the sweep net samples by a factor unique to each pond. The conversion factor was an average ratio of the approximate volume sampled by the sweep net divided by the approximate volume sampled by the Ekman dredge. On average, sweep net samples consisted of ~ 2.5 times more volume relative to the Ekman samples. Thus, the average abundance of each species in each pond consisted of the geometric mean of 27 individual Ekman samples plus nine sweep net samples. Combined pond area sampled during the study was $\sim 2.5 m^2$ or between 3% and 6% of the total pond areas.

Community structure was summarized by calculating total and proportional abundance for each order, richness (number of species) and Shannon-Wiener diversity and equitability indices. Shannon-Wiener diversity H was calculated as follows (Krebs 1985):

$$H = \sum_{i=1}^S (p_i)(\log_2 p_i) \quad (\text{Eq. 3})$$

and equitability E was calculated as follows:

$$E = \frac{H}{\log_2(S)}, \text{ where} \quad (\text{Eq. 4})$$

H = information content of sample (bits individual⁻¹) = species diversity;

E = equitability;

S = number of species;

p_i = proportion of total sample belonging to the i th species.

Habitat Structure

Pond morphometry was determined once in August, 1989. A 1 m² grid pattern was superimposed on each pond. Depth measurements were taken at 1 m intervals along each latitudinal transect. Contour maps with 0.25 m isobaths were compiled. Area of the total pond and that enclosed by each isobath was determined using a planimeter. The pond circumference was determined using a plan measure. Pond volume was calculated from the following formula (Wetzel 1983):

$$V = \left(\frac{h}{3}\right) \left[(A_1 + A_2 + \sqrt{(A_1)(A_2)}) \right], \text{ where} \quad (\text{Eq. 5})$$

V = the volume (m^3) of the pond between one depth stratum and the successive one;

h = vertical height between the strata (m);

A_1 and A_2 = the surface area of the respective strata (m^2);

A reference marker was placed in each pond at the start of the study. Water levels were measured to the nearest 0.5 cm at the reference markers during each site visit.

The distribution of aquatic macrophytes was mapped using the line transects that were in place for pond morphology measurements. Specimens were identified to species where possible. Macrophyte beds were plotted and area of each species or species-association was measured.

Five representative bottom sediment samples were collected, aggregated and submitted to the Manitoba Provincial Soil Testing Laboratory (presently Norwest Laboratories Inc., 203 - 545 University Crescent, Winnipeg MB R3T 5S6) for size fraction composition (TABLE 1). Samples were placed in polyethylene bags and stored at 4°C until analyses could be completed.

Water Chemistry

Water samples for chemical analyses were taken coincidentally with site visits for invertebrate sampling. Samples were analyzed at the W.M. Ward Technical Services

TABLE 1. Summary of methods used to analyze bottom sediment collected from the six Sandilands Provincial Forest study ponds.

Variable	Units	Methods
Organic Matter Content	%	dichromate digestion
Texture	-	visual estimation
Sand Content	%	digestion/sedimentation
Silt Content	%	digestion/sedimentation
Clay Particle Content	%	digestion/sedimentation

Laboratory (presently Environmental Sciences Centre, 745 Logan Avenue, Winnipeg MB R3E 1M8). Methods, summarized in TABLE 2, followed Sorba *et al.* (1980) and subsequent revisions, except where stated. Sample containers and caps were rinsed three times with pond water and water was collected from ~ 0.25 m depth. Sample containers were capped under water in order to minimize air space in the container. Samples were immediately placed in coolers with ice. Sample containers destined for metal analyses were first preserved with 5.0 mL of 50 % HNO_3 L^{-1} . Dissolved oxygen samples were preserved with the addition of 2.0 mL manganous sulphate and 2.0 mL alkali-iodide-azide reagent. Pond temperature was measured with an alcohol thermometer to the nearest 0.5°C . General conditions (*e.g.*, time, cloud cover, wind direction, as well as any unusual pond conditions) observed at the time of sample collection were recorded.

Aliquots destined for nutrient analyses (nitrogen, phosphorus, and carbon) were collected in duplicate. One series was submitted for the analyses of total species whereas the other was filtered, and submitted for analyses of dissolved species. Samples were filtered in the field using a Geotech Backflushing Filter apparatus through cellulose acetate filters of $0.45\ \mu\text{m}$ pore size (142 mm diameter). Filtration was preceded by rinsing the filter, apparatus, and all associated tubing with ~ 100 mL deionized water, followed by ~ 200 mL pond water. Sample containers were triple rinsed with filtered pond water.

Statistical Analysis

Canonical Correspondence Analysis was performed using CANOCO version 3.12 (ter Braak 1991). Species data were input as log-transformed densities ($\ln(a y + c)$, where $a = 1.0000$ and $c = 1.0001$). Environmental data were appropriately transformed and normality was tested with χ^2 goodness-of-fit ($\alpha = 0.05$), following distribution-fitting

TABLE 2. Summary of methods used to analyze water chemistry collected from the six Sandilands Provincial Forest study ponds.

Variable	Units	Method
Field Temperature	°C	Field measurement with alcohol thermometer.
Field Laboratory pH	Units	Field measurement with Metrohm Model E 588 meter.
pH	Units	Electrometric.
Field Laboratory Conductivity (25 °C)	$\mu\text{S cm}^{-1}$	Field measurement with YSI Model 33 conductivity meter. Results were standardized to 25 °C with linear conversion function (Greenberg <i>et al.</i> 1992).
Conductivity (25 °C)	$\mu\text{S cm}^{-1}$	Automated--conductivity bridge.
Solids (Total Dissolved)	mg L^{-1}	Gravimetric.
Solids (Total Suspended)	mg L^{-1}	Gravimetric.
Solids (Total)	mg L^{-1}	Calculated: Total dissolved solids plus total suspended solids
Alkalinity (Total)	mg L^{-1}	Potentiometric.
Alkalinity (Bicarbonate)	mg L^{-1}	Calculation.
Alkalinity (Carbonate)	mg L^{-1}	Calculation.
Alkalinity (Hydroxide)	mg L^{-1}	Calculation.
Calcium (Extractable)	mg L^{-1}	ICAP.
Magnesium (Extractable)	mg L^{-1}	ICAP.
Hardness	mg L^{-1}	Calculated from calcium and magnesium. Hardness (mg equivalents of CaCO_3) = $2.497 [\text{Ca, mg L}^{-1}] + 4.118 [\text{Mg, mg L}^{-1}]$ (Greenberg <i>et al.</i> 1992).
Sodium (Extractable)	mg L^{-1}	Inductively Coupled Argon Plasma (ICAP).
Potassium (Extractable)	mg L^{-1}	Automated atomic adsorption.
Iron (Extractable)	mg L^{-1}	ICAP.
Manganese (Extractable)	mg L^{-1}	ICAP.
Dissolved Oxygen	mg L^{-1}	Winkler titration after addition of 2.0 mL of manganous sulphate and 2.0 mL alkali-iodide-azide in the field.
Dissolved Oxygen	% Sat.	Calculated: Equilibrium functions reported by Bowie <i>et al.</i> (1985).
Colour (True)	Units	Colourimetric comparison.
Turbidity	NTU	Field measurement, H.F. Instruments Model DRT 15 B meter.
Nitrogen (Total)	mg L^{-1}	Calculated: Total Kjeldahl nitrogen plus dissolved nitrate - nitrite nitrogen.
Nitrogen (Dissolved)	mg L^{-1}	Calculated: Dissolved Kjeldahl nitrogen plus dissolved nitrate - nitrite nitrogen.
Nitrogen (Particulate)	mg L^{-1}	Calculated: Total nitrogen minus dissolved nitrogen.
Nitrogen (Total Kjeldahl)	mg L^{-1}	Automated phenate.
Nitrogen (Total Organic)	mg L^{-1}	Calculated: Total Kjeldahl nitrogen minus total ammonia nitrogen.
Nitrogen (Dissolved Kjeldahl)	mg L^{-1}	Automated phenate after field filtration through 0.45 μm pore size cellulose acetate filters.
Nitrogen (Particulate Kjeldahl)	mg L^{-1}	Calculated: Total Kjeldahl nitrogen minus dissolved Kjeldahl nitrogen.
Nitrogen (Total Ammonia)	mg L^{-1}	Automated phenate.
Nitrogen (Un-ionized Ammonia)	mg L^{-1}	Calculated: Equilibrium function reported by Emerson <i>et al.</i> (1975).
Nitrogen (Dissolved Nitrate-Nitrite)	mg L^{-1}	Automated Cd reduction.
Phosphorus (Total)	mg L^{-1}	Automated stannous chloride.
Phosphorus (Dissolved)	mg L^{-1}	Automated stannous chloride after field filtration through 0.45 μm pore size cellulose acetate filters.
Phosphorus (Particulate)	mg L^{-1}	Calculated: Total phosphorus minus dissolved phosphorus.
Chloride (Soluble)	mg L^{-1}	Automated thiocyanate.
Sulphate (Soluble)	mg L^{-1}	Automated methylthymol blue.

TABLE 2. Continued.

Variable	Units	Method
Carbon (Total Organic)	mg L ⁻¹	Infrared analyzer
Carbon (Dissolved Organic)	mg L ⁻¹	Infrared analyzer after field filtration through 0.45 µm pore size cellulose acetate filters.
Carbon (Particulate Organic)	mg L ⁻¹	Calculated: Total organic carbon minus dissolved organic carbon.
Carbon (Total Inorganic)	mg L ⁻¹	Infrared analyzer.
Carbon (Dissolved Inorganic)	mg L ⁻¹	Infrared analyzer after field filtration through 0.45 µm pore size cellulose acetate filters.
Carbon (Particulate Inorganic)	mg L ⁻¹	Calculated: Total inorganic carbon minus dissolved organic carbon.

procedures (STATGRAPHICS version 5.1, STSC Corporation 1992). Distributions were normal, log-normal, and arcsine. In some cases (*e.g.*, water chemistry variables that were influenced by data at or near the limit of detection), normality could not be obtained even after numerous alternate transformations. Data expressed as proportions were transformed into radians by the arcsine function (Sokal and Rohlf 1981). Selected species input options included weighting species scores by mean sample scores. All species, including rare species, were given equal weight. The least numbers of environmental variables that best explained the observed variability in the species data were chosen using forward selection procedures. Unrestricted Monte Carlo permutation of the residuals under the null model was used to test both the fit of the overall model and the fit of the first canonical axis ($\alpha = 0.05$) based upon the selected environmental variables.

The non-parametric Kruskal-Wallis one-way analysis of variance by ranks (STATGRAPHICS version 5.1, STSC Corporation 1992) was used to test for water chemistry differences among ponds ($\alpha = 0.05$). This test was chosen since the parametric one-way analysis of variance could be influenced by heteroscedastic variances and these remained for several variables despite numerous alternate transformations. Duncan's multiple range test, applied to each univariate water chemistry variable, followed Kruskal-Wallis tests in order to group ponds that were statistically indistinguishable from one another. This test conformed well with the results of Kruskal-Wallis test, but should be considered approximate for those water chemistry variables with unequal variances. Duncan's multiple range test is applied to parametric data and therefore can be affected by non-normality.

Multivariate cluster analysis (STATGRAPHICS version 5.1, STSC Corporation 1992 and STATGRAPHICS *PLUS* version 7, Manugistics 1993) was used to group

ponds into similar units in order to further explore the relationships derived by CCA. Ponds were grouped based upon insect abundances, general numerical descriptors of community structure, the complete complement of environmental variables as well as several subsets, including those selected during CCA. All data were appropriately transformed as previously described and standardized (Johnson and Wichern 1988). The hierarchical centroid method of clustering was chosen, with input being euclidean distance. Several clustering methods were tested (*e.g.*, seeded, average, nearest neighbour, furthest neighbour, median) and all yielded equivalent results. Therefore, the choice of method appeared not to influence the result with the data set generated from this study.

Estimation of Niche Width and Niche Overlap in Canonical Space

A species tolerance or ecological amplitude is estimated in CCA by the standard deviation of a Gaussian response curve (Dueser and Shugart 1978, 1979, 1982; Carnes and Slade 1982; Van Horne and Ford 1982; Chessel *et al.* 1982, 1987; ter Braak and Barendregt 1986; ter Braak and Looman 1986; Lebreton *et al.* 1988; ter Braak and van Dam 1989). The species range or niche width can be estimated by the approximate 95% confidence region around its optimum. If the ecological tolerance or amplitude is equal to one standard deviation, then the species range or niche width is approximately four to six tolerance units (ter Braak and Gremmen 1987).

Methods have not been developed to estimate confidence regions around species tolerances when input to CCA has been abundance data. Confidence regions have been estimated for CCA and for a Gaussian-logit response where input has been presence-absence data (ter Braak and Looman 1986, ter Braak and Gremmen 1987, ter Braak 1987b). Gaussian-logit response is a generalized linear approach modified for use with

presence-absence data. ter Braak (1987b) estimated confidence intervals from the regression coefficients in the final reciprocal averaging algorithm of CCA to compare changes in plant species along a gradient created by rising shore-line. However he cautioned that the confidence intervals were likely underestimated since the axes in CCA are chosen optimally; a factor not included in the estimation of confidence intervals. Most researchers have chosen to represent the approximate range of a species along an environment gradient with species scores plus and minus one standard deviation (*e.g.*, Chessel *et al.* 1982, Lebreton *et al.* 1988), thus approximating 66% confidence regions.

It was desirable in the present study to use abundance data rather than presence-absence values since abundance provides an important measure of a species success at a given site. Dueser and Shugart (1979) noted that niche pattern consisted of three factors, niche position (*i.e.*, species score), niche breadth or ecological amplitude (*i.e.*, standard deviation), and population abundance. Presence-absence data may be more useful when the number of sites is relatively large (*e.g.*, > 1000 in the study by ter Braak and Gremmen 1987). As the number of sites increase, better estimates can be obtained of species preferences for certain habitats, and population success becomes less important. In the present study, the number of sites was small (*i.e.*, six ponds), thus considerable information would be lost on the variability or success of populations within any one pond if CCA were run with presence-absence data. Canonical Correspondence Analysis applied to abundance data, on the other hand, should provide as much information on the distribution of species as with nominal data, and should provide additional information on the success of a species at any one site.

Simultaneous $100(1-\alpha)\%$ confidence regions were estimated by the F-ratio method around the optimum for each species for each of the first four canonical axes (Johnson and

Wichern 1988). ter Braak (1991) reported that inter-species and inter-site distances in CCA orthogonal space are approximate χ^2 distances. The F-ratio can therefore be used to estimate confidence regions with χ^2 distances (Carnes and Slade 1982). Calculations were as follows:

$$U_k \pm \sqrt{\frac{p(n-1)}{(n-p)} F_{p,n-p}(\alpha) \frac{S_{ii}^2}{\sqrt{n}}}, \text{ where} \quad (\text{Eq. 6})$$

U_k = species score (its optimum) on each canonical axis;

S_{ii}^2 = species sample standard deviation (tolerance) on each canonical axis;

p = number of environmental variables retained in the CCA model (3);

n = number of sites (6).

Output from CCA provides population standard deviations as estimates of tolerances for species. Sample standard deviations were obtained by dividing population standard deviations by $\sqrt{\left(1 - \frac{1}{n}\right)}$ (ter Braak 1991) prior to calculation of simultaneous confidence regions.

Consequently, projection of the 95% confidence regions around a species score on each of the first four canonical axes results in a series of ellipses representing the approximate niche widths for that species. This method is a better estimate of a species' niche in multivariate space than the method proposed by Green (1974) and the methods used by Chessel *et al.* (1982) and Lebreton *et al.* (1988). Green (1974) suggested that niche width in multivariate space can be estimated by the 50% confidence ellipse and the

methods used by Chessel *et al.* (1982) and Lebreton *et al.* (1988) estimated approximate 66% confidence regions. Subsequent workers have similarly used 95% confidence regions to define niche widths (Dueser and Shugart 1979).

Once niche widths were estimated for each species along all canonical axes, asymmetrical niche overlap between species and between species and sites was calculated (Eq. 7). Niche widths were projected on each axis, then proportional overlap (Figure 2) was determined as follows:

$$\begin{aligned} &\text{Percent Overlap of Species 2 on Species 1 along the 1st} \\ &\text{Canonical Axis} = \left(\frac{b-c}{b-a} \right) \times 100, \text{ where} \end{aligned} \quad (\text{Eq. 7})$$

a and b = 95% F-ratio coordinates calculated from

$$u_k \pm \sqrt{\frac{p(n-1)}{(n-p)} F_{p,n-p}(\alpha) \frac{S_{ii}^2}{\sqrt{n}}} \quad (\text{Eq. 6) for Species 1;}$$

c and d = 95% F-ratio coordinates calculated from

$$u_k \pm \sqrt{\frac{p(n-1)}{(n-p)} F_{p,n-p}(\alpha) \frac{S_{ii}^2}{\sqrt{n}}} \quad (\text{Eq. 6) for Species 2;}$$

● = Species score u_k for Species 1 and Species 2;

■ = Site score x_i at Site 1.

The canonical axes are in standard deviation units. Depending upon the relative species scores and niche widths, Eq. 7 can assume ~ 14 forms, although the overall structure remains the same. Species 2 overlaps Species 1 by ~ 75% along the first canonical axis in this example. Typically, values > 60% or 70% would be considered significant overlap (Macdonald 1983, Fuller and Hynes 1987). The large overlap

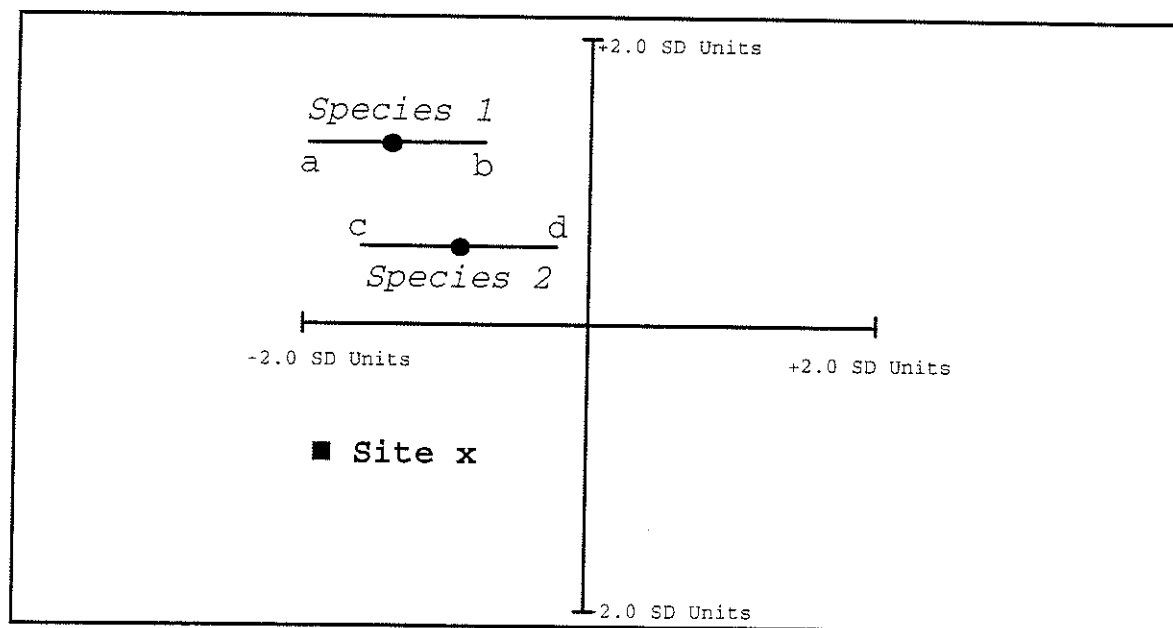


Figure 2. Niche overlap estimation in CCA orthogonal space, showing location and ecological tolerance for *Species 1* and *Species 2* along with the plotting position of hypothetical **Site x**. *Species 1* overlaps *Species 2* ~ 75% along the first canonical axis. Only *Species 1* overlaps **Site x**.

observed in the example could be interpreted to mean that *Species 2* might be able to replace the ecological function of *Species 1*. However, CCA allows more objective estimations of potential replacement, at least concerning overlap along environmental axes. Since *Species 1* overlaps the environment in **Site x**, it is inferred that *Species 1* can occupy or colonize **Site x**. The environment is represented by the site score. However, similar inference cannot be made about the ability of *Species 2* to occupy **Site x** since the niche width of *Species 2* does not overlap the score at **Site x**. Thus, while *Species 2* has high overlap with *Species 1*, *Species 2* may not be able to colonize a specific habitat to replace the ecological function of hypothetically lost *Species 1*.

Site scores in CCA are calculated by two methods (Palmer 1993). The weighted average (WA) method generates site scores that are weighted by species, whereas the linear combination (LC) method predicts site scores based upon linear combination of environmental variables. Overlap of individual species on WA site scores is not too useful since the WA site scores and species scores are not independent. Indeed, in cases where there is no environmental gradient but the species assemblage differs between sites, WA site scores would still appear well separated in orthogonal space. In contrast, the LC method produces site scores independent of species that are completely constrained by the environment; thus, overlap of species scores on LC site scores is meaningful. Palmer (1993) recommended the use of LC site scores for all CCA applications but Kenkel (pers. comm.¹) argued that the WA scores provide a more biologically relevant site score because they account for both environment and species composition. In the present application, sites scores representing only environment are required since the intent is to infer whether a potential replacement species may be able to colonize a new pond based

¹ Dr Norman Kenkel, Professor, Department of Botany, University of Manitoba.

upon species tolerance and pond environment. Linear combination site scores are available only for the first three canonical axes. In CCA, the number of constrained or canonical axes cannot exceed the number of external variables. Residual variability in the insect community not accounted for in the first three constrained axes is included in the fourth or additional unconstrained axes (Prentice and Cramer 1990).

Projection of relative niche widths on single dimensional axes has been used by Green (1971, 1974), Chessel *et al.* (1982, 1987), and Lebreton *et al.* (1988) to show niche position. May (1975) cautioned that calculation of overlap following projection of confidence ellipses generated from discriminant analysis may overestimate niche overlap for some species in multidimensional space with independent axes depending upon the geometric configuration of a species' ellipse. In discriminant analysis and other multivariate techniques however, the orientation of an ellipse is affected by the covariance structure of the matrix. In contrast, the axes in CCA are not simply derived by rotation; thus, the original geometric configuration of a species ellipse may not be retained. It is therefore not possible to construct ellipses with correct orientation.

Niche width calculations are affected by sample size, since the table value for the t statistic becomes larger as the degrees of freedom are reduced. Degrees of freedom are typically determined by the number of sites actually occupied by a species. Thus, information on the absence of a species is not included. Consequently, a species limited to two or three sites may have a larger niche width when estimated by the 95% confidence region than a species occupying five or six sites. This undesirable property has been discussed by Dueser and Shugart (1979, 1982), Van Horne and Ford (1982), and Carnes and Slade (1982). Green (1971) suggested that the presence of a species conveyed considerably more information than its absence. A species may be absent for a number of

reasons, including: (1) the species cannot live at that site; (2) the species has not yet dispersed to that site; or (3) the species does live at the site but was missed by chance during sampling. Carnes and Slade (1982) argued that the absence of a species at a given site provides valuable information which should be retained in data analysis. They reasoned that Green's (1971) rationale may be appropriate for sedentary forms where dispersion rates are low, but may not apply to highly mobile forms. Mobile animals may occupy a site merely by chance for a limited period of time although that site may not be within its preferred niche range (*e.g.*, adult Coleoptera). For discriminant analysis, Carnes and Slade (1982) suggested that samples be collected using a complete or stratified random design and that habitat variables be measured and incorporated into the statistical analysis even when species were absent. In discriminant analysis, this has the effect of extending the range of habitat to that which is available rather than only that which is occupied, thereby eliminating the effect of sample size on niche width as reported by Dueser and Shugart (1979, 1982).

The method of Carnes and Slade (1982) was extended to CCA in order to calculate niche widths without the influence of unequal species occurrences, with one modification. In CCA, population standard deviations are calculated only from occupied sites. By adding 0.0001 to all species abundances (*i.e.*, as previously mentioned, $c = 1.0001$ in the log-transformed abundances), CCA treated all species as being present at all sites, thereby calculating standard deviations across all available habitat. The addition of 0.0001 to all species abundances is the equivalent of finding one additional specimen of each taxon approximately once each 17 years, given the present sampling strategy. This simple assumption is realistic and is consistent with both Green (1971) and Carnes and Slade (1982). It is assumed that these highly mobile taxa will colonize all ponds occasionally by accident, but may not establish successful populations; their absence in

the samples is caused by chance alone. Confidence regions were calculated with five degrees of freedom for all species ($n-1$, where $n = 6$ sites).

It is recognized that both the method used to calculate 95% confidence regions around a species optimum and the method used to calculate niche overlap in canonical space are approximate. Both methods are simple extensions of previous work (*e.g.*, Chessel *et al.* 1982, Lebreton *et al.* 1988); however, the extensions are thought to better represent niche width than previous work and to adequately estimate niche overlap.

RESULTS AND DISCUSSION

Pond Characterization

Pond 34 had a total volume of $\sim 41 \text{ m}^3$, a surface area of 57 m^2 (TABLE 3) and a maximum depth of 1.5 m (Figure 3). The entire bottom was covered with dense beds of *Chara* sp. with *Typha* sp. encroaching well into the pond along most margins (TABLE 4). Pond sediment was mainly coarse sand (TABLE 5). Water chemistry was characterized by low colour (~ 15 colour units), low dissolved organic carbon (8.8 mg L^{-1}), pH in the low alkaline range, and moderate concentrations of dissolved minerals (total dissolved solids of $\sim 186 \text{ mg L}^{-1}$; TABLE 6). Total phosphorus and total nitrogen concentrations were relatively low ($\bar{X} = 0.0264$ and 0.53 mg L^{-1} , respectively). The majority of phosphorus and nitrogen was present in dissolved forms rather than bound to suspended sediment particles or in algal cell walls. In addition, virtually all of the observed dissolved nitrogen was of organic origin, indicating that most nitrogen is probably being cycled within the pond through macrophyte tissue followed by senescence, rather than by the introduction of new inorganic forms. Dissolved inorganic carbon concentration was

TABLE 3. Summary of morphological features of the six Sandilands Provincial Forest study ponds.

Variable	Units	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Circumference	m	16.40	16.38	31.49	31.01	17.09	31.01
Area	m ²	57.35	40.45	82.00	78.45	54.38	81.20
Volume	m ³	41.65	19.38	58.52	58.43	52.16	67.67
Maximum Depth	m	1.50	0.95	1.35	1.39	1.65	1.70
Circumference / Volume Ratio	m m ⁻³	0.39	0.85	0.54	0.53	0.33	0.46
Water Level Variation	Coef. of Var.	0.30	0.54	0.32	0.46	0.51	0.53

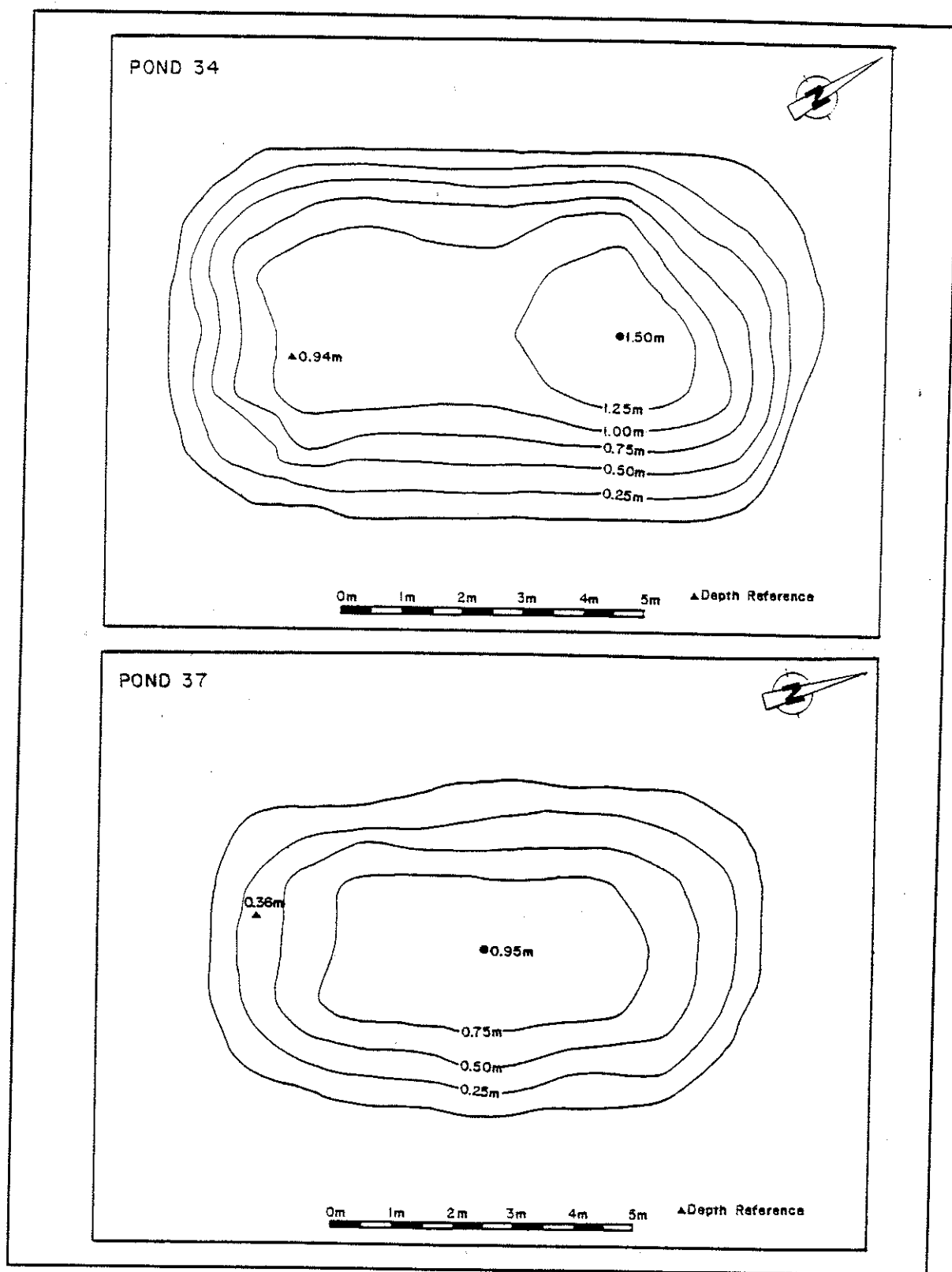


Figure 3. Bathymetric maps of the six Sandilands Provincial Forest study ponds.

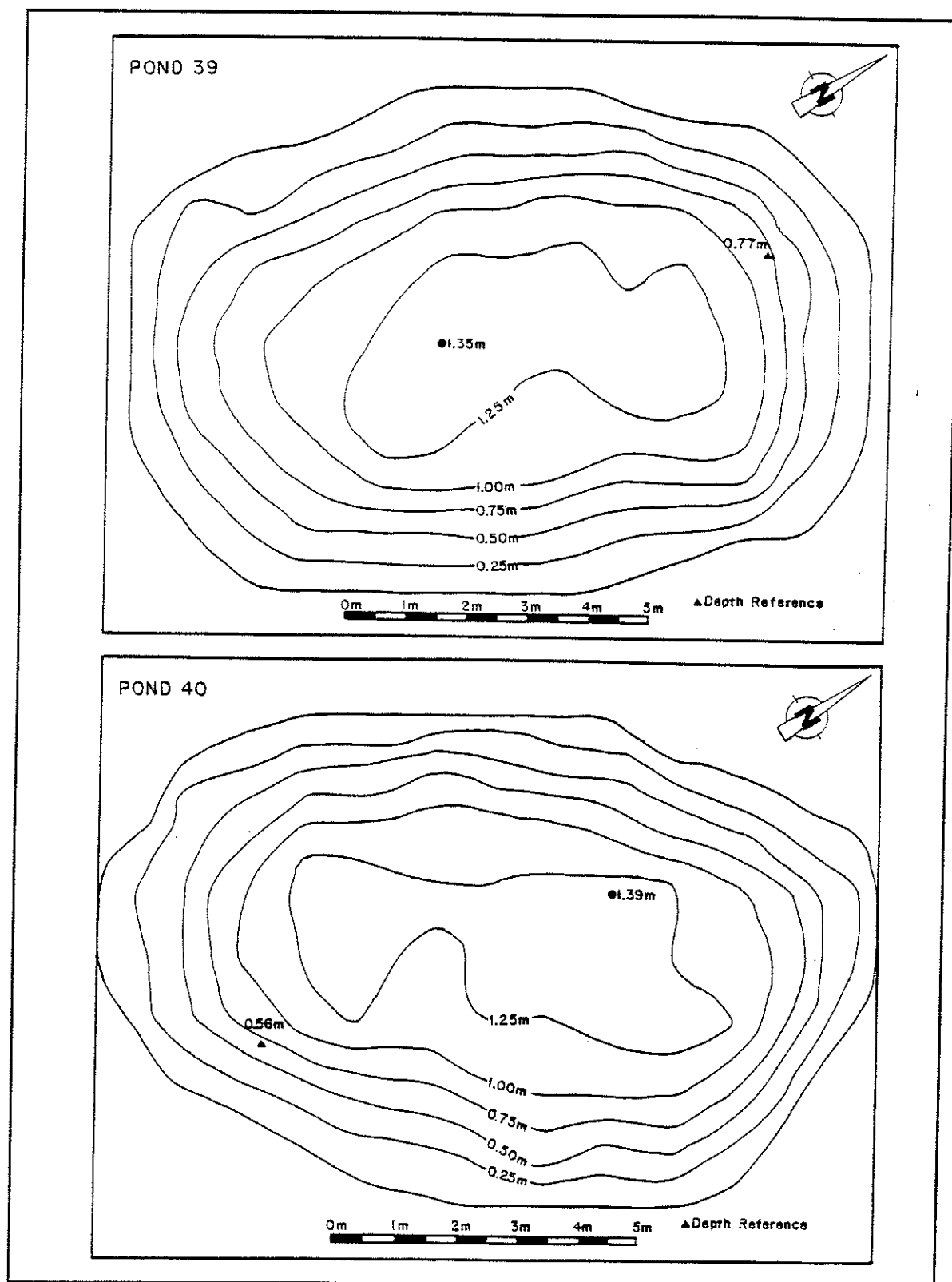


Figure 3. Continued.

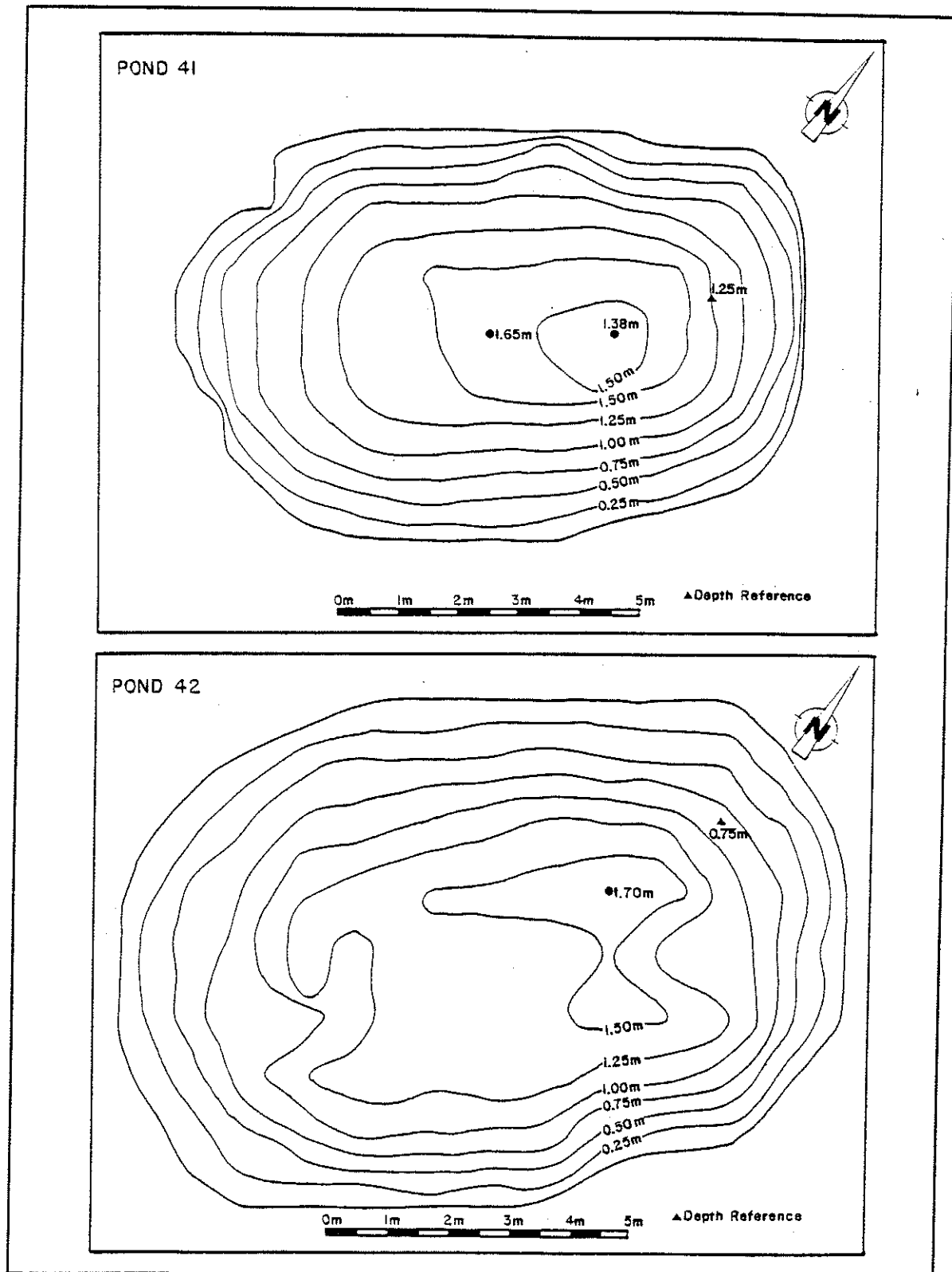


Figure 3. Continued.

TABLE 4. Area colonized by macrophyte species in the six Sandilands Provincial Forest study ponds. All values are percent of total pond area.

Plant Species or Association	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
<i>Carex</i> sp.	0	0	6	0	0	0
<i>Chara</i> sp.	48	0	6	9	0	0
<i>Chara</i> sp. and <i>Sphagnum</i> sp.	0	5	0	0	0	0
<i>Chara</i> sp., <i>U. vulgaris</i> L. and <i>Sphagnum</i> sp.	0	0	0	0	0	44
<i>Chara</i> sp., <i>Potamogeton foliosus</i> Raf. and <i>Sphagnum</i> sp.	0	6	0	0	0	0
Filamentous algae and <i>Sphagnum</i> sp.	0	8	0	0	0	0
<i>P. foliosus</i> Raf., <i>Chara</i> sp. and <i>Sphagnum</i> sp.	0	0	0	0	0	38
<i>P. foliosus</i> Raf.	0	23	19	31	0	0
<i>P. foliosus</i> Raf. and <i>P. gramineus</i> L.	0	0	4	0	0	0
<i>P. foliosus</i> Raf. and <i>Sphagnum</i> sp.	0	10	0	0	0	0
<i>P. foliosus</i> Raf., <i>Chara</i> sp., <i>P. gramineus</i> L. and <i>Sphagnum</i> sp.	0	0	0	0	67	0
<i>P. gramineus</i> L.	0	0	15	0	0	0
<i>P. natans</i> L.	0	0	0	3	0	0
<i>Polygonum coccineum</i> Muhl.	0	0	0	0	12	0
<i>Ranunculus aquatilis</i> L. and <i>Sphagnum</i> sp.	0	0	0	0	0	1
<i>Scirpus</i> sp., <i>Carex</i> sp. and <i>Sphagnum</i> sp.	0	0	0	0	0	11
<i>Sparganium</i> sp.	0	0	0	2	0	0
<i>Sphagnum</i> sp.	0	13	0	0	0	0
<i>Typha</i> sp.	0	0	0	0	21	0
<i>Typha</i> sp. and <i>Chara</i> sp.	52	0	0	0	0	0
<i>Utricularia vulgaris</i> L. and <i>Sphagnum</i> sp.	0	0	0	0	0	0
<i>U. vulgaris</i> L., <i>Chara</i> sp. and <i>P. natans</i> L.	0	0	0	4	0	0
<i>U. vulgaris</i> L. and <i>Chara</i> sp.	0	0	0	35	0	0
<i>Polygonum coccineum</i> Muhl. and <i>Sphagnum</i> sp.	0	0	0	0	0	1
<i>Sparganium</i> sp. and <i>Sphagnum</i> sp.	0	0	0	0	0	5
Plant association with <i>Sphagnum</i> sp.	0	42	0	0	67	100
Plant association with <i>Chara</i> sp.	100	11	6	48	67	82
Plant association with <i>Potamogeton</i> spp.	0	39	53	34	0	38
Plant association with <i>Sphagnum</i> sp. and area covered with detritus	0	77	50	17	67	100
Detritus	0	35	50	17	0	0
Plant Cover	100	65	50	83	100	100

TABLE 5. Characteristics of bottom sediments in the six Sandilands Provincial Forest study ponds. All values are percent of sample mass.

Sediment Type	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Organic	3	2	1	3	2	2
Silt	3	1	1	1	2	1
Clay	2	1	0	2	3	1
Very Fine Sand	2	2	0	2	6	1
Fine Sand	2	32	17	33	49	36
Medium Sand	9	38	59	45	36	39
Coarse Sand	43	15	18	15	4	17
Very Coarse Sand	39	11	5	2	0	5
Textural Class	coarse sand	coarse sand	medium sand	medium sand	medium sand	medium sand

TABLE 6. Summary of water chemistry in the six Sandilands Provincial Forest study ponds.

Variable	Units	Kruskal-Wallis ¹	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Field Temperature	°C	not sig.	13.4	13.1	12.8	14.4	13.9	13.2
Field pH	Units	<0.001	8.1 ^a	8.0 ^a	7.6 ^b	7.7 ^{ab}	7.4 ^b	7.6 ^b
Laboratory pH	Units	<0.0001	8.05 ^a	7.84 ^{ab}	7.55 ^c	7.65 ^{bc}	7.20 ^d	7.47 ^c
Field Conductivity (25 °C)	µS cm ⁻¹	<0.0001	324.9 ^a	305.7 ^a	202.9 ^b	327.8 ^a	125.9 ^c	266.3 ^{ab}
Laboratory Conductivity (25 °C)	µS cm ⁻¹	<0.0001	324.1 ^a	323.3 ^a	224.3 ^b	380.2 ^c	137.3 ^d	308.1 ^a
Solids (Total Dissolved)	mg L ⁻¹	<0.001	186 ^{ac}	180 ^{ac}	147 ^{ab}	257 ^d	129 ^b	207 ^{cd}
Solids (Total Suspended)	mg L ⁻¹	not sig.	<5	<5	<5	<5	<6	<6
Solids (Total)	mg L ⁻¹	<0.001	189 ^{ac}	184 ^{ac}	151 ^{ab}	260 ^d	132 ^b	208 ^{cd}
Alkalinity (Total)	mg L ⁻¹	<0.0001	165 ^a	166 ^a	105 ^b	198 ^d	60 ^c	157 ^a
Alkalinity (Bicarbonate)	mg L ⁻¹	<0.0001	198 ^a	202 ^a	128 ^b	242 ^d	73 ^c	192 ^a
Alkalinity (Carbonate)	mg L ⁻¹	not sig.	2.1	0.0	0.0	0.0	0.0	0.0
Alkalinity (Hydroxide)	mg L ⁻¹	not sig.	0.00	0.00	0.00	0.00	0.00	0.00
Calcium (Extractable)	mg L ⁻¹	<0.0001	46.0 ^a	48.6 ^a	35.5 ^b	64.2 ^c	22.4 ^d	52.0 ^a
Magnesium (Extractable)	mg L ⁻¹	<0.0001	15.0 ^a	12.0 ^b	6.7 ^c	10.8 ^b	3.5 ^d	8.7 ^e
Hardness	mg L ⁻¹	<0.0001	177 ^{ab}	171 ^a	117 ^c	205 ^b	70 ^d	166 ^a
Sodium (Extractable)	mg L ⁻¹	<0.01	1.9 ^{ab}	1.7 ^a	2.1 ^{ab}	2.2 ^b	2.4 ^b	2.3 ^b
Potassium (Extractable)	mg L ⁻¹	not sig.	<5	<5	<5	<5	<5	<5
Iron (Extractable)	mg L ⁻¹	<0.0001	0.06 ^a	<0.05 ^a	0.17 ^b	0.26 ^b	0.36 ^b	0.53 ^c
Manganese (Extractable)	mg L ⁻¹	not sig.	<0.03	<0.02	<0.03	<0.03	<0.05	<0.03
Dissolved Oxygen	mg L ⁻¹	not sig.	9.0	7.5	6.4	6.1	<8.5	7.9
Dissolved Oxygen	% Sat.	not sig.	86.4	71.4	61.9	60.5	80.2	75.7
Colour (True)	Units	<0.0001	15 ^a	14 ^a	44 ^{bc}	38 ^b	45 ^{bc}	47 ^c
Turbidity	NTU	not sig.	0.6	0.4	0.7	0.6	1.0	1.3
Nitrogen (Total)	mg L ⁻¹	<0.0001	0.53 ^{ab}	0.37 ^a	0.70 ^{bc}	0.72 ^{bc}	1.09 ^d	1.02 ^{cd}
Nitrogen (Dissolved)	mg L ⁻¹	<0.0001	0.42 ^a	0.28 ^b	0.50 ^a	0.58 ^a	0.95 ^c	0.87 ^c
Nitrogen (Particulate)	mg L ⁻¹	not sig.	<0.22	<0.21	<0.23	<0.23	<0.23	<0.22
Nitrogen (Total Kjeldahl)	mg L ⁻¹	<0.0001	0.49 ^{ab}	0.36 ^b	0.66 ^{ac}	0.70 ^{ac}	1.07 ^d	0.94 ^{cd}
Nitrogen (Total Organic)	mg L ⁻¹	<0.0001	0.48 ^{ab}	0.35 ^a	0.65 ^{bc}	0.69 ^{bc}	1.03 ^d	0.92 ^{cd}
Nitrogen (Dissolved Kjeldahl)	mg L ⁻¹	<0.0001	0.38 ^{ab}	<0.27 ^a	0.47 ^{bc}	0.57 ^{cd}	0.93 ^e	0.79 ^{de}
Nitrogen (Particulate Kjeldahl)	mg L ⁻¹	not sig.	<0.22	<0.21	<0.23	<0.23	<0.23	<0.22
Nitrogen (Total Ammonia)	mg L ⁻¹	not sig.	0.006	0.007	0.011	0.009	0.021	0.012
Nitrogen (Un-ionized Ammonia)	mg L ⁻¹	not sig.	0.0002	0.0002	0.0001	0.0001	0.0002	0.0001
Nitrogen (Dissolved Nitrate-Nitrite)	mg L ⁻¹	not sig.	<0.03	<0.01	<0.02	<0.01	<0.01	<0.02
Phosphorus (Total)	mg L ⁻¹	not sig.	0.0264	0.0301	0.0421	0.0413	0.0562	0.0526
Phosphorus (Dissolved)	mg L ⁻¹	<0.001	<0.0096 ^a	0.0132 ^{ab}	0.0128 ^{ab}	0.0123 ^{ab}	0.0276 ^c	0.0174 ^b
Phosphorus (Particulate)	mg L ⁻¹	not sig.	0.0153	0.0159	0.0268	0.0366	0.0271	0.0317
Chloride (Soluble)	mg L ⁻¹	<0.05	1.0 ^{ab}	0.8 ^a	1.0 ^{ab}	1.2 ^b	1.4 ^b	1.3 ^b
Sulphate (Soluble)	mg L ⁻¹	<0.05	6 ^{ab}	5 ^a	8 ^{ab}	5 ^a	10 ^b	6 ^{ab}
Carbon (Total Organic)	mg L ⁻¹	<0.0001	10.2 ^a	<7.3 ^a	17.1 ^b	17.2 ^b	24.2 ^b	22.5 ^b
Carbon (Dissolved Organic)	mg L ⁻¹	<0.0001	8.8 ^a	<6.8 ^a	15.5 ^b	15.7 ^b	22.9 ^b	19.9 ^b
Carbon (Particulate Organic)	mg L ⁻¹	not sig.	<5.2	<5.0	<5.1	<5.3	<5.2	<5.8

TABLE 6. Continued.

Variable	Units	Kruskal-Wallis ¹	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Carbon (Total Inorganic)	mg L ⁻¹	<0.0001	32.0 ^{ac}	30.7 ^{ab}	22.8 ^b	37.7 ^a	11.6 ^c	30.1 ^{abc}
Carbon (Dissolved Inorganic)	mg L ⁻¹	<0.0001	31.1 ^a	30.1 ^a	20.7 ^b	34.8 ^a	11.0 ^c	26.7 ^{ab}
Carbon (Particulate Inorganic)	mg L ⁻¹	not sig.	<5.0	<5.0	<5.7	<6.2	<5.0	<5.6

¹ Probabilities that a statistically significant difference exists between at least two ponds, as demonstrated by the non-parametric Kruskal-Wallis One-Way Analysis by Ranks test.

a,b,c,d,e Values for each variable with the same letter are not statistically different ($\alpha = 0.05$), as determined by Duncan's multiple range test.

relatively high ($\bar{X} = 31.1 \text{ mg L}^{-1}$). Inorganic carbon often increases as a result of photosynthetic activity in the presence of cations, principally calcium and magnesium (Horne 1978). Thus, elevated dissolved inorganic carbon can often be used as an indicator of relative primary productivity. Relatively high dissolved inorganic carbon in Pond 34 may therefore be consistent with the expected high rate of primary productivity occurring in the dense beds of *Chara* sp..

The clear, mineralized water within Pond 34 is a reflection of the nature of the surrounding catchment area. This pond is situated on relatively high ground; the pond probably intercepts the ground water table within the surficial aquifer. The pond is surrounded by stands of mature cedar, spruce, and aspen. The surface organic mantle is thin ($< 3 \text{ cm}$ in most areas) and overlies extensive sand deposits. Percolation of precipitation through the thin organic mantle and through the coarse sand deposits would be rapid with little opportunity for dissolution of materials associated with the surface organic material.

Thirty-seven arthropod species were identified from Pond 34; *Leucorrhinia intacta* Hagen was clearly dominant [$> 80\%$ of the total identified arthropod fauna; ($\bar{X} = 275.49 \text{ individuals m}^{-2}$; TABLE 7)]. Both Shannon-Wiener diversity and equitability were lowest in Pond 34 relative to the other study sites (TABLE 8), reflecting the overwhelming dominance of *L. intacta*. Two odonate and six coleopteran species were unique to Pond 34.

Pond 37, the smallest of the study ponds, had a volume of 19.38 m^3 , a circumference of 16.38 m , and a maximum depth of 0.95 m . Water level fluctuation throughout the study was greatest in this pond (coefficient of variation = 54%).

TABLE 7. Abundance of arthropods collected from the six Sandilands Provincial Forest study ponds. Values are means (numbers m⁻²) of all samples collected during the study period.

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Amphipoda	Talitridae	<i>Hyalella azteca</i> (Saussure)	adult	Hya azt	28.92	1.68	94.82	128.76	4.67	1.07
Emphemeroptera	Siphonuridae	<i>Siphonurus alternata</i> (Say) (probably)	larvae	Sip alt	0.00	0.00	0.00	0.00	0.00	0.13
Emphemeroptera	Baetidae	<i>Callibaetis</i> sp. Eaton	larvae	Cal sp.	0.00	0.41	0.91	0.36	2.16	0.87
Emphemeroptera	Caenidae	<i>Caenis diminuta</i> Walker	larvae	Cae dim	0.00	0.00	0.20	0.00	0.00	0.16
Emphemeroptera	Caenidae	<i>Caenis youngi</i> Roemhild	larvae	Cae you	0.00	0.00	1.10	0.27	0.08	0.00
Anisoptera	Aeshnidae	<i>Aeshna canadensis</i> Walker	nymph	Aes can	0.39	0.00	0.00	0.00	0.19	0.00
Anisoptera	Aeshnidae	<i>Aeshna interrupta</i> Walker	nymph	Aes int	0.22	0.15	0.10	0.21	0.17	0.00
Anisoptera	Aeshnidae	<i>Anax junius</i> Drury	nymph	Anx jun	0.08	0.00	0.00	0.00	0.00	0.00
Anisoptera	Corduliidae	<i>Cordulia shurtleffi</i> Scudder	nymph	Cor shu	0.92	0.00	0.00	0.00	0.00	0.09
Anisoptera	Corduliidae	<i>Somatochlora williamsoni</i> Walker	nymph	Som wil	0.06	0.18	0.18	0.12	0.15	0.08
Anisoptera	Libellulidae	<i>Leucorrhinia frigida</i> Hagen	nymph	Leu fri	0.06	0.00	0.00	0.00	0.00	0.00
Anisoptera	Libellulidae	<i>Leucorrhinia hudsonica</i> (Selys)	nymph	Leu hud	0.20	0.00	0.00	0.00	0.00	0.00
Anisoptera	Libellulidae	<i>Leucorrhinia intacta</i> Hagen	nymph	Leu int	275.49	43.88	0.23	7.19	0.17	0.87
Anisoptera	Libellulidae	<i>Leucorrhinia proxima</i> Calvert	nymph	Leu pro	0.33	0.00	0.00	0.00	0.09	0.09
Anisoptera	Libellulidae	<i>Libellula quadrimaculata</i> Linne	nymph	Lib qua	0.09	0.00	0.33	1.55	0.06	0.20
Anisoptera	Libellulidae	<i>Sympetrum danae</i> Sulzer	nymph	Sym dan	0.00	0.00	0.00	0.00	0.00	0.26
Anisoptera	Libellulidae	<i>Sympetrum obtrusum</i> (Hagen)	nymph	Sym obt	0.00	0.18	0.09	0.00	0.00	0.00
Zygoptera	Lestidae	<i>Lestes congener</i> Hagen	nymph	Les con	0.20	0.00	0.18	0.43	0.78	0.18
Zygoptera	Lestidae	<i>Lestes disjunctus disjunctus</i> Selys	nymph	Les dis	0.00	0.00	0.07	0.00	0.09	0.06
Zygoptera	Lestidae	<i>Lestes dryas</i> Kirby	nymph	Les dry	0.00	0.00	0.00	0.08	0.00	0.00
Zygoptera	Lestidae	<i>Lestes unguiculatus</i> Hagen	nymph	Les ung	0.09	0.00	0.07	0.00	0.00	0.31
Zygoptera	Coenagrionidae	<i>Coenagrion angulatum</i> Hagen	nymph	Coe ang	0.00	0.00	0.00	0.43	0.30	0.36
Zygoptera	Coenagrionidae	<i>Coenagrion resolutum</i> (Hagen)	nymph	Coe res	0.20	0.00	0.00	1.03	0.61	1.31
Zygoptera	Coenagrionidae	<i>Enallagma cyathigerum</i> (Charpentier)	nymph	Ena cya	27.40	40.19	13.63	80.99	17.66	2.32
Hemiptera	Veliidae	<i>Microvelia pulchella</i> Westwood (probably)	immature	Mic pul	0.00	0.00	0.00	0.00	0.00	0.14
Hemiptera	Gerridae	<i>Gerris buenoi</i> Kirkaldy	adult	Ger bue	0.06	0.00	0.17	0.08	0.17	0.06
Hemiptera	Gerridae	<i>Gerris dissortis</i> Drake and Harris	adult	Ger dis	0.13	0.05	0.12	0.00	0.00	0.00
Hemiptera	Belostomatidae	<i>Lethocerus americanus</i> (Leidy)	adult	Let ame	0.00	0.00	0.00	0.06	0.00	0.00
Hemiptera	Nepidae	<i>Ranatra fusca</i> Palisot de Beauvois	adult	Ran fus	0.00	0.00	0.07	0.00	0.00	0.00
Hemiptera	Corixidae	<i>Callicorixa audeni</i> Hungerford	adult	Cal aud	0.00	0.00	0.00	0.06	0.30	0.16
Hemiptera	Corixidae	<i>Hesperocorixa atopodonta</i> (Hungerford)	adult	Hes ato	0.00	0.18	0.18	0.45	0.13	0.75
Hemiptera	Corixidae	<i>Hesperocorixa minorella</i> (Hungerford)	adult	Hes min	0.00	0.00	0.00	0.00	0.00	0.18
Hemiptera	Corixidae	<i>Hesperocorixa vulgaris</i> (Hungerford)	adult	Hes vul	0.00	0.09	0.07	0.19	0.60	0.09
Hemiptera	Corixidae	<i>Sigara (Vermicorixa) alternata</i> (Say)	adult	Sig alt	0.20	0.09	0.34	0.33	0.64	0.75
Hemiptera	Corixidae	<i>Sigara (Arctosigara) conocephala</i> (Hungerford)	adult	Sig con	0.00	0.00	0.00	0.06	0.00	0.00
Hemiptera	Corixidae	<i>Sigara (Arctosigara) decoratella</i> (Hungerford)	adult	Sig dec	0.00	0.00	0.00	0.00	0.00	0.06

TABLE 7. Continued

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Hemiptera	Corixidae	<i>Sigara (Vermicorixa) grossolineata</i> Hungerford	adult	Sig gro	0.00	0.00	0.07	0.00	0.09	0.09
Hemiptera	Notonectidae	<i>Notonecta borealis</i> Bueno and Hussey	adult	Not bor	0.18	0.00	0.00	0.00	0.00	0.00
Hemiptera	Notonectidae	<i>Notonecta irrorata</i> Uhler	adult	Not irr	0.09	0.00	0.00	0.00	0.08	0.00
Hemiptera	Notonectidae	<i>Notonecta kirbyi</i> Hungerford	adult	Not kir	0.00	0.00	0.07	0.06	0.00	0.00
Hemiptera	Notonectidae	<i>Notonecta undulata</i> Say	adult	Not und	0.00	0.15	0.21	0.28	0.52	0.36
Trichoptera	Phryganeidae	<i>Banksiola crotchii</i> Banks	larvae	Ban cro	0.11	0.09	0.00	0.16	0.09	0.29
Trichoptera	Phryganeidae	<i>Ptilostomis</i> sp. Kolenati	larvae	Pti sp.	0.00	0.00	0.10	0.09	0.00	0.00
Trichoptera	Limnephilidae	<i>Anobolia</i> sp. Stephens	larvae	Ana sp.	0.00	0.00	0.10	0.00	0.00	0.00
Trichoptera	Limnephilidae	<i>Limnephilus</i> sp. 1 Leach	larvae	Lim sp1	0.00	0.00	0.09	0.00	0.00	0.00
Trichoptera	Limnephilidae	<i>Limnephilus</i> sp. 2 Leach	larvae	Lim sp2	0.00	0.00	0.10	0.00	0.00	0.00
Trichoptera	Limnephilidae	<i>Nemotaulius hostilis</i> (Hagen)	larvae	Nem hos	0.00	0.00	0.10	0.00	0.00	0.00
Trichoptera	Leptoceridae	<i>Oecetis inconspicua</i> (Walker) Complex	larvae	Oec inc	0.00	0.40	0.33	0.45	0.29	0.12
Coleoptera	Gyrinidae	<i>Gyrinus aquiris</i> LeConte	adult	Gyr aqu	0.00	0.05	0.00	0.00	0.00	0.00
Coleoptera	Halplidae	<i>Haliphus canadensis</i> Wallis	adult	Hal can	0.20	0.11	0.17	0.00	0.00	0.00
Coleoptera	Halplidae	<i>Haliphus connexus</i> Matheson	adult	Hal con	0.06	0.00	0.00	0.00	0.00	0.00
Coleoptera	Halplidae	<i>Haliphus immaculicollis</i> Harris	adult	Hal imm	0.06	0.17	0.17	0.09	0.51	0.13
Coleoptera	Halplidae	<i>Haliphus longulus</i> LeConte	adult	Hal lon	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Halplidae	<i>Haliphus salinarius</i> Wallis	adult	Hal sal	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Halplidae	<i>Haliphus</i> sp. Latreille	larvae	Hal sp.	0.51	1.13	0.18	2.27	0.17	0.75
Coleoptera	Halplidae	<i>Haliphus strigatus</i> Roberts	adult	Hal str	0.00	0.00	0.07	0.00	0.00	0.00
Coleoptera	Halplidae	<i>Haliphus subguttatus</i> Crotch	adult	Hal sub	0.00	0.00	0.07	0.06	0.00	0.00
Coleoptera	Halplidae	<i>Peltodytes edentulus</i> (LeConte)	adult	Pel ede	0.00	0.00	0.00	0.06	0.00	0.00
Coleoptera	Halplidae	<i>Peltodytes</i> sp. Regimbart	larvae	Pel sp.	0.00	0.00	0.00	0.11	0.00	0.00
Coleoptera	Halplidae	<i>Peltodytes tortuosus</i> Roberts	adult	Pel tor	0.00	0.00	0.00	0.38	0.00	0.00
Coleoptera	Dytiscidae	<i>Acilius semisulcatus</i> Aube	adult	Aci sem	0.18	0.00	0.00	0.15	0.17	0.28
Coleoptera	Dytiscidae	<i>Acilius</i> sp. Leach	larvae	Aci sp.	0.00	0.00	0.21	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Agabus anthracinus</i> Mannerheim	adult	Aga ant	0.00	0.09	0.00	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Agabus</i> sp. Leach	larvae	Aga sp.	0.00	0.00	0.00	0.70	0.17	0.54
Coleoptera	Dytiscidae	<i>Colymbetes longulus</i> LeConte	adult	Col lon	0.09	0.00	0.00	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Colymbetes sculptilis</i> Harris	adult	Col scu	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Dytiscidae	<i>Coptotomus longulus</i> LeConte	adult	Cop lon	0.00	0.00	0.00	0.06	0.00	0.00
Coleoptera	Dytiscidae	<i>Desmopachria convexa</i> (Aube)	adult	Des con	0.00	0.00	0.00	0.00	0.09	0.00
Coleoptera	Dytiscidae	<i>Dytiscus dauricus</i> Gebler	adult	Dyt dau	0.00	0.09	0.07	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Dytiscus</i> sp. Linnaeus	larvae	Dyt sp.	0.00	0.09	0.00	0.28	0.00	0.06
Coleoptera	Dytiscidae	<i>Graphoderus liberus</i> (Say)	adult	Grp lib	0.00	0.00	0.18	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Graphoderus perplexus</i> Sharp	adult	Grp per	0.00	0.00	0.00	0.00	0.06	0.00

TABLE 7. Continued

Order or Sub-Order	Family	Species	Life Stage	Code	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Coleoptera	Dytiscidae	<i>Graphoderus</i> sp. Dejean	larvae	Grp sp.	0.00	0.00	0.00	0.00	0.09	0.16
Coleoptera	Dytiscidae	<i>Hydaticus aruspex</i> Clark	adult	Hda aru	0.21	0.00	0.00	0.09	0.00	0.00
Coleoptera	Dytiscidae	<i>Hydaticus</i> sp. Leach	larvae	Hda sp.	0.00	0.00	0.00	0.31	0.00	0.00
Coleoptera	Dytiscidae	<i>Hydroporus paugus</i> Fall	adult	Hdp pau	0.00	0.05	0.00	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Hydroporus rubyi</i> Larson	adult	Hdp rub	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Dytiscidae	<i>Hydroporus rufinasus</i> Mannerheim	adult	Hdp ruf	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Dytiscidae	<i>Hydroporus</i> sp. Clairville	larvae	Hdp sp.	0.00	0.12	0.00	0.09	0.00	0.00
Coleoptera	Dytiscidae	<i>Hydroporus</i> sp. 1 Clairville	adult	Hdp sp1	0.09	0.00	0.07	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Hygrotus patruelis</i> (LeConte)	adult	Hyg pat	0.00	0.00	0.07	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Hygrotus salinarius</i> (Wallis)	adult	Hyg sal	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Dytiscidae	<i>Hygrotus sayi</i> Balfour-Browne	adult	Hyg say	0.00	0.05	0.15	0.09	0.57	0.18
Coleoptera	Dytiscidae	<i>Hygrotus</i> sp. 1 Stephens	adult	Hyg sp1	0.00	0.00	0.10	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Hygrotus</i> sp. 2 Stephens	adult	Hyg sp2	0.00	0.00	0.00	0.00	0.08	0.06
Coleoptera	Dytiscidae	<i>Laccophilus biguttatus</i> Kirby	adult	Lac big	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Dytiscidae	<i>Laccophilus maculosus</i> Say	adult	Lac mac	0.00	0.00	0.10	0.06	0.06	0.06
Coleoptera	Dytiscidae	<i>Laccophilus</i> sp. Leach	larvae	Lac sp.	0.00	0.00	0.00	0.12	0.00	0.00
Coleoptera	Dytiscidae	<i>Liodessa affinis</i> (Say)	adult	Lio aff	0.00	0.09	0.09	0.06	0.69	0.15
Coleoptera	Dytiscidae	<i>Rhantus binotatus</i> (Harris)	adult	Rha bin	0.15	0.09	0.10	0.06	0.00	0.06
Coleoptera	Dytiscidae	<i>Rhantus frontalis</i> (Marshall)	adult	Rha fro	0.15	0.00	0.00	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Rhantus</i> sp. Dejean	larvae	Rha sp.	0.00	0.00	0.07	0.00	0.00	0.00
Coleoptera	Dytiscidae	<i>Rhantus suturellus</i> (Harris)	adult	Rha sut	0.09	0.00	0.10	0.00	0.00	0.00
Coleoptera	Hydrophilidae	<i>Anacaena limbata</i> (Fabricius)	adult	Anc lim	0.17	0.00	0.00	0.00	0.00	0.20
Coleoptera	Hydrophilidae	<i>Berosus striatus</i> (Say)	adult	Ber str	0.00	0.00	0.00	0.00	0.00	0.06
Coleoptera	Hydrophilidae	<i>Cymbiodyta minima</i> Notman	adult	Cym min	0.00	0.00	0.00	0.09	0.00	0.00
Coleoptera	Hydrophilidae	<i>Cymbiodyta vindicata</i> Fall	adult	Cym vin	0.00	0.00	0.00	0.00	0.00	0.18
Coleoptera	Hydrophilidae	<i>Enochrus (Lumetus) hamiltoni</i> (Horn)	adult	Eno ham	0.06	0.00	0.00	0.00	0.00	0.00
Coleoptera	Hydrophilidae	<i>Enochrus (Methyrus) ochraceus</i> (Melsheimer)	adult	Eno och	0.00	0.00	0.00	0.00	0.06	0.00
Coleoptera	Hydrophilidae	<i>Helophorus (Rhopaleophorus) angusticollis</i> d'Orchymont	adult	Hel ang	0.00	0.00	0.00	0.00	0.00	0.06
Coleoptera	Hydrophilidae	<i>Helophorus (Rhopaleophorus) lacustris</i> LeConte	adult	Hel lac	0.00	0.05	0.00	0.00	0.00	0.00
Coleoptera	Hydrophilidae	<i>Hydrobius fuscipes</i> (Linne)	adult	Hdb fus	0.00	0.09	0.00	0.00	0.00	0.00
Coleoptera	Hydrophilidae	<i>Hydrochara obtusata</i> (Say)	adult	Hdc obt	0.20	0.00	0.00	0.00	0.00	0.00
Coleoptera	Hydrophilidae	<i>Hydrochus pseudosquamifer</i> D.C. Miller	adult	Hdu pse	0.00	0.00	0.07	0.00	0.06	0.00
Coleoptera	Hydrophilidae	<i>Tropisternus lateralis nimbatus</i> (Say)	adult	Tro lat	0.06	0.00	0.00	0.00	0.06	0.00
Coleoptera	Hydrophilidae	<i>Tropisternus</i> sp. Solier	larvae	Tro sp.	0.00	0.00	0.00	0.00	0.00	0.11
Coleoptera	Hydraenidae	<i>Hydraena angulicollis</i> Notman	adult	Hdr ang	0.06	0.00	0.00	0.00	0.58	0.18
Coleoptera	Scitidae	<i>Cyphon</i> sp. Paykull	adult	Cyp sp.	0.00	0.00	0.00	0.00	0.06	0.00

TABLE 8. Summary measures of arthropod community composition in the six Sandilands Provincial Forest study ponds.

Community Variable	Pond 34	Pond 37	Pond 39	Pond 40	Pond 41	Pond 42
Abundance Aggregated by Order (organisms m ⁻²)						
Amphipoda	28.92	1.68	94.82	128.76	4.67	1.07
Ephemeroptera	0.00	0.41	2.21	0.63	2.24	1.15
Anisoptera	277.84	44.39	0.92	9.07	0.84	1.59
Zygoptera	27.89	40.19	13.95	82.96	19.43	4.54
Hemiptera	0.65	0.56	1.31	1.59	2.52	2.63
Trichoptera	0.11	0.49	0.81	0.69	0.38	0.41
Coleoptera	2.35	2.27	2.04	5.14	3.92	3.24
Total Abundance (organisms m ⁻²)	337.76	89.99	116.06	228.84	33.99	14.64
Number of Species	37	28	46	43	47	45
Proportional Abundance Aggregated by Order (%)						
Amphipoda	8.56	1.87	81.70	56.27	13.74	7.32
Ephemeroptera	0.00	0.45	1.90	0.27	6.58	7.89
Anisoptera	82.26	49.33	0.80	3.96	2.47	10.84
Zygoptera	8.26	44.66	12.02	36.25	57.17	31.02
Hemiptera	0.19	0.62	1.13	0.70	7.40	17.99
Trichoptera	0.03	0.54	0.70	0.30	1.11	2.82
Coleoptera	0.70	2.52	1.76	2.25	11.52	22.13
Diversity and Equitability						
Shannon-Wiener Diversity (H)	1.022	1.527	1.182	1.606	3.013	4.690
Equitability (E)	0.196	0.318	0.214	0.296	0.542	0.854

Macrophytes in Pond 37 were *Potamogeton foliosus* Raf., the moss *Sphagnum* sp., and *Chara* sp.. *Potamogeton foliosus* Raf. and *Sphagnum* sp. were dominant. About 35% of the area lacked well developed macrophytes and was covered in detritus. Bottom substrate consisted predominantly of coarse sand and was similar to that observed in Pond 34.

Dissolved minerals and colour in Pond 37 were similar to Pond 34. Nitrogen, phosphorus, and carbon varied slightly relative to Pond 34 although only dissolved nitrogen differed significantly (TABLE 6). These similarities were not unexpected since Pond 37 was also situated on relatively high, well drained topography, with a thin mantle of organic surface deposits overlying sand.

Twenty-eight species of arthropods were identified in Pond 37, the lowest observed from any of the ponds. However, total abundance was ~ 90 arthropods m^{-2} , a density substantially lower than that observed in Pond 34, but not the lowest relative to other study ponds. Shannon-Wiener diversity was 1.527 and equitability was 0.318, values slightly higher than those calculated for Pond 34. Although odonates dominated, *L. intacta* and *Enallagma cyathigerum* (Charpentier) were approximately equal in abundance. Coleoptera were more abundant in Pond 37 relative to Pond 34 and comprised $\sim 2.5\%$ of the identified arthropods (Figure 4). Four species of Coleoptera were unique to this site.

Pond 39 had the largest area ($\sim 82 m^2$), a volume of $\sim 58 m^3$, nearly twice the volumes in ponds 34 and 37, and a maximum depth of 1.35 m. Bottom macrophyte cover was composed of several species of *Potamogeton*, scattered *Chara* sp., and some limited

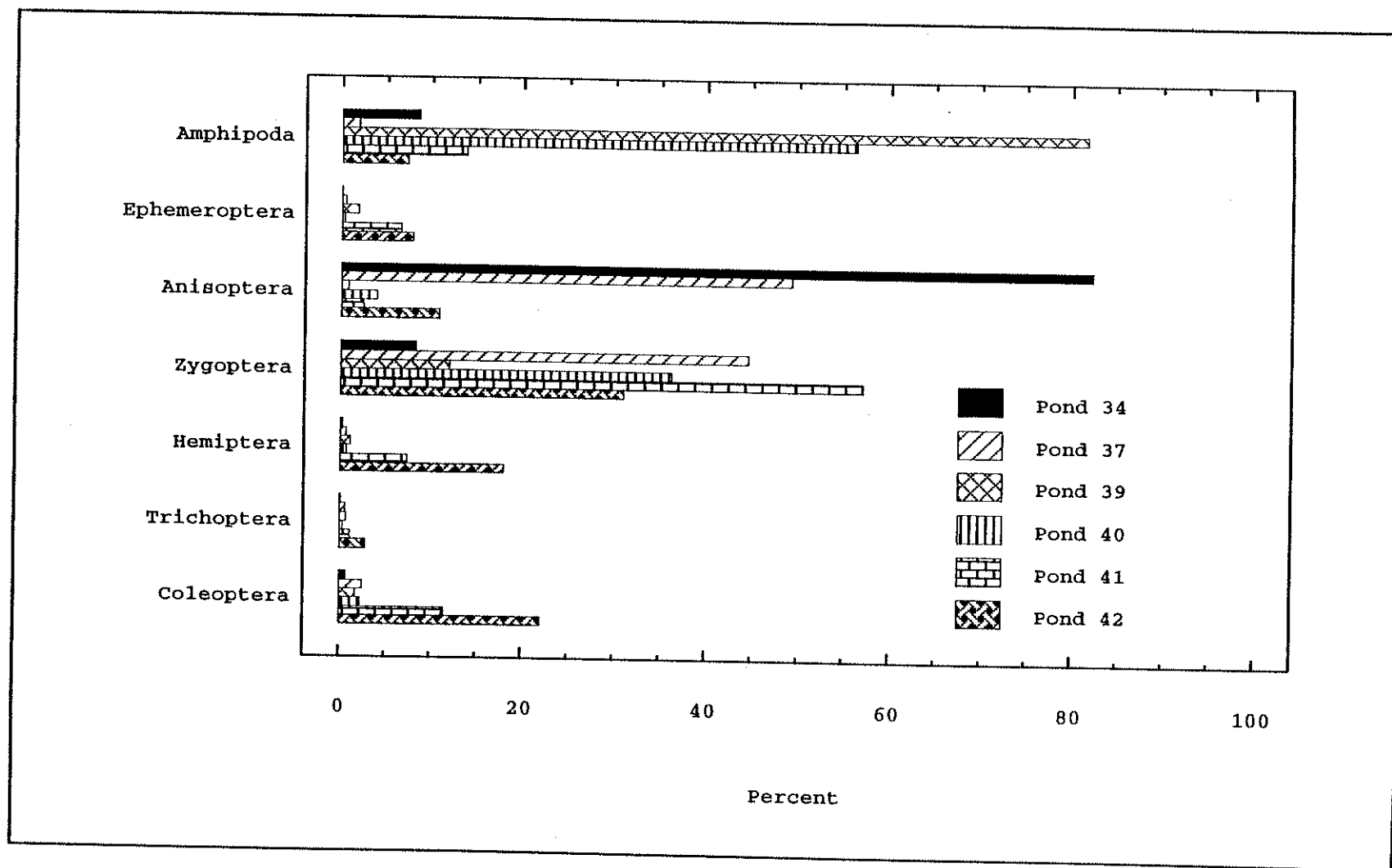


Figure 4. Bar graph showing percent composition of the arthropod community, aggregated by order, collected from the six Sandilands Provincial Forest study ponds.

Carex sp. colonized pond margins. Detritus covered 50% of the bottom area. Bottom substrate in Pond 39 was principally medium sand.

Water chemistry in Pond 39 differed significantly from ponds 34 and 37. Principal among these differences were elevated colour, organic carbon, and several forms of nitrogen, whereas dissolved minerals, pH, and inorganic carbon were lower. These differences in water chemistry were a reflection of subtle differences in the surrounding surface deposits. Organic soils near Pond 39 were deeper than at either pond 34 or 37. Surrounding vegetation consisted of alder and willow, typical of poorly drained sites, along with mixed deciduous trees. The thicker organic mantle combined with the finer underlying sands would result in slower infiltration of precipitation relative to ponds 34 or 37, which would allow more opportunity for dissolution of organic materials present in the upper-most layers of soil. In addition, nearby marsh and bog areas may provide a source of highly coloured water.

Hyalella azteca (Saussure) comprised over 80% of the arthropods in Pond 39. *Enallagma cyathigerum* was the only other species to contribute over 10% to total abundance. Although 46 species were identified, diversity and equitability were low (1.182 and 0.214, respectively), reflecting the dominance of one or two taxa. Ten species were present in Pond 39 that were not identified from other ponds, including all four species of Limnephilidae larvae. Total abundance of all arthropods was 116.06 m⁻², indicating a standing stock slightly higher than Pond 37 but substantially less than Pond 34.

Pond 40 was similar in physical configuration to Pond 39. *Potamogeton foliosus* Raf., *Utricularia vulgaris* L., and *Chara* sp. were the dominant macrophytes in a diverse

community. The bottom sediments in Pond 40 were composed principally of medium and fine sands. Water chemistry resembled that of Pond 39, except for slightly reduced colour and elevated concentrations of inorganic carbon and dissolved minerals. The elevated inorganic carbon, similar to Pond 34, was indicative of enhanced primary productivity in the presence of calcium or magnesium. Calcium concentration was significantly higher in Pond 40 than in other study ponds; the likely source being nearby calcareous till derived from carbonate rocks and deposited during glaciation. The surrounding vegetation and surface soils were similar to Pond 34, although the surface organic mantle was deeper at Pond 40.

Diversity and equitability in Pond 40 were similar to ponds 34, 37, and 39. As in Pond 39, *H. azteca* was dominant and comprised over 50% of the taxa. *Enallagma cyathigerum* was more abundant in Pond 40 ($\bar{X} = 81 \text{ m}^{-2}$) than in other study ponds. Nine species, mainly Coleoptera, were unique to Pond 40.

Pond 41 was similar in size to ponds 34 and 37 but was substantially smaller in area and volume than ponds 39 and 40. Maximum depth was 1.65 m. The macrophyte community consisted of an association of *P. foliosus* Raf., *Chara* sp., *P. gramineus* L., and *Sphagnum* sp.. *Typha* sp. colonized the eastern margin of the pond. Bottom sediment consisted of medium and fine sands, similar to that observed in Pond 40.

Water chemistry in Pond 41 was characterized by highly coloured water with low pH, dissolved minerals, and inorganic carbon, and elevated nitrogen, phosphorus, and organic carbon, relative to the other study ponds. Pond 41 is located on the periphery of an extensive marsh and bog area characterized by *Carex* sp. along with sparse groups of willow and alder. Thus, the observed chemistry reflects contributions of water from the

adjacent bog. Flooding of Pond 41 from the surrounding bog occurred on at least one occasion during a period of high rainfall in the summer of 1990 and may occur with some frequency during spring melt.

Although nitrogen and phosphorus were higher in Pond 41 than other ponds, overall primary productivity was probably lower, as indicated by low inorganic carbon concentrations. Although the nutrient yield of the surrounding extensive marsh and bog area was probably greater than observed in other study ponds, as evidenced by high organic nitrogen concentrations, overall primary productivity may have been limited by the highly coloured water. Phosphorus therefore, may be remaining in solution rather than being incorporated into macrophyte tissue. The macrophyte community was well developed, but sparse relative to most other ponds.

Pond 41 was the richest site, with 47 taxa being identified. Diversity and equitability, at 3.013 and 0.542, respectively, were substantially greater than observed in ponds 34, 37, 39, or 40. However, total overall abundance ($\bar{X} \sim 34$ arthropods m^{-2}) was about one order of magnitude lower. *Enallagma cyathigerum* was the dominant species and comprised nearly 60% of the fauna. Eleven species, all Coleoptera, were unique to Pond 41.

Pond 42 was the deepest pond and held the greatest volume, although it was similar in area to ponds 39 and 40. As in Pond 39, the macrophyte community was diverse, but sparse relative to other study ponds. The community was composed of an association of *Chara* sp., *U. vulgaris* L., *Sphagnum* sp., *P. foliosus* Raf., with *Scirpus* sp. and *Carex* sp. encroaching into the pond along some margins. Bottom sediments were principally medium and fine sands.

Water chemistry in Pond 42 was similar to that observed in Pond 41, probably because of the nearby bog area. Dissolved minerals, as evidenced by conductivity and total dissolved solids, were higher in Pond 42 and were similar to concentrations observed at other study sites. Overland flooding was unlikely. Pond 42 was located on slightly higher, relatively well-drained soils, unlike Pond 41, with surrounding aspen, birch and alder. Primary productivity was similar to other ponds, as indicated by similar inorganic carbon concentrations. However, some of this productivity may have been occurring in phytoplankton rather than rooted macrophytes. Total phosphorus concentrations were similar to those observed in Pond 41, but dissolved phosphorus was lower, suggesting that more phosphorus was being incorporated into plant tissue in Pond 41 than in Pond 42. The highly coloured water may limit light penetration required for macrophyte growth, allowing algae some competitive advantage. This observation is partly supported by the relatively higher turbidity and particulate phosphorus concentrations, which would be expected as a result of increased algal growth.

Pond 42 had the highest arthropod diversity and equitability of all study sites. Equitability was 0.854, indicating that abundance was relatively evenly distributed among a larger number of taxa. Anisoptera, Zygoptera, Hemiptera, and Coleoptera all contributed more than 10% to the overall abundance (Figure 4). Pond 42 was similar in richness to ponds 39, 40, and 41; 45 species were identified and enumerated. However, overall abundance ($\bar{X} \sim 15$ arthropods m^{-2}) was lowest of all study ponds. Nine species were unique to Pond 42.

Canonical Correspondence Analysis

Species, sites and vectors representing pH, area of pond bottom covered with macrophytes, and percent bottom sediment comprised of silt are shown on the first two canonical axes in Figure 5. In this CCA ordination triplot, environmental variables are shown as arrows whose direction is towards the greatest variability. The length of the environmental vector is determined by the predicted rate of change in weighted average and thus explains the variation observed in species distribution or abundance along the arrow (Dixit *et al.* 1989). Longer arrows are therefore more important in explaining observed variation in species abundance. Vectors positioned close to a canonical axis indicate high correlation with that axis. Species common to all ponds and present in all ponds in relatively similar abundances will be plotted close to the origin. Ponds midway along the environmental gradient will also be plotted close to the origin.

The combination of pH, total area of bottom covered with macrophytes, and percent silt accounted for the greatest amount of variability in abundance of the species of interest. The fit of the overall model and the fit on the first canonical axis were highly significant ($p = 0.005$ and 0.004 , respectively) when tested with Monte Carlo permutation under the null model (TABLE 9). Variance inflation factors (TABLE 10) were all less than 3.0, indicating that each variable provided unique information to the model. ter Braak (1991) advised that if variance inflation factors are greater than 20, the two variables are correlated and therefore not providing unique information to the model. Variance inflation factors greater than 20 yield a highly unstable model (ter Braak 1991).

The gradient length for the first canonical axis is ~ 2.75 standard deviation units. The gradient length represents the approximate species turnover rate along the axis (Allen

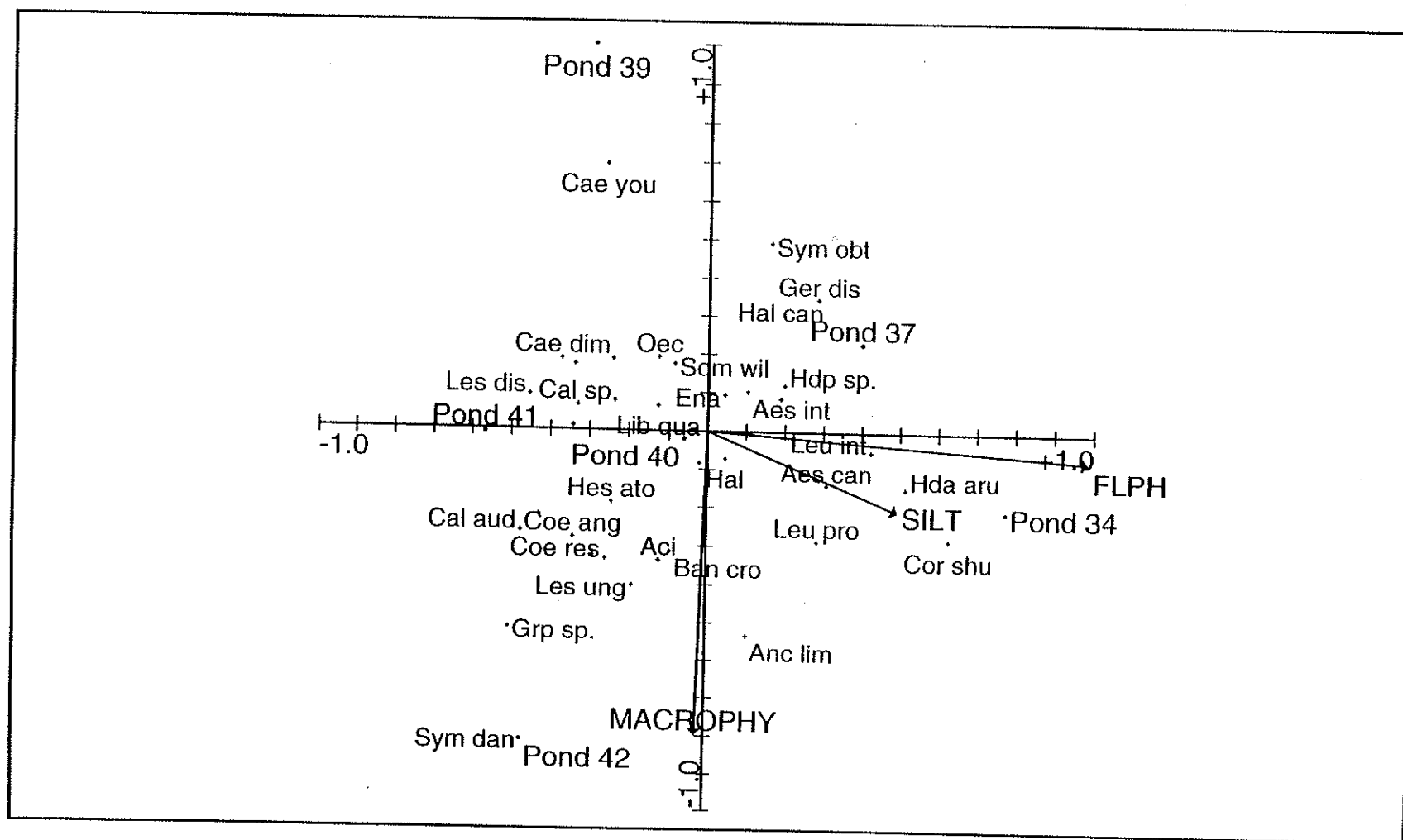


Figure 5. Ordination triplot showing species, environmental vectors, and the six Sandilands Provincial Forest study ponds along the first two canonical axes. Species codes are listed in TABLE 8. FLPH = pH, MACROPHY = area covered by macrophytes, and SILT = % bottom substrate comprised of silt.

TABLE 9. Results of the Monte Carlo permutation test on the fit of the CCA model of arthropods with pH, silt, and area covered by macrophytes in the six Sandilands Provincial Forest study ponds.

Monte Carlo Permutation Test	Variable	Value
Number of permutations under null model		1000
Test of significance of first canonical axis	Eigenvalue	0.365
	F-ratio	1.08
	P-value	0.004
Overall test	Trace	0.77
	F-ratio	1.85
	P-value	0.005

TABLE 10. Regression/canonical coefficients for standardized variables and variance inflation factors generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds.

	Axis 1	Axis 2	Axis 3	Axis 4	Variance Inflation Factors
Eigenvalue	0.3650	0.2438	0.1564	0.1597	
pH	0.8843	-0.5103	-0.6453	0.0000	1.4587
Silt	0.2497	0.9556	1.2770	0.0000	2.6063
Macrophyte Cover	-0.1463	-1.4573	-0.2770	0.0000	2.2217

and Peet 1990). ter Braak (1991) advised that data sets with gradient lengths less than 1.5 should be analyzed with multivariate methods based upon linear correlations, such as principal components analysis. Species correlations with environment data over a narrow range are likely linear rather than uni-modal, making indirect gradient methods more appropriate. When gradient lengths along the first axis are between 1.5 and 3.0, data sets can be analyzed by either indirect or direct gradient methods (ter Braak and Prentice 1988). Data sets with gradient lengths greater than 3.0 are ideally suited for direct gradient methods such as CCA. Because the gradient length of the first canonical axis exceeds ter Braak's (1991) minimum, and is near the upper bounds of the range where either method could be used (ter Braak and Prentice 1988), CCA was considered appropriate.

Species and environment axes 1, 2, and 3 are highly correlated ($r = 0.9994$, 0.9962 , and 0.9734 , respectively; TABLE 11). pH was correlated with the first constrained canonical axis, which accounted for the greatest observed variability in the species data ($\sim 35\%$; TABLE 12). Area covered by macrophytes was correlated with the second constrained canonical axis, which accounted for an additional 23.4% of the observed species variability. Percent silt was correlated with the third canonical axis. The third constrained canonical axis accounted for an additional 15.0% of the species variability. Remaining variability (27.5%) was accounted for in the fourth and, if extracted, subsequent unconstrained axes. The remaining variability not accounted for in the first three constrained axes is relatively small, indicating that most observed variability in the species distribution and abundance is related to the three supplied environmental variables. It is probable that the correlations of the three environmental factors with the three canonical axes are significant, since the t -values of the regression/canonical

TABLE 11. CCA weighted correlations of arthropod species collected from the six Sandilands Provincial Forest study ponds and environment axes formed with pH, silt, and area covered by macrophytes.

	Species Axis 1	Species Axis 2	Species Axis 3	Species Axis 4	Environment Axis 1	Environment Axis 2	Environment Axis 3	Environment Axis 4
Species Axis 1	1.0000							
Species Axis 2	-0.0023	1.0000						
Species Axis 3	-0.0004	-0.0124	1.0000					
Species Axis 4	-0.0348	0.0671	0.0064	1.0000				
Environment Axis 1	0.9994	0.0000	0.0000	0.0000	1.0000			
Environment Axis 2	0.0000	0.9962	0.0000	0.0000	0.0000	1.0000		
Environment Axis 3	0.0000	0.0000	0.9734	0.0000	0.0000	0.0000	1.0000	
Environment Axis 4	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
pH	0.9871	-0.0725	-0.1350	0.0000	0.9877	-0.0728	-0.1385	0.0000
Silt	0.4940	-0.2092	0.8211	0.0000	0.4943	-0.2100	0.8435	0.0000
Macrophyte Cover	-0.0217	-0.7953	0.5857	0.0000	-0.0217	-0.7984	0.6017	0.0000

TABLE 12. Summary statistics of the CCA model of arthropods with pH, silt, and area covered by macrophytes in the six Sandilands Provincial Forest study ponds.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.365	0.244	0.156	0.160	1.041
Species-environment correlations	0.999	0.996	0.973	0.000	
Cumulative percentage variance of species data	35.1	58.5	73.5	88.8	
Cumulative percentage variance of species-environment relation	47.7	79.6	100.0		
Sum of all unconstrained eigenvalues					1.041
Sum of all canonical eigenvalues					0.765

coefficients are all greater than 4 ($df = 3$; TABLE 13). TABLE 13 is a combination of both regression and canonical coefficients. It is therefore not possible to compare the t -values directly to Student's t probabilities since canonical coefficients are inherently more variable than regression coefficients (ter Braak 1991).

The goal of CCA application to the aquatic insect data within the pond habitat was to account for the greatest variability of as many species as possible, but more importantly, to ensure the best fit for those species with replacement potential (*i.e.*, the output from Chapter IV). It is for the latter species that judgments must be made concerning their ability to colonize and to achieve similar population success as the hypothetically lost species. The environmental variables that best describe the overall community structure may not be the ones that best describe the variability in the principal species of interest. Thus, numerous attempts were made not only to select the CCA model that best accounted for the entire community structure, but also to select the model that accounted for the greatest variability in the species with replacement potential.

The CCA model that best described the overall species distribution and abundance involved the environmental variables pH, pond circumference, and percent bottom area covered with *Sphagnum* sp.. Both the fit of the overall model and the first canonical axis were significant ($p = 0.004$ and 0.018 , respectively), and all variables had low variance inflation factors. Abundance of the amphipod *Hyaella azteca* was directly correlated with the extent of bottom surface covered by *Sphagnum* sp.. However, *H. azteca*, a dominant arthropod in most ponds, was not of principal interest since it did not have replacement potential. pH, pond circumference, and area of bottom covered with *Sphagnum* sp. explained, on average, 63.7% of the variability in distribution and abundance of the 36 species of interest that have replacement potential.

TABLE 13. *t* values of regression coefficients generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds and pH, silt, and area covered by macrophytes.

	Axis 1	Axis 2	Axis 3	Axis 4
Fraction of Variance Explained	0.4770	0.3186	0.2044	0.0000
pH	29.7182	-6.7796	-3.2113	0.0000
Silt	6.2789	9.5258	4.7546	0.0000
Macrophyte Cover	-3.9845	-15.7333	-1.1170	0.0000

Hyaella azteca was deleted from the data set, and CCA was re-run with forward selection of variables. pH, area of bottom covered by macrophytes, and area of bottom covered by plant communities associated with *Potamogeton* spp. provided the best fit model. This model was attractive since all variables had low variance inflation factors, and the fit of the overall model and the first canonical axis were significant ($p = 0.005$ and 0.002). This selection of environmental variables, on average, accounted for 69.2% of the observed variability in distribution and abundance of the 36 species of interest, and was therefore considered an improvement over the previous model.

The data set was examined in detail to determine if minor adjustments could be made to the selection of environmental variables to yield an overall better fit. Area covered by plant communities associated with *Potamogeton* spp. was inversely related with percent silt ($r = -0.9317$, $\beta \neq 0$, $p = 0.007$). When percent silt was substituted into the CCA model for area covered by plant communities associated with *Potamogeton* spp., the model had the same attractive features and the fit of the overall model was the same as before ($p = 0.005$), but the fit of the first canonical axis was marginally poorer ($p = 0.004$ rather than $p = 0.002$). However, this latter model explained a greater proportion of the observed variability in distribution and abundance of the 36 key species (cf. 69.2% with 71.7%), even when adjusted for the slightly poorer overall fit. Approximately 30% of the key species had cumulative fits $> 90\%$, over half of the key species had cumulative fits $> 75\%$, and $< 15\%$ of the key species had cumulative fits $< 50\%$. Thus, the CCA model with pH, percent silt, and percent bottom area covered by macrophytes accounted well for the overall distribution and abundance of aquatic insect species in the six study ponds, and in particular, accounted best for the variability observed in the 36 key species.

There was a negligible effect to adding 0.0001 to the abundance of all species. The significance of both the fit of the first canonical axis and the overall fit did not change. Species scores did not change (Student's *t* paired difference test, $\alpha = 0.05$), although standard deviations predictably increased mainly because of the increase in standard deviations from zero for species occupying a single pond. Standard deviations for species found in more than one pond changed by less than 1%. The cumulative fit of the 36 key species changed by less than 0.002%. Consequently, this transformation did not significantly affect the model but provided output that could be used to calculate niche widths based upon both species presences and absences.

The appropriateness of the niche width representation by 95% confidence ellipses was tested through calibration using the species present only in single ponds. Niche width of species occurring in only one pond should overlap only the site score of that pond. If the estimated niche width is too wide, successful recovery of original plotting position would not be possible along any of the axes, resulting in predicted location of a given species in several other ponds. If the estimated niche width is too small, overlap with the environment of ponds in nearby orthogonal space would occur infrequently or not at all. Of the original 108 taxa, 56 occurred in only one pond. Calculation of species-environment overlap for these 56 species yielded correct pond placement 100% of the time when all three constrained axes were considered; this outcome was not too surprising because the species scores were weighted by the site scores. Even so, the calibration exercise was not trivial since estimated species niche width overlapped more than one pond between 30% and 40% of the cases along the first three canonical axes. The implication was that the niche widths may be overestimated. However, in cases where misclassification occurred, it always occurred with the same ponds. Species that occurred in single ponds were never misclassified into more than two ponds and in none of

the cases did misclassification occur in two ponds simultaneously along all three canonical axes. Thus, in all cases, species were classified into the correct single pond along at least one of the axes; even canonical Axis 3 was an important component of the CCA model. When misclassification occurred along canonical Axis 1, it was consistently with ponds 41 and 42. Similarly, misclassification along canonical Axis 2 always occurred with ponds 40 and 41, and misclassification along canonical Axis 3 always occurred with ponds 40 and 42. There was very little separation in orthogonal space along the respective axes (*e.g.*, < 8% of the gradient length) for the misclassified ponds. Rather than niche widths being overestimated, ponds 41 and 42 could not be successfully separated along canonical Axis 1, simply because these ponds were very similar in those attributes represented by the first axis (*i.e.*, pH). Similarly, ponds 40 and 41 were not well separated on the basis of macrophyte cover, represented by canonical Axis 2, and ponds 40 and 42 were not well separated on the basis of canonical Axis 3.

A similar pattern emerged when only the 36 key species were examined. Of the 36 key species, eight were present in single ponds. In all eight cases, species niche width, estimated by the 95% confidence ellipse projected onto the first canonical axis, overlapped only with the LC site score of the pond in which the species was actually found. A similar success in recovering species position along the second and third canonical axes was observed in six of the eight cases.

The calibration exercise was re-run using species scores plus or minus one standard deviation to represent niche width, as used by Chessel *et al.* (1982) and Lebreton *et al.* (1988). Niche widths appeared to be underestimated because all species were correctly placed along the first canonical axis. If one were using strictly a mathematical approach, this outcome would be expected given the algorithms used by CCA. However,

this result is intuitively unrealistic since it is expected that at least some species should be incorrectly placed given the similarity in the pond environment represented by canonical Axis 1. Therefore, it is inferred that the method of estimating niche width using 95% confidence regions is more appropriate than merely representing niche width by species score plus or minus one standard deviation.

Detrending is sometimes necessary in CCA to remove the "arch" effect that results when the first and second axes are correlated by a second-order polynomial function (ter Braak 1991). The arch effect occurs when a superfluous variable is highly correlated with the second canonical axis (ter Braak 1991). Because percent area covered by macrophytes is highly correlated with the second axis, the need for detrending was explored. Detrended Canonical Correspondence Analysis (DCCA), with detrending by second-order polynomials, was used with the same three input variables. The eigenvalue for the second axis did not change significantly (0.2297) relative to no detrending (0.2449), an indication that detrending was not necessary. Detrending by third- and fourth-order polynomials was not necessary. ter Braak (1991) suggested that when the eigenvalues for the third and fourth axes steadily decline, detrending by second-order polynomials may not be sufficient. Although both eigenvalues for the third and fourth axes were less than those for the first and second axes, they did not decline in the manner stated by ter Braak (1991); further detrending was therefore, unwarranted. Thus, percent bottom area covered by macrophyte vegetation is an important variable in the selected model. ter Braak (1991) advised that the need for detrending can be avoided when the variables are carefully selected and the number of selected variables is small. The selected CCA model therefore, meets these requirements. The finding that detrending was not necessary, at least with this data set, is consistent with Palmer (1993).

Typically, CCA is used with nominal (presence-absence) species data when relationships between species tolerance and environment are examined. CCA was re-run using nominal data with forward selection of variables. The same three variables selected when CCA was run with abundance data were also selected once *H. azteca* was removed from the data set. However, the fit of the first canonical axis was not significant ($p = 0.10$) although the overall model was ($p = 0.04$). Sixty-five percent of variation in distribution of the key species was accounted for in the nominal data model. This is substantially less than the variation in key species accounted for when abundance data was used. Because the overall nominal-data model was significant and the variables selected provided the best fit, the same three variables may influence colonization potential as well as affecting population success following colonization. Thus, the abundance-data model provided the same information concerning colonization potential as the nominal-data model, but also provided additional information concerning variability in population success in relation to the same environmental variables.

The selected variables should be considered as representative of a larger set of inter-related environmental variables or processes rather than sole explanatory variables. pH, percent silt, and percent bottom area covered by macrophytes were individually correlated with a number of other measured variables. For example, pH was correlated with dissolved phosphorus, dissolved organic carbon, several species of nitrogen, and colour. Silt was correlated with area covered by macrophyte community associated with *Potamogeton* spp., and percent bottom area covered by macrophytes is the inverse of pond area covered with detritus. Consequently, although the selected variables provided the best model, they likely represented a number of other related factors that, in combination, accounted for the distribution and abundance of the aquatic insect community.

pH or the larger set of correlated environmental variables that it represents can only be considered to influence community structure should there be a significant difference in such variables among the study ponds. Such differences were examined using Kruskal-Wallis and Duncan's multiple range tests (TABLE 6). The ponds can be separated into three groups, based upon pH. Ponds 34 and 37 both have pH ~ 8.0. Ponds 39, 41, and 42 all have a more acidic pH than ponds 34 and 37. Pond 40 has a pH midway between the two groups and is not distinguishable from either group. The ponds also form two roughly similar groups based upon dissolved organic carbon, several forms of nitrogen and dissolved phosphorus.

Pond Similarity Assessment

Multivariate cluster analysis should link ponds with similar community structure in an identical manner to linkages formed independently based upon environmental factors, and thereby provide a second test of the data. Based upon log-transformed species abundance and deletion of *H. azteca*, ponds 37 and 40 were most similar, followed by ponds 41 and 42. Both ponds 39 and 34 were subsequently linked with ponds 37 and 40 (Figure 6A). The same pattern appeared when the variables selected by CCA were used as input to cluster analysis. Minor differences occurred in the last linkage; Pond 34 was grouped with Pond 42, whereas it was linked with ponds 37, 40, and 39 when insect abundances were used (Figure 6B).

The ponds were then clustered using all 91 measured or derived environmental variables as input. However, the linkages formed did not match those formed by either insect abundances or CCA selected variables although there were several similarities

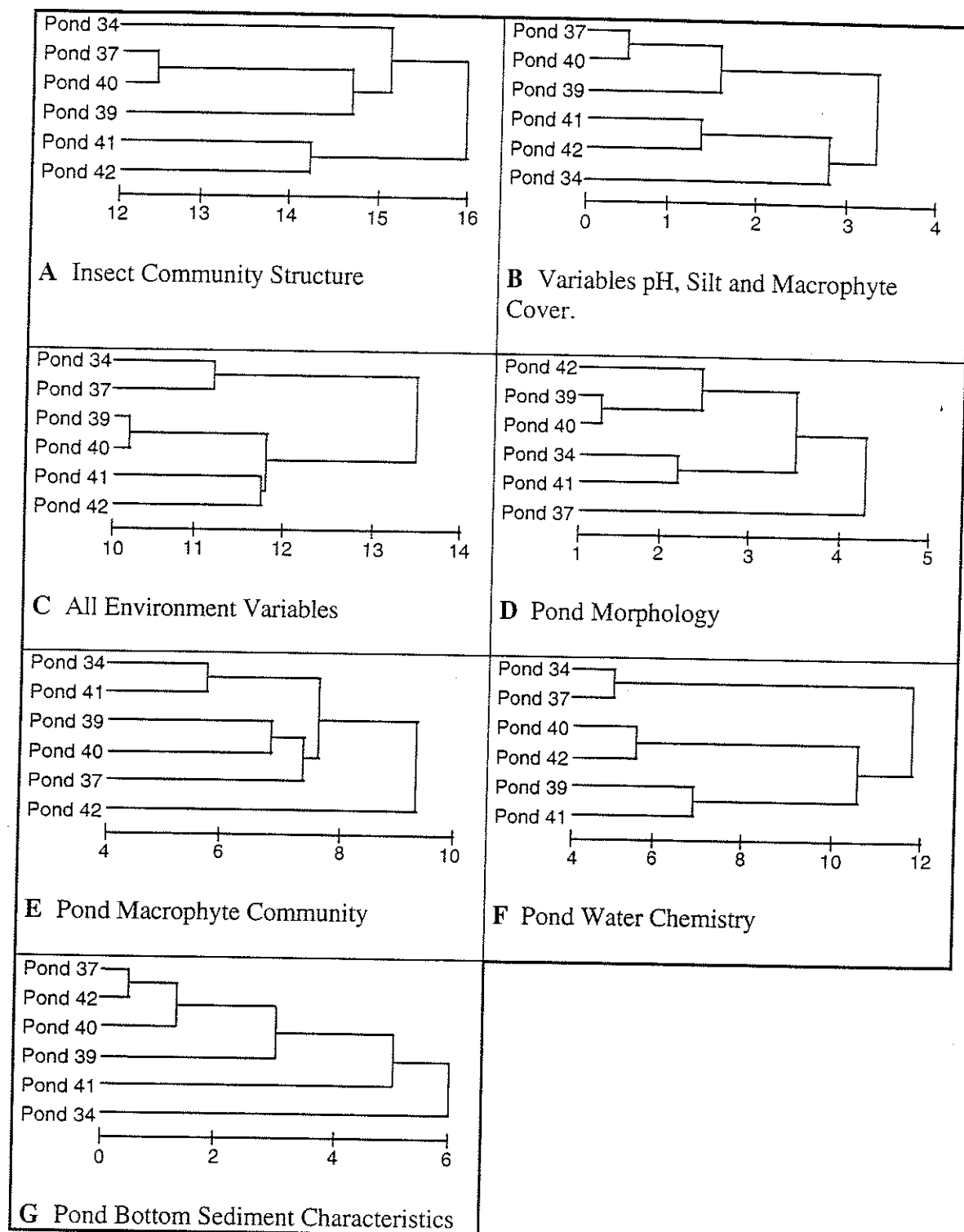


Figure 6. Cluster dendrograms showing linkages between the six Sandilands Provincial Forest study ponds based upon arthropod community structure and various measures of environment. Euclidean distances are shown on the absissae.

(Figure 6C). Thus, not all of the 91 environmental variables appear to influence the aquatic insect community. The similarity between the cluster dendograms formed by insect abundance and by the variables selected by CCA, appears more than a coincidence; the aquatic insect community is probably influenced by pH, percent silt, and percent area of bottom covered with macrophyte beds.

Since many of the environmental variables are correlated, it is possible that the observed variability in the arthropod community can be explained solely on the basis of either water chemistry, pond morphology, structure of the macrophyte community or bottom sediment composition rather than a limited combination of variables. To examine this possibility, all water chemistry variables, all measures of pond morphology, all descriptors of macrophyte community, and all bottom sediment characteristics were used as input to cluster analyses. A simpler univariate approach would be suggested if ponds were linked by any one of these four groups of variables in the same manner as linkages based upon arthropod community structure. However, none of the linkages formed by the four categories of environmental variables matched those formed by measures of arthropod community structure (Figure 6D, 6E, 6F, and 6G). Thus, it is apparent that the structure of the arthropod community is influenced by a limited combination of environmental factors and that the three variables selected by CCA best describe this influence.

Community Structure and Environment

Communities are shaped by density-dependent influences, such as competition for resources and predation, or density-independent factors, such as environmental limitations and disturbances (May 1986, Sousa 1979). Dytiscid beetles were shown by Larson (1985)

to be affected by a number of environmental factors including pH of the water, elevation, flow, habitat stability, salinity, pond size, mineral content, mosses, hydrophytes, and terrestrial plant material. The structure of Coleoptera and Hemiptera communities is influenced by salinity in the study sites examined by Lancaster and Scudder (1987). Odonata in bog pools in Newfoundland appeared to be influenced by habitat stability and pool size (Larson and House 1990). Odonata, although influenced by environmental factors, may subsequently affect the presence and abundance of other aquatic insects through intense predation (Benke 1976, 1978; Thorp and Cothran 1984; Larson 1990; Larson and House 1990).

An environmental variable must have sufficient range for the arthropod community to respond to it. pH did not influence the aquatic insect community in a study on bog communities in Newfoundland (Larson 1990) but the pH range of the bog ponds was relatively narrow (4.2 to 4.6). Changes within the insect community in response to pH variation within this narrow range may be difficult to detect or may not exist. In contrast, pH strongly influenced the richness of invertebrates in acid streams in southern England (Hildrew *et al.* 1984). These streams had mean annual pHs ranging from 4.8 to 6.1. It was concluded that the number of species available for colonization increased with pH. Species richness increased principally because within the region there was a large pool of colonizing species tolerant of higher pH.

The nature of the pH influence on the invertebrate community appears to be much different between the Hildrew *et al.* (1984) study and the Sandilands Provincial Forest study ponds. Species richness increased in the present study with declining pH. Ponds 41 and 42 had the highest number of species and had the lowest pH. The lowest individual pH value observed during the present study (6.2) was near the highest mean annual pH

within the study sites examined by Hildrew *et al.* (1984). Hence, the response observed by Hildrew *et al.* (1984) may be related to physiological intolerance of aquatic insects to low pH, whereas the response within the present study appears related to phenomena other than direct stress caused by pH.

Macrophyte cover is an important factor affecting the structure of aquatic communities (*e.g.*, Larson 1985). In the Sandilands Provincial Forest pond habitat, overall macrophyte cover was an important factor. Secondly, the composition of the macrophyte community may also have been important because aquatic arthropod distribution and abundance was related to the area covered by various species of *Potamogeton*. Further, population success of *H. azteca* appeared to be directly related to the extent of pond substrate covered with *Sphagnum* sp.. Rodríguez and Magnan (1993) found aquatic vegetation to be an important factor in Laurentian Shield lakes, although information was not available on the composition of the macrophyte community. These authors also found sand and gravel to be important factors in shaping the macrobenthic community. Sand and gravel did not appear to be important factors in the Sandilands pond habitat. However, percent silt provided an equivalent fit as percent area covered by *Potamogeton* spp..

Insect communities in bog pools in Newfoundland were structured by water level stability and by pool size (Larson and House 1990). Water level stability in the present study did not appear to be a significant factor. Water levels in Larson and House's (1990) study varied so substantially that some pools actually dried. Therefore, the determinant in Larson and House (1990) may have been temporary versus permanent habitats, rather than water-level fluctuation. Temporary pools can only sustain species that are highly mobile or species with life-history adaptations for periods of habitat loss. Larson and House

(1990) also suggested that small pools may be affected to a greater extent than large pools by substrate freezing during the winter period because there may be a smaller pool of tolerant species available that can withstand winter freezing. Water level fluctuations in the six Sandilands Provincial Forest sites were minor by comparison; all of the ponds were permanent and all of the ponds probably were similarly affected by winter freezing.

Pond size was a factor both in Larson and House's (1990) study and the present study. In the present study, pond size was a contributing variable in the original model prior to elimination of the dominant *H. azteca*. Total abundance increased with pool size probably because of pond stability; small pools were more likely to be temporary or to freeze completely during the winter period, whereas large pools were permanent and had less substrate freezing during winter (Larson and House 1990). The relationship between increasing arthropod abundance and pool size may also be related to changes in the macrophyte community or the increased availability of refugia; Larson and House (1990) observed an increase in density of rooted macrophytes as pond size increased. Pond circumference, although not significant by itself, improved the overall CCA model fit and provided unique information to this study. However, the influence of pond size on the structure of the arthropod community is not clear, since there is no apparent correlation between the abundance of any taxon or group and pond size. This is not unexpected in multivariate ordination methods, especially when attempts are made to understand the significance of the second or third axes, because all factors are acting in concert. Pond circumference may relate to site selection for oviposition or oviposition success of one or more pond taxa. Pond circumference or other measures of pond size did not contribute significantly to the final model once *H. azteca* was removed from the analysis.

The distribution and abundance of aquatic insect communities may be influenced by odonate predation (Benke 1976, 1978; Baker 1980; Thorp and Cothran 1984; Larson 1990; Larson and House 1990); a similar relationship may exist in the ponds of this study. The reduced number of unique species in Pond 37 relative to other ponds might support this hypothesis. Intense predation by both *E. cyathigerum* and *L. intacta* may have extirpated unique species from Pond 37. Larson (1990) attributed the absence of Coleoptera larvae from certain habitats to odonate predation. Coleoptera did not appear to be similarly affected in the ponds of this study because total Coleoptera abundance was relatively similar in all ponds, with or without dominant odonate populations. Pond 40 had the greatest density of Coleoptera, but also had an abundant population of *E. cyathigerum*. Thorp and Cothran (1984) and Baker (1980) also found odonate predation capable of significantly influencing the structure of aquatic invertebrate communities, although it was not the only factor. However, the few unique species located in Pond 37 may be a result of its small size; this pond was ~ 20% smaller in area than other ponds, suggesting that it may have fewer available niches than other larger ponds (Briand 1983).

Replacement Potential Based Upon Niche Overlap in Canonical Space

Confidence regions for each species are shown in Appendix I along with general output from CCA. Detailed niche overlap and potential for replacement information are listed in Appendix II. An example of the detailed information generated from the niche overlap in canonical space analysis is shown in TABLE 14.

In the example shown in TABLE 14, *Caenis youngi* and *C. diminuta* were identified as potential replacements for each other (see Chapter IV). *Caenis youngi* can only replace *C. diminuta* by Model I in Pond 42, since this is the only pond in which *C.*

TABLE 14. Example output from the niche overlap in canonical space analysis using two species of Ephemeroptera collected from the Sandilands Provincial Forest study ponds. Complete analysis is shown in Appendix II.

Lost Species	Replacement Species
<i>Caenis diminuta</i>	<i>Caenis youngi</i>
Inter-Species Overlap: Axis 1	97.18%
Inter-Species Overlap: Axis 2	51.60%
Inter-Species Overlap: Axis 3	100.00%
Inter-Species Overlap: Axis 4	100.00%
Species-Environment Overlap: Axis 1	Pond 39; Pond 40; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;
Species-Environment Overlap: Axis 4	LC site scores not calculated for Axis 4
Model I: Available Ponds	Pond 42;
Model I: Potential for Replacement	Pond 42 (No);
Model II or III: Available Ponds	Pond 39;
Model II or III: Potential for Replacement	Pond 39 (Possible);
<i>Caenis youngi</i>	<i>Caenis diminuta</i>
Inter-Species Overlap: Axis 1	65.78%
Inter-Species Overlap: Axis 2	100.00%
Inter-Species Overlap: Axis 3	66.31%
Inter-Species Overlap: Axis 4	9.17%
Species-Environment Overlap: Axis 1	Pond 39; Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 3	Pond 39; Pond 40; Pond 42;
Species-Environment Overlap: Axis 4	LC site scores not calculated for Axis 4
Model I: Available Ponds	Pond 40; Pond 41;
Model I: Potential for Replacement	Pond 40 (No); Pond 41 (No);
Model II or III: Available Ponds	Pond 39;
Model II or III: Potential for Replacement	Pond 39 (Possible);

diminuta is present and *C. youngi* is absent. Overlap between *C. youngi* and *C. diminuta* is high along canonical Axis 1 (97.18%), and relatively low (51.60%) along canonical Axis 2. *Caenis youngi* overlaps Pond 42 along canonical Axis 1 but not along canonical Axis 2. Should *C. diminuta* be lost from Pond 42, *C. youngi* may not be able to replace its ecological function since it would not be able to colonize this specific habitat.

Canonical axes 1 and 2 accounted for the greatest variation in species distribution and abundance (35.1% and 23.4%, respectively; TABLE 12). Using only species that occurred in single ponds, all three constrained axes were important. Thus, judgments concerning inter-species overlap and species-environment overlap were made using information from the first three constrained axes.

Caenis youngi can only replace *C. diminuta* by Model II or Model III in Pond 39; this is the only pond in which both species co-exist. The principal consideration in Model II and III replacement is whether the replacement species can reach similar population success as the hypothetically lost species. Replacements were considered "probable" given the following considerations: (1) under present co-existence, the potential replacement species was at least as abundant as the hypothetically lost species; (2) when the potential replacement species overlapped the specific pond habitat available for Model II or III replacement along the first three canonical axes; and (3) when there was > 60% inter-species overlap along the first three canonical axes. When all three conditions were not met, the potential replacement was considered "possible". Inter-species overlap of 60% was arbitrary, but is a value widely used in overlap studies (*e.g.*, Fuller and Hynes 1987) and is consistent with the extent of overlap chosen in Chapter III to determine similarity between species. In any case, inter-species overlap played only a small role in determining whether a lost species could potentially be replaced by another. *Caenis*

youngi met only two of the three conditions, thus replacement was considered "possible". Although the niche overlap method used here is asymmetrical, the overall outcome of *C. youngi* replacement by *C. diminuta* and *C. diminuta* replacement by *C. youngi* was the same. Neither could replace each other in the available ponds by Model I, and replacement by Model II or III in the available pond was judged to be only "possible".

Niche overlap in canonical space did not result in the rejection of any of the 36 species identified in Chapter IV as having replacement potential. Rather, the conditions under which specific replacement could occur were refined considerably. Specific replacement hypotheses were developed for each pond and for each species across all ponds (TABLE 15).

Some generalizations can be made (TABLE 16 and TABLE 17). On average, ~ 33% of the original species in the overall ponds have potential replacements. The range of potential replacements is quite variable among ponds, with Pond 34 having potential replacements for > 50% of the total species, whereas only ~ 18% of the total species in Pond 37 have potential replacements. Replacement by Model I appears to be limited to a few species in the pond habitat. Out of 148 initial combinations of available ponds and species with Model I replacement potential, all but 16 (10.8%) were rejected through niche analysis in canonical space. In some ponds (Pond 34 and Pond 39), there were no species with potential for replacement by a Model I mechanism. All other ponds had at least one species with Model I replacement potential. On the other hand, there were 153 combinations of available ponds and species with Model II or III replacement potential; predictions were modified by niche overlap in canonical space such that only 38 (24.8%) remained "probable" replacements. The remaining combinations could not be rejected, but were qualified as having only "possible" potential.

TABLE 15. Hypothetically lost taxa (first column) and potential replacement taxa (subsequent columns) collected from the six Sandilands Provincial Forest study ponds with habitat and mode of replacement.

Lost Species	Replacement Species	
<i>Caenis diminuta</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Caenis youngi</i> Pond 42 (No) ^(a) ; Pond 39 (Possible) ^{(b)(c)} ;	
<i>Caenis youngi</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Caenis diminuta</i> Pond 40 (No); Pond 41 (No); Pond 39 (Possible);	
<i>Aeshna canadensis</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Anax junius</i> Pond 41 (No); Pond 34 (Possible);	
<i>Aeshna interrupta</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Anax junius</i> Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No); Pond 34 (Possible);	
<i>Anax junius</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Aeshna interrupta</i> None Available Pond 34 (Probable);	<i>Aeshna canadensis</i> None Available Pond 34 (Probable);

TABLE 15. Continued.

Lost Species		Replacement Species				
<i>Cordulia shurtleffi</i>	<i>Sympetrum danae</i>					
Model I: Potential for Replacement	Pond 34 (No);					
Model II and III: Potential for Replacement	Pond 42 (Possible);					
<i>Somatochlora williamsoni</i>	<i>Sympetrum obtrusum</i>	<i>Sympetrum danae</i>				
Model I: Potential for Replacement	Pond 34 (No); Pond 40 (Yes); Pond 41 (Yes); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No);				
Model II and III: Potential for Replacement	Pond 37 (Possible); Pond 39 (Possible);	Pond 42 (Possible);				
<i>Leucorrhinia hudsonica</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Banksiola crotchii</i>			
Model I: Potential for Replacement	None Available	None Available	None Available			
Model II and III: Potential for Replacement	Pond 34 (Probable);	Pond 34 (Probable);	Pond 34 (Possible);			
<i>Leucorrhinia intacta</i>	<i>Sympetrum danae</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia hudsonica</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No);	Pond 37 (No); Pond 39 (Yes); Pond 40 (Yes);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (Yes); Pond 40 (Yes); Pond 41 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 40 (No);
Model II and III: Potential for Replacement	Pond 42 (Possible);	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Possible); Pond 39 (Possible); Pond 42 (Possible);	Pond 40 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);

TABLE 15. Continued.

Lost Species		Replacement Species							
<i>Leucorrhinia proxima</i>	<i>Sympetrum danae</i>	<i>Ptilostomis</i> sp.	<i>Leucorrhinia intacta</i>	<i>Leucorrhinia hudsonica</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>	<i>Lestes congener</i>	<i>Banksiola crotchi</i>
Model I: Potential for Replacement	Pond 34 (No); Pond 41 (No);	Pond 34 (No); Pond 41 (No); Pond 42 (No);	None Available	Pond 41 (No); Pond 42 (No);	Pond 41 (No);	Pond 34 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No);	None Available	None Available
Model II and III: Potential for Replacement	Pond 42 (Possible);	None Available	Pond 34 (Probable); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Possible); Pond 42 (Probable);	None Available	Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 41 (Probable); Pond 42 (Probable);	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Probable);
<i>Libellula quadrimaculata</i>	<i>Somatochlora williamsoni</i>								
Model I: Potential for Replacement	None Available								
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 39 (Possible); Pond 40 (Possible); Pond 41 (Probable); Pond 42 (Possible);								
<i>Sympetrum danae</i>	<i>Somatochlora williamsoni</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Cordulia shurtleffi</i>					
Model I: Potential for Replacement	None Available	None Available	None Available	None Available					
Model II and III: Potential for Replacement	Pond 42 (Possible);	Pond 42 (Possible);	Pond 42 (Possible);	Pond 42 (Possible);					
<i>Sympetrum obtrusum</i>	<i>Somatochlora williamsoni</i>								
Model I: Potential for Replacement	None Available								
Model II and III: Potential for Replacement	Pond 37 (Possible); Pond 39 (Probable);								

TABLE 15. Continued.

Lost Species		Replacement Species			
<i>Lestes congener</i>	<i>Leuchorrhinia proxima</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>		
Model I: Potential for Replacement	Pond 39 (Yes); Pond 40 (Yes);	Pond 34 (No); Pond 39 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 40 (No);		
Model II and III: Potential for Replacement	Pond 34 (Probable); Pond 41 (Possible); Pond 42 (Possible);	Pond 40 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);		
<i>Lestes disjunctus disjunctus</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes congener</i>
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 41 (No);	Pond 39 (No); Pond 41 (No); Pond 42 (No); None Available	None Available
Model II and III: Potential for Replacement	Pond 41 (Possible); Pond 42 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 39 (Possible); Pond 42 (Probable);		Pond 39 (Possible); Pond 41 (Probable); Pond 42 (Probable);
<i>Lestes dryas</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes disjunctus disjunctus</i>	<i>Lestes congener</i>
Model I: Potential for Replacement	Pond 40 (Yes);	None Available	Pond 40 (Yes);	Pond 40 (No);	None Available
Model II and III: Potential for Replacement	None Available	Pond 40 (Probable);	None Available	None Available	Pond 40 (Probable);

TABLE 15. Continued.

Lost Species		Replacement Species		
<i>Lestes unguiculatus</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus disjunctus</i>
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 34 (No); Pond 39 (No); Pond 42 (No); None Available	Pond 34 (No);
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 39 (Possible); Pond 42 (Possible);		Pond 39 (Possible); Pond 42 (Possible);
<i>Coenagrion angulatum</i>	<i>Ptilostomis</i> sp.	<i>Enallagma cyathigerum</i>	<i>Banksiola crotchii</i>	
Model I: Potential for Replacement	Pond 41 (No); Pond 42 (No);	None Available	None Available	
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 40 (Probable); Pond 41 (Probable); Pond 42 (Probable);	Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);	
<i>Coenagrion resolutum</i>	<i>Ptilostomis</i> sp.	<i>Banksiola crotchii</i>		
Model I: Potential for Replacement	Pond 34 (No); Pond 41 (No); Pond 42 (No);	None Available		
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Possible); Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);		

TABLE 15. Continued.

Lost Species		Replacement Species			
<i>Enallagma cyathigerum</i>	<i>Ptilostomis</i> sp.	<i>Coenagrion angulatum</i>	<i>Banksiola crotchii</i>		
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No);	Pond 39 (No);		
Model II and III: Potential for Replacement	Pond 39 (Possible); Pond 40 (Possible);	Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 37 (Possible); Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);		
<i>Notonecta borealis</i>	<i>Notonecta irrorata</i>	<i>Hydaticus aruspex</i>			
Model I: Potential for Replacement	None Available	None Available			
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Probable);			
<i>Notonecta irrorata</i>	<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta borealis</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>
Model I: Potential for Replacement	Pond 34 (No);	Pond 34 (No); Pond 41 (No);	Pond 41 (No);	Pond 41 (Yes);	Pond 41 (No);
Model II and III: Potential for Replacement	Pond 41 (Possible);	None Available	Pond 34 (Possible);	Pond 34 (Possible);	Pond 34 (Possible);
<i>Notonecta kirbyi</i>	<i>Notonecta undulata</i>	<i>Notonecta irrorata</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>	
Model I: Potential for Replacement	None Available	Pond 39 (No); Pond 40 (No);	Pond 40 (No);	Pond 39 (No);	
Model II and III: Potential for Replacement	Pond 39 (Probable); Pond 40 (Probable);	None Available	Pond 39 (Possible);	Pond 40 (Possible);	

TABLE 15. Continued.

Lost Species		Replacement Species				
<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>				
Model I: Potential for Replacement	Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 42 (No);				
Model II and III: Potential for Replacement	Pond 39 (Possible); Pond 40 (Possible);	Pond 41 (Possible);				
<i>Banksiola crotchi</i>	<i>Ptilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia hudsonica</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (No); Pond 40 (Yes);	Pond 37 (No); Pond 40 (No); Pond 41 (No); Pond 42 (No);	None Available	Pond 37 (Yes);	Pond 34 (No); Pond 37 (No);
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Probable); Pond 37 (Probable); Pond 40 (Probable); Pond 41 (Probable); Pond 42 (Probable);	Pond 34 (Possible); Pond 40 (Probable); Pond 41 (Probable); Pond 42 (Probable);	Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);
<i>Ptilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>	<i>Banksiola crotchi</i>	
Model I: Potential for Replacement	Pond 39 (No); Pond 40 (Yes);	None Available	Pond 39 (No);	Pond 39 (No);	Pond 39 (No);	
Model II and III: Potential for Replacement	None Available	Pond 39 (Probable); Pond 40 (Probable);	Pond 40 (Possible);	Pond 40 (Probable);	Pond 40 (Probable);	
<i>Haliphus subguttatus</i>	<i>Peltodytes tortulosus</i>					
Model I: Potential for Replacement	Pond 39 (No);					
Model II and III: Potential for Replacement	Pond 40 (Possible);					

TABLE 15. Continued.

Lost Species		Replacement Species		
<i>Peltodytes tortulosus</i>	<i>Haliphus subguttatus</i>			
Model I: Potential for Replacement	None Available			
Model II and III: Potential for Replacement	Pond 40 (Possible);			
<i>Graphoderus liberus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>		
Model I: Potential for Replacement	None Available	Pond 39 (No);		
Model II and III: Potential for Replacement	Pond 39 (Possible);	None Available		
<i>Hydaticus aruspex</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Notonecta borealis</i>	
Model I: Potential for Replacement	Pond 34 (No);	Pond 40 (No);	Pond 40 (No);	
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Possible);	Pond 34 (Possible);	
<i>Hydroporus</i> sp. 1	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Laccophilus maculosus</i>	<i>Hygrotus</i> sp. 2
Model I: Potential for Replacement	Pond 34 (No);	Pond 39 (No);	Pond 34 (No);	Pond 34 (No);
Model II and III: Potential for Replacement	Pond 39 (Possible);	Pond 34 (Possible);	Pond 39 (Probable);	Pond 39 (No); None Available
<i>Hygrotus</i> sp. 2	<i>Hydroporus</i> sp. 1			
Model I: Potential for Replacement	Pond 41 (Yes); Pond 42 (No);			
Model II and III: Potential for Replacement	None Available			

TABLE 15. Continued.

Lost Species		Replacement Species	
<i>Laccophilus maculosus</i>	<i>Hydroporus</i> sp. I		
Model I: Potential for Replacement	Pond 40 (No); Pond 41 (Yes); Pond 42 (No);		
Model II and III: Potential for Replacement	Pond 39 (Possible);		
<i>Rhantus binotatus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	
Model I: Potential for Replacement	Pond 37 (No); Pond 40 (No); Pond 42 (No);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 42 (No);	
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 39 (Possible);	Pond 34 (Possible);	
<i>Rhantus frontalis</i>	<i>Rhantus suturellus</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>
Model I: Potential for Replacement	None Available	None Available	Pond 34 (No);
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Possible);	None Available
<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 34 (No);
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Probable); Pond 39 (Possible);	Pond 39 (Possible);

TABLE 15. Continued.

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- a* Replacement by Model I considered likely when the replacement species overlaps the specific pond from which the original species is hypothetically lost along the first three canonical axes.
 - b* Replacement by Model II or Model III considered "Possible" when the replacement species co-exists in lesser abundance than the hypothetically lost species, and there is either less than 60% inter-species overlap on the first three canonical axes or there is no overlap with the specific pond from which the original species is hypothetically lost along the first three canonical axes.
 - c* Replacement by Model II or Model III considered "Probable" when the replacement species co-exists in greater abundance than the hypothetically lost species, there is greater than 60% inter-species overlap on the first three canonical axes, and there is overlap with the specific pond from which the original species is hypothetically lost along the first three canonical axes.
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TABLE 16. Summary statistics of replacement potential of arthropods collected from the six Sandilands Provincial Forest study ponds, based upon abundance and distribution characteristics of the hypothetically lost taxa.

	Total Number of Species	Total Number of Species With Potential Replacements	Number of Species With Potential Model I Replacements	Number of Species With Potential Model II or III Replacements	Number of Species With Both Potential Model I and Model II or III Replacements	Number of Replacements / Number of Original Species With Potential for Model I Replacement	Number of Replacements / Number of Original Species With Potential for Model II or Model III Replacement	Number of Replacements / Number of Original Species With Potential for Model I and Model II or Model III Replacement
Pond 34	37	19 (51.4%)	0 (0.00%)	19 (100.0%)	0 (0.00%)	0.00	2.05	0.00
Pond 37	28	5 (17.8%)	1 (20.0%)	3 (60.0%)	1 (20.0%)	1.00	1.00	2.00
Pond 39	46	18 (39.1%)	0 (0.00%)	18 (100.0%)	0 (0.0%)	0.00	1.39	0.00
Pond 40	43	15 (34.8%)	1 (6.7%)	9 (60.0%)	5 (33.3%)	1.00	1.67	2.38
Pond 41	47	14 (29.8%)	3 (21.4%)	10 (71.4%)	1 (7.1%)	1.00	2.20	2.00
Pond 42	45	13 (28.9%)	0 (0.0%)	13 (100.0%)	0 (0.00%)	1.00	2.69	0.00
Combined Ponds	108	36 (33.3%)	1 (2.8%)	20 (55.6%)	15 (41.7%)	1.00	2.15	3.93

TABLE 17. Summary statistics of replacement potential of arthropods collected from the six Sandilands Provincial Forest study ponds, based upon abundance and distribution characteristics of the potential replacement taxa.

	Model I Replacement			Model II or III Potential Replacement				
	Potential Replacement		Total Available Opportunities ^(a)	Probable Potential Replacement		Possible Potential Replacement		Total Available Opportunities
	Congeneric Replacement	Confamilial or Higher Replacement		Congeneric Replacement	Confamilial or Higher Replacement	Congeneric Replacement	Confamilial or Higher Replacement	
Pond 34	0 (0.0%)	0 (0.0%)	27	5 (12.8%)	5 (12.8%)	10 (25.6%)	19 (48.7%)	39
Pond 37	0 (0.0%)	2 (10.5%)	19	0 (0.0%)	1 (25.0%)	0 (0.0%)	3 (75.0%)	
Pond 39	1 (3.7%)	1 (3.7%)	27	1 (4.0%)	3 (12.0%)	8 (32.0%)	13 (52.0%)	
Pond 40	2 (8.0%)	6 (24.0%)	25	2 (7.4%)	7 (25.9%)	3 (11.1%)	15 (55.6%)	
Pond 41	0 (0.0%)	4 (13.8%)	29	1 (4.3%)	5 (21.7%)	4 (17.4%)	13 (56.5%)	
Pond 42	0 (0.0%)	0 (0.0%)	21	3 (8.5%)	5 (14.2%)	4 (11.4%)	23 (65.7%)	23
Combined Ponds	3 (2.0%)	13 (8.8%)	148	12 (7.8%)	26 (17.0%)	29 (19.0%)	86 (56.2%)	35
(a)								153

(a) Total Available Opportunities is the sum of all available species with potential opportunity for replacement within each pond (from Appendix II).

Most hypothetically lost species had several potential replacements. This greatly increases the odds that functional replacement could actually occur. However, those species identified as having only Model I potential replacements available, tended to have only single replacements available (TABLE 16). In cases where species had only replacements available through Model II or III replacement mechanisms, multiple replacements were usually available, with ratios of hypothetically lost to potential replacement ranging to 2.69:1. Some hypothetically lost species in ponds 37, 40, and 41 had a combination of potentially available species for replacement by both Model I and Model II or III mechanisms. In these cases, the ratio of hypothetically lost : potential replacement species was at least 2:1 and probably offers the highest probability that functional replacement could actually occur.

There appeared to be a subtle pattern regarding placement of a pond in canonical space, the number of species with potential replacements, and the predominate type of replacement potential. It is expected that, at least in the case of Model I replacement, there should be more species in the available colonizing pool capable of inhabiting average conditions relative to conditions at the more distal ends of the gradient. For example, Pond 40 was plotted in a central location along both canonical axes 1 and 2. Habitat located centrally in canonical correspondence bi-plots is representative of average environmental conditions and therefore, may be more common. Pond 40 had a larger number of species with potential capability for Model I replacement relative to other ponds (32.0% versus 0.0% to 13.8% in other ponds). Further, the ponds located at the extreme ends of the gradient represented by the first two canonical axes (ponds 34, 39, and 42) had the lowest number of species with Model I potential replacement (0.0%, 7.4% and 0.0%, respectively). This pattern tended to hold for Model II or III replacement.

Pond 40, located centrally in the bi-plot, had the greatest number of species identified as "probable" Model II or III replacements (33.3%) whereas Pond 39, located at the extreme end of the gradient represented by canonical Axis 2, had the fewest number of "probable" Model II or III potential replacement species (16.0%). All other ponds had similar proportions of Model II or III "probable" potential replacement species. This pattern held regardless of the total number of species within each of the ponds and the number of transient species found in any one of the ponds. One would expect habitat representative of average conditions to be suitable for a greater number of species than habitat at the more extreme end of a gradient. However, within the study ponds, most available niches may be filled, and the number of available niches may be similar among ponds, thus placing similar limits on the total number of species that any one pond may be able to support. As previously mentioned, pond size and the related number of available niches may account for the fewer species found in Pond 37. Pond 37 is ~ 20% smaller than the other ponds and simply may have fewer available niches. Similarly, one would expect greater numbers of transients in ponds at the extreme ends of the gradients than in average habitat, because successful colonization should be more likely in less extreme habitat. However, the number of transients were similar in all ponds. Habitat may not be a factor affecting distribution of transient species. Interspecific interaction may play a role in the colonization potential of transients. Transient species may simply be poor competitors, and remain poor competitors regardless of the nature of the habitat.

CHAPTER VI

GENERAL DISCUSSION

It is now possible to return to the studies cited in Chapter I and re-order observations on the apparent presence of functional replacement. Cairns (1974) and Stauffer and Hocutt (1980) probably were referring to Model I (re-colonization) when describing change in community composition below an effluent outfall. It is almost certain that Odum *et al.* (1979) were referring to Model I when the conceptual response of aquatic communities to stress was described. Similarly, Minns *et al.* (1990) were referring to Model I when they indicated that acid-tolerant species may increase species richness in lakes affected by acid precipitation, following initial taxonomic losses. Conversely, Cairns and Dickson (1976) and Kimball and Levins (1985) referred to systems with structural and functional redundancy, but their meaning was not clearly defined. They probably meant replacement by Model II (niche width expansion) or Model III (redundant species). Similarly, Stephan *et al.* (1985) were probably inferring Model II or Model III replacement.

Schindler *et al.* (1985) referred to acidified Lake 223 as having "redundant features", but both Model I and Model III were involved in Lake 223 recovery. *Semotilus margarita* (Cope) - *Pimephales promelas* Rafinesque and *Daphnia catawba* Coker - *Daphnia galeata mendota* Birge were identified as redundant features of the lake (Schindler *et al.* 1985). *Semotilus* abundance increased following the loss of *Pimephales* and *D. catawba* abundance increased following the disappearance of *D. galeata mendota*. Schindler *et al.* (1985) reported that there was substantial overlap in diet between *S. margarita* and *P. promelas* (see also Tallman *et al.* 1984). Hence, replacement probably occurred by Model III since *Semotilus* increased D_{ui} without apparently increasing niche

width. Conversely, *D. catawba* first appeared in 1980, following the decline of *D. galeata mendota* (Malley and Chang 1986), a Model I replacement. By this latter model, *D. catawba* is able to successfully re-colonize following release of competition by the disappearance of *D. galeata mendota*. Malley and Chang (1986) speculated that *D. catawba* increased dramatically following re-colonization because of reduced predation, since acidification resulted in the collapse of the small cyprinid predators. In any case, *Daphnia catawba* re-colonized following the loss of *Daphnia galeata mendota*, and then increased its overall processing of resources (*i.e.*, D_{ui} increased).

Schindler *et al.* (1985) reported that the loss of *P. promelas* from an experimental lake undergoing acidification was predicted, based upon the known sensitivity of this species. However, its replacement by *S. margarita* was not predicted. Using data from existing niche overlap studies conducted on the two species, and interpreted according to the methods advanced here (Chapter III), it could have been predicted that *S. margarita* is a potential replacement for *P. promelas* and that replacement would occur by Model III.

The concept of functional replacement has been reported in the scientific literature for a considerable period of time, but reference to guiding theory and application to apparent observations of functional replacement has been confused. As evidenced by the principle advanced here, the mode of replacement can clearly differ among systems and among species.

Stephan *et al.* (1985) assumed that all but 5% of the genera at any one site required protection from the impact of toxic materials. It is possible to make some qualified comment on the whether 5% is a reasonable estimate of the number of taxa that may have replacements at a given site. During examination of the resource partitioning

studies reported in the literature, 13% of the aquatic insects had potential replacements, and slightly less than half of these or 6% had potential replacements within the same family but different genera. About 8.8% of the 33% of taxa with potential Model I replacement, or ~ 3% of all taxa in the present study, had replacements available at the confamilial level. The percentage of all taxa available for Model II or Model III replacement at the confamilial level ranged from 5.6% to 18.5% for "probable" and "possible" replacements, respectively. Thus, the arbitrary level of 5% chosen by Stephan *et al.* (1985) seems reasonable, although perhaps slightly high. It is probably not reasonable to consider replacement at a lower taxonomic level for toxic materials, since the responses of congeneric taxa are generally similar (Stephan *et al.* 1985). It would be unlikely that a potential replacement taxon within the same genus as the lost species would be more tolerant, and thus capable of surviving in the altered habitat. The responses among congeneric taxa may differ for conventional pollutants (Resh and Unzicker 1975).

It is not possible to compare directly the findings from the re-interpretation of resource partitioning studies in Chapter III to the results of niche overlap analysis in canonical space in Chapter V using aquatic arthropods from the six study ponds. However, there are some apparent similarities. First, in both cases, the potential for replacement is not widespread, although the percentage of potential replacement is slightly higher in the aquatic arthropod community in the six study ponds relative to the studies reviewed in the literature. The reasons for this difference are not clear because the reverse might be expected. Replacement should be more common within functional guilds. The literature studies on resource partitioning generally were restricted to examining relationships within functional guilds, whereas the field study conducted in the six ponds examined the overall aquatic arthropod community regardless of functional guild. Intuitively, there should be a lower percentage of potential replacements in the six pond

habitats relative to the studies reviewed from the literature. It is possible that this may change once further studies are conducted on the identified potential replacements within the six study ponds. Second, using both approaches, Model I replacement appears to be the least common of all types of replacement. This finding has further implications for the maintenance of ecosystem integrity, because Model I replacement is the only type in which original species diversity is maintained. Although system function is preserved in Model II and Model III replacement, there may be residual effects on community stability, resilience or other measures of community response (*e.g.*, Cherfas 1994, Kay and Schneider 1994). These residual effects have not been considered.

Niche overlap and species replacement theory presented in Chapter II can be directly linked to the underlying principals of CCA, adding internal consistency to the overall approach advanced in this study. There are many similarities between the bell-shaped species response curve modelled in CCA and the curve describing a species niche presented in Chapter II (*cf.* Figure 1, Chapter V and Figure 1, Chapter II). First, the variables defining the Gaussian response curve can be directly related to those in the equations used by MacArthur (1972). K_j , the asymptote of resource j (Eqs. 4 and 5, Chapter II) is equivalent to C_k , the maximum of the response curve for species k (Eq. 1, Chapter V); K_j occurs at some optimum location on the resource axis, equivalent to u_k (Eq. 1, Chapter V); K_j has variability equivalent to t_k (Eq. 1, Chapter V). Second, ter Braak (1986) listed four assumptions about species response models inherent in CCA, and he advised that three of these assumptions derive from the species packing model discussed by Whittaker *et al.* (1973) but which can be directly traced to MacArthur (1972). Model II and Model III replacement were derived from the species packing model of MacArthur (1972). Finally, one option available for weighting species abundances in CCA to derive species scores (the option chosen for this assessment) is to

use Hill's (1973) N_2 diversity. N_2 diversity is equivalent to the inverse Simpson index, described by Eq. 7, Chapter II and used in Eq. 1, Chapter II and most importantly, Eq. 8, Chapter II.

Habitat factors have been included in the overall potential replacement analysis in several places. First, genera with preferences for broadly similar microhabitat characteristics were grouped together in Chapter IV and, along with other factors (not all independent of habitat), led to the clustering of functionally similar taxa. Second, the analysis in Chapter V is a refinement of the previous analysis, except now preferences for habitat at the species level are included. The analysis in Chapter V may also represent possible mechanisms used by functionally similar species to partition resources; this is consistent with the findings of resource partitioning studies in which a large percentage of aquatic insects co-exist by habitat partitioning. In any case, habitat has played a large role in separating functionally similar species. Additional information generated in future studies, (*e.g.*, prey species preferences of predators), may similarly result in considerable refinement of the clustering at the generic level, as done in Chapter IV.

According to Prigogine *et al.* (1972) and Nicolis and Prigogine (1977), living systems that maintain entropy-reducing mechanisms are self-organized. The inherent ability to self-organize may form the basis for any given ecosystem to adjust to a certain degree of stress, while still maintaining normal ecosystem function as evidenced by material cycling and energy flow. Paine and Suchanek (1983, p. 821) viewed the role of an organism in terms of its "behaviour, the type and range of its ecological interactions, and especially its influence on other community members". After demonstrating that functional convergence of ecological traits had occurred in two distantly related organisms, they then suggested that ecologists must add a new dimension to their

examination of communities. A unique analysis of community ecology has been presented here given the new dimension suggested by Paine and Suchanek (1983). The potential for functional replacement offers some hope that self-organized, natural systems are able to compensate for external perturbations, at least to some degree, but its continued use in environmental management applications must be guided by a thoughtful and responsible ethic. It is most important to understand better the various modes by which functional replacement may occur and the constraints or limitations associated with each.

SUMMARY AND CONCLUSIONS

The phenomenon of functional replacement of lost species following environmental disturbance has not previously been rigorously examined. Three models of potential functional replacement are developed. Generalized equations are fitted that can be used to relate original community function in terms of type, abundance and diversity of resource use, species overlap, and species diversity of the original, undisturbed community to the community after species replacement. The first, Model I (re-colonization), follows from literature on classic succession. As environmental conditions change following environmental disturbance, sensitive species are displaced while more tolerant taxa colonize the vacated niches. The replacement species, following this hypothesis, would be a poor competitor relative to the original taxon, would have an inflexible niche width and would have good dispersal capability. Predictive evidence for the likelihood of Model I replacement may be significant niche overlap between allopatric populations of functionally similar species and the presence of competitive exclusion. The second and third models follow from theory on species packing. Model II (niche width expansion) predicts that remaining species in a community will expand their niche width to utilize resources left unused by the lost taxon. Replacement species would have the ability to

alter niche width through behavioural or short-term phenotypical response to competition, may co-exist as part of a functional guild, and would co-exist with the original taxon by partitioning resources. Predictive evidence for the likelihood of Model II replacement may be significant niche overlap in allopatric populations with wider niche width in allopatric populations relative to sympatric populations. Model III (redundant species) predicts that co-existing functionally similar species would have large niche overlap such that, even with removal of sensitive species, all available resources would continue to be utilized. Replacement species would co-exist as part of a functional guild and would co-exist without resource partitioning prior to disturbance. Predictive evidence for the likelihood of Model III replacement would be significant niche overlap in sympatric populations of functionally equivalent species.

Over 200 studies were reviewed on niche overlap and resource partitioning to determine how widespread potential replacement might be, based upon the predictive tools associated with each of the models. Approximately 120 of the studies contained sufficient detail to make judgments on the potential for replacement. The potential for replacement does not appear widespread, but would be limited to ~ 20% of guild-forming organisms. Replacement by Model II would be most likely, followed by Model III and Model I.

The aquatic arthropod community was examined in six study ponds located in Sandilands Provincial Forest in order to begin the task of experimentally assessing the hypotheses concerning potential replacement. The six ponds were excavated ~ 35 years ago to hold water for fire suppression purposes. The study ponds are relatively uniform in configuration with surface areas ranging from ~ 40 to 80 m² and maximum depths of ~ 1.0 to 1.7 m. The ponds were sampled from September 1988 to October 1990. Over 100

aquatic arthropod taxa were identified and ~ 90 environmental variables were measured or derived.

Relative to the original taxa, potential replacement species must process similar food materials in the same microhabitat, at the same time, and using the same feeding method. The size spectrum of the replacement community must remain unchanged in order to ensure that energy flow and material cycling remain unaltered in the replacement community. Out of the original 108 taxa, 36 (33.3%) had at least one potential replacement species that performed an equivalent ecological function and was similar in size.

Despite the six ponds being similar in size, uniform in morphology, located in the same area, and having been colonized for the same period of time, the aquatic arthropod community differed substantially among ponds. Canonical Correspondence Analysis was used to relate the distribution and abundance of aquatic arthropods in the six study ponds to the measured environmental variables. When all aquatic arthropods were included in the model, pond pH, area covered by *Sphagnum* sp., and pond circumference best explained the observed variability in distribution and abundance (overall model fit: $p = 0.004$; first canonical axis: $p = 0.018$). The abundance of the amphipod *Hyaella azteca*, a dominant species without a potential replacement, was directly related to the area of pond substrate covered by *Sphagnum* sp.. The model was re-run excluding *H. azteca*. The resulting model that best explained the observed variability in the remaining 107 species was pond pH, area covered by macrophyte, and percent substrate comprised of silt (overall model fit: $p = 0.005$; first canonical axis: $p = 0.004$). This model explained 88.8% of the variability in species distribution and abundance of the 107 species and 71.7% of the variability in the key 36 species with replacement potential.

A method was derived to calculate niche overlap in canonical space in order to predict which of the 36 candidate replacement species had potential to colonize available pond habitat and to successfully achieve similar abundance as the hypothetically lost taxa. There were 148 "opportunities" for replacement by Model I, based upon a combination of available ponds and potential replacement species. Replacement by Model I was limited to 16 cases or ~ 10% of the total available. There were 153 "opportunities" for replacement by Model II or III. Although none could be rejected completely by this analysis, replacement by these latter models was probable in 38 cases or ~ 25% of the total available. In many cases, each hypothetically lost taxon was associated with multiple potential replacement species. However, on average, hypothetically lost taxa with only Model I replacements could be replaced by only a single species, whereas hypothetically lost taxa with Model II or III replacements could be replaced by up to two species. In cases where a hypothetically lost taxon could be replaced by any of the models, such species had, on average, nearly four potential replacements. Actual replacement would occur with greater probability in cases where multiple species were available and this occurred more often under Models II or III than Model I. Replacement by any model was more likely for species located in ponds of "average" environmental conditions relative to those located near the lower or upper ends of a gradient.

FUTURE STUDIES

Unequivocal species replacement can be demonstrated only through systematic experimentation. This includes: (1) developing hypotheses concerning available potential replacement species; (2) estimating diversity and amount of resources processed by the community (D_r from Eq. 1, Chapter II); (3) removing target species; (4) tracking

ecosystem structure during the post-removal period; and (5) comparing D_r of the community before and after species removal to determine replacement success (*i.e.*, Eq. 9, Chapter II). The work here was focused on developing the theoretical basis for potential functional replacement and then achieving the objective in (1). The basis for the larger experiment involving species removal has now been set. Hypotheses concerning available potential replacement species in the six study ponds have been developed from the preliminary work and candidate taxa can be targetted for removal. Candidate removal taxa are listed in TABLE 1 along with the type of replacement expected and the pond in which replacement would occur. These predictions lend themselves to further experimentation with the opportunity for replication by species, habitat and type of replacement. It is now possible to follow key variables describing system function after replacement, using the equations fitted to the generic model of community interaction and function, to ensure that the ecological function of the system has not be disrupted.

Several modifications are suggested for future studies aimed at testing the hypotheses developed here. First, biomass size spectra should be used rather than simply size spectra. Although this may not affect the overall outcome, the use of biomass size spectra is more comparable to data generated elsewhere. The use of the techniques suggested here have greater value if they can be used for predictive purposes with data that are commonly generated. Second, CCA is a powerful tool for gaining a better understanding of complex relationships among species distribution and abundance and environmental variables. Mathematical statisticians should be encouraged to validate or improve the method developed in this study for defining niche width in canonical space and for subsequently calculating inter-species and species-environment overlap. Third, analysis of food resource consumption should be included in studies on species distribution and abundance when the goal is to develop predictions concerning the

TABLE 1. List of taxa collected from the six Sandilands Provincial Forest study ponds suitable for field verification of replacement, with replication by species, habitat, and mode of replacement.

Lost Species	Replacement Species			
<i>Anax junius</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Aeshna interrupta</i> Pond 34	<i>Aeshna canadensis</i> Pond 34		
<i>Somatochlora williamsoni</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Sympetrum obtrusum</i> Pond 40; Pond 41			
<i>Leucorrhinia hudsonica</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leucorrhinia proxima</i> Pond 34	<i>Leucorrhinia intacta</i> Pond 34		
<i>Leucorrhinia intacta</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leucorrhinia proxima</i> Pond 39; Pond 40	<i>Lestes unguiculatus</i> Pond 37; Pond 40		
<i>Leucorrhinia proxima</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leucorrhinia intacta</i> Pond 34	<i>Lestes unguiculatus</i> Pond 42	<i>Lestes congener</i> Pond 41; Pond 42	<i>Banksiola crotchii</i> Pond 42
<i>Libellula quadrimaculata</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Somatochlora williamsoni</i> Pond 41			

TABLE I. Continued.

Lost Species	Replacement Species			
<i>Sympetrum obtrusum</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Somatochlora williamsoni</i> Pond 39			
<i>Lestes congener</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leucorrhinia proxima</i> Pond 39; Pond 40 Pond 34			
<i>Lestes disjunctus disjunctus</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Lestes unguiculatus</i> Pond 42	<i>Lestes congener</i> Pond 41; Pond 42		
<i>Lestes dryas</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leucorrhinia proxima</i> Pond 40	<i>Leucorrhinia intacta</i> Pond 40	<i>Lestes unguiculatus</i> Pond 40	<i>Lestes congener</i> Pond 40
<i>Coenagrion angulatum</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Enallagma cyathigerum</i> Pond 40; Pond 41; Pond 42			
<i>Notonecta borealis</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Hydaticus aruspex</i> Pond 34			

TABLE 1. Continued.

Lost Species		Replacement Species			
<i>Notonecta irrorata</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Hydroporus</i> sp. 1 Pond 41				
<i>Notonecta kirbyi</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Notonecta undulata</i> Pond 39; Pond 40				
<i>Banksiola crotchii</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leuchorrhinia proxima</i> Pond 40 Pond 34	<i>Enallagma cyathigerum</i> Pond 34; Pond 37; Pond 40; Pond 41; Pond 42	<i>Coenagrion resolutum</i> Pond 37 Pond 40; Pond 41; Pond 42		
<i>Ptilostomis</i> sp. Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Leuchorrhinia proxima</i> Pond 40	<i>Enallagma cyathigerum</i> Pond 39; Pond 40	<i>Coenagrion angulatum</i> Pond 40	<i>Banksiola crotchii</i> Pond 40	
<i>Hydroporus</i> sp. 1 Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Laccophilus maculosus</i> Pond 39				
<i>Hygrotus</i> sp. 2 Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Hydroporus</i> sp. 1 Pond 41				

TABLE 1. Continued.

Lost Species	Replacement Species
<i>Laccophilus maculosus</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Hydroporus</i> sp. 1 Pond 41
<i>Rhantus suturellus</i> Model I: Potential for Replacement Model II and III: Potential for Replacement	<i>Rhantus binotatus</i> Pond 34

potential for replacement. This will allow overlap to be better estimated along this important resource axis rather than reliance upon generalizations reported in the available literature. On the other hand, generalizations from the literature on food consumption are readily available for many species; this therefore enables the more widespread use of the methods suggested here for predictive purposes. At the very least, specific food consumption by each species in each community needs to be compared with generalized food resource use reported in the literature.

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APPENDIX I

CONFIDENCE REGIONS AND GENERAL OUTPUT FROM CANONICAL CORRESPONDENCE ANALYSIS

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TABLE 1. 95% confidence regions calculated from CCA species scores and sample standard deviations for arthropods collected from the six Sandilands Provincial Forest study ponds.

Species Code	Species Scores				Sample Standard Deviation				95% Confidence Regions				Root Mean Square Tolerance	Weight	N ₂ (Effective Number of Occurrences)	Number of Actual Occurrences
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4				
Sip alt	-0.9526	-1.6595	-0.6973	1.3123	0.1009	0.1568	0.0914	0.1213	0.2142	0.3328	0.1940	0.2575	10.97	0.12	1.01	1
Cal sp.	-0.6801	0.1316	0.2017	0.0403	0.6790	1.3204	1.1496	1.2568	1.4416	2.8037	2.4408	2.6686	103.14	3.08	4.03	5
Cae dim	-0.7634	0.3777	-0.3034	1.4004	0.1978	2.0212	0.3946	0.1135	0.4201	4.2916	0.8378	0.2410	94.57	0.33	1.98	2
Cae you	-0.5392	1.4223	-0.0560	0.7340	0.2923	1.0429	0.5950	1.2376	0.6206	2.2143	1.2635	2.6278	79.82	1.06	1.83	3
Aes can	0.6338	-0.2852	1.1896	-0.0309	1.4321	0.2160	0.2365	0.7675	3.0407	0.4587	0.5022	1.6296	75.59	0.50	1.83	2
Aes int	0.2097	0.2109	0.1571	-0.2473	1.1140	0.8134	1.1481	0.9581	2.3652	1.7270	2.4378	2.0343	92.85	0.78	4.73	5
Anx jun	1.5720	-0.4222	1.0307	0.4750	0.1855	0.1163	0.1395	0.1054	0.3938	0.2470	0.2961	0.2238	12.78	0.08	1.01	1
Cor shu	1.2871	-0.5704	0.8353	0.5755	0.8951	0.4384	0.6129	0.2975	1.9005	0.9308	1.3014	0.6317	55.11	0.74	1.26	2
Som wil	-0.1729	0.3548	-0.0997	0.0323	0.9639	1.1992	1.0877	1.1648	2.0466	2.5462	2.3094	2.4732	101.11	0.72	5.36	5
Leu fri	1.5679	-0.4210	1.0281	0.4741	0.2126	0.1335	0.1599	0.1209	0.4515	0.2835	0.3396	0.2568	14.66	0.06	1.02	1
Leu hud	1.5794	-0.4244	1.0355	0.4766	0.1209	0.0758	0.0909	0.0686	0.2568	0.1610	0.1931	0.1456	8.33	0.18	1.01	1
Leu int	0.8649	-0.1055	-0.0474	-0.0545	0.8844	0.6439	1.1378	0.7805	1.8777	1.3672	2.4160	1.6572	80.37	12.52	3.08	6
Leu pro	0.5874	-0.5826	0.7931	0.3585	1.4058	0.5986	0.8108	0.7958	2.9849	1.2709	1.7217	1.6898	86.91	0.46	2.18	3
Lib qua	-0.2558	0.1318	-0.4387	-0.1876	0.6109	1.1442	0.6739	1.2099	1.2972	2.4294	1.4309	2.5690	86.61	1.55	2.39	5
Sym dan	-0.9546	-1.6635	-0.6989	1.3150	0.0735	0.1143	0.0665	0.0883	0.1561	0.2426	0.1412	0.1875	8.00	0.23	1.00	1
Sym obt	0.3247	1.0055	-0.7844	0.1158	0.7395	0.8217	0.6392	1.0719	1.5702	1.7447	1.3572	2.2759	76.10	0.25	1.83	2
Les con	-0.4738	-0.0282	0.4483	-0.2632	0.9690	0.9910	1.1028	1.1200	2.0575	2.1043	2.3415	2.3780	95.65	1.45	3.82	5
Les dis	-0.9275	0.1854	0.4132	0.4267	0.2686	1.5724	1.0115	1.2898	0.5703	3.3387	2.1478	2.7386	104.40	0.21	2.93	3
Les dry	-0.1245	-0.0386	-0.7770	-0.9889	0.0948	0.1070	0.1195	0.1458	0.2012	0.2272	0.2538	0.3096	10.80	0.08	1.01	1
Les ung	-0.3840	-0.8217	-0.2318	1.1703	1.0983	1.4693	0.7583	0.3932	2.3320	3.1198	1.6100	0.8348	92.36	0.42	2.12	3
Coe ang	-0.6943	-0.5733	-0.1158	-0.2287	0.5032	0.8446	1.0977	1.1935	1.0685	1.7933	2.3308	2.5341	86.56	0.93	2.96	3
Coe res	-0.5240	-0.6856	-0.1121	0.0050	0.8335	0.8503	1.0579	1.2061	1.7698	1.8054	2.2462	2.5609	91.19	2.20	3.32	4
Ena cya	0.0867	0.1951	-0.0502	-0.1297	1.0515	1.0016	1.1067	1.0540	2.2327	2.1266	2.3499	2.2380	96.23	18.28	5.42	6
Mic pul	-0.9529	-1.6601	-0.6975	1.3127	0.0975	0.1515	0.0883	0.1171	0.2070	0.3217	0.1875	0.2486	10.60	0.13	1.01	1
Ger bue	-0.4947	0.3794	0.3830	0.2025	0.9066	1.3366	0.9817	1.2543	1.9249	2.8379	2.0845	2.6632	103.54	0.51	4.16	5
Ger dis	0.5768	0.7105	0.2467	0.6894	1.0992	1.2368	0.8853	0.8093	2.3338	2.6260	1.8798	1.7184	93.28	0.28	2.69	3
Let ame	-0.1244	-0.0384	-0.7751	-0.9862	0.1088	0.1228	0.1371	0.1673	0.2310	0.2607	0.2912	0.3552	12.39	0.06	1.02	1
Ran fus	-0.6035	2.0265	0.0186	1.4597	0.1147	0.2326	0.1012	0.1746	0.2435	0.4938	0.2149	0.3708	15.00	0.07	1.01	1
Cal aud	-0.9684	-0.5430	0.5076	-0.2625	0.3665	0.8388	1.1982	1.1785	0.7783	1.7810	2.5441	2.5022	87.35	0.47	2.34	3

TABLE 1. Continued.

Species Code	Species Scores				Sample Standard Deviation				95% Confidence Regions				Root Mean Square Tolerance	Weight	N ₂ (Effective Number of Occurrences)	Number of Actual Occurrences
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4				
Hes ato	-0.4986	-0.3860	-0.5044	0.2826	0.6650	1.3424	0.7553	1.2381	1.4121	2.8502	1.6037	2.6288	95.17	1.38	3.68	5
Hes min	-0.9537	-1.6617	-0.6982	1.3138	0.0868	0.1348	0.0785	0.1043	0.1842	0.2863	0.1668	0.2214	9.44	0.17	1.01	1
Hes vul	-0.7038	0.0212	0.4476	-0.5409	0.7016	0.8575	1.2357	0.9786	1.4898	1.8207	2.6237	2.0778	87.94	0.88	2.89	5
Sig alt	-0.5082	-0.2070	0.1091	0.2253	0.9127	1.3178	1.0752	1.2191	1.9380	2.7981	2.2829	2.5885	104.20	1.90	4.72	6
Sig con	-0.1244	-0.0384	-0.7751	-0.9862	0.1088	0.1228	0.1371	0.1673	0.2310	0.2607	0.2912	0.3552	12.39	0.06	1.02	1
Sig dec	-0.9479	-1.6503	-0.6937	1.3059	0.1456	0.2261	0.1319	0.1748	0.3091	0.4801	0.2800	0.3712	15.83	0.06	1.02	1
Sig gro	-0.9309	-0.0296	0.2840	0.5301	0.2528	1.6150	1.0282	1.2524	0.5368	3.4291	2.1831	2.6592	105.06	0.24	2.97	3
Not bor	1.5788	-0.4242	1.0351	0.4765	0.1269	0.0795	0.0954	0.0720	0.2693	0.1689	0.2026	0.1528	8.74	0.17	1.01	1
Not irr	0.2866	-0.2333	1.2418	-0.2155	1.5022	0.2343	0.2627	0.8068	3.1896	0.4975	0.5578	1.7131	79.47	0.16	2.00	2
Not kir	-0.3831	1.0751	-0.3505	0.3281	0.2745	1.1409	0.4439	1.3477	0.5829	2.4225	0.9425	2.8616	84.04	0.13	2.00	2
Not und	-0.6250	-0.0581	0.0350	-0.0454	0.6829	1.2431	1.1431	1.2335	1.4500	2.6395	2.4271	2.6190	100.41	1.30	4.39	5
Ban cro	-0.1870	-0.6413	-0.2390	0.1484	1.0690	0.9079	1.0321	1.1228	2.2699	1.9277	2.1915	2.3841	94.58	0.68	4.11	5
Pti sp.	-0.3777	1.0514	-0.3606	0.2986	0.2718	1.1416	0.4428	1.3500	0.5771	2.4239	0.9401	2.8665	84.11	0.18	2.00	2
Ana sp.	-0.6049	2.0315	0.0187	1.4631	0.0967	0.1963	0.0854	0.1474	0.2054	0.4168	0.1814	0.3131	12.66	0.10	1.01	1
Lim sp1	-0.6045	2.0302	0.0187	1.4622	0.1017	0.2064	0.0898	0.1550	0.2158	0.4382	0.1907	0.3291	13.31	0.09	1.01	1
Lim sp2	-0.6049	2.0315	0.0187	1.4631	0.0967	0.1963	0.0854	0.1474	0.2054	0.4168	0.1814	0.3131	12.66	0.10	1.01	1
Nem hos	-0.6049	2.0315	0.0187	1.4631	0.0967	0.1963	0.0854	0.1474	0.2054	0.4168	0.1814	0.3131	12.66	0.10	1.01	1
Oec inc	-0.2582	0.3905	-0.2893	-0.1860	0.7807	1.1004	1.0351	1.1523	1.6577	2.3364	2.1978	2.4467	93.76	1.36	4.52	5
Gyr aqu	0.8012	0.4633	-1.1912	-0.5816	0.1595	0.1423	0.1849	0.1505	0.3387	0.3021	0.3926	0.3196	14.62	0.05	1.02	1
Hal can	0.6261	0.6576	0.1499	0.5776	1.0539	1.1857	0.9571	0.8546	2.2378	2.5176	2.0322	1.8145	93.13	0.44	2.87	3
Hal con	1.5679	-0.4210	1.0281	0.4741	0.2126	0.1335	0.1599	0.1209	0.4515	0.2835	0.3396	0.2568	14.66	0.06	1.02	1
Hal imm	-0.4864	0.1553	0.3328	-0.1695	0.9489	1.1089	1.2018	1.1452	2.0147	2.3545	2.5518	2.4315	100.89	0.99	4.03	6
Hal lon	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hal sal	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hal sp.	0.0927	-0.1441	-0.4845	-0.1873	0.9259	0.9482	0.8885	1.0388	1.9659	2.0133	1.8866	2.2057	86.90	3.24	4.17	6
Hal str	-0.6035	2.0265	0.0186	1.4597	0.1147	0.2326	0.1012	0.1746	0.2435	0.4938	0.2149	0.3708	15.00	0.07	1.01	1
Hal sub	-0.3831	1.0751	-0.3505	0.3281	0.2745	1.1409	0.4439	1.3477	0.5829	2.4225	0.9425	2.8616	84.04	0.13	2.00	2
Pel ede	-0.1244	-0.0384	-0.7751	-0.9862	0.1088	0.1228	0.1371	0.1673	0.2310	0.2607	0.2912	0.3552	12.39	0.06	1.02	1
Pel sp.	-0.1246	-0.0388	-0.7785	-0.9912	0.0815	0.0920	0.1028	0.1254	0.1730	0.1954	0.2182	0.2663	9.29	0.10	1.01	1
Pel tor	-0.1248	-0.0392	-0.7814	-0.9955	0.0464	0.0525	0.0587	0.0716	0.0986	0.1114	0.1247	0.1521	5.30	0.32	1.00	1

TABLE 1. Continued.

Species Code	Species Scores				Sample Standard Deviation				95% Confidence Regions				Root Mean Square Tolerance	Weight	N ₂ (Effective Number of Occurrences)	Number of Actual Occurrences
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4				
Aci sem	-0.2454	-0.6916	0.1716	0.1536	1.1736	0.7998	1.0945	1.1223	2.4918	1.6982	2.3238	2.3829	96.55	0.71	3.80	4
Aci sp.	-0.6065	2.0377	0.0188	1.4674	0.0686	0.1392	0.0605	0.1045	0.1456	0.2956	0.1284	0.2219	8.97	0.19	1.01	1
Aga ant	0.8058	0.4654	-1.1973	-0.5853	0.1205	0.1074	0.1398	0.1137	0.2559	0.2279	0.2968	0.2414	11.04	0.09	1.01	1
Aga sp.	-0.5913	-0.6644	-0.4337	-0.1038	0.4914	0.8712	0.8475	1.2343	1.0434	1.8498	1.7996	2.6209	82.19	1.12	2.55	3
Col lon	1.5734	-0.4226	1.0316	0.4753	0.1754	0.1100	0.1319	0.0996	0.3724	0.2335	0.2800	0.2114	12.09	0.09	1.01	1
Col scu	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Cop lon	-0.1244	-0.0384	-0.7751	-0.9862	0.1088	0.1228	0.1371	0.1673	0.2310	0.2607	0.2912	0.3552	12.39	0.06	1.02	1
Des con	-1.1567	-0.0193	1.4684	-0.9867	0.1333	0.1010	0.1633	0.1377	0.2831	0.2145	0.3468	0.2924	12.38	0.09	1.01	1
Dyt dau	0.1863	1.1570	-0.6645	0.3158	0.7738	0.8617	0.6693	1.1212	1.6430	1.8296	1.4211	2.3806	79.67	0.15	1.98	2
Dyt sp.	-0.0425	-0.1697	-0.8624	-0.5620	0.5906	0.7232	0.2088	0.8815	1.2539	1.5356	0.4433	1.8717	59.38	0.39	2.14	3
Grp lib	-0.6063	2.0368	0.0188	1.4667	0.0735	0.1493	0.0650	0.1121	0.1561	0.3170	0.1379	0.2379	9.63	0.17	1.01	1
Grp per	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Grp sp.	-1.0306	-1.0596	0.0997	0.4678	0.1331	0.8736	1.1508	1.2211	0.2826	1.8549	2.4434	2.5927	86.56	0.24	1.88	2
Hda aru	1.0501	-0.3048	0.4707	0.0187	0.8697	0.2046	0.9248	0.7494	1.8466	0.4345	1.9636	1.5912	67.93	0.28	1.76	2
Hda sp.	-0.1248	-0.0392	-0.7811	-0.9951	0.0507	0.0573	0.0641	0.0782	0.1077	0.1216	0.1361	0.1661	5.79	0.27	1.00	1
Hdp pau	0.8012	0.4633	-1.1912	-0.5816	0.1595	0.1423	0.1849	0.1505	0.3387	0.3021	0.3926	0.3196	14.62	0.05	1.02	1
Hdp rub	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hdp ruf	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hdp sp.	0.4058	0.2484	-1.0199	-0.7635	0.5118	0.2832	0.2440	0.2352	1.0867	0.6013	0.5180	0.4994	30.86	0.20	1.97	2
Hdp sp1	0.6176	0.6580	0.5880	0.9118	1.1929	1.3431	0.5592	0.5466	2.5329	2.8518	1.1874	1.1606	89.43	0.15	1.98	2
Hyg pat	-0.6035	2.0265	0.0186	1.4597	0.1147	0.2326	0.1012	0.1746	0.2435	0.4938	0.2149	0.3708	15.00	0.07	1.01	1
Hyg sal	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hyg say	-0.8294	0.0226	0.4793	-0.1562	0.5625	1.1917	1.1525	1.2264	1.1944	2.5304	2.4471	2.6039	97.56	0.89	3.06	5
Hyg sp1	-0.6049	2.0315	0.0187	1.4631	0.0967	0.1963	0.0854	0.1474	0.2054	0.4168	0.1814	0.3131	12.66	0.10	1.01	1
Hyg sp2	-1.0705	-0.7265	0.5372	0.0026	0.1516	0.8975	1.1825	1.2540	0.3219	1.9056	2.5109	2.6625	88.97	0.14	1.97	2
Lac big	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Lac mac	-0.6977	0.3480	0.0056	0.3734	0.4065	1.5303	0.9234	1.3083	0.8632	3.2493	1.9605	2.7779	102.79	0.27	3.79	4
Lac sp.	-0.1247	-0.0389	-0.7788	-0.9917	0.0782	0.0883	0.0987	0.1204	0.1661	0.1875	0.2096	0.2556	8.91	0.11	1.01	1
Lio aff	-0.8199	-0.0327	0.5919	-0.3568	0.6621	1.0143	1.1938	1.1119	1.4058	2.1536	2.5348	2.3608	92.74	0.90	2.56	5
Rha bin	0.3888	0.1738	-0.0988	0.3990	1.0871	1.2731	0.9600	0.9905	2.3083	2.7032	2.0385	2.1031	99.01	0.44	4.48	5

TABLE 1. Continued.

Species Code	Species Scores				Sample Standard Deviation				95% Confidence Regions				Root Mean Square Tolerance	Weight	N _e (Effective Number of Occurrences)	Number of Actual Occurrences
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4				
Rha fro	1.5777	-0.4239	1.0344	0.4762	0.1380	0.0865	0.1037	0.0783	0.2931	0.1837	0.2203	0.1663	9.51	0.14	1.01	1
Rha sp.	-0.6035	2.0265	0.0186	1.4597	0.1147	0.2326	0.1012	0.1746	0.2435	0.4938	0.2149	0.3708	15.00	0.07	1.01	1
Rha sut	0.4315	0.8684	0.5016	0.9968	1.1997	1.3517	0.5614	0.5494	2.5474	2.8700	1.1920	1.1665	89.95	0.18	2.00	2
Anc lim	0.2186	-1.0913	0.1041	0.9279	1.3878	0.6817	0.9504	0.4625	2.9467	1.4474	2.0180	0.9820	85.49	0.34	1.99	2
Ber str	-0.9479	-1.6503	-0.6937	1.3059	0.1456	0.2261	0.1319	0.1748	0.3091	0.4801	0.2800	0.3712	15.83	0.06	1.02	1
Cym min	-0.1246	-0.0387	-0.7776	-0.9898	0.0896	0.1011	0.1130	0.1379	0.1903	0.2147	0.2400	0.2928	10.21	0.09	1.01	1
Cym vin	-0.9537	-1.6617	-0.6982	1.3138	0.0868	0.1348	0.0785	0.1043	0.1842	0.2863	0.1668	0.2214	9.44	0.17	1.01	1
Eno ham	1.5679	-0.4210	1.0281	0.4741	0.2126	0.1335	0.1599	0.1209	0.4515	0.2835	0.3396	0.2568	14.66	0.06	1.02	1
Eno och	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1
Hel ang	-0.9479	-1.6503	-0.6937	1.3059	0.1456	0.2261	0.1319	0.1748	0.3091	0.4801	0.2800	0.3712	15.83	0.06	1.02	1
Hel lac	0.8012	0.4633	-1.1912	-0.5816	0.1595	0.1423	0.1849	0.1505	0.3387	0.3021	0.3926	0.3196	14.62	0.05	1.02	1
Hdb fus	0.8058	0.4654	-1.1973	-0.5853	0.1205	0.1074	0.1398	0.1137	0.2559	0.2279	0.2968	0.2414	11.04	0.09	1.01	1
Hdc obt	1.5794	-0.4244	1.0355	0.4766	0.1209	0.0758	0.0909	0.0686	0.2568	0.1610	0.1931	0.1456	8.33	0.18	1.01	1
Hdu pse	-0.8617	1.0841	0.6911	0.3296	0.3175	1.1303	0.8008	1.3461	0.6741	2.3999	1.7003	2.8581	89.34	0.13	2.00	2
Tro lat	0.2089	-0.2215	1.2523	-0.2564	1.5040	0.2392	0.2717	0.8089	3.1935	0.5080	0.5768	1.7175	79.68	0.12	2.01	2
Tro sp.	-0.9519	-1.6581	-0.6967	1.3113	0.1091	0.1696	0.0988	0.1311	0.2317	0.3601	0.2098	0.2784	11.87	0.10	1.01	1
Hdr ang	-0.8780	-0.4545	0.9108	-0.3062	0.8316	0.7633	1.0099	1.1019	1.7656	1.6207	2.1443	2.3397	85.49	0.68	1.94	3
Cyp sp.	-1.1531	-0.0190	1.4635	-0.9830	0.1617	0.1227	0.1982	0.1671	0.3433	0.2605	0.4208	0.3547	15.02	0.06	1.02	1

TABLE 2. Weighted average (WA) site scores with various measures of site variability generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds and pH, silt, and area covered by macrophytes.

	Site Scores (Weighted Average)				Site Heterogeneity (Root Mean Squared Deviation for Samples)				Root Mean Square Tolerance	Weight	N ₂ Diversity
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4			
Pond 34	1.5685	-0.3753	0.9648	0.4778	1.1451	0.4571	0.9805	0.5139	82.85	14.20	4.57
Pond 37	0.8308	0.3336	-0.8137	-0.5902	0.7056	0.4631	1.1181	0.5246	74.79	11.14	4.23
Pond 39	-0.6591	2.1623	-0.0513	1.4716	0.5581	1.6706	0.2558	1.3243	110.92	9.26	9.56
Pond 40	-0.0888	-0.0258	-1.1266	-0.9975	0.4706	0.3592	0.6821	0.8924	63.48	15.49	8.51
Pond 41	-1.1302	-0.1254	1.6331	-0.9943	0.8776	0.3353	1.3040	0.8993	92.08	12.09	11.72
Pond 42	-1.0031	-1.5956	-0.6233	1.3181	0.7783	1.4000	0.7114	1.2347	107.20	10.34	21.75
Gradient Length (Standard Deviation Units)	2.6987	3.7579	2.7597	2.4691							

TABLE 3. Site scores generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds and pH, silt, and area covered by macrophytes, calculated as linear combination of environmental variables (LC).

	Site Scores (Linear Combination of Environmental Variables)				
	Axis 1	Axis 2	Axis 3	Axis 4	% Species Fit
Pond 34	1.5848	-0.4260	1.0390	0.0000	98.89
Pond 37	0.8119	0.4683	-1.2055	0.0000	55.48
Pond 39	-0.6082	2.0439	0.0190	0.0000	99.19
Pond 40	-0.1249	-0.0394	-0.7828	0.0000	58.84
Pond 41	-1.1642	-0.0198	1.4788	0.0000	95.03
Pond 42	-0.9569	-1.6679	-0.7006	0.0000	99.26
Gradient Length (Standard Deviation Units)	2.7490	3.7118	2.6843	0.0000	

TABLE 4. Cumulative fit per species as fraction of variance of species, generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds, and pH, silt, and area covered by macrophytes.

	Axis 1	Axis 2	Axis 3	Axis 4	Variance (y)	Percent Variance Explained
Fraction Fitted	0.3506	0.2342	0.1502	0.1534		
Sip alt	0.1524	0.6149	0.6966	0.9858	5.95	69.66
Cal sp.	0.7641	0.7927	0.8600	0.8626	0.61	86.00
Cae dim	0.2095	0.2608	0.2939	0.9989	2.78	29.39
Cae you	0.0932	0.7421	0.7431	0.9159	3.12	74.31
Aes can	0.2115	0.2543	0.9993	0.9998	1.90	99.93
Aes int	0.2504	0.5037	0.6442	0.9924	0.18	64.42
Anx jun	0.6112	0.6553	0.9180	0.9738	4.04	91.80
Cor shu	0.5385	0.6443	0.8711	0.9787	3.08	87.11
Som wil	0.1389	0.7234	0.7696	0.7745	0.22	76.96
Leu fri	0.6111	0.6552	0.9180	0.9738	4.02	91.80
Leu hud	0.6112	0.6554	0.9181	0.9738	4.08	91.81
Leu int	0.9540	0.9682	0.9711	0.9749	0.78	97.11
Leu pro	0.2392	0.4745	0.9106	0.9997	1.44	91.06
Lib qua	0.0596	0.0754	0.2507	0.2827	1.10	25.07
Sym dan	0.1524	0.6150	0.6967	0.9858	5.98	69.67
Sym obt	0.0388	0.4103	0.6364	0.6414	2.72	63.64
Les con	0.4383	0.4398	0.8324	0.9677	0.51	83.24
Les dis	0.6569	0.6832	0.8136	0.9526	1.31	81.36
Les dry	0.0043	0.0047	0.1714	0.4415	3.62	17.14
Les ung	0.0655	0.3656	0.3895	0.9981	2.25	38.95
Coe ang	0.5099	0.8576	0.8718	0.9271	0.95	87.18
Coe res	0.3391	0.9196	0.9352	0.9352	0.81	93.52
Ena cya	0.1154	0.6997	0.7383	0.9965	0.07	73.83
Mic pul	0.1524	0.6149	0.6966	0.9858	5.96	69.66
Ger bue	0.4150	0.6592	0.9080	0.9776	0.59	90.80
Ger dis	0.2421	0.6096	0.6539	0.9999	1.37	65.39
Let ame	0.0043	0.0047	0.1715	0.4415	3.60	17.15
Ran fus	0.0542	0.6658	0.6659	0.9832	6.71	66.59
Cal aud	0.5694	0.7484	0.9048	0.9466	1.65	90.48
Hes ato	0.3387	0.5417	0.8883	0.9971	0.73	88.83
Hes min	0.1524	0.6150	0.6966	0.9858	5.97	69.66
Hes vui	0.4717	0.4722	0.6629	0.9415	1.05	66.29
Sig alt	0.7067	0.8239	0.8565	0.9954	0.37	85.65
Sig con	0.0043	0.0047	0.1715	0.4415	3.60	17.15
Sig dec	0.1525	0.6147	0.6963	0.9857	5.89	69.63
Sig gro	0.6699	0.6705	0.7329	0.9501	1.29	73.29
Not bor	0.6112	0.6554	0.9181	0.9738	4.08	91.81
Not irr	0.0470	0.0782	0.9608	0.9873	1.75	96.08
Not kir	0.0655	0.5811	0.6359	0.6840	2.24	63.59
Not und	0.9321	0.9402	0.9431	0.9480	0.42	94.31
Ban cro	0.0663	0.8460	0.9542	0.9960	0.53	95.42
Pti sp.	0.0648	0.5672	0.6263	0.6668	2.20	62.63
Ana sp.	0.0542	0.6659	0.6659	0.9832	6.75	66.59
Lim sp1	0.0542	0.6658	0.6659	0.9832	6.74	66.59
Lim sp2	0.0542	0.6659	0.6659	0.9832	6.75	66.59
Nem hos	0.0542	0.6659	0.6659	0.9832	6.75	66.59

TABLE 4. Continued.

	Axis 1	Axis 2	Axis 3	Axis 4	Variance (y)	Percent Variance Explained
Oec inc	0.1913	0.6287	0.8688	0.9681	0.35	86.88
Gyr aqu	0.1193	0.1592	0.4229	0.4858	5.38	42.29
Hal can	0.3266	0.6868	0.7056	0.9836	1.20	70.56
Hal con	0.6111	0.6552	0.9180	0.9738	4.02	91.80
Hal imm	0.4295	0.4733	0.6743	0.7265	0.55	67.43
Hal lon	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hal sal	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hal sp.	0.0277	0.0945	0.8499	0.9629	0.31	84.99
Hal str	0.0542	0.6658	0.6659	0.9832	6.71	66.59
Hal sub	0.0655	0.5811	0.6359	0.6840	2.24	63.59
Pel ede	0.0043	0.0047	0.1715	0.4415	3.60	17.15
Pel sp.	0.0043	0.0047	0.1713	0.4415	3.64	17.13
Pel tor	0.0042	0.0047	0.1712	0.4414	3.67	17.12
Aci sem	0.0999	0.8934	0.9422	0.9813	0.60	94.22
Aci sp.	0.0542	0.6659	0.6659	0.9831	6.79	66.59
Aga ant	0.1194	0.1593	0.4230	0.4860	5.44	42.30
Aga sp.	0.2886	0.6529	0.8081	0.8170	1.21	80.81
Col lon	0.6112	0.6553	0.9180	0.9738	4.05	91.80
Col scu	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Cop lon	0.0043	0.0047	0.1715	0.4415	3.60	17.15
Des con	0.2714	0.2715	0.7088	0.9063	4.93	70.88
Dyt dau	0.0137	0.5409	0.7147	0.7540	2.54	71.47
Dyt sp.	0.0014	0.0230	0.5822	0.8197	1.33	58.22
Grp lib	0.0542	0.6659	0.6659	0.9831	6.78	66.59
Grp per	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Grp sp.	0.4080	0.8394	0.8432	0.9273	2.60	84.32
Hda aru	0.5904	0.6401	0.7587	0.7589	1.87	75.87
Hda sp.	0.0043	0.0047	0.1712	0.4414	3.66	17.12
Hdp pau	0.1193	0.1592	0.4229	0.4858	5.38	42.29
Hdp rub	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hdp ruf	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hdp sp.	0.0839	0.1154	0.6455	0.9426	1.96	64.55
Hdp spl	0.1815	0.3875	0.5520	0.9476	2.10	55.20
Hyg pat	0.0542	0.6658	0.6659	0.9832	6.71	66.59
Hyg sal	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hyg say	0.6661	0.6666	0.8890	0.9127	1.03	88.90
Hyg spl	0.0542	0.6659	0.6659	0.9832	6.75	66.59
Hyg sp2	0.5149	0.7520	0.8817	0.8817	2.23	88.17
Lac big	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Lac mac	0.6124	0.7648	0.7648	0.9402	0.79	76.48
Lac sp.	0.0043	0.0047	0.1713	0.4415	3.64	17.13
Lio aff	0.4859	0.4867	0.7400	0.8320	1.38	74.00
Rha bin	0.4314	0.5176	0.5455	1.0000	0.35	54.55
Rha fro	0.6112	0.6553	0.9181	0.9738	4.07	91.81
Rha sp.	0.0542	0.6658	0.6659	0.9832	6.71	66.59
Rha sut	0.0811	0.4095	0.5190	0.9517	2.30	51.90
Anc lim	0.0226	0.5869	0.5920	1.0000	2.11	59.20
Ber str	0.1525	0.6147	0.6963	0.9857	5.89	69.63
Cym min	0.0043	0.0047	0.1714	0.4415	3.63	17.14
Cym vin	0.1524	0.6150	0.6966	0.9858	5.97	69.66
Eno ham	0.6111	0.6552	0.9180	0.9738	4.02	91.80

TABLE 4. Continued.

	Axis 1	Axis 2	Axis 3	Axis 4	Variance (y)	Percent Variance Explained
Eno och	0.2715	0.2716	0.7089	0.9062	4.90	70.89
Hel ang	0.1525	0.6147	0.6963	0.9857	5.89	69.63
Hel lac	0.1193	0.1592	0.4229	0.4858	5.38	42.29
Hdb fus	0.1194	0.1593	0.4230	0.4860	5.44	42.30
Hdc obt	0.6112	0.6554	0.9181	0.9738	4.08	91.81
Hdu pse	0.2944	0.7605	0.9499	0.9929	2.52	94.99
Tro lat	0.0248	0.0527	0.9448	0.9822	1.76	94.48
Tro sp.	0.1524	0.6149	0.6965	0.9858	5.94	69.65
Hdr ang	0.3581	0.4541	0.8395	0.8831	2.15	83.95
Cyp sp.	0.2715	0.2716	0.7089	0.9062	4.90	70.89

TABLE 5. Squared residual length per pond with four axes generated from the CCA model with arthropods collected from the six Sandilands Provincial Forest study ponds and pH, silt, and area covered by macrophytes.

	Axis 1	Axis 2	Axis 3	Axis 4	Squared Residual Length	Percent Fit
Fraction Fitted	0.3506	0.2342	0.1502	0.1534		
Pond 34	0.2274	0.1937	0.0490	0.0125	1.13	98.89
Pond 37	0.4867	0.4639	0.3844	0.3288	0.74	55.48
Pond 39	1.4955	0.3589	0.3592	0.0134	1.65	99.19
Pond 40	0.5779	0.5777	0.3977	0.2388	0.58	58.84
Pond 41	0.6267	0.6256	0.2122	0.0543	1.09	95.03
Pond 42	0.9667	0.3472	0.2874	0.0099	1.33	99.26

TABLE 6. Biplot scores of pH, silt, and area covered by macrophytes generated from the CCA model with arthropods collected in six Sandilands Provincial Forest study ponds.

	Axis 1	Axis 2	Axis 3	Axis 4
Correlation Coefficient (r) Species vs Environment	0.9994	0.9962	0.9734	0.0000
pH	0.9877	-0.0728	-0.1387	0.0000
Silt	0.4943	-0.2100	0.8435	0.0000
Macrophyte Cover	-0.0217	-0.7984	0.6017	0.0000

APPENDIX II

**INTER-SPECIES OVERLAP, SPECIES-ENVIRONMENT OVERLAP,
AVAILABLE PONDS, AND REPLACEMENT POTENTIAL**

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TABLE 1. Inter-species overlap, species-environment (LC site scores) overlap, available habitat, and potential for functional replacement in the six Sandilands Provincial Forest study ponds.

Lost Species		Replacement Species
<i>Caenis diminuta</i>	<i>Caenis youngi</i>	
Inter-Species Overlap: Axis 1	97.18%	
Inter-Species Overlap: Axis 2	51.60%	
Inter-Species Overlap: Axis 3	100.00%	
Inter-Species Overlap: Axis 4	100.00%	
Species-Environment Overlap: Axis 1	Pond 39; Pond 40; Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	
Species-Environment Overlap: Axis 4 ^(a)		
Model I: Available Ponds	Pond 42;	
Model I: Potential for Replacement	Pond 42 (No) ^(b) ;	
Model II and III: Available Ponds	Pond 39;	
Model II and III: Potential for Replacement	Pond 39 (Possible) ^{(c)(d)} ;	
<i>Caenis youngi</i>	<i>Caenis diminuta</i>	
Inter-Species Overlap: Axis 1	65.78%	
Inter-Species Overlap: Axis 2	100.00%	
Inter-Species Overlap: Axis 3	66.31%	
Inter-Species Overlap: Axis 4	9.17%	
Species-Environment Overlap: Axis 1	Pond 39; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 3	Pond 39; Pond 40; Pond 42;	

TABLE 1. Continued.

Lost Species	Replacement Species
Species-Environment Overlap: Axis 4	
Model I: Available Ponds	Pond 40; Pond 41;
Model I: Potential for Replacement	Pond 40 (No); Pond 41 (No);
Model II and III: Available Ponds	Pond 39;
Model II and III: Potential for Replacement	Pond 39 (Possible);
<i>Aeshna canadensis</i>	<i>Anax junius</i>
Inter-Species Overlap: Axis 1	12.95%
Inter-Species Overlap: Axis 2	53.85%
Inter-Species Overlap: Axis 3	58.96%
Inter-Species Overlap: Axis 4	13.73%
Species-Environment Overlap: Axis 1	Pond 34;
Species-Environment Overlap: Axis 2	Pond 34;
Species-Environment Overlap: Axis 3	Pond 34;
Species-Environment Overlap: Axis 4	
Model I: Available Ponds	Pond 41;
Model I: Potential for Replacement	Pond 41 (No);
Model II and III: Available Ponds	Pond 34;
Model II and III: Potential for Replacement	Pond 34 (Possible);
<i>Aeshna interrupta</i>	<i>Anax junius</i>
Inter-Species Overlap: Axis 1	16.65%
Inter-Species Overlap: Axis 2	14.30%
Inter-Species Overlap: Axis 3	12.15%
Inter-Species Overlap: Axis 4	11.00%

TABLE 1. Continued.

Lost Species		Replacement Species	
Species-Environment Overlap:	Pond 34;		
Axis 1			
Species-Environment Overlap:	Pond 34;		
Axis 2			
Species-Environment Overlap:	Pond 34;		
Axis 3			
Species-Environment Overlap:			
Axis 4			
Model I: Available Ponds	Pond 37; Pond 39; Pond 40; Pond 41;		
Model I: Potential for Replacement	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No);		
Model II and III: Available Ponds	Pond 34;		
Model II and III: Potential for Replacement	Pond 34 (Possible);		
<i>Anax junius</i>	<i>Aeshna interrupta</i>	<i>Aeshna canadensis</i>	
Inter-Species Overlap: Axis 1	100.00%	100.00%	
Inter-Species Overlap: Axis 2	100.00%	100.00%	
Inter-Species Overlap: Axis 3	100.00%	100.00%	
Inter-Species Overlap: Axis 4	100.00%	100.00%	
Species-Environment Overlap:	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Axis 1			
Species-Environment Overlap:	Pond 34; Pond 37; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;	
Axis 2			
Species-Environment Overlap:	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 41;	
Axis 3			
Species-Environment Overlap:			
Axis 4			

TABLE 1. Continued.

Lost Species		Replacement Species	
Model I: Available Ponds	None Available	None Available	
Model I: Potential for Replacement	None Available	None Available	
Model II and III: Available Ponds	Pond 34;	Pond 34;	
Model II and III: Potential for Replacement	Pond 34 (Probable);	Pond 34 (Probable);	
<i>Cordulia shurtleffi</i>	<i>Sympetrum danae</i>		
Inter-Species Overlap: Axis 1	0.00%		
Inter-Species Overlap: Axis 2	4.32%		
Inter-Species Overlap: Axis 3	0.00%		
Inter-Species Overlap: Axis 4	6.31%		
Species-Environment Overlap: Axis 1	Pond 42;		
Species-Environment Overlap: Axis 2	Pond 42;		
Species-Environment Overlap: Axis 3	Pond 40; Pond 42;		
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 34;		
Model I: Potential for Replacement	Pond 34 (No);		
Model II and III: Available Ponds	Pond 42;		
Model II and III: Potential for Replacement	Pond 42 (Possible);		
<i>Somatochlora williamsoni</i>	<i>Sympetrum obtrusum</i>	<i>Sympetrum danae</i>	
Inter-Species Overlap: Axis 1	76.21%	7.63%	
Inter-Species Overlap: Axis 2	68.52%	9.53%	
Inter-Species Overlap: Axis 3	58.77%	6.11%	
Inter-Species Overlap: Axis 4	92.02%	7.58%	

TABLE 1. Continued.

Lost Species		Replacement Species	
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 42;	
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 40; Pond 42;	
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 34; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	
Model I: Potential for Replacement	Pond 34 (No); Pond 40 (Yes); Pond 41 (Yes); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No);	
Model II and III: Available Ponds	Pond 37; Pond 39;	Pond 42;	
Model II and III: Potential for Replacement	Pond 37 (Possible); Pond 39 (Possible);	Pond 42 (Possible);	
<i>Leucorrhinia hudsonica</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Banksiola crotchii</i>
Inter-Species Overlap: Axis 1	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 2	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 3	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 4	100.00%	100.00%	100.00%

TABLE 1. Continued.

Lost Species		Replacement Species				
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond			
Axis 1	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond			
Axis 2	37; Pond 40; Pond 41; Pond 42;	37; Pond 40; Pond 41; 42;	37; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond			
Axis 3	39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap:						
Axis 4						
Model I: Available Ponds	None Available	None Available	None Available			
Model I: Potential for Replacement	None Available	None Available	None Available			
Model II and III: Available Ponds	Pond 34;	Pond 34;	Pond 34;			
Model II and III: Potential for Replacement	Pond 34 (Probable);	Pond 34 (Probable);	Pond 34 (Possible);			
<i>Leucorrhinia intacta</i>	<i>Sympetrum</i>	<i>Leucorrhinia</i>	<i>Leucorrhinia</i>	<i>Lestes</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus</i>
	<i>danae</i>	<i>proxima</i>	<i>hudsonica</i>	<i>unguiculatus</i>		<i>disjunctus</i>
Inter-Species Overlap: Axis 1	5.71%	100.00%	13.68%	100.00%	10.71%	17.46%
Inter-Species Overlap: Axis 2	1.89%	79.03%	11.77%	100.00%	16.62%	100.00%
Inter-Species Overlap: Axis 3	5.84%	68.24%	7.99%	66.64%	10.50%	84.92%
Inter-Species Overlap: Axis 4	11.31%	88.52%	8.79%	38.23%	18.68%	100.00%
Species-Environment Overlap:	Pond 42;	Pond 34; Pond	Pond 34;	Pond 34; Pond	Pond 40;	Pond 39; Pond
Axis 1		37; Pond 39; Pond 40; Pond 41; Pond 42;		37; Pond 39; Pond 40; Pond 41; Pond 42;		41; Pond 42;
Species-Environment Overlap:	Pond 42;	Pond 34; Pond	Pond 34;	Pond 34; Pond	Pond 40; Pond	Pond 34; Pond
Axis 2		37; Pond 40; Pond 41; Pond 42;		37; Pond 39; Pond 40; Pond 41; Pond 42;	41;	37; Pond 39; Pond 40; Pond 41; Pond 42;

TABLE 1. Continued.

Lost Species		Replacement Species							
Species-Environment Overlap: Axis 3	Pond 40; Pond 42;	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap: Axis 4									
Model I: Available Ponds	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 37; Pond 39; Pond 40;	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 37; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40;			
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No);	Pond 37 (No); Pond 39 (Yes); Pond 40 (Yes);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (Yes); Pond 40 (Yes); Pond 41 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 40 (No);			
Model II and III: Available Ponds	Pond 42;	Pond 34; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 39; Pond 42;	Pond 40;	Pond 39; Pond 41; Pond 42;			
Model II and III: Potential for Replacement	Pond 42 (Possible);	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Possible); Pond 39 (Possible); Pond 42 (Possible);	Pond 40 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);			
<i>Leucorrhinia proxima</i>	<i>Sympetrum danae</i>	<i>Ptilostomis</i> sp.	<i>Leucorrhinia intacta</i>	<i>Leucorrhinia hudsonica</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus</i>	<i>Lestes congener</i>	<i>Banksiola crotchii</i>
Inter-Species Overlap: Axis 1	5.23%	19.33%	62.91%	8.60%	72.79%	6.74%	19.11%	66.69%	75.05%
Inter-Species Overlap: Axis 2	17.02%	81.08%	85.02%	12.66%	100.00%	17.88%	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 3	8.20%	43.80%	100.00%	11.21%	66.99%	11.77%	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 4	11.09%	100.00%	86.82%	8.62%	49.40%	18.32%	100.00%	100.00%	100.00%
Species-Environment Overlap: Axis 1	Pond 42;	Pond 39; Pond 40;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40;	Pond 39; Pond 41; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 40; Pond 41;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;

TABLE 1. Continued.

Lost Species		Replacement Species							
Species-Environment Overlap: Axis 3	Pond 40; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4									
Model I: Available Ponds	Pond 34; Pond 41;	Pond 34; Pond 41; Pond 42;	None Available	Pond 41; Pond 42;	Pond 41;	Pond 34; Pond 41; Pond 42;	Pond 34;	None Available	None Available
Model I: Potential for Replacement	Pond 34 (No); Pond 41 (No);	Pond 34 (No); Pond 41 (No); Pond 42 (No);	None Available	Pond 41 (No); Pond 42 (No);	Pond 41 (No);	Pond 34 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No);	None Available	None Available
Model II and III: Available Ponds	Pond 42;	None Available	Pond 34; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 42;	None Available	Pond 41; Pond 42;	Pond 34; Pond 41; Pond 42;	Pond 34; Pond 41; Pond 42;
Model II and III: Potential for Replacement	Pond 42 (Possible);	None Available	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Possible); Pond 42 (Probable);	None Available	Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 41 (Probable); Pond 42 (Probable);	Pond 34 (Possible); Pond 41 (Possible); Pond 42 (Probable);
<i>Libellula quadrimaculata</i>	<i>Somatochlora williamsoni</i>								
Inter-Species Overlap: Axis 1	100.00%								
Inter-Species Overlap: Axis 2	97.81%								
Inter-Species Overlap: Axis 3	100.00%								
Inter-Species Overlap: Axis 4	93.86%								
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;								
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;								
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;								
Species-Environment Overlap: Axis 4									

TABLE 1. Continued.

Lost Species		Replacement Species			
Model I: Available Ponds	None Available				
Model I: Potential for Replacement	None Available				
Model II and III: Available Ponds	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;				
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 39 (Possible); Pond 40 (Possible); Pond 41 (Probable); Pond 42 (Possible);				
<i>Sympetrum danae</i>	<i>Somatochlora williamsoni</i>	<i>Leucorrhinia proxima</i>	<i>Leucorrhinia intacta</i>	<i>Cordulia shurtleffi</i>	
Inter-Species Overlap: Axis 1	100.00%	100.00%	68.66%	0.00%	
Inter-Species Overlap: Axis 2	100.00%	89.16%	10.67%	16.56%	
Inter-Species Overlap: Axis 3	100.00%	100.00%	100.00%	0.00%	
Inter-Species Overlap: Axis 4	100.00%	100.00%	100.00%	100.00%	
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;	
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 39; Pond 41;	
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	None Available	None Available	None Available	None Available	
Model I: Potential for Replacement	None Available	None Available	None Available	None Available	

TABLE 1. Continued.

Lost Species		Replacement Species			
Model II and III: Available Ponds	Pond 42;	Pond 42;	Pond 42;	Pond 42;	
Model II and III: Potential for Replacement	Pond 42 (Possible);	Pond 42 (Possible);	Pond 42 (Possible);	Pond 42 (Possible);	
<i>Sympetrum obtrusum</i>	<i>Somatochlora williamsoni</i>				
Inter-Species Overlap: Axis 1	100.00%				
Inter-Species Overlap: Axis 2	100.00%				
Inter-Species Overlap: Axis 3	100.00%				
Inter-Species Overlap: Axis 4	100.00%				
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;				
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;				
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;				
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	None Available				
Model I: Potential for Replacement	None Available				
Model II and III: Available Ponds	Pond 37; Pond 39;				
Model II and III: Potential for Replacement	Pond 37 (Possible); Pond 39 (Probable);				
<i>Lestes congener</i>	<i>Leucorrhinia proxima</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus</i>		
Inter-Species Overlap: Axis 1	96.75%	9.78%	27.72%		
Inter-Species Overlap: Axis 2	60.40%	10.80%	100.00%		
Inter-Species Overlap: Axis 3	73.53%	10.84%	91.73%		

TABLE 1. Continued.

Lost Species		Replacement Species			
Inter-Species Overlap: Axis 4	71.06%	13.02%	93.07%		
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40;	Pond 39; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	Pond 39; Pond 40;	Pond 34; Pond 39; Pond 41; Pond 42;	Pond 34; Pond 40;		
Model I: Potential for Replacement	Pond 39 (Yes); Pond 40 (Yes);	Pond 34 (No); Pond 39 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 40 (No);		
Model II and III: Available Ponds	Pond 34; Pond 41; Pond 42;	Pond 40;	Pond 39; Pond 41; Pond 42;		
Model II and III: Potential for Replacement	Pond 34 (Probable); Pond 41 (Possible); Pond 42 (Possible);	Pond 40 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);		
<i>Lestes disjunctus disjunctus</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes dryus</i>	<i>Lestes congener</i>
Inter-Species Overlap: Axis 1	100.00%	57.48%	100.00%	0.00%	100.00%
Inter-Species Overlap: Axis 2	38.07%	40.95%	81.64%	6.81%	63.03%
Inter-Species Overlap: Axis 3	80.16%	100.00%	72.47%	11.82%	100.00%
Inter-Species Overlap: Axis 4	61.70%	60.51%	30.48%	11.30%	80.82%

TABLE 1. Continued.

Lost Species		Replacement Species			
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40;	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 42;	Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	Pond 39;	None Available	Pond 41;	Pond 39; Pond 41; Pond 42;	None Available
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 41 (No);	Pond 39 (No); Pond 41 (No); Pond 42 (No);	None Available
Model II and III: Available Ponds	Pond 41; Pond 42;	Pond 39; Pond 41; Pond 42;	Pond 39; Pond 42;	None Available	Pond 39; Pond 41; Pond 42;
Model II and III: Potential for Replacement	Pond 41 (Possible); Pond 42 (Possible);	Pond 39 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 39 (Possible); Pond 42 (Probable);	None Available	Pond 39 (Possible); Pond 41 (Probable); Pond 42 (Probable);
<i>Lestes dryas</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes unguiculatus</i>	<i>Lestes disjunctus disjunctus</i>	<i>Lestes congener</i>
Inter-Species Overlap: Axis 1	100.00%	100.00%	100.00%	0.00%	100.00%
Inter-Species Overlap: Axis 2	100.00%	100.00%	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 3	79.86%	100.00%	100.00%	100.00%	100.00%
Inter-Species Overlap: Axis 4	100.00%	100.00%	0.00%	100.00%	100.00%

TABLE 1. Continued.

Lost Species		Replacement Species			
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond	Pond 39; Pond	Pond 37; Pond
Axis 1	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;	41; Pond 42;	39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond
Axis 2	37; Pond 40; Pond 41; Pond 42;	37; Pond 40; Pond 41;	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond	Pond 34; Pond
Axis 3	39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap:					
Axis 4					
Model I: Available Ponds	Pond 40;	None Available	Pond 40;	Pond 40;	None Available
Model I: Potential for Replacement	Pond 40 (Yes);	None Available	Pond 40 (Yes);	Pond 40 (No);	None Available
Model II and III: Available Ponds	None Available	Pond 40;	None Available	None Available	Pond 40;
Model II and III: Potential for Replacement	None Available	Pond 40 (Probable);	None Available	None Available	Pond 40 (Probable);
<i>Lestes unguiculatus</i>	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia intacta</i>	<i>Lestes dryas</i>	<i>Lestes disjunctus</i>	<i>disjunctus</i>
Inter-Species Overlap: Axis 1	93.17%	63.48%	8.63%	24.46%	
Inter-Species Overlap: Axis 2	40.74%	43.82%	7.28%	87.37%	
Inter-Species Overlap: Axis 3	71.64%	100.00%	15.76%	96.67%	
Inter-Species Overlap: Axis 4	100.00%	100.00%	0.00%	100.00%	
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 40;	Pond 39; Pond	
Axis 1	37; Pond 39; Pond 40; Pond 41; Pond 42;	37; Pond 39; Pond 40; Pond 42;		41; Pond 42;	
Species-Environment Overlap:	Pond 34; Pond	Pond 34; Pond	Pond 40; Pond	Pond 34; Pond	
Axis 2	37; Pond 40; Pond 41; Pond 42;	37; Pond 40; Pond 41;	41;	37; Pond 39; Pond 40; Pond 41; Pond 42;	

TABLE 1. Continued.

Lost Species		Replacement Species		
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	Pond 39;	None Available	Pond 34; Pond 39; Pond 42;	Pond 34;
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 34 (No); Pond 39 (No); Pond 42 (No);	Pond 34 (No);
Model II and III: Available Ponds	Pond 34; Pond 42;	Pond 34; Pond 39; Pond 42;	None Available	Pond 39; Pond 42;
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 39 (Possible); Pond 42 (Possible);	None Available	Pond 39 (Possible); Pond 42 (Possible);
<i>Coenagrion angulatum</i>	<i>Ptilostomis</i> sp.	<i>Enallagma cyathigerum</i>	<i>Banksiola crotchii</i>	
Inter-Species Overlap: Axis 1	54.01%	100.00%	100.00%	
Inter-Species Overlap: Axis 2	72.28%	87.87%	100.00%	
Inter-Species Overlap: Axis 3	40.34%	99.00%	94.02%	
Inter-Species Overlap: Axis 4	96.15%	88.32%	89.60%	
Species-Environment Overlap: Axis 1	Pond 39; Pond 40;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 4				

TABLE 1. Continued.

Lost Species		Replacement Species	
Model I: Available Ponds	Pond 41; Pond 42;	None Available	None Available
Model I: Potential for Replacement	Pond 41 (No); Pond 42 (No);	None Available	None Available
Model II and III: Available Ponds	Pond 40;	Pond 40; Pond 41; Pond 42; Pond 40	Pond 40; Pond 41; Pond 42; Pond 40
Model II and III: Potential for Replacement	Pond 40 (Possible);	(Probable); Pond 41 (Probable); Pond 42 (Probable);	(Possible); Pond 41 (Possible); Pond 42 (Possible);
<i>Coenagrion resolutum</i>	<i>Ptilostomis</i> sp.	<i>Banksiola crotchii</i>	
Inter-Species Overlap: Axis 1	32.61%	100.00%	
Inter-Species Overlap: Axis 2	69.02%	100.00%	
Inter-Species Overlap: Axis 3	41.86%	95.96%	
Inter-Species Overlap: Axis 4	100.00%	93.10%	
Species-Environment Overlap: Axis 1	Pond 39; Pond 40;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 34; Pond 41; Pond 42;	None Available	
Model I: Potential for Replacement	Pond 34 (No); Pond 41 (No); Pond 42 (No);	None Available	
Model II and III: Available Ponds	Pond 40;	Pond 34; Pond 40; Pond 41; Pond 42;	

TABLE 1. Continued.

Lost Species		Replacement Species	
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Possible); Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);	
<i>Enallagma cyathigerum</i>	<i>Ptilostomis</i> sp.	<i>Coenagrion angulatum</i>	<i>Banksiola crotchii</i>
Inter-Species Overlap: Axis 1	25.85%	47.86%	100.00%
Inter-Species Overlap: Axis 2	86.86%	74.10%	75.66%
Inter-Species Overlap: Axis 3	40.01%	98.20%	92.61%
Inter-Species Overlap: Axis 4	100.00%	100.00%	97.05%
Species-Environment Overlap: Axis 1	Pond 39; Pond 40;	Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 34; Pond 37; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39;	Pond 39;
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 34 (No); Pond 37 (No); Pond 39 (No);	Pond 39 (No);
Model II and III: Available Ponds	Pond 39; Pond 40;	Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;

TABLE 1. Continued.

Lost Species		Replacement Species			
Model II and III: Potential for Replacement	Pond 39 (Possible); Pond 40 (Possible);	Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible); Pond 37 (Possible); Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);		
<i>Notonecta borealis</i>	<i>Notonecta irrorata</i>	<i>Hydaticus aruspex</i>			
Inter-Species Overlap: Axis 1	100.00%	100.00%			
Inter-Species Overlap: Axis 2	100.00%	100.00%			
Inter-Species Overlap: Axis 3	100.00%	100.00%			
Inter-Species Overlap: Axis 4	100.00%	100.00%			
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40;			
Species-Environment Overlap: Axis 2	Pond 34; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;			
Species-Environment Overlap: Axis 3	Pond 34; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	None Available	None Available			
Model I: Potential for Replacement	None Available	None Available			
Model II and III: Available Ponds	Pond 34;	Pond 34;			
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Probable);			
<i>Notonecta irrorata</i>	<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta borealis</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>
Inter-Species Overlap: Axis 1	45.46%	18.27%	8.44%	79.41%	57.89%
Inter-Species Overlap: Axis 2	100.00%	100.00%	33.94%	100.00%	86.48%
Inter-Species Overlap: Axis 3	100.00%	0.00%	36.32%	100.00%	100.00%

TABLE 1. Continued.

Lost Species		Replacement Species			
Inter-Species Overlap: Axis 4	100.00%	100.00%	8.92%	50.97%	89.61%
Species-Environment Overlap: Axis 1	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39; Pond 40; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 40; Pond 41;
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34;	Pond 34; Pond 39; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4					
Model I: Available Ponds	Pond 34;	Pond 34; Pond 41;	Pond 41;	Pond 41;	Pond 41;
Model I: Potential for Replacement	Pond 34 (No);	Pond 34 (No); Pond 41 (No);	Pond 41 (No);	Pond 41 (Yes);	Pond 41 (No);
Model II and III: Available Ponds	Pond 41;	None Available	Pond 34;	Pond 34;	Pond 34;
Model II and III: Potential for Replacement	Pond 41 (Possible);	None Available	Pond 34 (Possible);	Pond 34 (Possible);	Pond 34 (Possible);
<i>Notonecta kirbyi</i>	<i>Notonecta undulata</i>	<i>Notonecta irrorata</i>	<i>Hydroporus</i> sp. 1	<i>Hydaticus aruspex</i>	
Inter-Species Overlap: Axis 1	100.00%	100.00%	100.00%	85.46%	
Inter-Species Overlap: Axis 2	100.00%	20.54%	100.00%	17.94%	
Inter-Species Overlap: Axis 3	100.00%	0.00%	63.20%	100.00%	
Inter-Species Overlap: Axis 4	89.24%	59.86%	40.56%	55.60%	
Species-Environment Overlap: Axis 1	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 40; Pond 41;	

TABLE 1. Continued.

Lost Species		Replacement Species		
Species-Environment Overlap: Axis 3	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 41;	Pond 34; Pond 39; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	None Available	Pond 39; Pond 40;	Pond 40;	Pond 39;
Model I: Potential for Replacement	None Available	Pond 39 (No); Pond 40 (No);	Pond 40 (No);	Pond 39 (No);
Model II and III: Available Ponds	Pond 39; Pond 40;	None Available	Pond 39;	Pond 40;
Model II and III: Potential for Replacement	Pond 39 (Probable); Pond 40 (Probable);	None Available	Pond 39 (Possible);	Pond 40 (Possible);
<i>Notonecta undulata</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>		
Inter-Species Overlap: Axis 1	40.20%	100.00%		
Inter-Species Overlap: Axis 2	74.42%	18.85%		
Inter-Species Overlap: Axis 3	38.83%	22.98%		
Inter-Species Overlap: Axis 4	97.50%	65.41%		
Species-Environment Overlap: Axis 1	Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;		
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 41;		
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	Pond 37; Pond 41; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 42;		

TABLE 1. Continued.

Lost Species		Replacement Species				
Model I: Potential for Replacement	Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 42 (No);				
Model II and III: Available Ponds	Pond 39; Pond 40;	Pond 41;				
Model II and III: Potential for Replacement	Pond 39 (Possible); Pond 40 (Possible);	Pond 41 (Possible);				
<i>Banksiola crotchii</i>	<i>Prilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Leuchorrhinia hudsonica</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>
Inter-Species Overlap: Axis 1	25.42%	98.69%	11.31%	93.15%	77.97%	47.07%
Inter-Species Overlap: Axis 2	68.96%	65.93%	8.35%	83.46%	93.65%	93.03%
Inter-Species Overlap: Axis 3	42.90%	65.73%	8.81%	99.31%	98.35%	100.00%
Inter-Species Overlap: Axis 4	100.00%	70.88%	6.11%	91.10%	100.00%	100.00%
Species-Environment Overlap: Axis 1	Pond 39; Pond 40;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4						
Model I: Available Ponds	Pond 34; Pond 37; Pond 41; Pond 42;	Pond 37; Pond 40;	Pond 37; Pond 40; Pond 41; Pond 42;	None Available	Pond 37;	Pond 34; Pond 37;
Model I: Potential for Replacement	Pond 34 (No); Pond 37 (No); Pond 41 (No); Pond 42 (No);	Pond 37 (No); Pond 40 (Yes);	Pond 37 (No); Pond 40 (No); Pond 41 (No); Pond 42 (No);	None Available	Pond 37 (Yes);	Pond 34 (No); Pond 37 (No);

TABLE 1. Continued.

Lost Species		Replacement Species				
Model II and III: Available Ponds	Pond 40;	Pond 34; Pond 41; Pond 42;	Pond 34;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 40; Pond 41; Pond 42;	Pond 40; Pond 41; Pond 42;
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Probable); Pond 41 (Possible); Pond 42 (Possible);	Pond 34 (Possible);	Pond 34 (Probable); Pond 37 (Probable); Pond 40 (Probable); Pond 41 (Probable); Pond 42 (Probable);	Pond 34 (Possible); Pond 40 (Probable); Pond 41 (Probable); Pond 42 (Probable);	Pond 40 (Possible); Pond 41 (Possible); Pond 42 (Possible);
<i>Ptilostomis</i> sp.	<i>Leuchorrhinia proxima</i>	<i>Enallagma cyathigerum</i>	<i>Coenagrion resolutum</i>	<i>Coenagrion angulatum</i>	<i>Banksiola crotchii</i>	
Inter-Species Overlap: Axis 1	100.00%	100.00%	100.00%	100.00%	100.00%	
Inter-Species Overlap: Axis 2	42.51%	76.20%	51.41%	53.48%	54.85%	
Inter-Species Overlap: Axis 3	80.21%	100.00%	100.00%	100.00%	100.00%	
Inter-Species Overlap: Axis 4	58.95%	78.08%	89.34%	85.00%	83.17%	
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	
Species-Environment Overlap: Axis 4						
Model I: Available Ponds	Pond 39; Pond 40;	None Available	Pond 39;	Pond 39;	Pond 39;	
Model I: Potential for Replacement	Pond 39 (No); Pond 40 (Yes);	None Available	Pond 39 (No);	Pond 39 (No);	Pond 39 (No);	
Model II and III: Available Ponds	None Available	Pond 39; Pond 40;	Pond 40;	Pond 40;	Pond 40;	

TABLE 1. Continued.

Lost Species		Replacement Species			
Model II and III: Potential for Replacement	None Available	Pond 39 (Probable); Pond 40 (Probable);	Pond 40 (Possible);	Pond 40 (Probable);	Pond 40 (Probable);
<i>Haliphus subguttatus</i>	<i>Peltodytes tortulosus</i>				
Inter-Species Overlap: Axis 1	16.92%				
Inter-Species Overlap: Axis 2	4.60%				
Inter-Species Overlap: Axis 3	13.23%				
Inter-Species Overlap: Axis 4	5.32%				
Species-Environment Overlap:	Pond 40;				
Axis 1					
Species-Environment Overlap:	Pond 40; Pond				
Axis 2	41;				
Species-Environment Overlap:	Pond 40; Pond				
Axis 3	42;				
Species-Environment Overlap:					
Axis 4					
Model I: Available Ponds	Pond 39;				
Model I: Potential for Replacement	Pond 39 (No);				
Model II and III: Available Ponds	Pond 40;				
Model II and III: Potential for Replacement	Pond 40 (Possible);				
<i>Peltodytes tortulosus</i>	<i>Haliphus subguttatus</i>				
Inter-Species Overlap: Axis 1	100.00%				
Inter-Species Overlap: Axis 2	100.00%				
Inter-Species Overlap: Axis 3	100.00%				
Inter-Species Overlap: Axis 4	100.00%				
Species-Environment Overlap:	Pond 39; Pond				
Axis 1	40; Pond 42;				
Species-Environment Overlap:	Pond 34; Pond				
Axis 2	37; Pond 39;				
	Pond 40; Pond				
	41;				
Species-Environment Overlap:	Pond 37; Pond				
Axis 3	39; Pond 40;				
	Pond 42;				

TABLE 1. Continued.

Lost Species		Replacement Species	
Species-Environment Overlap:			
Axis 4			
Model I: Available Ponds	None Available		
Model I: Potential for Replacement	None Available		
Model II and III: Available Ponds	Pond 40;		
Model II and III: Potential for Replacement	Pond 40 (Possible);		
<i>Graphoderus liberus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	
Inter-Species Overlap: Axis 1	100.00%	0.00%	
Inter-Species Overlap: Axis 2	100.00%	0.00%	
Inter-Species Overlap: Axis 3	100.00%	0.00%	
Inter-Species Overlap: Axis 4	100.00%	0.00%	
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 41;	Pond 34;	
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	None Available	Pond 39;	
Model I: Potential for Replacement	None Available	Pond 39 (No);	
Model II and III: Available Ponds	Pond 39;	None Available	
Model II and III: Potential for Replacement	Pond 39 (Possible);	None Available	
<i>Hydaticus aruspex</i>	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Notonecta borealis</i>
Inter-Species Overlap: Axis 1	26.98%	100.00%	14.59%
Inter-Species Overlap: Axis 2	100.00%	99.03%	38.87%

TABLE 1. Continued.

Lost Species		Replacement Species		
Inter-Species Overlap: Axis 3	48.00%	28.41%	10.32%	
Inter-Species Overlap: Axis 4	100.00%	100.00%	9.60%	
Species-Environment Overlap: Axis 1	Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;	Pond 34;	
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 41;	Pond 34;	
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	Pond 34;	Pond 40;	Pond 40;	
Model I: Potential for Replacement	Pond 34 (No);	Pond 40 (No);	Pond 40 (No);	
Model II and III: Available Ponds	Pond 40;	Pond 34;	Pond 34;	
Model II and III: Potential for Replacement	Pond 40 (Possible);	Pond 34 (Possible);	Pond 34 (Possible);	
<i>Hydroporus</i> sp. 1	<i>Notonecta kirbyi</i>	<i>Notonecta irrorata</i>	<i>Laccophilus maculosus</i>	<i>Hygrotus</i> sp. 2
Inter-Species Overlap: Axis 1	23.01%	100.00%	34.08%	12.71%
Inter-Species Overlap: Axis 2	84.94%	17.45%	100.00%	59.14%
Inter-Species Overlap: Axis 3	50.17%	45.96%	100.00%	100.00%
Inter-Species Overlap: Axis 4	100.00%	100.00%	100.00%	100.00%
Species-Environment Overlap: Axis 1	Pond 39; Pond 40; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39; Pond 40; Pond 41; Pond 42;	Pond 41; Pond 42;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41;	Pond 34; Pond 40; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 40; Pond 41; Pond 42;

TABLE 1. Continued.

Lost Species		Replacement Species		
Species-Environment Overlap: Axis 3	Pond 37; Pond 39; Pond 40; Pond 42;	Pond 34; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	Pond 34;	Pond 39;	Pond 34;	Pond 34; Pond 39;
Model I: Potential for Replacement	Pond 34 (No);	Pond 39 (No);	Pond 34 (No);	Pond 34 (No);
Model II and III: Available Ponds	Pond 39;	Pond 34;	Pond 39;	Pond 39 (No); None Available
Model II and III: Potential for Replacement	Pond 39 (Possible);	Pond 34 (Possible);	Pond 39 (Probable);	None Available
<i>Hygrotylus</i> sp. 2	<i>Hydroporus</i> sp. 1			
Inter-Species Overlap: Axis 1	100.00%			
Inter-Species Overlap: Axis 2	88.50%			
Inter-Species Overlap: Axis 3	47.29%			
Inter-Species Overlap: Axis 4	43.59%			
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;			
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 41;			
Species-Environment Overlap: Axis 4				
Model I: Available Ponds	Pond 41; Pond 42;			
Model I: Potential for Replacement	Pond 41 (Yes); Pond 42 (No);			
Model II and III: Available Ponds	None Available			

TABLE I. Continued.

Lost Species		Replacement Species	
Model II and III: Potential for Replacement		None Available	
<i>Laccophilus maculosus</i>	<i>Hydroporus</i> sp. I		
Inter-Species Overlap: Axis 1	100.00%		
Inter-Species Overlap: Axis 2	87.77%		
Inter-Species Overlap: Axis 3	60.56%		
Inter-Species Overlap: Axis 4	41.78%		
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;		
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 41;		
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 40; Pond 41; Pond 42;		
Model I: Potential for Replacement	Pond 40 (No); Pond 41 (Yes); Pond 42 (No);		
Model II and III: Available Ponds	Pond 39;		
Model II and III: Potential for Replacement	Pond 39 (Possible);		
<i>Rhantus binotatus</i>	<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	
Inter-Species Overlap: Axis 1	100.00%	12.70%	
Inter-Species Overlap: Axis 2	90.24%	6.80%	
Inter-Species Overlap: Axis 3	58.48%	10.81%	
Inter-Species Overlap: Axis 4	55.46%	7.91%	

TABLE 1. Continued.

Lost Species		Replacement Species	
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34;	
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 41;	Pond 34;	
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 37; Pond 40; Pond 42;	Pond 37; Pond 39; Pond 40; Pond 42;	
Model I: Potential for Replacement	Pond 37 (No); Pond 40 (No); Pond 42 (No);	Pond 37 (No); Pond 39 (No); Pond 40 (No); Pond 42 (No);	
Model II and III: Available Ponds	Pond 34; Pond 39;	Pond 34;	
Model II and III: Potential for Replacement	Pond 34 (Possible); Pond 39 (Possible);	Pond 34 (Possible);	
<i>Rhantus frontalis</i>	<i>Rhantus suturellus</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>
Inter-Species Overlap: Axis 1	100.00%	100.00%	0.00%
Inter-Species Overlap: Axis 2	100.00%	100.00%	0.00%
Inter-Species Overlap: Axis 3	100.00%	100.00%	0.00%
Inter-Species Overlap: Axis 4	100.00%	100.00%	0.00%
Species-Environment Overlap: Axis 1	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;
Species-Environment Overlap: Axis 2	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;

TABLE 1. Continued.

Lost Species		Replacement Species	
Species-Environment Overlap: Axis 3	Pond 34; Pond 39; Pond 41;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	None Available	None Available	Pond 34;
Model I: Potential for Replacement	None Available	None Available	Pond 34 (No);
Model II and III: Available Ponds	Pond 34;	Pond 34;	None Available
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Possible);	None Available
<i>Rhantus suturellus</i>	<i>Rhantus frontalis</i>	<i>Rhantus binotatus</i>	<i>Graphoderus liberus</i>
Inter-Species Overlap: Axis 1	11.50%	90.61%	6.13%
Inter-Species Overlap: Axis 2	6.40%	84.99%	11.05%
Inter-Species Overlap: Axis 3	18.48%	100.00%	11.57%
Inter-Species Overlap: Axis 4	14.26%	100.00%	20.40%
Species-Environment Overlap: Axis 1	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;
Species-Environment Overlap: Axis 2	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;
Species-Environment Overlap: Axis 3	Pond 34;	Pond 34; Pond 37; Pond 39; Pond 40; Pond 41; Pond 42;	Pond 39;
Species-Environment Overlap: Axis 4			
Model I: Available Ponds	Pond 39;	None Available	Pond 34;
Model I: Potential for Replacement	Pond 39 (No);	None Available	Pond 34 (No);
Model II and III: Available Ponds	Pond 34;	Pond 34; Pond 39;	Pond 39;

TABLE 1. Continued.

Lost Species		Replacement Species	
Model II and III: Potential for Replacement	Pond 34 (Possible);	Pond 34 (Probable); Pond 39 (Possible);	Pond 39 (Possible);
<p><i>a</i> Species - environment overlap along Axis 4 is not estimated since LC site scores are provided in CCA for only the constrained axes. The number of constrained axes cannot be greater than the number of supplied environmental variables (<i>e.g.</i>, three in the present application).</p> <p><i>b</i> Replacement by Model I considered likely when the replacement species overlaps the specific pond from which the original species is hypothetically lost along the first three canonical axes.</p> <p><i>c</i> Replacement by Model II or Model III considered "Possible" when the replacement species co-exists in lesser abundance than the hypothetically lost species, and there is either less than 60% inter-species overlap on the first three canonical axes or there is no overlap with the specific pond from which the original species is hypothetically lost along the first three canonical axes.</p> <p><i>d</i> Replacement by Model II or Model III considered "Probable" when the replacement species co-exists in greater abundance than the hypothetically lost species, there is greater than 60% inter-species overlap on the first three canonical axes, and there is overlap with the specific pond from which the original species is hypothetically lost along the first three canonical axes.</p>			