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DETERMINANTS OF AQUATIC SNAIL COMMUNITY STRUCTURE
IN GREAT LAKES (LAKE HURON) COASTAL WET MEADOWS

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DETERMINANTS OF AQUATIC SNAIL COMMUNITY STRUCTURE IN GREAT LAKES (LAKE HURON) COASTAL WET MEADOWS

By

Brian E. Keas

A DISSERTATION

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ABSTRACT

DETERMINANTS OF AQUATIC SNAIL COMMUNITY STRUCTURE IN GREAT LAKES (LAKE HURON) COASTAL WET MEADOWS

By

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Previous studies examining aquatic snail community structure have used a wide variety of explanatory variables including water chemistry, area effects, habitat diversity, and biotic interactions. Almost all have focused on within-patch characteristics and have generally ignored the surrounding landscape context. The northern shoreline of Lake Huron includes a dynamic wetland complex containing numerous Great Lakes coastal wet meadows. I sampled aquatic snails from 26 coastal wet meadows in 1997 and 1998, and measured 28 within-patch characteristics used to describe the water chemistry, habitat structure, and plant community. A GIS database was used to calculate 27 landscape-level characteristics describing the adjacent and nearby patches and the complexity of the shoreline. I used canonical correspondence analysis (CCA) to identify patterns in the distribution and abundance of snails associated with the within-patch characteristics. Landscape effects were examined by CCA after accounting for within-patch effects. Additional associations with water depth were examined using multiple regression analyses and laboratory experiments.

Nineteen species of snails were collected with six species occurring abundantly in most wet meadows. The occurrence of various plant species explained the greatest amount of within-patch variation in the snail community, followed by characteristics of habitat structure. Water chemistry explained the least amount, as expected. Significant associations with multiple landscape context variables, especially bulrush, cattail, and upland meadows, were observed after accounting for within-patch effects. In 1997 only, there were significant associations with shoreline complexity as measured by sinuosity and fractal dimension at multiple scales. A suite of variables that were related to urban land use and habitat fragmentation was included in a 1998 model, suggesting some concern for anthropogenic impacts on the snail community and the need for conservation of these wetlands. In an analysis of water levels, mean depth was the most common predictor, followed by spatial and temporal variation in water levels. Laboratory experiments showed interspecific variation in snail motility and desiccation resistance that were consistent in explaining snail community structure.

A conceptual model of the Great Lakes coastal wet meadow snail community was developed based on a depth gradient from deeper wet meadows that remain permanently flooded to shallow and hydrologically semi-isolated wet meadows in which periodic drying occurred. The model included interactions at various scales, from within-patch to shoreline complexity, and the proximate behavioral and physiological differences among snail species. Further testing of the pathways in this model will help to clarify the mechanisms behind the observed patterns.

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Many enjoyable memories were made along the northern Lake Huron shoreline and in the lab through the help and encouragement of Joe Gathman, Donna Kashian, and Sam Riffell. Special thanks to Sam Riffell who helped with habitat design and sampling, with construction of the GIS database, and with suggestions for data analyses.

Residents of Cedarville, DeTour Village, and Hessel provided access to coastal wetlands on their properties. Computing resources were provided by the Department of Geography and water analyses by the Department of Geological Sciences at Michigan State. Support for my research was provided by grants from the Michigan Chapter of the Nature Conservancy (to Tom Burton), the Department of Zoology and the Graduate School at Michigan State University, and the John G. Shedd Aquarium.

Thanks to Angela Roberts for her loving encouragement and the inspiration to finish writing, and to my parents for their support and patience.

Yes, my dissertation is finished!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Aquatic snails are usually an important component of freshwater invertebrate communities (e.g. Weatherhead and James 2001). Many play key roles as consumers by grazing upon algal and bacterial communities present in biofilms on the surfaces of submersed objects and vegetation (Russel-Hunter 1978). Snails affect the microbial biofilm by influencing the abundance and diversity of species within the biofilm itself (Doremus and Harman 1977, Lowe and Hunter 1988), as well as invertebrate grazers feeding upon it (Hawkins and Furnish 1987, Harvey and Hill 1991, Hill 1992). Other snail species may consume living vegetation or act as detritivores by feeding on decaying vegetation (Calow 1970, Reavell 1980). Snails, in turn, are often the prey of a variety of predators (leeches: Townsend and McCarthy 1980, Brönmark and Malmqvist 1986; crayfish: Crowl 1990, Weber and Lodge 1990; insects: Kesler and Munns 1989; and fish: Brown and DeVries 1985, Turner 1996). Because of their importance in most aspects of the aquatic food web, it is not surprising that many researchers have investigated factors thought to affect snail distribution and abundance (e.g. Dussart 1976, Brönmark 1985, Lodge et al. 1987).

Traditionally, explanations of the patterns seen in freshwater snail distributions have focused on water chemistry, especially calcium concentration. Because calcium is a major component of snail shells, the explanation seems obvious. However, many studies have failed to find a significant correlation between environmental calcium and shell calcium content (Hunter and Lull 1977, Mackie and Flippance 1983a,b). In some cases, the abundance of snails was related to calcium (Dussart 1976, 1979), though diversity declined only in lakes with very low calcium concentrations (<5 mg/l) in a study of 1500

Norwegian lakes (Økland 1983). Even in calcium-poor lakes, some species were found in abundance (Rooke and Mackie 1984). The variability among previous studies suggests a complex, inconsistent relationship between water calcium levels and snail communities that is not well understood, and suggests that other factors should be investigated. Lodge et al. (1987) summarized other examples and supported the suggestion that, in most contexts, physicochemical factors (including calcium) were not the primary determinants of snail distribution and abundance.

In addition to chemical factors, other studies have investigated how habitat diversity and macrophytes (or productivity in general) affected snail communities. High habitat diversity coupled with interspecific differences among snails in habitat and food preferences may result in higher snail diversity (Ross and Ultsch 1980, Lodge et al. 1987). Numerous studies have shown either a general association between snails and macrophytes (Brönmark 1985) or associations between snails and specific macrophyte species (Bickel 1965, Pip and Stewart 1976, Pip 1978, 1985, 1991, Lodge 1985, 1986, Beckett et al. 1992). Costil and Clement (1996) examined snail and plant communities in relation to trophic levels of the lakes, and underscored possible interactions between snail distribution and physicochemical factors (especially nutrients), lake productivity, and macrophyte abundance/diversity. Brown and Lodge (1993) cautioned that apparent snail-macrophyte associations could be better explained by the greater surface area of these habitats rather than a distinct preference *per se*.

The application of the theory of island biogeography (MacArthur and Wilson 1967) in which lakes are treated as islands within the surrounding land has been used with some success in describing the mollusk species richness of lakes within a region

(Lassen 1975, Aho 1978a, Browne 1981, Jokinen 1987). In general, the number of species was expected to increase with the surface area of the lake in a dynamic equilibrium maintained by primarily biotic factors (e.g. dispersal rates, macrophyte heterogeneity, etc.) rather than by abiotic chemical factors. Some studies have examined the effects of variables above and beyond the species-area effect in an attempt to further discern their role in determining snail distributions. For example, Aho (1978b) found that oligotrophic lakes generally followed the predictions of the theory (i.e. biotic factors were important), and that, only in lakes with low calcium concentrations, did the latter variable better explain the variation in species distributions; likewise, the model did not hold for larger lakes in the study. Lassen (1975) found differences in oligotrophic versus eutrophic lakes, and Brönmark (1985) found that macrophyte diversity and the snail species in nearby ponds added explanatory ability beyond area.

Clearly, a multitude of factors influence snail community structure, and the interactions among them are not well understood. Lodge et al. (1987) attempted to clarify the importance of physicochemical and biotic factors in the development of a conceptual model that differentiated between three spatial scales. In this model, chemistry (especially calcium) was the most important factor at the largest, regional scale. If calcium levels were sufficient, then habitat diversity and food selectivity became important among lakes and among habitats within lakes. Additional biotic factors included disturbance, competition, and predation, but their effects were constrained by a habitat continuum from temporary ponds to permanent lakes.

In order to further identify important determinants of freshwater snail community structure, I conducted a multifaceted study in northern Lake Huron coastal wetlands of

Michigan's Upper Peninsula. Coastal wetlands and their dominant vegetation types are influenced by water depth and length of hydroperiod (e.g. permanent or seasonal inundation). In most cases, there is a distinct zonation of vegetation types from the open water of Lake Huron to the shoreline that includes bulrush, cattail, wet meadow, and shrub zones (Minc and Albert 1998) (Figure 1). In the present study, snails were collected from 26 *wet meadows* during 1997 and 1998 along with numerous environmental characteristics based on field measurements and a geographic information system (GIS). Additionally, laboratory experiments were conducted to help clarify the effects of a drastic decrease in water levels that occurred during the study.

Three sets of analyses were performed to answer specific questions regarding the aquatic snail community structure. Each of these analyses, which corresponds to a separate chapter, is briefly described below.

Chapter One includes a description of the aquatic snail community along the northern Lake Huron shoreline and tests for associations between the snail community and the more traditional determinants of structure: water chemistry, habitat structure (heterogeneity), and the aquatic plant community. While there have been many similar analyses (see above), my approach was unique because I combined them into one overall analysis. If the patterns of previous studies in which no one factor strongly influenced the snail community hold true, each of the three analyses alone would not provide strong explanatory power, but by using a variance partitioning method, I hoped to describe the relative importance of all three aspects.

Chapter Two expands upon the first by examining the less well-studied effects of

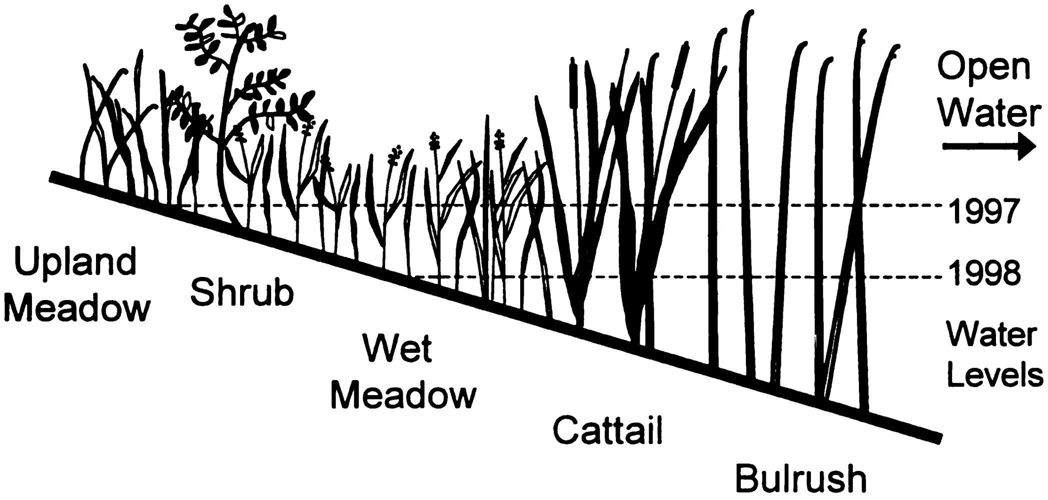

Figure 1. Schematic cross-section of a typical coastal wetland showing the vegetation zones as they change with water depth. Approximate water levels are indicated for 1997 and 1998.

the surrounding landscape on the snail community. While landscape ecology, which deals with the effects of spatial patterns (e.g. patch size, shape, connectivity, fragmentation and edge-effects) on organisms (see Forman 1995), has gained prominence as a distinct field over the past two decades, only recently has it been applied to aquatic systems (e.g. Palmer et al. 2000, Wiens 2002). I know of only two studies that specifically examine the effects of landscape on snail communities. Magnin et al. (1995) examined the effects of cultivation patterns and temporal changes on land snail communities and Lewis and Magnuson (2000) found that differences in snail species richness in lakes were dependent on the position of the lake in the catchment and their stream connectivity. The success of landscape ecology in answering questions regarding the distribution of a variety of animals suggested that it might be useful in explaining wetland snail distributions. Because I wanted to know the effects of landscape patterns on the snail community, I examined these relationships after factoring out the effects of chemistry, structure and plant community. Thus, any significant effects were above and beyond those of chemistry and habitat characteristics.

Between sampling periods from 1997 to 1998, the water levels of Lake Huron dropped considerably (Figure 1) leaving many sampling sites shallower or without standing water – an obvious influence on aquatic snail communities. While water depth was included directly in analyses of Chapter One and indirectly in Chapter Two, the effects of water level changes were not specifically addressed. In Chapter Three, I examined in more detail the effects of water level changes on the snail community through regression modeling. The proximate causes of the observed changes were then investigated using laboratory experiments of snail behavior and desiccation resistance.

Lastly, the results of my analyses were used in the construction of a conceptual model describing the aquatic snail community structure in northern Lake Huron coastal wetlands. My results add to the current understanding of determinants of snail distribution as well as suggest further areas of research likely to increase knowledge of these wetlands. In addition, the model can aid investigations of processes that affect the biodiversity of this very important and declining habitat.

CHAPTER ONE

RELATIVE IMPORTANCE OF WATER CHEMISTRY, HABITAT STRUCTURE AND THE PLANT COMMUNITY TO COASTAL WET MEADOW SNAIL DISTRIBUTION

INTRODUCTION

Patterns in freshwater snail distributions have traditionally been explained on the basis of water chemistry, especially calcium concentration. Because calcium is a major component of snail shells, the explanation seems obvious. However, many studies have failed to find a significant correlation between environmental calcium and shell calcium content (Hunter and Lull 1977, Mackie and Flippance 1983a,b). In some cases, the abundance of snails was related to calcium (Dussart 1976, 1979), though diversity declined only in water with very low (<5 mg/l) calcium concentrations (Økland 1983). Even in calcium-poor lakes, some mollusks were found in abundance (Rooke and Mackie 1984). The variability among previous studies suggests a complex, inconsistent relationship between water calcium levels and snail communities that is not well understood, and suggests that other factors should be investigated. Lodge et al. (1987) summarized other examples and supported the suggestion that physicochemical factors (including calcium) are not the primary determinants of snail distribution and abundance in most contexts.

In addition to chemical factors, other studies have investigated how habitat diversity and macrophytes (or productivity in general) affected snail communities. Because each type of habitat or macrophyte assemblage (often a major component of aquatic habitats) may support different species, higher species richness may be correlated with increasing habitat diversity (Brönmark 1985). High habitat diversity coupled with interspecific differences among snails in habitat and food preferences may result in higher snail diversity (Ross and Ultsch 1980, Lodge et al. 1987). Numerous studies have shown either a general association between snails and macrophytes (Brönmark 1985) or associations between snails and specific macrophyte species (Bickel 1965, Pip and Stewart 1976, Pip 1978, 1985, 1991, Lodge 1985, 1986, Beckett et al. 1992). Costil and Clement (1996) examined snail and plant communities in relation to trophic levels of the lakes, and underscored possible interactions between physicochemical (especially nutrients), lake productivity, and macrophyte abundance/diversity. Brown and Lodge (1993) cautioned that apparent snail-macrophyte associations could be better explained by the greater surface area of these habitats rather than a distinct preference *per se*. Even so, most studies agree that habitat diversity alone, and possibly the types of macrophytes present affect the distribution of snails to some degree.

The application of the theory of island biogeography (MacArthur and Wilson 1967), in which lakes are treated as islands within the surrounding land, has been used with some success in describing the mollusk species richness of lakes within a region (Lassen 1975, Aho 1978a,b, Browne 1981, Jokinen 1987). In general, the number of species was expected to increase with the surface area of the lake in a dynamic equilibrium maintained by primarily biotic factors (e.g. dispersal rates, macrophyte heterogeneity, etc.) rather than by abiotic chemical factors. Some researchers have used this theory to examine the effects of variables above and beyond the species-area effect in an attempt to further define their role in determining snail distributions. For example, Aho (1978b) found that oligotrophic lakes generally followed the predictions of the theory (i.e. biotic factors were important), and that only in lakes with low calcium concentrations did the latter variable better explain the variation in species distributions; likewise, the model did not hold for larger lakes in the study. Lassen (1975) found differences in oligotrophic versus eutrophic lakes and Brönmark (1985) found that macrophyte diversity and the snail species in nearby ponds added explanatory power beyond area.

Clearly, a multitude of factors influence snail community structure, and the interactions among them are not well understood. Lodge et al. (1987) attempted to clarify the importance of physicochemical and biotic factors by developing a conceptual model that differentiated between three spatial scales. In this model, chemistry (especially calcium) was the most important factor at the largest, regional scale. If calcium levels were sufficient, then habitat diversity and food selectivity became important among lakes and among habitats within lakes. Additional biotic factors included disturbance, competition, and predation, but their effects were constrained by a habitat continuum from temporary ponds to permanent lakes.

The objective of the present study was to describe the aquatic snail community of a Great Lakes coastal wetland complex and evaluate the relative importance of water chemistry, habitat structure, and the plant community in explaining snail distribution and abundance. Because of the lack of research on these wetlands in general (Krieger 1992) and specifically on the snail community, my approach was explorative in nature, with my only hypothesis being that habitat structure and the plant community should be more important than water chemistry in determining snail distributions. According to the conceptual model of Lodge et al. (1987), this was to be expected because the wetlands were located in the same biogeographic region.

METHODS

Study Area

I sampled 26 distinct coastal wet meadows along a 60 km length of the northern Lake Huron shoreline in Michigan's Upper Peninsula (Figure 2, Table 1). The wet meadows all were part of a complex of Great Lakes marshes that were among some of the most pristine coastal wetlands (Minc and Albert 1998). The area was part of the Niagaran Escarpment composed of Silurian-age limestone and dolomite bedrock. The vegetation was predominantly hummock-forming grasses (*Calamagrostis canadensis*) and sedges (*Carex stricta*, *C. aquatilis*, and *C. latifolia*) with low densities of bulrush (primarily *Scirpus acutus*) and cattail (primarily *Typha angustifolia*). The substrate, composed of muck or mucky-peat sediments covered by dense layers of the previous season's grass and sedge leaves, provided a structurally complex habitat (along with the hummock structure) in which most snails were found. Some sites also contained a shrub zone including *Salix* spp., *Myrica gale*, and *Alnus rugosa* with *Potentilla* spp. scattered throughout. Additional information was given by Burton et al. (1999).

Snail Collection

Transects running perpendicular to the shoreline of Lake Huron were established in each wet meadow and divided into 50 m sections. The number of sections sampled in each wet meadow ranged from 1 to 3 depending on the size of the wet meadow (Table 1) and the presence of standing water deep enough to sample with a dip net (~10 cm). Each wet meadow was assumed to by hydrologically connected with Lake Huron although, in some, this was modified by natural barriers (sandy ridges creating a swale-like effect) or roads (with culverts maintaining water flow) (Table 1). Snails were

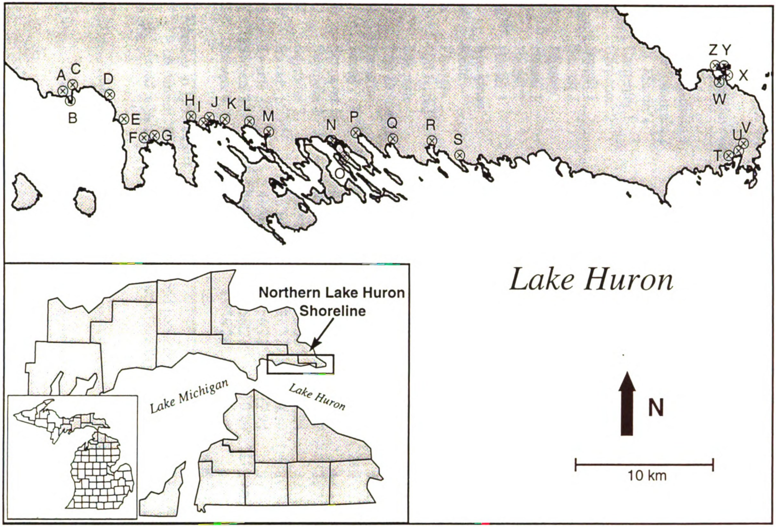

Figure 1. Study area showing the locations of 26 wet meadows along the northern Lake Huron shoreline of Michigan, USA. Names of the wet meadows are in Table 1.

Table 1. Wet meadows of the northern Lake Huron shoreline sampled for aquatic snails.

Site label	Wet meadow site	Latitude (N)	Longitude (W)	Area (ha)	Sections sampled[1]	Barrier[2]
A	Pontchartrain 1	46°01'45"	84°35'14"	1.18	2 / 1	S
B	Pontchartrain 2	46°01'33"	84°34'58"	2.47	3 / 0	S
C	St. Martin's	46°01'59"	84°34'48"	3.24	2 / 0	-R
D	Carpenter 1	46°01'15"	84°32'24"	2.60	2 / 1	-R
E	Carpenter 2	46°00'49"	84°32'16"	3.28	1 / 0	-R
F	Search 1	46°00'01"	84°30'26"	2.67	2 / 0	S
G	Search 2	46°00'02"	84°30'13"	0.12	1 / 1	S
H	Mismer	46°00'37"	84°27'44"	11.12	3 / 2	-
I	Hessel 1	46°00'36"	84°27'09"	8.93	2 / 1	R
J	Hessel 2	46°00'37"	84°26'52"	2.28	2 / 2	-R
K	Hessel 3	46°00'36"	84°26'13"	1.83	2 / 1	-
L	Mackinac	46°00'24"	84°24'46"	13.70	3 / 1	-R
M	Rudd	46°00'10"	84°23'30"	7.52	3 / 0	-
N	Flowers	45°59'28"	84°19'25"	3.84	3 / 2	-
O	Hill Island	45°59'15"	84°19'00"	1.94	1 / 0	-
P	Lakeside	45°59'56"	84°18'02"	1.92	2 / 1	-R
Q	Port Dolomite	45°59'43"	84°16'12"	2.82	3 / 3	R
R	Prentiss	45°59'36"	84°13'41"	22.09	3 / 2	R
S	Scotty	45°58'56"	84°12'12"	11.74	3 / 3	-R
T	Seymour 1	45°58'29"	83°55'54"	3.53	1 / 1	R
U	Seymour 2	45°58'36"	83°55'38"	1.27	3 / 2	R
V	Seymour 3	45°58'44"	83°55'30"	25.24	3 / 0	R
W	Sweets 1	46°01'28"	83°56'37"	4.80	3 / 3	-R
X	Sweets 2	46°01'40"	83°56'22"	2.94	3 / 3	-
Y	Sweets 3	46°01'40"	83°56'27"	0.89	2 / 2	-
Z	Sweets 4	46°01'46"	83°56'29"	0.69	1 / 1	-
					(59/33)	

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1. Number in 1997 / 1998
2. '-' = no barrier; 'S'= sandy ridge; 'R' = road between wet meadow and Lake Huron; '-R' = road adjacent to wet meadow but not separating site from Lake Huron

collected between 11-14 July 1997 and 7-10 July 1998 using timed D-frame aquatic dip net samples (Brown 1979). Analyses were based on only these collections to minimize variation in snail abundances caused by differences in life histories among species. Sampling at this time minimized variation caused by both the late summer death of annual, semelparous species and the early recruitment of juveniles into the population. Two 1-minute sweeps using a standard D-frame aquatic dip net were conducted in each section covering an area of approximately 10 m^2 (Figure 3). The contents were combined and washed through a 1 mm sieve bucket, and then preserved in 95% ethanol. In the laboratory, snails in the preserved samples were sorted to species and enumerated (empty shells were not included). Taxonomic nomenclature followed that of Clarke (1981) and Burch and Jung (1992).

Environmental Variables

Three variable groups were used to describe the wet meadow environment.

The first group contained seven water chemistry (CHEMISTRY) variables measured in the center of each section (Figure 3) at the time of snail sampling (pH and conductivity using an Altec monitor II meter and YSI model 31 conductivity bridge, respectively) or in the laboratory using water samples collected during snail sampling. Alkalinity was measured within 4 hours of collection by sulfuric acid titration to the bromcresol green endpoint, and the cations (calcium, potassium, magnesium and sodium) were measured using flame atomic absorption spectroscopy; samples were frozen until analyzed. Only alkalinity, conductivity and pH were measured in 1998.

Nine variables describing the habitat structure (STRUCTURE) were measured for each 50-meter section using two techniques at each of 20 habitat-sampling points located

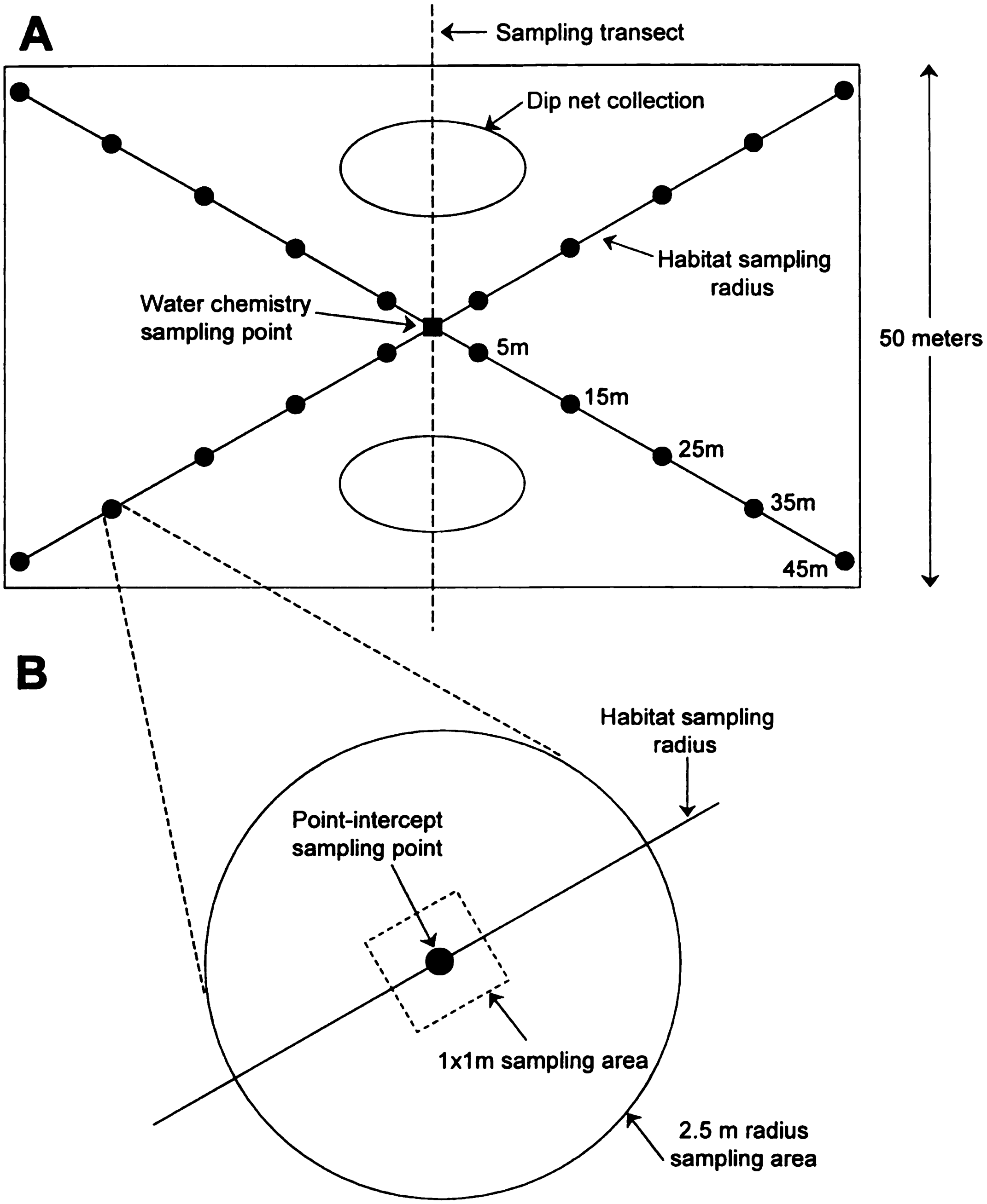


Figure 3. Diagram of snail and habitat sampling procedures used in the wet meadows during this study. A) Locations of timed aquatic dip net samples for snail collections, of water chemistry sampling point, and habitat sampling points along four radii.
B) Detailed diagram of the three methods used at each of the 20 habitat sampling points.

on four habitat sampling radii originating at the center of each section (Figure 3). Five sampling points were located at 10-m intervals along each of the four sampling radii.

Point-intercept sampling was conducted using a 2-m metal rod, stratified into eight 25 cm sections (strata), that was passed through the vegetation (Rotenberry and Wiens 1980). Using the rod, one of each of the following measurements was made at each sampling point. Grass density was measured as the total number of grass and sedge stems or leaves touching the rod (i.e. number of hits) in any of the eight strata; shrub density was measured as the total number of hits by shrubs in all strata; and vegetation density was measured as the total number of hits in all strata by any living vegetation (grasses, other macrophytes, and shrubs). Foliage diversity, a measure of the shrub cover and shading, was calculated as the number of 25-cm sections with at least one shrub hit. Water depth, hummock height and grass height were also measured using the metal rod. Water depth and grass height were standardized among sampling points by measuring these from the bases of hummocks (i.e. positioning the rod in a valley between hummocks) near the sampling point. This approach eliminated the possibility of variation in grass height and water depth caused by random positioning of the rod on the side or top of a hummock.

Hummock frequency and open water frequency were estimated by placing a 1-m^2 sampling quadrat (Figure 2) at each sampling point and recording the presence or absence of hummocks and open water (areas >0.25 m^2). The frequency of occurrence was calculated as the proportion of sampling points at which each of these were present (out of 20 sampling points per section).

The third group (PLANT) included 12 variables describing the frequency of occurrence of common plant species or types. The frequency of occurrence for macrophytes was measured as described above using a 1-m^2 sampling quadrat. Macrophytes measured were graminoids (including *Calamagrostis canadensis*, *Carex stricta*, *C. aquatilis*, and *C. latifolia*), cattail (primarily *Typha angustifolia*; also *T. latifolia* and hybrids), bulrush (primarily *Scirpus acutus*; also *S. americanus* and *S. validus*), duckweed (primarily *Lemna minor*; also *L. trisulca*), *Nuphar* (*N. variegatum*), *Polygonum* (*P. amphibium*), *Potamogeton* (*P. natans*), and submersed vegetation (*Potamogeton* spp., *Myriophyllum* spp., *Utricularia* spp.; also filamentous green algae). Woody vegetation occurrence was sampled using a 2.5-m radius circle centered on each habitat sampling point (Figure 2) and the presence/absence recorded. The variables measured were alder (*Alnus rugosa*), willow (primarily *Salix petiolaris*), shrub (any other shrub species <2.0 m in height, primarily *Potentilla palustris* and *Myrica gale*), and tree (any >2.0 m in height, including *Larix laricina* and *Populus* spp.). Trees and shrubs were measured in 1997 only because there was little or no change between years.

Statistical Analyses

Patterns of abundance and diversity. Abundance was estimated as the total number of individuals collected in each 50-m section of wet meadow. The change in abundance for each species from 1997 to 1998 was examined with t-tests for each species; a Bonferroni technique was used to correct for multiple tests as part of the SYSTAT software (SPSS 1999). Three measures of diversity were calculated for each wet meadow using the average abundance in each section (in sites containing multiple 50-m sections, Table 1). Species richness (S) was measured as the total number of species recorded at a site. Shannon Index (H') (see Magurran 1988) was calculated as:

$$H' = -\Sigma p_i \log p_i \qquad (1)$$

where p_i is the proportion of individuals of species i. This index takes into account both the richness and the evenness of the community. Because each wet meadow was not sampled with replicates, the variance of H' was approximated by:

$$s^2_{H'} = [\ \Sigma f_i \log^2 f_i - (\ \Sigma f_i \log f_i\ )^2 / n\ ] / n^2 \qquad (2)$$

where f_i is the number of snails of species i, and n is the total number of snails (Zar 1999). No statistical tests were used to compare H' among wet meadows, however, confidence intervals were constructed using the square root of the variance calculated in (2) as an estimate of the standard deviation. The 95% confidence interval was then considered as mean ± 2 s.d. J', a measure of evenness only, was calculated as:

$$J' = H' / H_{max}' \qquad (3)$$

where:

$$H_{max}' = \log S \qquad (4)$$

The effect of wet meadow size on abundance and diversity was investigated through regression analyses of each dependent variable separately with area (log transformed). Species richness values were log transformed prior to analysis as is customary (Rosenzweig 1995); other variables were untransformed. Regression analyses were performed using SYSTAT 9 (SPSS 1999).

Multivariate analyses of environmental variables and species data. Canonical correspondence analysis (CCA), using the statistical software CANOCO (ter Braak and Šmilauer 1999), was utilized to express major relationships between the species and environmental variables. CCA is a technique that integrates ordination with regression resulting in uncorrelated (i.e. canonical) linear combinations of environmental variables (ter Braak and Šmilauer 1998). CCA is especially appropriate when species show a unimodal response to an environmental gradient as is often recognized in mollusks (Bishop 1981). Over partial lengths of the gradient, the species response may appear linear, but CCA is robust enough to meet these conditions (ter Braak and Verdonschot 1995, ter Braak and Šmilauer 1998).

The three environmental variable groups were examined separately, limiting the number of variables used in each analysis, as suggested by Borcard et al. (1992). Abundance data were log (x+1) transformed to normalize the variance and rare species were down-weighted using an algorithm available in CANOCO prior to analysis. Down-weighting the rare species reduces the disproportionate effect that they may have on the ordination (ter Braak and Šmilauer 1998). Variables with high multicollinearity were examined and those with a variable inflation factor greater than 20 were removed (ter Braak and Šmilauer 1998).

Two separate analyses were conducted. First, I wanted to determine which of the environmental variables within each variable group were most significant in explaining the variation in species data and second, to examine the relative importance of the three variable groups. Data from individual sections were included in the data matrix rather than each wet meadow as a whole, in order to increase the power of the analyses. Although this did not account for effects of spatial autocorrelation, it was assumed that snails would be influenced most strongly by habitat differences within each 50-m section, and that any effects of spatial autocorrelation could be detected in the sites-environmental biplots from the CCA analyses.

I used the forward selection procedure within CANOCO (ter Braak and Šmilauer 1998) to select the largest number of variables from each environmental variable group that resulted in a significant model (to determine overall variance explained by the variable group). Significance was determined for both the 1st axis and all axes combined and a model was considered significant only if both of these met an *a priori* $\alpha < 0.10$. I used a more liberal value because of the variability inherent in field observations, and to maintain an acceptable Type II error rate. Significance testing was conducted using the Monte Carlo permutation testing (199 permutations) procedure within CANOCO (ter Braak and Šmilauer 1998).

After defining a significant model, significant variables (i.e. those that explained the greatest amount of species variation) were identified within each variable group. The results were interpreted with the use of CCA biplots, in which the environmental variables were represented as vectors among either site scores or species scores. Site or species scores with positive relationships to the environmental variable were in the vector direction whereas those with negative relationships were in the opposite direction. In addition, the length of the vector represented the relative importance of that environmental variable to the ordination (ter Braak and Verdonschot 1995).

In order to examine the overall variance explained and to partition the variance among variable groups, I conducted partial CCA using the method of Borcard et al. (1992), which removed the influence of covariables from the variable set in question. This method was similar to a normal CCA but with the extra requirement that the extracted gradients were uncorrelated with the covariables (ter Braak and Verdonschot 1995). The variation explained by a set of variables was calculated as the sum of all constrained eigenvalues divided by the total inertia, which is analogous to the total variance. In partial CCA, then, the variation explained by one variable group only was based on the sum of all constrained eigenvalues after removing the effects of the covariables (Borcard et al. 1992). In this way, the variance explained by one variable group was separated from the variance shared by two or more variable groups (Økland and Eilertsen 1994).

RESULTS

Patterns of abundance and diversity

A total of 20,410 individuals from 59 sections and 15,127 individuals from 33 sections were collected during 1997 and 1998, respectively. Fewer sections were sampled in 1998 because Lake Huron water levels dropped 28 cm from the levels in 1997 (USACE 2000) leaving sections or entire wet meadows without standing water. The snails were distributed among 19 species in seven families (Table 2). The four most abundant species were *Physa gyrina*, *Gyraulus parvus*, *Planorbula armigera*, and *G. deflectus* (Table 3). These four species along with *Planorbella trivolvis* and *Fossaria parva* were the most common, occurring in >40% of the sections sampled (Table 3). *Physa gyrina* and *F. parva* decreased significantly (P<0.10), and *G. deflectus* and *P. armigera* increased significantly (p<0.10) in abundance from 1997 to 1998; although variable, all others did not change significantly from one year to the next (Table 3). Of the 19 species collected, five were only collected in one year and were uncommon with fewer than five individuals being collected for each species (abundance <0.10/section in Table 3). Among wet meadows, the abundance varied greatly, ranging from only 27

Table 2. List of species found in the study area and labels used in CCA diagrams. Nomenclature follows Clarke (1981) and Burch and Jung (1992).

Species	Label
Pulmonata	
Physidae	
Physa gyrina Say, 1821	Pg
Aplexa elongata (Linnaeus, 1758)	Ae
Planorbidae	
Gyraulus deflectus (Say, 1824)	Gd
Gyraulus parvus (Say, 1817)	Gp
Gyraulus cristus (Linnaeus, 1758)	Gc
Planorbula armigera (Say, 1821)	Pa
Planorbella trivolvis (Say, 1817)	Pt
Planorbella campanulata (Say, 1821)	Pc
Promenetus exacuous (Say, 1821)	Pe
Lymnaeidae	
Stagnicola elodes (Say, 1821)	Se
Fossaria obrussa (Say, 1825)	Fo
Fossaria parva (Lea, 1841)	Fp
Acella haldemani (Binney, 1867)	Ah
Ancylidae	
Ferrissia parallela (Haldeman, 1841)	Fl
Prosobranchia	
Hydrobiidae	
Amnicola limosa (Say, 1817)	Al
Amnicola walkeri Pilsbry, 1898	Aw
Pyrgulopsis lustricus (Pilsbry, 1890)	Pl
Bithyniidae	
Bithynia tentaculata (Linnaeus, 1758)	Bt
Valvatidae	
Valvata tricarinata (Say, 1817)	Vt

Table 3. Mean abundance of snails from 26 wet meadows along the northern Lake Huron shoreline in 1997 and 1998.

	1997				1998				
	Abundance[1]	SE	Maximum[1]	Frequency[2]	Abundance	SE	Maximum	Frequency	P[3]
Physa gyrina	130.59	18.04	602	98.31	55.00	12.64	345	93.94	**
Aplexa elongata	5.02	2.79	130	16.95	2.45	2.42	80	6.06	ns
Gyraulus deflectus	40.29	11.16	484	71.19	165.27	24.47	701	96.97	**
Gyraulus parvus	90.68	14.05	476	96.61	124.12	24.31	540	96.97	ns
Gyraulus cristus	0.00	0.00	0	0.00	0.03	0.03	1	3.03	-
Planorbula armigera	60.31	10.50	313	84.75	92.27	24.67	559	87.88	*
Planorbella trivolvis	4.22	1.73	91	45.76	7.79	3.82	110	42.42	ns
Planorbella campanulata	0.71	0.40	17	6.78	0.21	0.21	7	3.03	ns
Promenetus exacuous	0.00	0.00	0	0.00	1.27	0.76	23	12.12	-
Stagnicola elodes	0.08	0.06	3	5.08	0.24	0.09	2	21.21	ns
Fossaria obrussa	2.68	1.66	94	16.95	0.39	0.29	9	9.09	ns
Fossaria parva	9.58	1.59	47	83.05	5.76	1.34	33	78.79	*
Acella haldemani	0.00	0.00	0	0.00	0.03	0.03	1	3.03	-
Ferrissia parallela	0.12	0.07	3	5.08	0.61	0.36	11	15.15	ns
Amnicola limosa	0.17	0.17	10	1.69	0.70	0.46	14	15.15	ns
Amnicola walkeri	0.07	0.05	2	3.39	0.00	0.00	0	0.00	-
Pyrgulopsis lustricus	0.03	0.02	1	3.39	0.00	0.00	0	0.00	-
Bithynia tentaculata	1.36	1.36	80	1.69	2.24	1.58	43	6.06	ns
Valvata tricarinata	0.03	0.03	2	1.69	0.00	0.00	0	0.00	-

1. Number collected per 50-meter section; 59 sections in 1997, 33 sections in 1998.
2. Percentage of sections in which species was collected.
3. * = significantly different ($P<0.10$) using paired t-test, df=90 only; **=significantly different ($P<0.10$) using both paired t-test, df=29 and two group t-test, df=90

snails per section in Hessel 3 to 1035 snails in Port Dolomite during 1997. During 1998, the range was similar, although values for particular wet meadows may have changed (Table 3).

Species richness ranged from 3-11 with a mean of 6.3 and 6.5 in 1997 and 1998, respectively (Table 4). Shannon Index diversity was relatively similar among the majority of wet meadows (Figure 4, Table 4) in 1997 (mean = 0.52). In 1998, the mean was the same (0.52) but Seymour 1 was unusually low ($H' = 0.18$) (Figure 4) because of low richness ($S = 3$) and evenness ($J' = 0.37$); of the 19 individuals collected, 17 were *G. deflectus*. In both years, values for the Shannon Index were normally distributed among wet meadows as indicated by the generally straight, diagonal line in the probability plots (Figure 4). Changes in H' from 1997 to 1998 occurred primarily in wet meadows that had lower than average H' in 1997 (then increased in 1998) or higher than average H' in 1997 (then decreased in 1998) (Figure 4).

Because the meadow Search 2 was much smaller (0.12 ha) than the other wet meadows and exerted a significant effect on the regression analyses, it was not included when examining the effects of area on abundance and diversity. Search 2 had the least diverse snail community in 1997 but not 1998 (Table 4). Without Search 2 included in the analyses, there were no significant area effects on abundance, species richness, Shannon Index or evenness in either year (Figure 5).

CCA Analyses: Environmental Patterns in Species Distributions

Although selected for use in this study because of a general similarity, the wet meadows did exhibit variation in the environmental variables selected for analyses (Table 5). A comparison between years was conducted using a t-test with Bonferroni correction.

Table 4. Summary statistics for the abundance and diversity of snails measured in 26 wet meadows along the northern Lake Huron shoreline in 1997 and 1998. S = species richness, H' = Shannon Index of diversity, and J' = Shannon evenness statistic. See text for calculations.

	1997				1998			
Wet meadow	Abundance[1]	S	H'	J'	Abundance	S	H'	J'
A Pontchartrain 1	232	5	0.48	0.68	294	4	0.47	0.78
B Pontchartrain 2	538	6	0.36	0.46	—	—	—	—
C St. Martin's	370	7	0.51	0.61	—	—	—	—
D Carpenter 1	127	6	0.71	0.91	134	5	0.61	0.87
E Carpenter 2	144	5	0.44	0.63	—	—	—	—
F Search 1	423	6	0.69	0.88	—	—	—	—
G Search 2	72	3	0.43	0.91	141	5	0.58	0.84
H Mismer	268	6	0.53	0.68	235	5	0.49	0.71
I Hessel 1	533	7	0.61	0.72	906	11	0.67	0.64
J Hessel 2	562	8	0.47	0.52	1038	7	0.46	0.54
K Hessel 3	27	4	0.51	0.84	268	7	0.45	0.53
L Mackinac	446	6	0.41	0.53	695	7	0.62	0.73
M Rudd	135	8	0.53	0.58	—	—	—	—
N Flowers	570	7	0.47	0.56	1008	8	0.59	0.66
O Hill Island	521	5	0.31	0.44	—	—	—	—
P Lakeside	278	7	0.58	0.68	55	4	0.59	0.97
Q Port Dolomite	1035	7	0.63	0.75	596	7	0.52	0.62
R Prentiss	219	8	0.55	0.60	258	6	0.42	0.53
S Scotty	198	6	0.65	0.83	481	5	0.56	0.79
T Seymour 1	94	5	0.48	0.68	19	3	0.18	0.37
U Seymour 2	255	7	0.59	0.70	293	8	0.65	0.72
V Seymour 3	471	6	0.47	0.60	—	—	—	—
W Sweets 1	360	7	0.52	0.61	452	8	0.55	0.61
X Sweets 2	198	6	0.52	0.67	380	7	0.55	0.66
Y Sweets 3	137	10	0.62	0.62	442	10	0.46	0.46
Z Sweets 4	130	6	0.49	0.63	344	6	0.40	0.51

1. Number collected per 50-meter section.

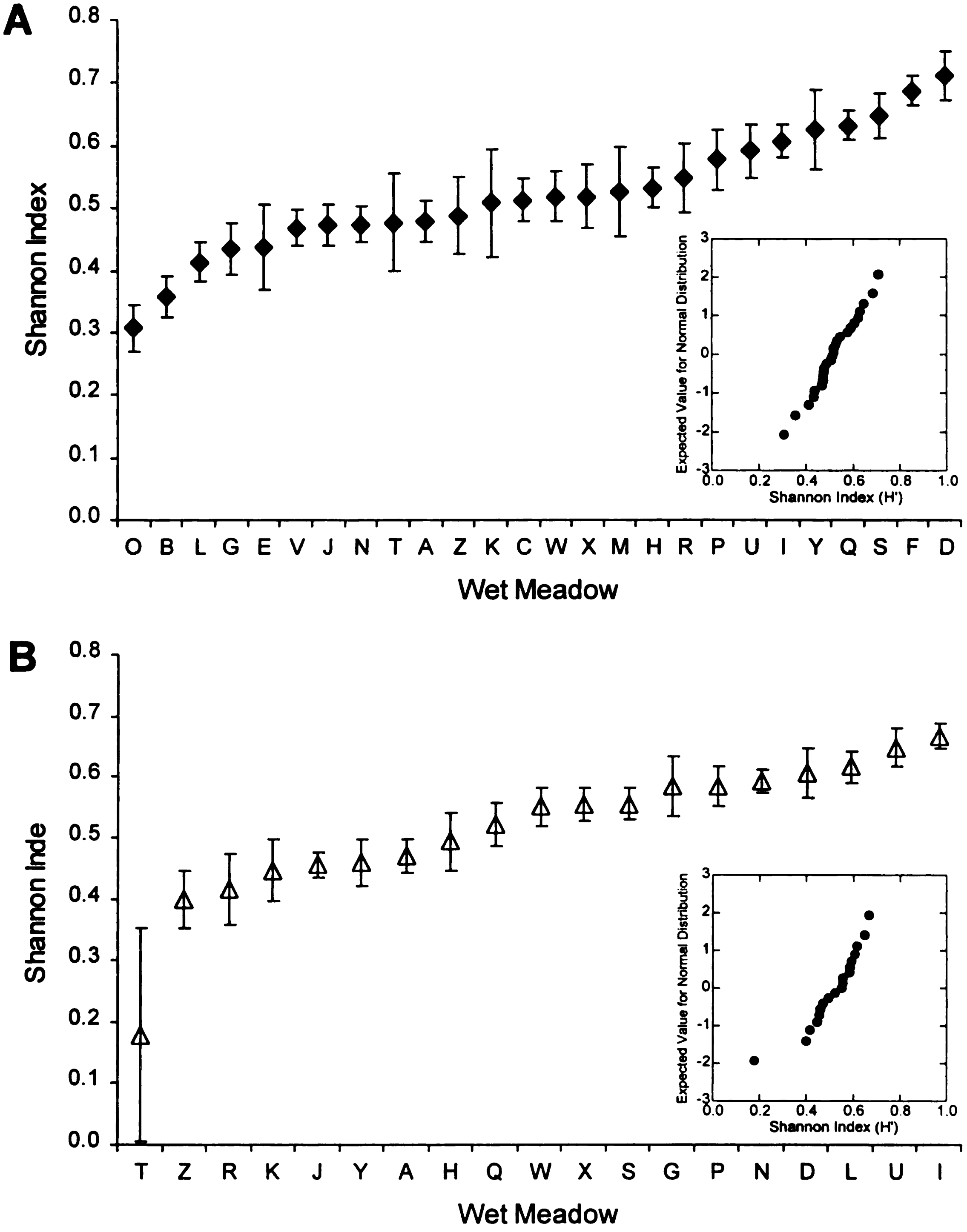
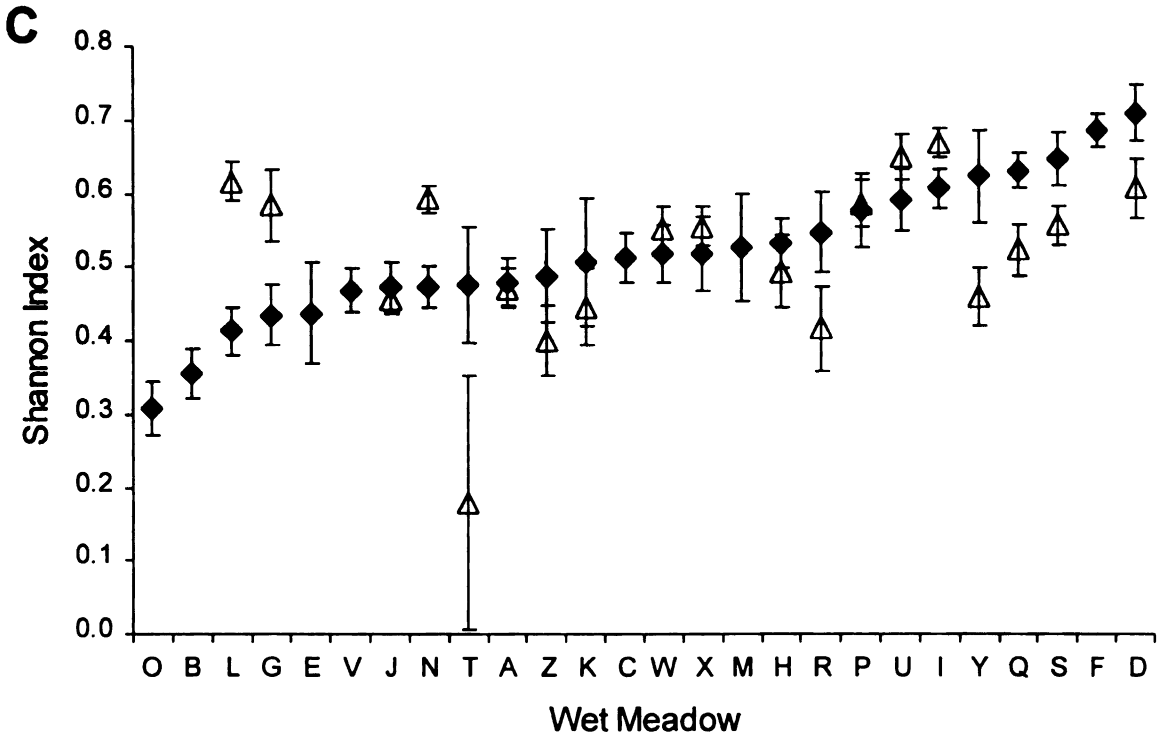


Figure 4. Shannon Index of diversity for wet meadows in the northern Lake Huron shoreline of Michigan. Data are arranged in order of the Shannon Index value. Insets are probability plots for a normal distribution. (A) 1997. (B) 1998. (C) 1997 and 1998 combined. Note that wet meadow order is different between (A) and (B) and that the number of wet meadows was 26 in 1997 and 19 in 1998 (7 sites were dry in 1998).



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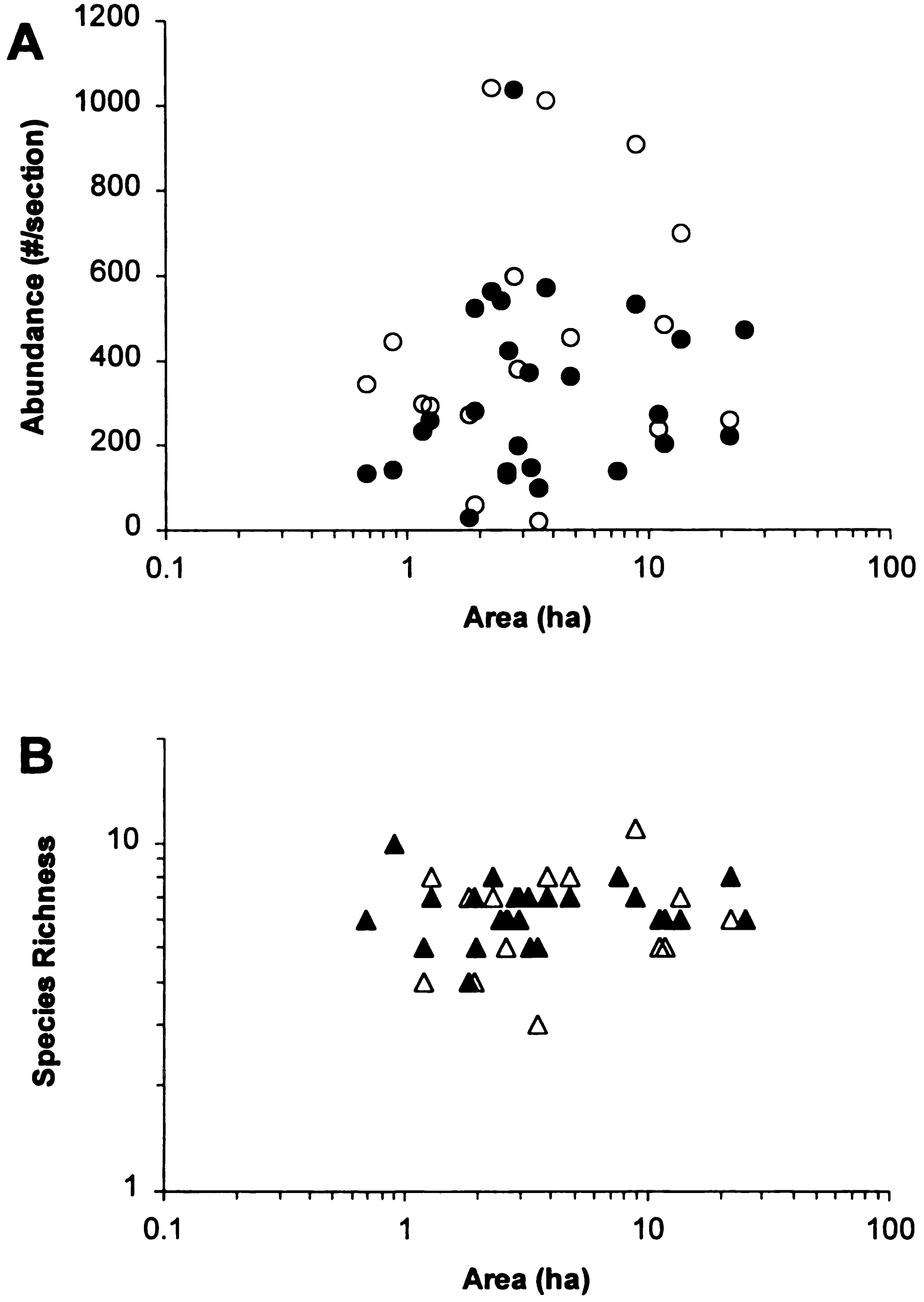
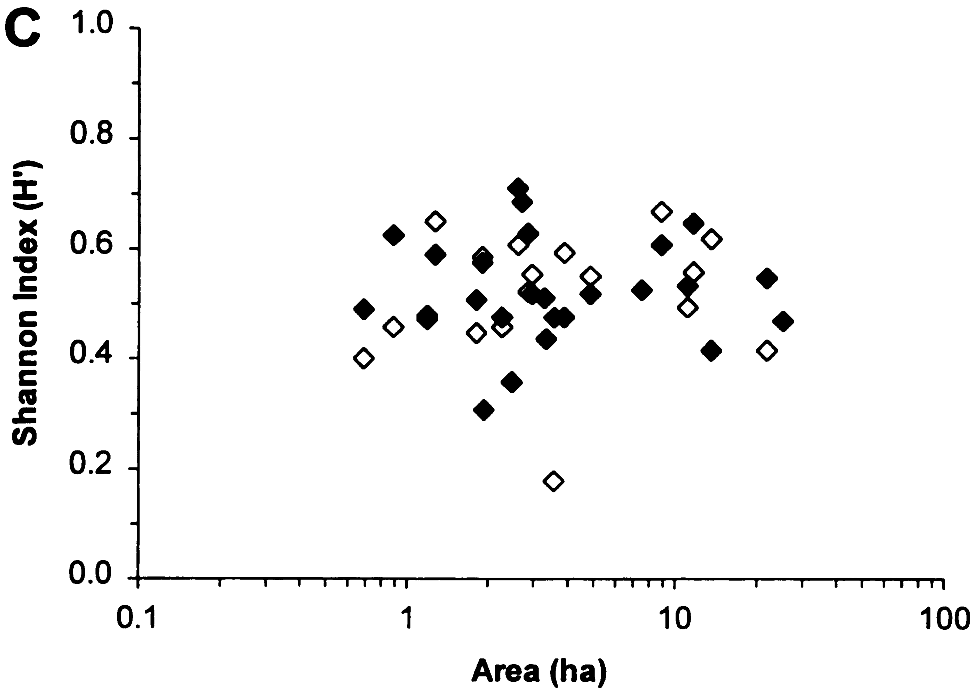


Figure 5. Area relationships to abundance (A), species richness (B), Shannon Index (C), and Shannon Evenness (D) of snail communities. 1997: solid symbols; 1998: open symbols. None of these comparisons showed significant correlations.



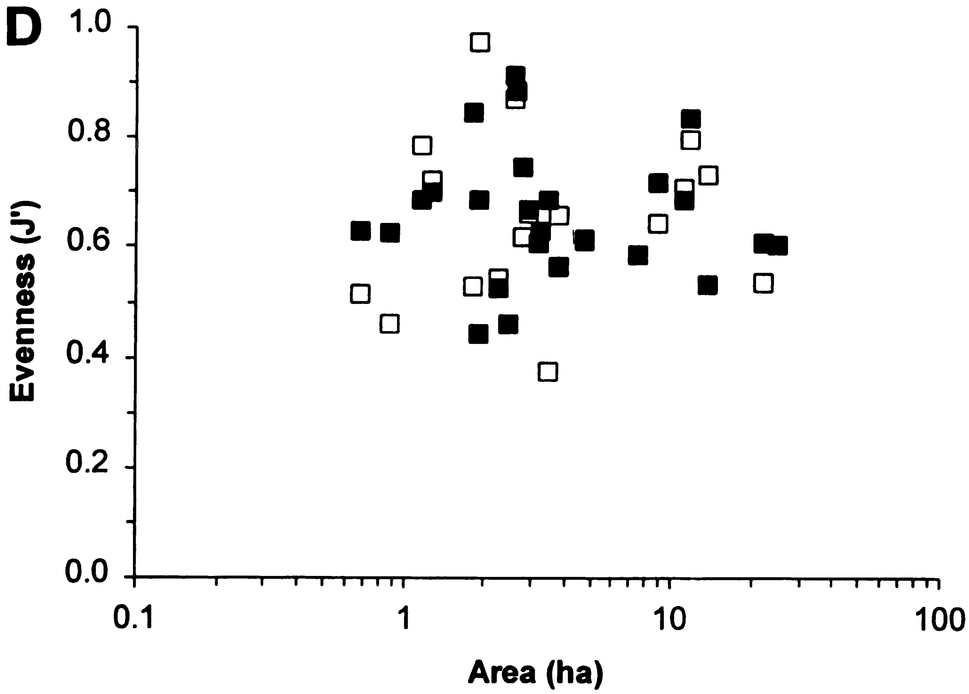


Figure 5. Continued.

Table 5. Summary statistics for three groups of environmental variables measured in 26 wet meadows along the northern Lake Huron shoreline in 1997 and 1998. P values are results of t-tests (with Bonferroni correction) examining differences between years.

Habitat Variable	Units	1997 Mean	1997 SE	1997 Range	1998 Mean	1998 SE	1998 Range	P[1]
CHEMISTRY								
Alkalinity	mg/l $CaCO_3$	168.00	8.06	55.00-328.00	147.12	8.46	57.00-244.00	ns
Conductivity	µS/cm	301.04	11.28	95.00-479.00	945.94	53.17	417.00-1636.00	<0.001
pH	—	7.40	0.04	6.77-8.12	7.27	0.07	6.59-8.01	ns
Ca	mg/l	40.77	1.79	13.50-81.75	—[2]	—	—	-
K	mg/l	0.78	0.07	0.10-2.50	—	—	—	-
Mg	mg/l	16.89	0.95	3.25-40.25	—	—	—	-
Na	mg/l	2.98	0.26	0.60-9.20	—	—	—	-
STRUCTURE								
Water Depth	cm	28.92	1.71	5.05-57.80	13.14	1.35	0.00-26.10	<0.001
Hummock Height	cm	19.50	1.03	0.00-33.86	19.89	1.63	0.00-33.60	ns
Hummock Frequency	%	57.79	4.22	0.00-100.00	47.96	5.98	0.00-100.00	ns
Grass Height	cm	108.95	1.99	74.25-143.68	111.52	2.54	64.17-136.50	ns
Grass Density	hits/point	4.88	0.22	0.40-9.90	5.07	0.34	0.21-10.90	ns
Shrub Density	hits/point	0.28	0.04	0.00-1.50	0.16	0.05	0.00-1.29	ns
Vegetation Density	hits/point	5.31	0.23	0.40-10.25	5.43	0.36	0.21-11.75	ns
Foliage Diversity	strata/patch	2.34	0.25	0.00-7.00	2.75	0.27	1.00-6.00	ns
Open Water Frequency	%	4.12	0.99	0.00-35.00	4.80	1.18	0.00-25.00	ns

Table 5. Continued.

Table 5. Continued.

Habitat Variable	Units	1997 Mean	1997 SE	1997 Range	1998 Mean	1998 SE	1998 Range	P
PLANT								
Graminoid	%	96.51	1.03	53.33-100.00	97.25	0.82	85.00-100.00	ns
Bulrush	%	19.77	3.64	0.00-100.00	35.33	6.03	0.00-100.00	ns
Cattail	%	7.18	2.27	0.00-78.95	14.22	4.25	0.00-83.33	ns
Duckweed	%	1.17	0.49	0.00-16.67	0.00	0.00	0.00-0.00	-
Nuphar	%	0.85	0.40	0.00-20.00	0.93	0.41	0.00-10.00	ns
Polygonum	%	12.63	2.55	0.00-85.00	1.07	0.36	0.00-5.26	<0.05
Potamogeton	%	0.85	0.35	0.00-15.00	0.61	0.36	0.00-10.00	ns
Submersed Vegetation	%	18.88	2.64	0.00-65.00	10.34	2.90	0.00-80.00	ns
Alder	%	5.00	1.02	0.00-31.58	4.45	1.28	0.00-23.53	ns
Willow	%	12.96	1.80	0.00-60.00	13.87	2.46	0.00-50.00	ns
Shrub	%	43.92	3.80	0.00-100.00	34.25	3.87	5.00-91.67	ns
Tree	%	4.03	0.94	0.00-35.00	2.74	0.77	0.00-16.67	ns

1. Results of t-test between years, df=90; ns=not significant.
2. Not measured in 1998.

Only three significant changes were observed. Conductivity was significantly higher in 1998 and water depth was significantly lower than in 1997 (Table 5). A decrease in the frequency of occurrence of *Polygonum amphibium* from 1997 to 1998 was the only significant change in the plant community.

Upon examination of the seven variables in the CHEMISTRY group (see Table 5) in 1997, alkalinity and calcium were highly correlated; alkalinity explained more variance and therefore calcium was removed from the analysis. The six remaining variables explained a total of 18.0% of the variation in the species data (Table 6). Axes 1 and 2 explained 10.2% and 3.6% of the species data and 57.0% and 20.2% of the species data when constrained by the environmental variables in the model (Table 6). Of the six variables, alkalinity, conductivity and pH were significant ($P<0.10$). The interset correlations (Table 7) were used to aid in the explanation of the CCA biplots with particular weight given to the significant variables. Axis 1 was most closely associated with pH and alkalinity. Examination of the sites plot (Figure 6) and the original data indicate that this axis was most strongly influenced by alkalinity. Sites to the lower right of the plot generally had much lower alkalinity (as low as 55 mg/l $CaCO_3$) than the other sites and only slightly higher pH. Four species, *Amnicola limosa, Valvata tricarinata, Stagnicola elodes,* and *Pyrgulopsis lustricus,* were associated with these low alkalinity sites (Figure 6). Conductivity was somewhat negatively associated with this first axis but also positively associated with the second axis. The tight clustering of the sites near the center of the plot indicated the overall similarity of the wet meadows in regards to water chemistry (Figure 6).

In 1997, total vegetation density and grass density were highly correlated in the

Table 6. Results of canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows in 1997.

	Axes				Σ canonical	Total	% Variance	1st axis		All axes	
	1	2	3	4	eigenvalues	inertia	explained	F-ratio	P	F-ratio	P
CHEMISTRY 1997					0.119	0.662	18.0	5.918	0.015	1.891	0.015
Eigenvalues	0.068	0.024	0.013	0.007							
Species-environment correlations	0.691	0.593	0.383	0.403							
Cumulative percentage variance											
of species data	10.2	13.8	15.8	16.8							
of species-environment correlation	57.0	77.2	88.1	93.8							
STRUCTURE 1997					0.154	0.662	23.3	4.256	0.075	1.890	0.005
Eigenvalues	0.052	0.043	0.026	0.016							
Species-environment correlations	0.603	0.697	0.604	0.531							
Cumulative percentage variance											
of species data	7.8	14.4	18.3	20.7							
of species-environment correlation	33.8	62.0	78.7	89.1							
PLANT 1997					0.225	0.662	34.0	6.354	0.020	1.974	0.005
Eigenvalues	0.080	0.041	0.032	0.025							
Species-environment correlations	0.742	0.631	0.649	0.651							
Cumulative percentage variance											
of species data	12.1	18.4	23.3	27.1							
of species-environment correlation	35.7	54.2	68.5	79.8							

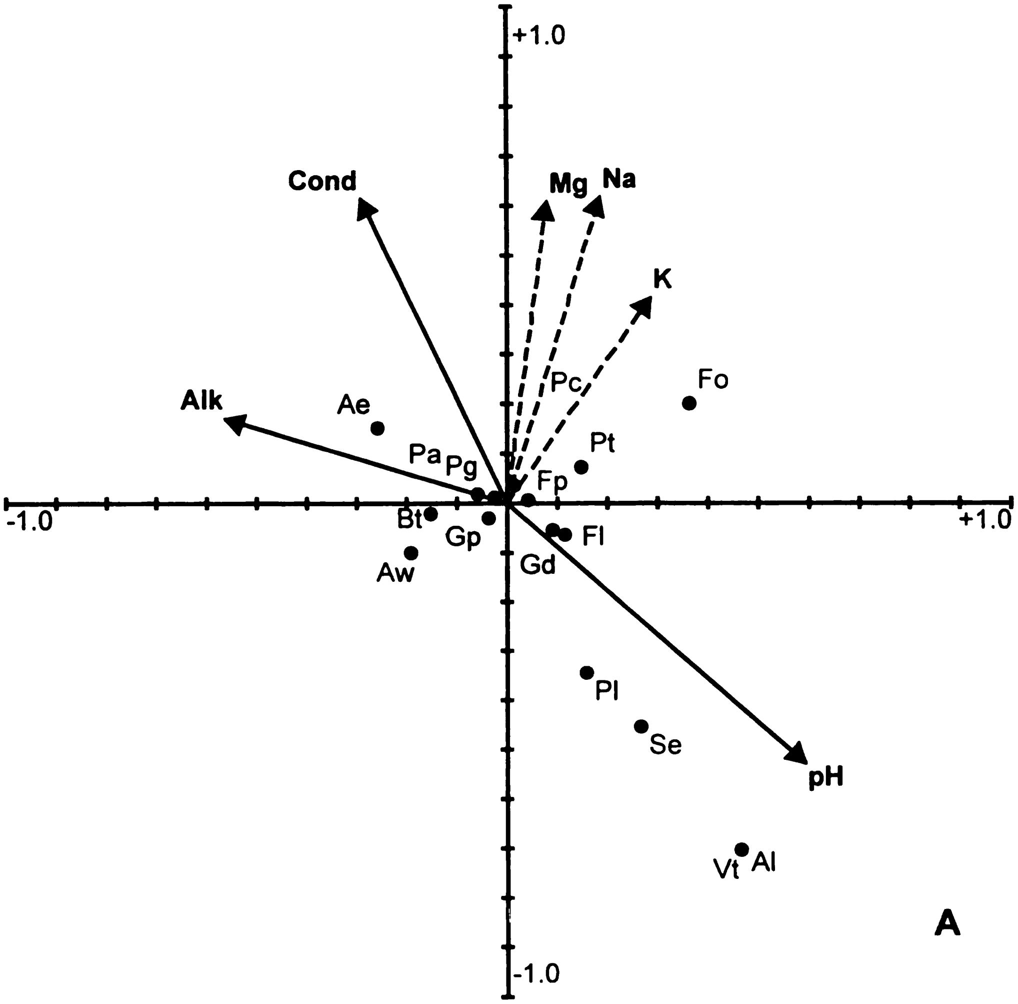


Figure 6. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 CHEMISTRY variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted environmental variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Environmental variable abbreviations as in Table 7, species labels as in Table 2, and site labels as in Table 1.

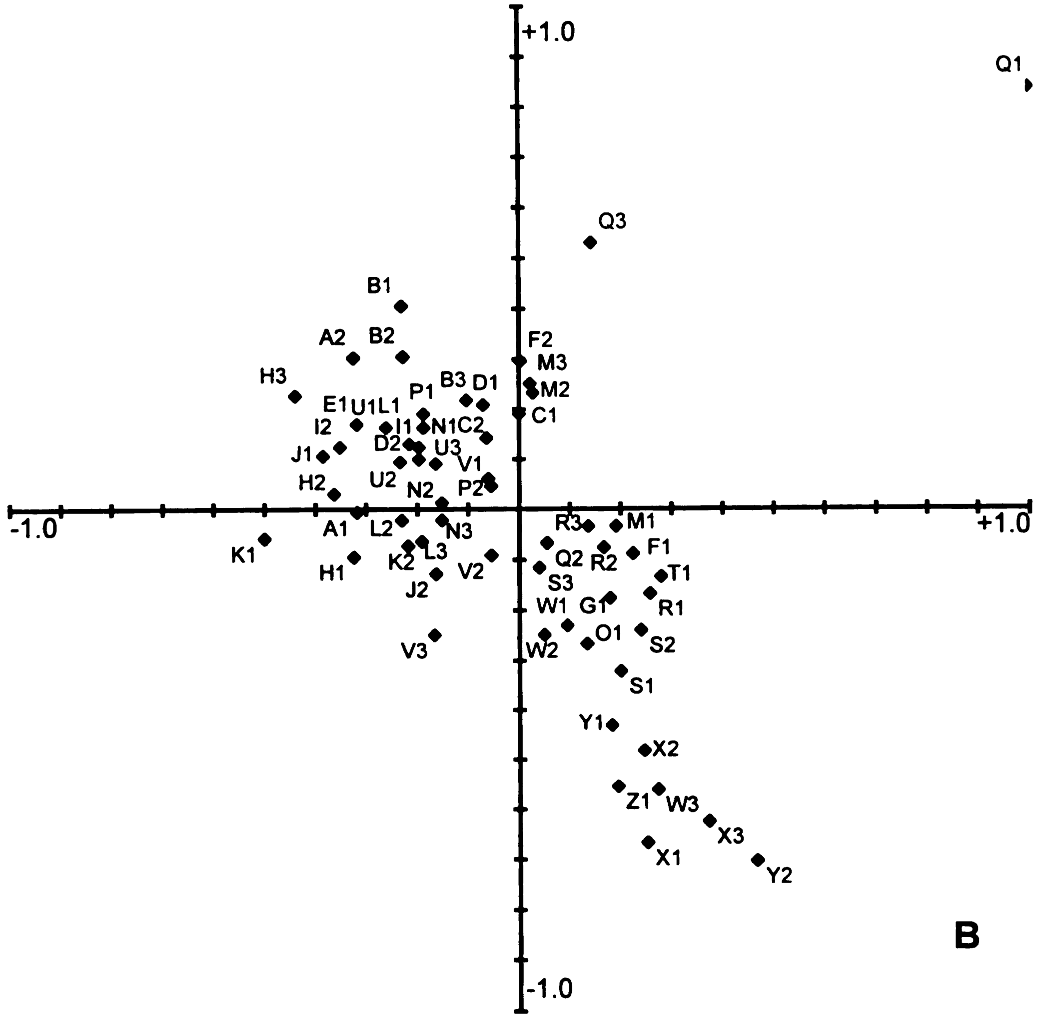


Figure 6. Continued.

STRUCTURE variable group (see Table 5), and vegetation density was removed leaving eight variables in the analysis. These variables explained a total of 23.3% of the variance in species data (Table 6) with axis 1 and axis 2 explaining 7.8% and 6.6% of the species data and 33.8% and 28.2% of the species data when constrained by the environmental variables (Table 6). Four variables: water depth, hummock frequency, shrub density and frequency of open water, were significant within the model (Table 7). The first axis was a gradient from deeper water to shallower water with a higher shrub density. The second axis was a gradient from more dense hummocks and grass habitats to sparsely vegetated habitat with more open water (Figure 7). *Amnicola limosa, V. tricarinata, S. elodes* and *Ferrissia parallela* all tended to be associated with deeper habitats, whereas *Aplexa elongata* was found in shallower, shrubby habitats with some open water pockets. *Bithynia tentaculata* and *Amnicola walkeri* were found to have fairly strong association with densely vegetated and hummock-filled habitats (Figure 7).

PLANT (see Table 5) accounted for the greatest proportion of variance explained with 34.0% in 1997 (Table 6). All 12 variables were included in the final model and six were significant (Table 7). Axis 1 and axis 2 accounted for 12.1% and 6.3% of the variance in the species data and 35.7% and 18.5% of the species data when constrained by the environmental variables (Table 6). A gradient from bulrush and cattails to shrub habitats was associated with axis 1, and axis 2 was a gradient from alder and bulrush to graminoid and *Potamogeton* habitats. *Ferrissia parallela* was strongly associated with increasing bulrush frequency (Figure 8). *Amnicola limosa, V. tricarinata*, and *S. elodes* were associated with axis 2, especially sites with lower frequency of graminoids and *Potamogeton* whereas *Planorbella campanulata* and *B. tentaculata* were associated with

Table 7. Interset correlations of environmental variables with CCA axes in 1997 for all variables included in significant model. Significant variables (P<0.10) are indicated in **bold type**. Environmental variable abbreviations are used in CCA diagrams.

		Interset Correlations			
Variable	Abbrev.	Axis 1	Axis 2	Axis 3	Axis 4
CHEMISTRY 1997					
Alkalinity	**Alk**	-0.388	0.101	0.142	-0.032
Conductivity	**Cond**	-0.200	0.362	0.084	-0.091
pH	**pH**	0.408	-0.311	0.085	-0.125
Potassium	K	0.197	0.245	-0.177	0.144
Magnesium	Mg	0.055	0.359	0.039	0.016
Sodium	Na	0.127	0.363	0.070	0.175
STRUCTURE 1997					
Water depth	**Depth**	-0.390	-0.266	0.045	0.273
Hummock freq.	**Hummfrq**	0.384	-0.391	-0.211	-0.045
Shrub density	**Shrubden**	0.408	0.110	0.357	0.049
Open water freq.	**Waterfrq**	-0.051	0.286	-0.192	0.250
Foliage diversity	Foldiv	0.380	0.060	0.270	0.071
Grass density	Grassden	0.130	-0.331	-0.067	-0.335
Grass height	Grassht	-0.055	-0.307	-0.202	0.020
Hummock height	Hummht	0.277	-0.156	-0.384	0.024
PLANT 1997					
Alder	**Alderfrq**	-0.108	0.282	-0.314	0.007
Bulrush	**Bulfrq**	0.507	0.223	-0.043	0.274
Cattail	**Catfrq**	0.442	-0.070	-0.084	-0.147
Graminoid	**Gramfrq**	-0.115	-0.259	-0.306	-0.418
Potamogeton	**Potfrq**	-0.112	-0.293	-0.103	0.397
Shrub	**Shrubfrq**	-0.221	-0.064	0.128	-0.249
Duckweed	Duckfrq	0.137	-0.116	0.101	-0.245
Nuphar	Nupfrq	0.186	-0.014	-0.106	0.290
Polygonum	Polyfrq	-0.031	-0.061	0.074	0.073
Submersed veg.	Subfrq	0.148	-0.206	0.097	0.083
Tree	Treefrq	-0.177	0.273	-0.085	-0.157
Willow	Wilfrq	-0.110	-0.061	0.186	0.008

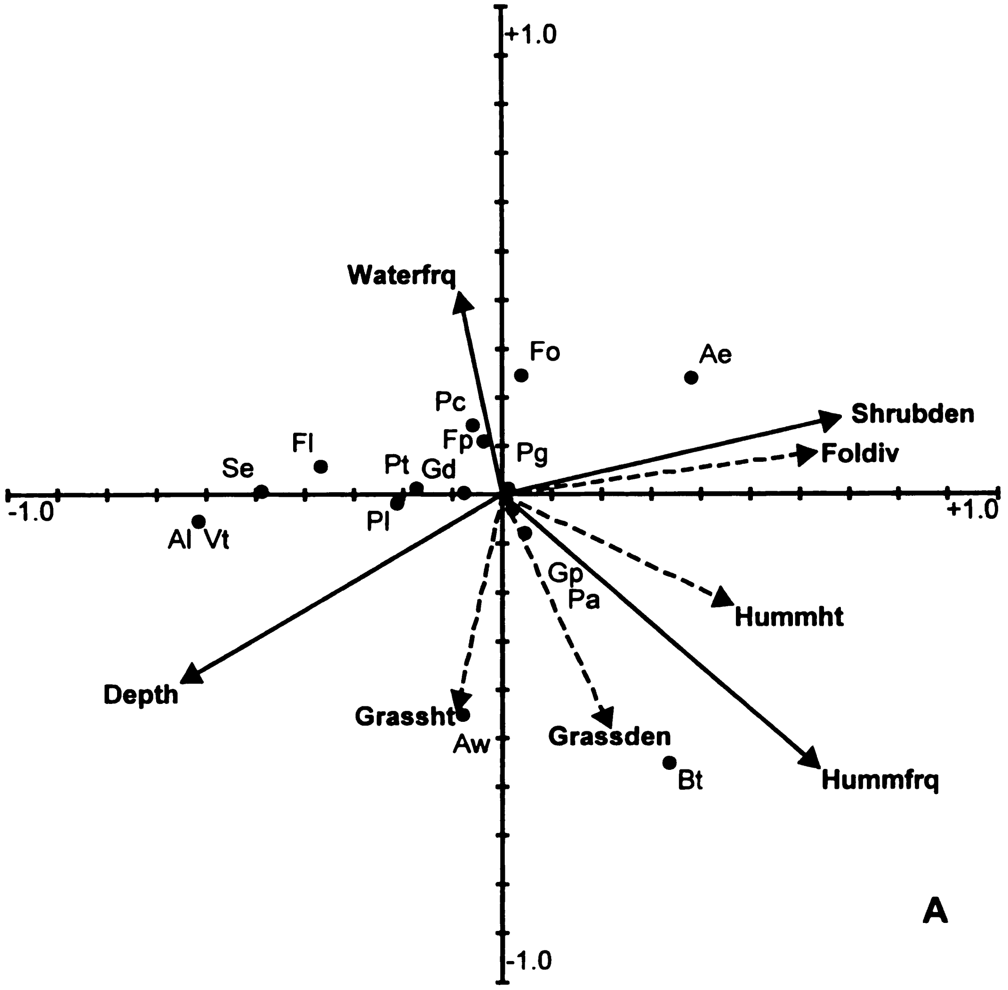
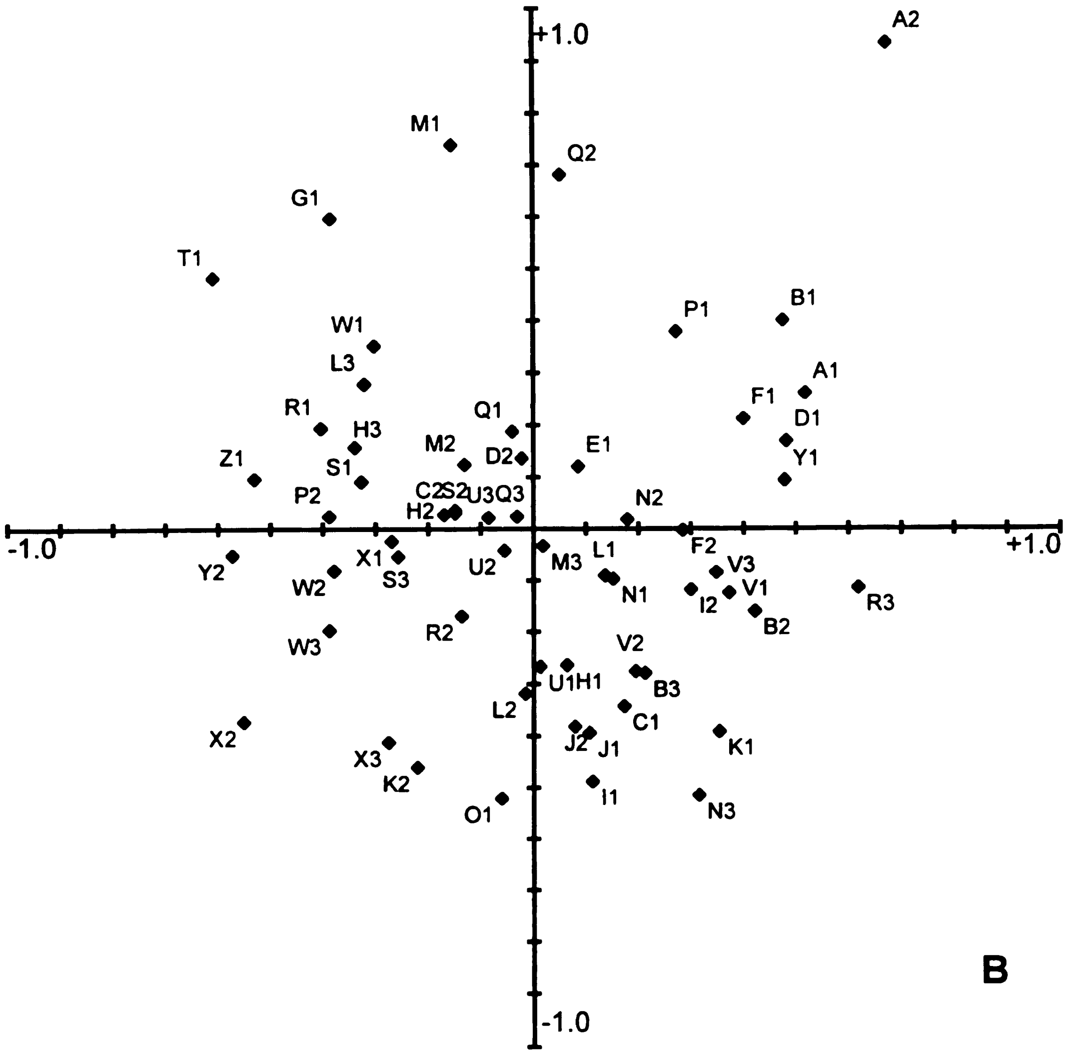


Figure 7. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 STRUCTURE variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted environmental variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Environmental variable abbreviations as in Table 7, species labels as in Table 2, and site labels as in Table 1.



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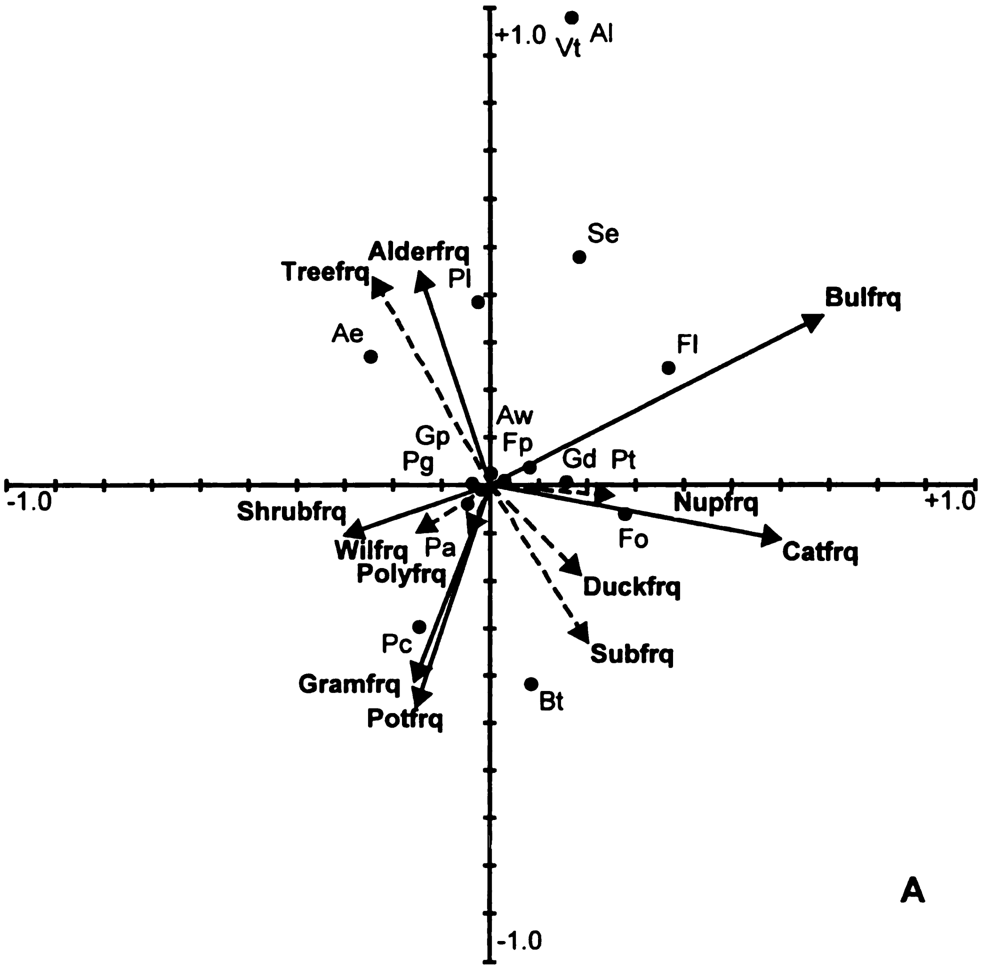

Figure 8. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 PLANT variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted environmental variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Environmental variable abbreviations as in Table 7, species labels as in Table 2, and site labels as in Table 1.

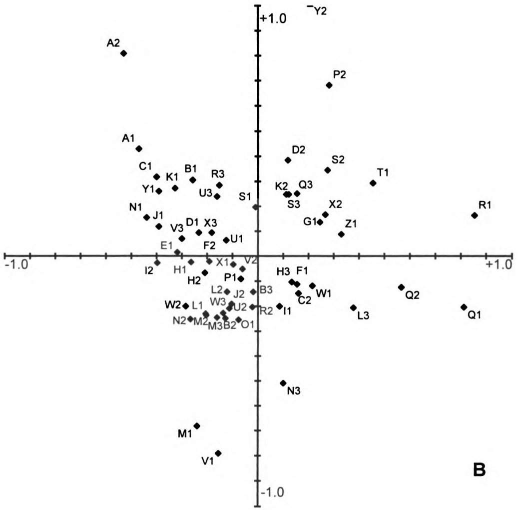

Figure 8. Continued.

a higher frequency of these. *Pyrgulopsis lustricus* was associated with higher alder frequency (Figure 8).

In 1998, there was no significant model for the CHEMISTRY group (P>0.10) and only hummock height was significant in STRUCTURE (Table 9). Thus, only one axis was generated in the CCA and therefore explained 100% of the variance in species data constrained by the environmental variable, but only 5.7% of the variance in species data (Table 8). There were no strong species associations with this gradient (Figure 9).

Five variables were included in the significant model for PLANT in 1998 and together they explained 24.2% of the species data. Bulrush, cattail and submersed vegetation were significant (Table 9). Axes 1 and 2 explained 9.7% and 8.0% of the variance in species data and 40.1% and 33.2% of the species data constrained by the environmental variables (Table 8). Axis 1 was a gradient of cattail frequency and axis 2 was a gradient from high bulrush to high submersed vegetation frequency (Figure 10). The majority of snail associations were with habitats containing low cattail frequency (Figure 10). *Bithynia tentaculata* associated strongly with submersed vegetation.

CCA Analyses: Importance of CHEMISTRY, STRUCTURE, and PLANT

The total inertia (i.e. sum of all unconstrained eigenvalues) for the 1997 data was 0.662. The proportion of variation explained by each of the three environmental variable groups was calculated by dividing the sum of the canonical eigenvalues for each by total inertia. The sums of unconstrained eigenvalues for CHEMISTRY, STRUCTURE, and PLANT were 0.119, 0.154, and 0.225, resulting in 18.0%, 23.3%, and 34.0%, respectively, of the variance explained by the environmental variables (Table 6). However, the correlation

Table 8. Results of canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows in 1998.

	Axes				Σ canonical	Total	% Variance	1st axis		All axes	
	1	2	3	4	eigenvalues	inertia	explained	F-ratio	P	F-ratio	P
CHEMISTRY 1998											
No significant model											
STRUCTURE 1998					0.035	0.612	5.7	1.869	0.050	—[1]	—
Eigenvalues	0.035	—[1]	—	—							
Species-environment correlations	0.722	—	—	—							
Cumulative percentage variance											
of species data	5.7	—	—	—							
of species-environment correlation	100.0	—	—	—							
PLANT 1998					0.148	0.612	24.2	2.895	0.080	1.721	0.020
Eigenvalues	0.059	0.049	0.021	0.012							
Species-environment correlations	0.762	0.793	0.552	0.477							
Cumulative percentage variance											
of species data	9.7	17.7	21.2	23.3							
of species-environment correlation	40.1	73.3	87.8	96.2							

1. Only one variable was included in model.

Table 9. Interset correlations of environmental variables with CCA axes in 1998 for all variables included in significant model. Significant variables (P<0.10) are indicated in **bold type**. Environmental variable abbreviations are used in CCA diagrams.

		Interset Correlations			
Variable	Abbrev.	Axis 1	Axis 2	Axis 3	Axis 4
CHEMISTRY 1998					
No significant model					
STRUCTURE 1998					
Hummock height	**Hummht**	-0.722	—[1]	—	—
PLANT 1998					
Bulrush	**Bulfrq**	0.120	-0.449	0.367	-0.221
Cattail	**Catfrq**	0.580	0.097	-0.144	0.095
Submersed veg.	**Subfrq**	0.063	0.540	0.390	0.086
Alder	Alderfrq	0.148	-0.254	-0.159	0.420
Shrub	Shrubfrq	0.279	0.132	0.028	0.193

1. With one variable only one canonical axis is produced.

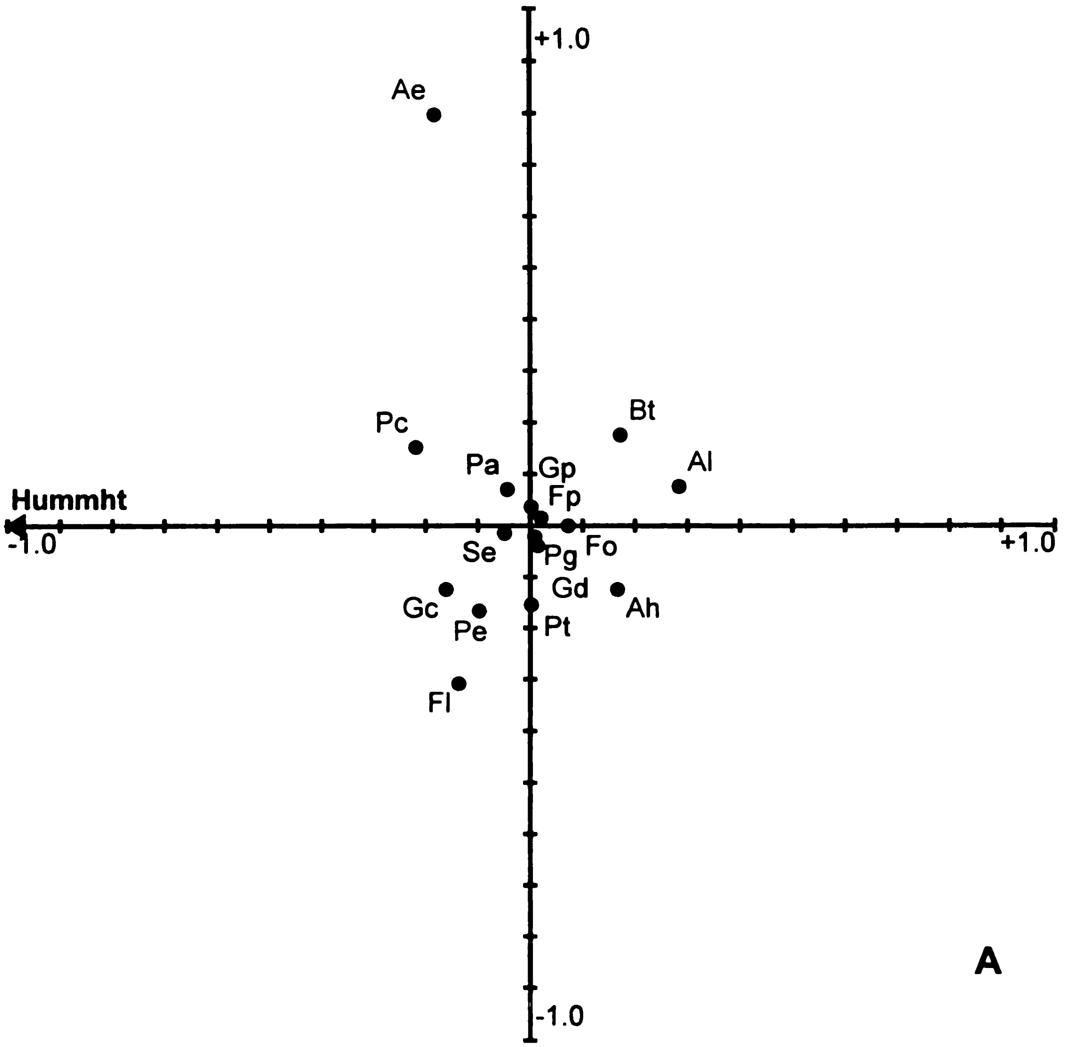

Figure 9. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1998 STRUCTURE variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. Species and sites scores are adjusted to scale = 0.3. Environmental variable abbreviation as in Table 8, species labels as in Table 2, and site labels as in Table 1.

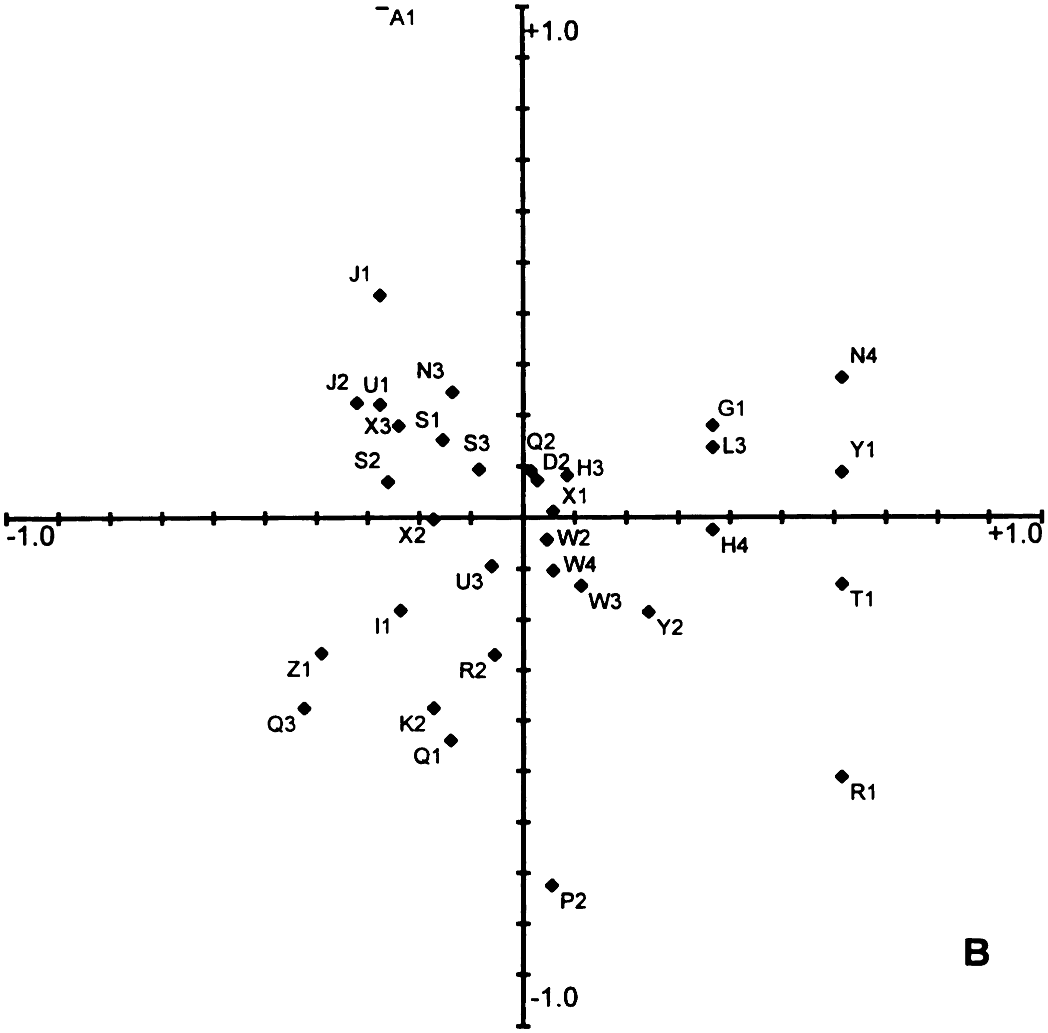

Figure 9. Continued.

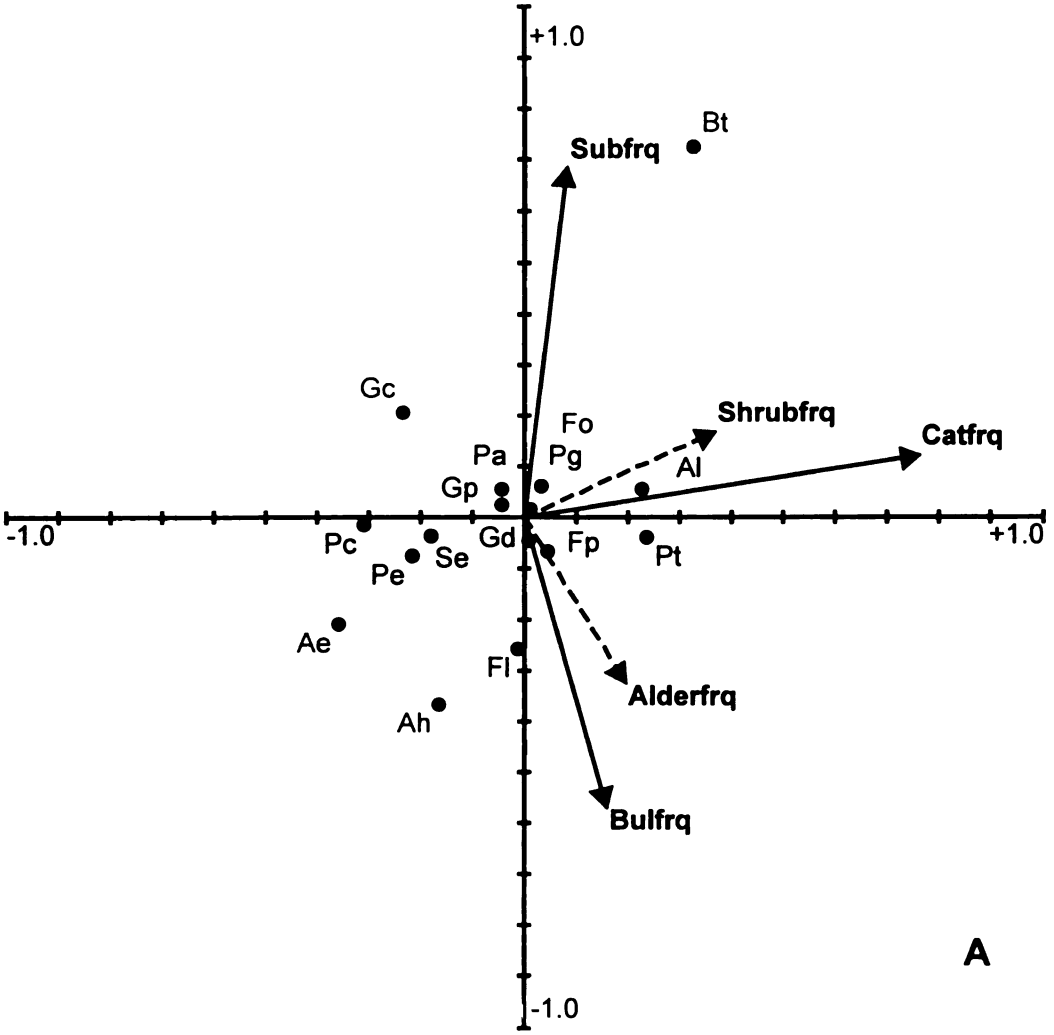

Figure 10. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1998 PLANT variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted environmental variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Environmental variable abbreviations as in Table 8, species labels as in Table 2, and site labels as in Table 1.

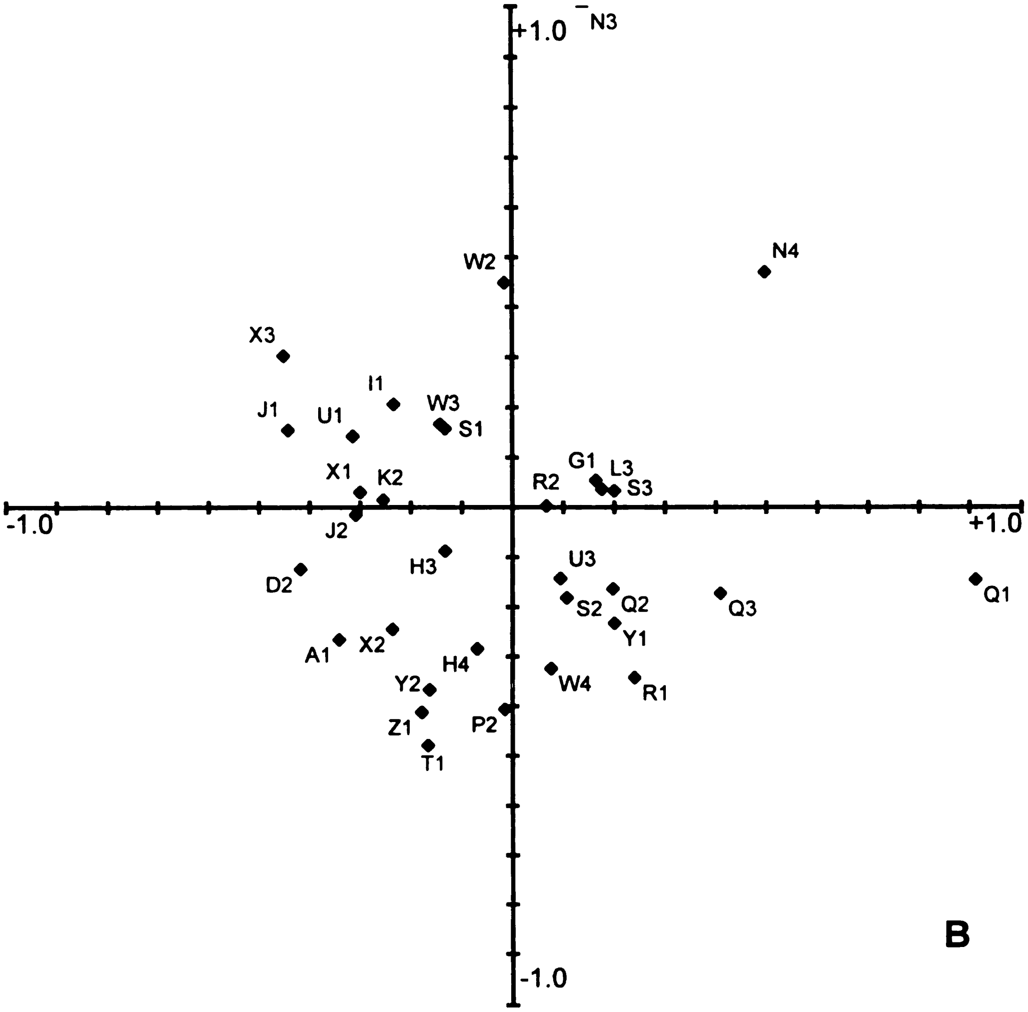

Figure 10. Continued.

that was likely to exist between environmental variables means that some of the variance explained by each group was likely shared with one or both of the other groups. The results of the partial CCA showed that less than half of the variance explained by CHEMISTRY was due to CHEMISTRY alone (7.9% of the 18.0%) (Figure 11). The remainder was shared with STRUCTURE and PLANT. Likewise, STRUCTURE alone and PLANT alone accounted for 15.6% and 21.8%, respectively, of the explained variance in the species data (Figure 11). A total of 58.2% of the variance in the species data was explained by the CCA. Nearly 13% of the variance was shared among the three variable groups, and 41.8% of the variance in species data was unexplained by the environmental variables included in the three models (Figure 11).

In 1998, the CCA models were able to explain much less of the variation in the species data (Table 8). There was no significant model for CHEMISTRY and only one variable in the STRUCTURE group. The canonical eigenvalues for STRUCTURE accounted for just 5.7% of the variance in species data (0.035 divided by the total inertia of 0.612) and PLANT accounted for 24.2% (0.148/0.612). PLANT alone accounted for 22.1% of the variance and STRUCTURE alone for 3.6%; 2.1% was shared between the two (Figure 12). The remaining 72.2% of the variance in species data was unexplained.

DISCUSSION

Snail Community Characteristics

Coastal wet meadows in the northern Lake Huron shoreline contained a very diverse aquatic snail community composed of 19 species (Table 2). There have been no systematic surveys of this habitat as far as this author can determine so comparisons are

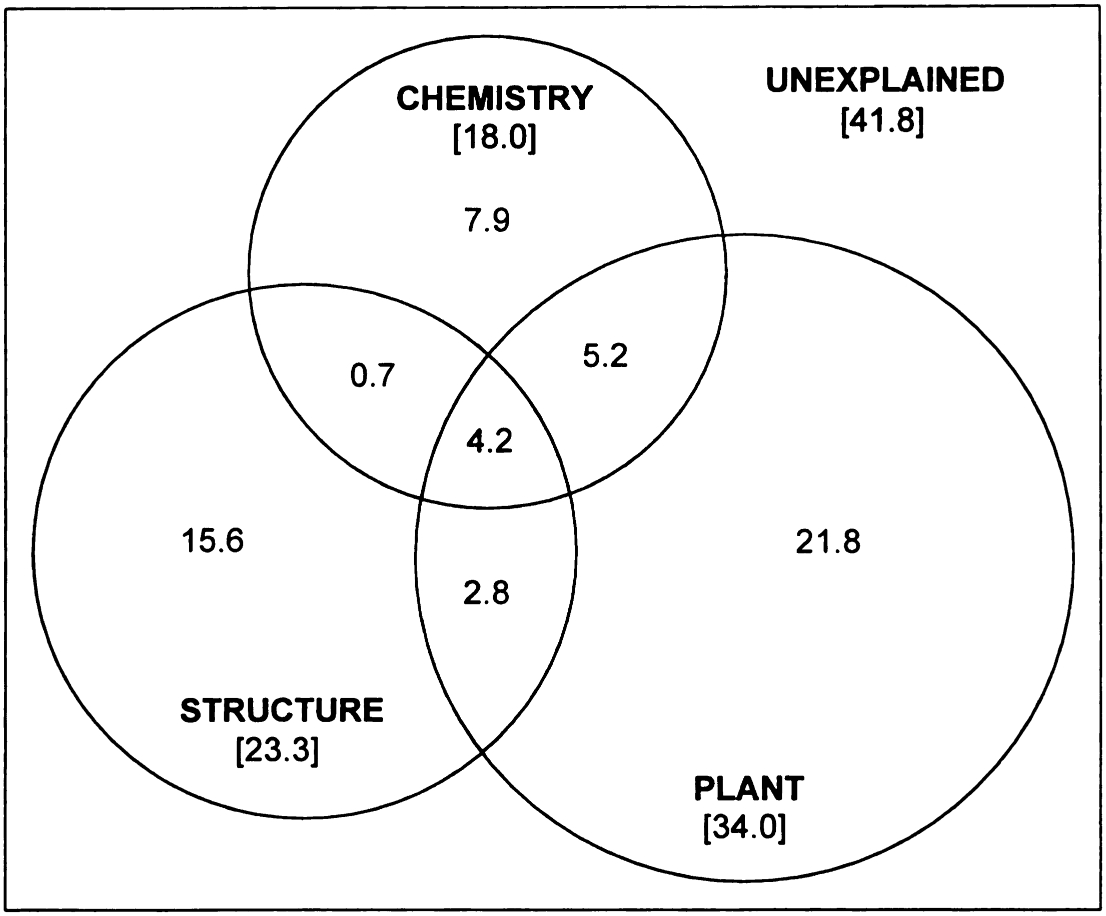

Figure 11. Venn diagram of the CCA variance partitioning of 1997 species data among three variable groups. Total variance explained by a variable group is enclosed in [ ] and represented by the size of the circle. Variance shared by variable groups is indicated in the appropriate intersections (although size is not proportional). Variance explained is calculated as the sum of all canonical eigenvalues for a particular analysis divided by the total inertia.

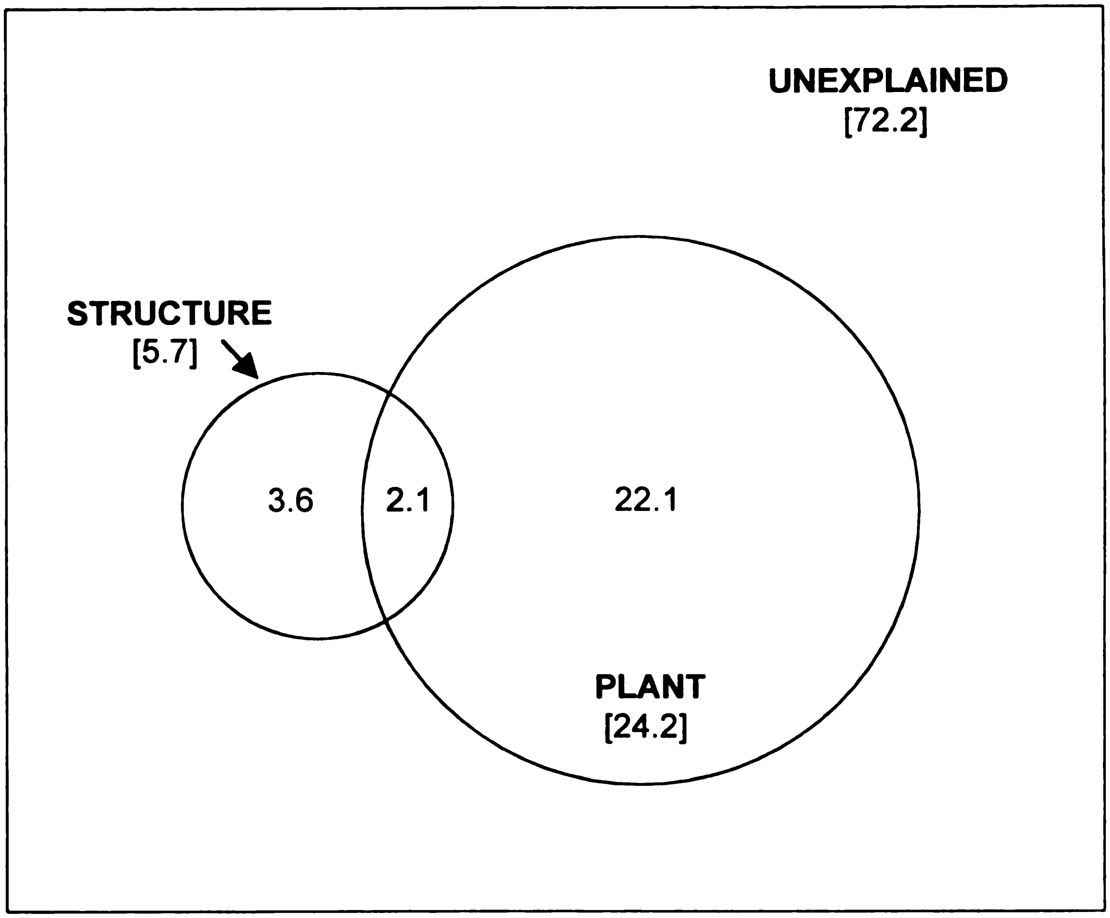

Figure 12. Venn diagram of the CCA variance partitioning of 1998 species data among two variable groups. There were not a significant model for the CHEMISTRY variable group in 1998. Total variance explained by a variable group is enclosed in [ ] and represented by the size of the circle. Variance shared by variable groups is indicated in the appropriate intersections (although size is not proportional). Variance explained is calculated as the sum of all canonical eigenvalues for a particular analysis divided by the total inertia.

difficult to make. Although not specifically listing wet meadows, Burch and Jung (1992) list 31 species that might be found in habitats similar to those found in these wet meadows (e.g. using categories such as quiet bay or pond, intermittent pool, or marsh species, etc.) in the northern Michigan region. Brönmark (1985) found 18 species in Swedish ponds, which were densely vegetated and provided similar habitats as those found in wet meadows, and Pip (1987) identified 40 species in a variety of aquatic habitats (41% were ponds, but also lakes and rivers) throughout central North America. The northern Lake Huron shoreline is considered to contain some of the most pristine of the remaining Great Lakes coastal wetlands (Minc and Albert 1998) and the snail community reflects this.

Further investigations of diversity used the Shannon Index, a diversity index that combined both species richness and a measure of the evenness of abundance among the different species (Magurran 1988). The distribution of Shannon Index scores for the wet meadows approximated a normal distribution (Figure 4), with the possible exception of Seymour 1 in 1998, indicating an underlying relationship among wet meadows. The normal distribution suggested that the snail communities within the wet meadows were similar enough to be considered together in the current analyses. Others have also found the distribution of Shannon Index scores to be normally distributed (see Magurran 1988).

In terms of the diversity represented by the Shannon Index, overall, the snail communities showed little change from 1997 to 1998 (Figure 4). Those wet meadows with low diversity in 1997 increased from 1997 to 1998 and those with relatively high diversity decreased from 1997 to 1998. This suggests that a dynamic equilibrium process may be important in structuring the snail communities.

Many studies of snails within lakes have found some evidence for an association of diversity with lake area (Lassen 1975, Aho 1978a,b, Browne 1981, Jokinen 1987). However, regressions of Shannon Index against area, and all other measures of diversity used in the present study showed no evidence of an area effect (Figure 5). Similarly, Brönmark (1985) found only a weak area effect in a study of aquatic snails in ponds. One of the most likely reasons for the increase in snail diversity within lakes was because lakes with greater area had higher habitat diversity that could support different snail species (Harman 1972, Ross and Ultsch 1980). In those studies, however, the measurement of habitat diversity was based primarily on substrate type, and macrophytes were only considered in a general sense as one type of substrate (Harman 1972). Because I sampled snails from sites that I identified as wet meadows, I automatically limited the variability in sediment type and habitat in general (though not completely, see Table 5) thereby reducing many effects of habitat type that might change as area increased. The lack of an area effect at my scale of sampling suggested a dynamic equilibrium that is more strongly influenced by other factors.

Habitat Characteristics of Coastal Wet Meadows

The 28 habitat characteristics used as explanatory variables provided a good description of the environment in which the snails were located. Analysis of the original data as well as CCA sites-environmental biplots suggested a relatively homogeneous environment, especially in terms of water chemistry.

The sites-environmental biplot for CHEMISTRY in 1997 exhibited a clustering effect of most points near the center of the two axes (Figure 6). This tight clustering was indicative of low variation in the overall combination of water chemistry variables examined (Jongman et al. 1995, ter Braak and Šmilauer 1998). An exception was that several wet meadows, Sweets 2-4, were separated and clustered in the lower right quadrant of the plot. This clustering suggested that these sites were somewhat distinct in their chemical characteristics, and direct analysis of the original data confirmed that these wet meadows were much lower in alkalinity and slightly higher in pH. Examination of the STRUCTURE and PLANT sites-environmental biplots (Figures 7-10) indicated moderate variability in these characteristics (i.e. less clustering of points).

The majority of environmental variables also were consistent from 1997 to 1998 (Table 5). This was somewhat surprising given the dynamic nature of the water level fluctuations in coastal wetlands. Not only do daily (seiches) and seasonal (due to precipitation patterns) fluctuations occur (Keough et al. 1999), but also a substantial decrease in water level occurred from 1997 to 1998. Lake Huron water level dropped by 28 cm (USACE 2000) during this time and the wet meadows showed a significant decline in depth from 29 cm to 13 cm in the sampled sections (Table 5). The average decrease of 16 cm in the wet meadows was less than the lake level decline because of natural and anthropomorphic barriers (Table 1) that affected water retention in the wet meadows.

The two other significant changes from 1997 to 1998 were most likely associated with the lower water levels. For example, higher conductivity levels that were recorded (Table 5) may have been an effect of concentrating solutes in the water column. The only change in plant structure or frequency was a decrease in the occurrence of *Polygonum amphibium* (Table 5). While the lower water levels will affect the plant community over time, the lack of additional plant changes in the present study was consistent with studies that show a lagged response to rapid water level changes (Keddy and Reznicek 1985, 1986).

Snail - Environmental Variable Relationships

The significant snail-environment relationships detected in the CCA for 1997 and 1998 are summarized in Figures 13 and 14, respectively.

As hypothesized, the water chemistry variables included in the CHEMISTRY variable group explained the least amount of variation in the species data. In 1997, 18.0% was explained and since there was no model in 1998, none was explained (Tables 6 and 8). The most significant variables from the CHEMISTRY group in 1997 were alkalinity, conductivity and pH (Figure 6). Calcium was not included in the analysis because of the strong correlation with alkalinity, which was expected in this region because of the dolomite and limestone bedrock. Whether the effect on snails was due to alkalinity or calcium concentrations or an interaction between the two was beyond the scope of this study. The first axis of this CCA ordination included both alkalinity and pH, which were common factors in other studies as well (e.g. Aho 1966, Mackie and Flippance 1983a, Økland 1983, McKillop 1985, Pip 1987). However, in the present study, alkalinity and pH were unexpectedly negatively related. An examination of the sites-environmental biplot (Figure 6) revealed that three sites were strongly related to this axis. The three sites were all located on Sweets Point on the northern tip of a peninsula (Figure 2). They were isolated from many of the other wet meadows and direct examination of the data revealed much lower alkalinities at these sites relative to the rest of the wet meadows. These sites also had slightly higher pH, leading to the negative relationship in the CCA. Thus, the observed negative relationship between pH and alkalinity should be regarded as a localized effect of a few influential wet meadows

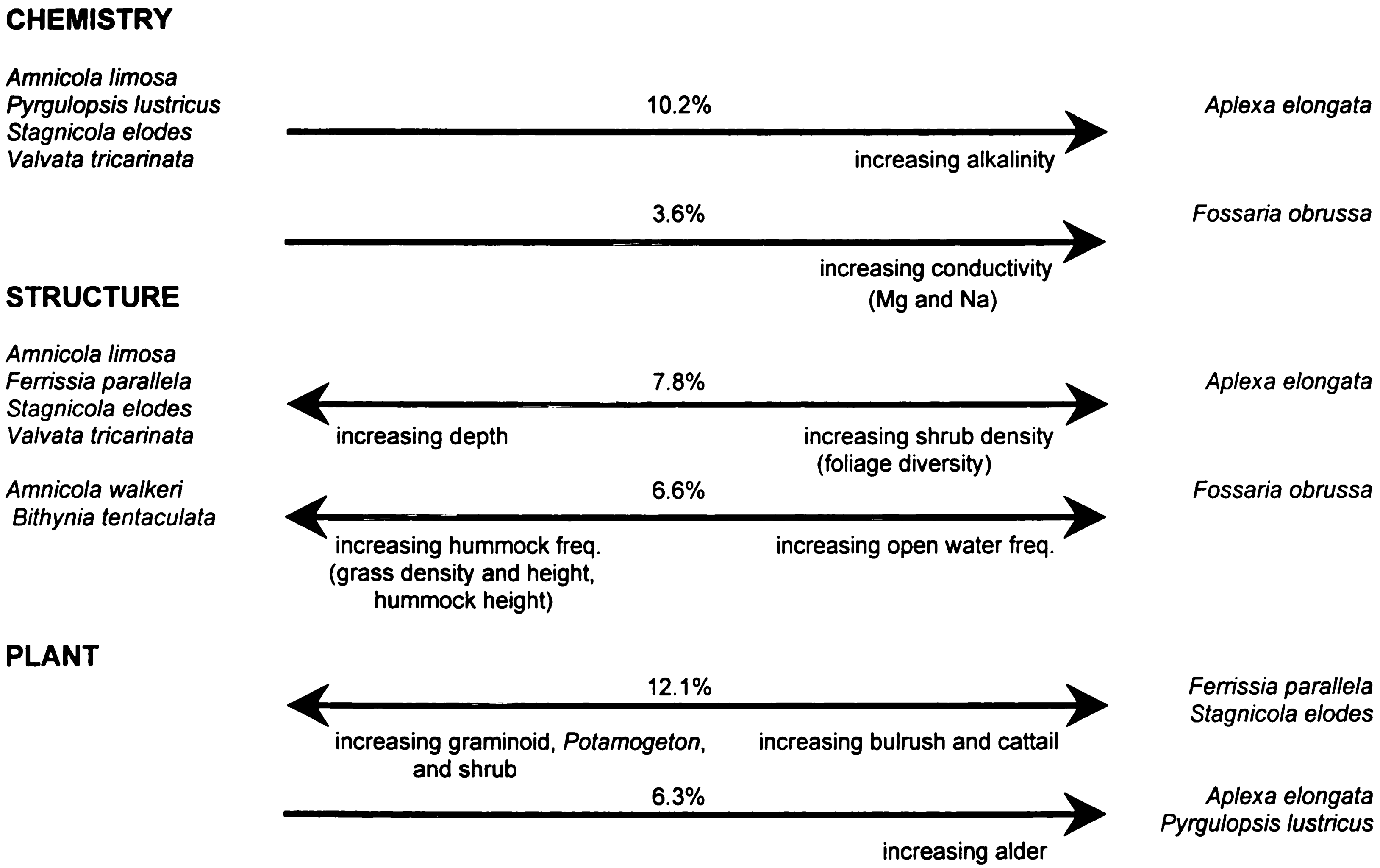

Figure 13. Summary of the 1997 snail-environment relationships using CCA for each of three environmental variable groups. Arrows represent environmental gradients for canonical axes with percentage of the species data explained above. Significant variables correlated with each axis are listed below; correlated, nonsignificant variable are in ( ). Snail species associated with each gradient are listed in the corresponding direction.

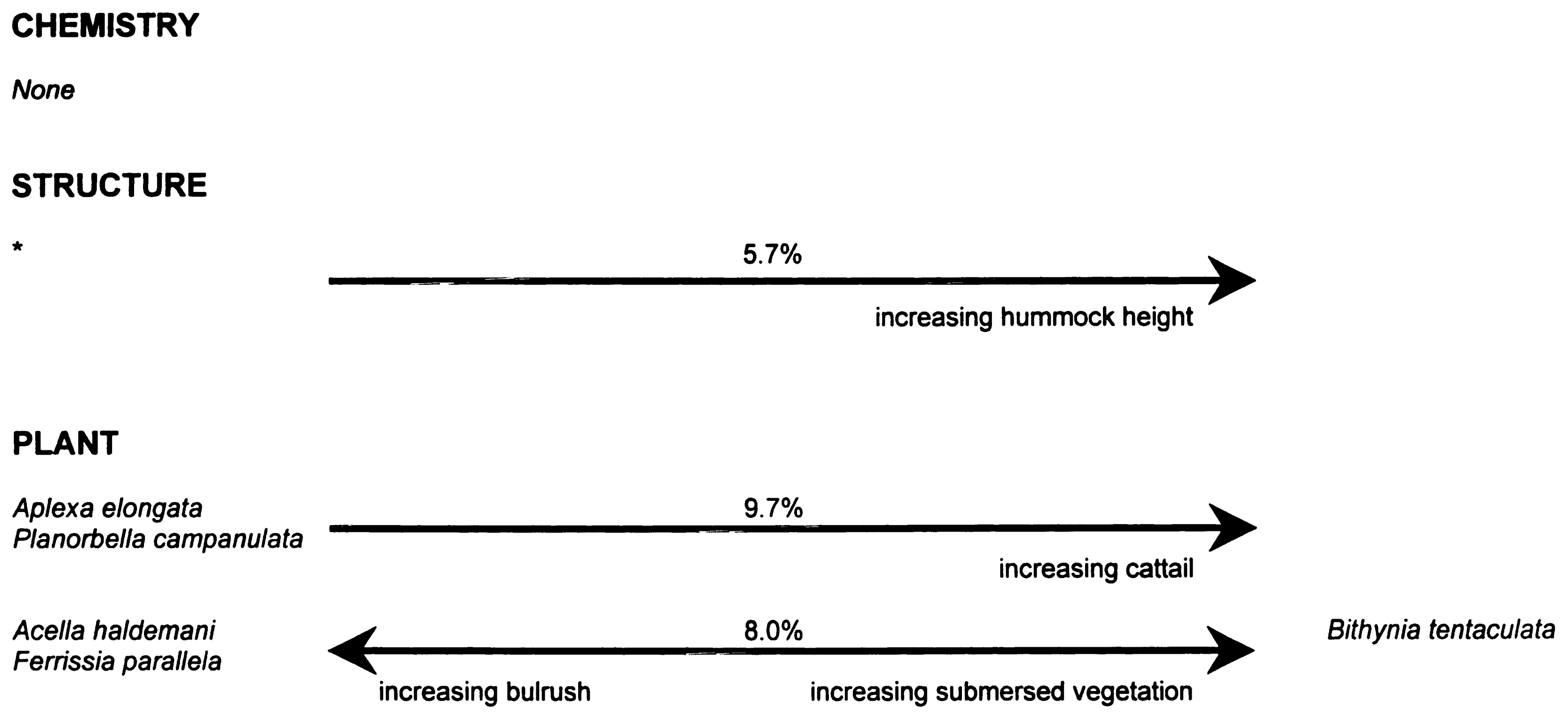

Figure 14. Summary of the 1998 snail-environment relationships using CCA for each of three environmental variable groups. Arrows represent environmental gradients for canonical axes with percentage of the species data explained above. Significant variables correlated with each axis are listed below. Snail species associated with each gradient are listed in the corresponding direction.

* No species were strongly associated with the STRUCTURE gradient.

among a generally homogeneous set, and therefore, the most significant variables were alkalinity and conductivity (Figure 13).

Snail species that showed a strong relationship in the CCA included four species that were more common than average in the Sweets point wet meadows (Figures 6 and 13). These included *Amnicola limosa* and *Valvata tricarinata*, which have been found in low alkalinity waters in other studies (Mackie and Flippance 1983a, Rooke and Mackie 1984) although not limited to these (McKillop 1985). *Fossaria obrussa* was influenced by environmental variables of the second axis, which is related to conductivity (as well as magnesium and sodium). Aho (1966) also found correlations between conductivity and the molluscan fauna in Finnish lakes and associated these with productivity.

The habitat structure or complexity as measured by the STRUCTURE variable group accounted for 23.3% in 1997 and 5.3% in 1998 of the variation in snail abundance and distribution (Tables 6 and 8). STRUCTURE was composed of primarily depth and non-specific plant characteristics that provided complexity to the environment. Nearly 5% of the variation explained by STRUCTURE was shared by the CHEMISTRY group in 1997, presumably as a result of interactions of the water chemistry variables on plant growth and the changes in water chemistry from shallower to deeper water.

In 1997, CCA of the STRUCTURE variable group revealed the most significant gradient as a change from deeper water to shallower water that contained a higher density of shrubs (Figure 13). This gradient may have reflected the role of fish predation in shaping the snail community. Snails in deeper water would likely be exposed to higher levels of fish predation to which some snails may be better adapted (Vermeij and Covich 1978). Both *A. limosa* and *V. tricarinata*, which are positively related to depth (Figure

7), are prosobranchs and contain an operculum that may confer some resistance to predators (Lodge et al. 1987). Furthermore the shell of *V. tricarinata* contains 2 or 3 raised carinae (keels) that help to strengthen the shell (Vermeij and Covich 1978). Conversely, *Aplexa elongata*, is a thin-shelled physid, lacking an operculum. It is not surprising that it was negatively related to depth and positively associated with shrub density. Increasing plant density may afford protection from fish predators (Covich and Knezevic 1978). A second gradient from higher occurrences of open water to increasing frequency of hummocks was also identified in 1997 (Figure 7) and in 1998 hummock height was the only significant variable (Figures 9 and 14). This gradient extended from more open regions to more densely structured habitat (hummocks) within the wet meadow, although it was independent of depth (as indicated by the right angle to the first gradient). It may also indicate the influence of predation as discussed above.

In addition to the interaction of depth/open water and plant/hummock density with predators, it is possible that these gradients affected the snail community in other ways. Although not examined in the present study, this gradient may have reflected a sun-shade gradient and/or a temperature gradient. The open water areas were exposed to more sun which may affect the periphyton community on which many snails feed (Doremus and Harman 1977, Russell-Hunter 1978, Lowe and Hunter 1988). In addition, the shading by the shrubs and hummocks (including the grasses forming the hummocks) may have maintained cooler temperatures in these regions that could have affected the snails directly or indirectly through the periphyton community. These possibilities deserve additional study.

The plant community explained the largest amount of variation in the species data. The PLANT variable group used the frequency of occurrence of plant species in the wet meadows as explanatory variables and explained 34.0% in 1997 and 24.2% in 1998 of the variation in snail distribution and abundance (Tables 6 and 8). In 1997, 9.4% of this explained variation is shared with the CHEMISTRY group and 7% shared with STRUCTURE, and 4.2% of this is shared among all three variable groups (Figure 11). In both years, bulrush and cattail were significant variables (Figures 13 and 14). These species may be found in large expanses just lakeward (Figure 1) of many of the wet meadows and in other cases, individual cattail or bulrush plants may be found scattered within the wet meadow (BEK: pers. obs.). In 1997, bulrush was included in a gradient in which the opposite direction was increasing graminoids, *Potamogeton natans* (a floating leaved pondweed species) and shrubs. This gradient was probably influenced more by the distribution of these plants within the wet meadow than by strong preferences for these species *per se* as occur in some snail-plant relationships (Calow 1973, Pip and Stewart 1976, Pip 1978). Bulrush was more common in deeper water whereas the others increased in frequency towards shallower depths. *Ferrissia parallela*, an ancylid limpet, showed a strong positive relationship with bulrush, as did *Stagnicola elodes*. Both of these species do not ingest live bulrush stems, but rather, can be found strongly attached to the stems where they are most likely feeding on the periphyton (BEK: pers. obs., Clarke 1981). *Planorbella campanulata* and *Bithynia tentaculata* showed a relationship with graminoids, *Potamogeton*, and shrub end of the gradient. In 1998, *B. tentaculata* was also associated with submersed vegetation. In 1997, the frequency of alder was significant and there was an association with *A. elongata* and *Pyrgulopsis lustricus*. It was unclear what accounts for this association.

Changes in the CCA from 1997 to 1998 (i.e. no significant model for CHEMISTRY, and less variation explained overall) (see Figures 13 and 14) were most likely due to the decrease in water levels that occurred. The elimination of a significant water chemistry model in 1998 supported the generally weak association of the snails with water chemistry observed in 1997. A decrease in water levels probably altered the water chemistry by changing the importance of the sources. Lowered water levels decreased the influence of Lake Huron and increased the importance of ground water and rainfall. These changes most likely added enough variability to reduce the likelihood of finding significant effects. In 1998 the only significant STRUCTURE gradient was hummock height whereas in 1997 there was a depth-shrub density gradient as well. The lower water levels in 1998 allowed only deeper sections from 1997 to be sampled in 1998. Thus, the depth gradient was reduced and the shallower sections that contain higher shrub density did not contain standing water. The hummock height gradient remained because hummock height was related to water depth; the taller hummocks were found in sections still containing water in 1998. The significant PLANT gradients also were plants generally associated with deeper portions of the coastal marshes: bulrush, cattails, and submersed vegetation.

Patterns in common and uncommon species

A number of species were found near the center of the CCA ordination biplots for the majority of the analyses, which indicated a limited association with the environmental gradients. These included the six most abundant and widely distributed species: *Physa gyrina*, *Gyraulus parvus*, *G. deflectus*, *Planorbula armigera*, *Planorbella trivolvis* and *Fossaria parva*. In contrast, the species that were frequently identified with each gradient were often less abundant and less widely distributed.

CCA is a technique widely used for the analysis of community composition data because of its ability to handle large numbers of zeroes in the data. However, rare species are known to have a disproportionately large influence on the analysis (ter Braak and Šmilauer 1998), and for this reason, they are given smaller weights in the analysis via a downweighting procedure found in CANOCO (ter Braak and Šmilauer 1998). I used the downweighting procedure in the present study to minimize the effect of rare species, thus reducing their influence in the analysis. The fact that they continued to appear in the gradient detected by CCA suggested that these gradients are biologically meaningful in comparison with the responses of the more abundant species, although caution should continue to be used in their interpretation. Also, it is important to stress that, even though the abundant species were not identified as having strong associations with the environmental axes, because of their abundance, they were still influential in the construction of the gradients.

The abundant species in the wet meadows were common throughout the region (e.g. Pip 1985, 1987) and were described as generalists, being found in many different environments (Burch and Jung 1992). The variation in their abundance and distribution within coastal wet meadows of the northern Lake Huron shoreline was not consistently associated with the environmental variables examined making it difficult to identify a gradient applicable to these species. And, this was especially true in comparison to the gradients detected with the less common species. Because these abundant species were such generalists, it made it more difficult to identify factors that affected their distribution. The environmental variables examined in the present study have shown only a limited ability to explain the observed distribution patterns. Other factors should be examined to further identify more important variables.

Conclusions

The coastal wet meadows of the northern Lake Huron shoreline contained a diverse assemblage of aquatic snails that included 19 species from seven different families. Snail abundance and diversity were not related to the size of the wet meadow due to the relative homogeneity of the habitat. Environmental variables that may affect the snail community composition were divided into three subsets, and the variance explained by each was partitioned. The occurrence of various plant species, including alder, bulrush, cattail, grasses and sedges, *Potamogeton natans*, various shrubs, and submersed vegetation, explained the greatest proportion of variation in the snail community. The structure of the habitat, as described by water depth, shrub density, hummock height and frequency, and the frequency of open water, explained the second greatest amount, and water chemistry (alkalinity and conductivity) explained the least. Although there were only a few changes in the habitat variables from 1997 to 1998, fewer significant snail-environment associations were observed in 1998, primarily because of decreased water depth. The environmental gradients detected were most closely associated with the less common snail species. The most common and abundant species were less associated with the variables examined, suggesting that other factors (e.g. surrounding landscape or fluctuating water levels) are more important determinants of their distribution patterns in wet meadow habitats.

CHAPTER TWO

SNAIL–LANDSCAPE ASSOCIATIONS IN COASTAL WET MEADOWS

INTRODUCTION

Landscape ecology is the study of the interaction between spatial patterns and ecological systems. Fundamental to this is the idea that landscapes are composed of relatively homogeneous, discrete elements called patches that when combined together form a mosaic pattern (Forman 1995). Patch quality, boundaries with other patches (that affect flow between them), patch context, and connectivity all may affect the ecological processes within a landscape. Additionally, the scale at which the landscape is examined, and the organisms involved are known to have an important influence (Wiens 2002).

As the name, "landscape", suggests, the theories underlying landscape ecology have been developed in terrestrial systems. It has been only relatively recently that many of these concepts have been applied to aquatic, primarily lotic, systems (see Wiens 2002). In addition to many other taxa and processes, these studies have shown that the stream and surrounding landscape influence aquatic invertebrate distributions (e.g. Palmer et al. 2000, Malmqvist 2002). Comparatively few landscape level analyses have been conducted that examine animal distributions in lentic systems. Lehtinen et al. (1999) found landscape level effects to be important in structuring wetland amphibian assemblages. In one of the earlier studies to include the importance of patch context, Brönmark (1985) examined pond isolation in an analysis of aquatic snail communities. In Minnesota lakes, Lewis and Magnuson (2000) found differences in species richness of snails to be dependent on the position of the lakes in the catchment and their stream connectivity.

The latter two studies demonstrate that the application of landscape level concepts has the potential to add to our understanding of aquatic snail communities. This is important since explaining the distribution and diversity of aquatic snails has proved troublesome (see Lodge et al. 1987). For example, early research espoused the importance of physicochemical factors, especially calcium content, of the water in determining snail distribution (Macan 1950, Aho 1966, Dussart 1976). More recently, some have concluded that physicochemical factors were important across biogeographical regions, but that within regions, other factors had greater influence (Lodge et al. 1987). The effect of lake size and area also received attention as the theory of island biogeography (MacArthur and Wilson 1967) was developed and applied to snail communities (Lassen 1975, Aho 1978a, Pip 1985, Jokinen 1987). The role that biotic interactions play in structuring aquatic snail communities has been less well studied, in part because of the difficulty in quantifying their importance. Although competition among snails is possible, there are few studies examining it (but see Eisenberg 1966). Lodge et al. (1987) suggested that other factors, such as predation by fish and crayfish (Brown and DeVries 1985, Lodge et al. 1987, Turner 1996), might limit snail population densities before competition became important.

The aquatic snail community found in 26 coastal wet meadows along the northern Lake Huron shoreline was composed of 19 species (*Chapter One*). Of these, six were relatively abundant and common; the others were found in relatively few of the wet meadow sites. Because of the generalist nature of the common species, few within-wet meadow characteristics were found to explain their distribution and abundance patterns, whereas for the less common species, habitat structure and plant community composition were important (*Chapter One*). The limited explanatory power of the within-patch characteristics that were examined suggests that other, perhaps landscape-level, processes (i.e. context or complexity) could help explain snail distributions.

The context of the wet meadow is likely important because of the potential interactions with surrounding habitat types. Coastal marshes participate in the exchange and transformation of inorganic and organic materials with adjacent waters and uplands (Sager et al. 1985, Mitsch and Gosselink 1993). It is likely that these fluxes will vary with the plant communities that are adjacent to the wet meadow; for example, whether the adjacent patch is a bulrush (*Scirpus* spp.) marsh or forested wetland or upland. Coastal marshes generally retain particulate matter rather than dissolved materials, which are released (Sager et al. 1985). The particulate matter may add to the detritus base, which is a food source for many species of snails (Russell-Hunter 1978, Reavell 1980, Brown 1982) and for which there may be specific snail-detritus preferences (Sterry et al. 1983, Lodge 1986) that affect a species presence or abundance. Wet meadow context may also affect the snail community composition by increasing or decreasing dispersal rates of snails from adjacent habitats (Brönmark 1985) or possibly by influencing the predator community.

Shoreline complexity may affect the import/export of materials and therefore the distribution of snails in coastal wet meadows by altering hydrological fluxes with the open water. Less complex shorelines should result in exposed wet meadows that are more strongly influenced by the open water from Lake Huron (see Lougheed et al. 2001). In addition, landscape theory suggests that complex landscapes are more stable (Forman 1995), which could allow for the development of more diverse snail communities. A number of other physical, chemical, and biological processes also are affected by shoreline complexity (Kent and Wong 1982).

The objective of the present study was to determine whether characteristics of the landscape surrounding the wet meadows could explain any additional variation in the snail communities. Specifically, I examined the context in which the wet meadows were located by measuring habitat patches immediately adjacent to the wet meadows and those present in the surrounding landscape (within 1 km of the wet meadow edge). I also examined the relationship of shoreline complexity (i.e. convolutedness) with snail community structure. These factors were examined after taking into account the variation explained by within-patch factors (i.e. chemistry, habitat structure, and plant community composition).

METHODS

Study Area

The northern Lake Huron shoreline in Michigan's Upper Peninsula contains numerous coastal wetlands (Figure 2). Twenty-six wet meadows among the extensive marsh complex were selected for this study (Table 1). General characteristics of these sites are described in *Chapter One: Methods, Study Area.*

Snail Collection

Snails were collected using timed dip net samples from 50-m sections in transects through each wet meadow in 1997 and 1998. Since I defined an entire wet meadow as one patch, I randomly selected a single section from sites in which multiple sections were sampled in order to remove bias due to differential sampling effort. In 1998, low water levels precluded sampling from seven wet meadows. Additional details of the snail sampling procedures are described in *Chapter One: Methods, Snail Collection.*

Within-Patch Environmental Characteristics

To account for within-patch characteristics that might explain snail distributions, I measured 28 environmental characteristics along each transect that were subdivided into chemistry, habitat structure, and plant community groups. The methods for sampling these characteristics, and descriptions of each of the variables are given in *Chapter One: Methods, Environmental Variables.*

Landscape Characteristics

A geographic information system was developed using ArcView (ESRI, Inc. 1999) to examine landuse-landcover patterns of the northern Lake Huron shoreline. Landuse-landcover patterns for the study area were interpreted based on color aerial photography from 1992. Because multiple images were required to cover the entire area, they were each georeferenced using existing digital data from the MIRIS (Michigan Resource Information System) database, rectified and mosaiked into one image that was used for digitizing landuse-landcover patterns. Landuse-landcover categories (Table 10) were verified/updated after comprehensive visual ground-truthing in 1999.

The landscape patterns surrounding the wet meadows were examined at two levels. First, patches that were immediately adjacent to the wet meadow perimeter were included in a PERIMETER variable group. Second, the landuse-landcover within 1-km of the edge of each wet meadow was included in a CONTEXT variable group.

The PERIMETER variable group contained 11 variables. For each wet meadow, the number of adjacent patches, the number of adjacent patch types, and the number of interfaces (discrete segments of wet meadow perimeter) with other patches were counted. Perimeter length of each wet meadow and proportion of perimeter length adjacent to

Table 10. Landuse-landcover categories used in the geographic information system of the northern Lake Huron shoreline, Michigan.

- Urban
- Agricultural
- Non-Forested Openings
- Forests
- Lakes, Ponds and Reservoirs
- Forested Wetlands
- Inland Emergent Wetlands
- Coastal Wetlands:
  - Alvar Wetland
  - Bulrush Marsh
  - Cattail Marsh
  - Fen Wetland
  - Sand flats
  - Wet Meadow
- Cobble Beaches
- Sand Beaches or Sand Dunes

Table 11. Landscape variables calculated for each of 26 wet meadows along the northern Lake Huron shoreline, Michigan.

Landscape Variable	Label	Description
PERIMETER		
# of adjacent patches	#Patches	Number of discrete patches adjacent to wet meadow perimeter.
# of adjacent patch types	#Types	Number of different patch types adjacent to wet meadow perimeter.
# of interfaces with other patches	#Interfaces	Number of different, discrete patch segments adjacent to wet meadow.
Proportion of patch perimeter adjacent to:		
Bulrush Marsh	%PBulrush	Emergent marsh dominated by *Scirpus acutus*.
Cattail Marsh	%PCattail	Emergent marsh dominated by *Typha angustifolia*.
Forested Wetlands	%PForWet	Northern white-cedar swamps with tamaracks and black spruce.
Total Wetlands	%PTotWet	Total of all wetland types from Table 10.
Open Water	%PWater	Lakes, Ponds, and Reservoirs (including Lake Huron)
Forests	%PForest	Uplands containing sugar maple, aspen, white birch, red and white pine.
Non-Forested Openings	%PNFO	Upland grasslands.
Urban	%PUrban	Primarily residential (homes and cottages); also commercial and industrial.
CONTEXT		
Within 1-km of patch perimeter:		
Bulrush Marsh	%Bulrush	Emergent marsh dominated by *Scirpus acutus*.
Cattail Marsh	%Cattail	Emergent marsh dominated by *Typha angustifolia*.
Wet Meadow	%WetMead	Grass and sedge dominated coastal wetland.
Inland Emergent Wetlands	%InWet	Inland marshes not hydrologically connected to Lake Huron.
Forested Wetlands	%ForWet	Northern white-cedar swamps with tamaracks and black spruce.
Total Wetlands	%TotWet	Total of all wetland types from Table 10.
Open Water	%Water	Lakes, Ponds, and Reservoirs (including Lake Huron)
Forests	%Forest	Uplands containing sugar maple, aspen, white birch, red and white pine.

Table 11. Continued.

Landscape Variable	Description	
Non-Forested Openings	%NFO	Upland grasslands.
Agricultural	%Agric	Cropland and pastures.
Urban	%Urban	Primarily residential (homes and cottages); also commercial and industrial.
Stream Density	Stream	Length of streams within context area.
Road Density	Road	Length of gravel and paved roads within context area.
COMPLEXITY		
Each of the following calculated at 3 scales: 500 m, 1 km, and 2 km		
Coastline Length		Measured length of Lake Huron shoreline.
	Coast-500m	
	Coast-1km	
	Coast-2km	
Sinuosity		Coastline length divided by the straight-line distance between endpoints.
	Sinuosity-500m	
	Sinuosity-1km	
	Sinuosity-2km	
Fractal Dimension		Fractal dimension of coastline.
	Fractal-500m	
	Fractal-1km	
	Fractal-2km	

eight landuse-landcover categories were calculated using ArcView (Table 11).

The CONTEXT variable group consisted of 13 variables describing the landscape surrounding the wet meadows for a distance of 1-km from the edge of each. The proportion of this buffer area assigned to 11 landuse-landcover categories was calculated as well as the length of streams and roads (Table 11).

The complexity or convolutedness of the shoreline in which the wet meadows were located was measured using vector shoreline data (Great Lakes Environmental Laboratory, Ann Arbor, MI). Buffer operations in Arc/Info were used to create shoreline vectors at three different scales (radii) from each wet meadow: 500-m, 1-km, and 2-km. Three separate measures of COMPLEXITY were calculated for each shoreline segment at each scale (Table 11); larger values of each of these metrics indicate greater complexity in the shoreline shape. Coastline length was the overall length of the shoreline in the buffer radius and was calculated directly from Arc/Info attribute tables. Sinuosity was a measure of the coastline length divided by the straight-line (Euclidean) distance between the endpoints. The fractal dimension was calculated using the walking divider method in the Fortran program, Fract_Line (Lam and de Cola 1993).

Statistical Analyses

Environmental characteristics. Canonical correspondence analysis (CCA), using CANOCO (ter Braak and Šmilauer 1999), was used to identify environmental variables from within each wet meadow (i.e. within-patch) that were related to snail distribution and abundance. Three separate analyses using water chemistry, habitat structure, and plant community composition were conducted using the forward selection procedure in CANOCO to select variables explaining the most variance within the species data.

Variables that were selected using this procedure were tested for significance ($\alpha < 0.10$) using Monte Carlo permutation testing (ter Braak and Šmilauer 1998). All significant variables from each analysis were combined for each year and used as covariables in further analyses. Detailed descriptions of these analyses are provided in *Chapter One: Methods, Statistical Analyses*.

Multivariate analyses of landscape variables and species data. Canonical correspondance analysis (CCA), using the statistical software CANOCO (ter Braak and Šmilauer 1999), was also utilized to express the major relationships between the species and landscape variables. The three landscape variable groups were examined separately, limiting the number of variables used in each analysis, as suggested by Borcard et al. (1992). Snail abundance data were log (x+1) transformed and rare species were down-weighted to reduce their influence using an algorithm available in CANOCO prior to analysis. Variables with high multicollinearity were examined and those with a variable inflation factor greater than 20 were removed (ter Braak and Šmilauer 1998).

I used the forward selection procedure within CANOCO (ter Braak and Šmilauer 1998) to select the largest number of variables from each landscape variable group that resulted in a significant model (to determine overall variance explained by the variable group). Because I was interested in the variation in snail data that could be accounted for by landscape variables above and beyond within-patch environmental characteristics, significant environmental variables were entered as covariables during the CCA (Borcard et al. 1992). In essence, this procedure removes the influence of covariables from the variable set in question, producing extracted gradients that are uncorrelated with the covariables (ter Braak and Verdonschot 1995). Significance was determined for both the

1st axis and all axes combined and a model was considered significant only if both of these met an *a priori* $\alpha < 0.10$. I used a more liberal value because of the variability inherent in field observations, and to maintain an acceptable Type II error rate. Significance testing was conducted using the Monte Carlo permutation testing (199 permutations) procedure within CANOCO (ter Braak and Šmilauer 1998).

After defining a significant model, significant variables (i.e. those that explained the greatest amount of species variation) were identified within each variable group. The results were interpreted with the use of CCA biplots, in which the landscape variables are represented as vectors among either site scores or species scores.

I conducted partial CCA using the method of Borcard et al. (1992) to determine the amount of variability shared between the PERIMETER and CONTEXT variable groups. Two of the wet meadows, Flowers and Hill Island, were located on islands; therefore, sinuosity and fractal dimension could not be calculated because no endpoints were present to measure straight-line distance. This prevented the inclusion of the COMPLEXITY variable group in the partial CCA (Økland and Eilertsen 1994). Additional details of this method are described in *Chapter One: Methods, Statistical Analyses*.

RESULTS

Wet meadows were located among a variety of surrounding habitats. All wet meadows were adjacent to at least two different patches and up to 17 interfaces with adjacent patches (Table 12), representing a very simple to very complex landscape configuration. The most common landuse-landcover category immediately adjacent to

Table 12. Summary statistics for three groups of landscape variables. *Complexity data are calculated for 24 wet meadows; sinuosity and fractal dimension were unable to be calculated for two meadows located on islands.

Landscape Variable	Units	Mean	SE	Range
PERIMETER				
# of adjacent patches	#/patch	4.46	0.49	2.00-11.00
# of adjacent patch types	#/patch	3.38	0.25	2.00-6.00
# of interfaces with other patches	#/patch	5.46	0.74	2.00-17.00
Proportion of patch perimeter adjacent to:				
Bulrush Marsh (*Scirpus* spp.)	%	19.26	3.66	0.00-58.29
Cattail Marsh (*Typha* spp.)	%	3.65	1.48	0.00-25.25
Forested Wetlands	%	5.37	2.82	0.00-68.05
Total Wetlands	%	28.28	4.50	0.00-75.39
Open water	%	8.61	3.65	0.00-76.50
Forests	%	53.00	4.51	13.27-93.10
Non-Forested Openings	%	0.90	0.54	0.00-12.13
Urban	%	7.52	2.74	0.00-62.40
CONTEXT				
Within 1-km of patch perimeter:				
Bulrush Marsh (*Scirpus* spp.)	%	4.13	0.84	0.00-16.45
Cattail Marsh (*Typha* spp.)	%	0.16	0.05	0.00-0.91
Wet meadow	%	4.24	0.68	0.23-11.01
Inland Emergent Wetlands	%	0.40	0.24	0.00-5.19
Forested Wetlands	%	2.14	0.58	0.12-12.34
Total Wetlands	%	11.13	1.29	1.48-26.55
Open water	%	37.29	3.56	11.48-71.01
Forests	%	70.50	3.47	23.14-94.32
Non-Forested Openings	%	3.83	0.84	0.00-17.96
Agricultural	%	0.18	0.10	0.00-1.96
Urban	%	14.09	2.80	0.00-55.4
Stream Density	m/ha	5.44	0.42	2.52-10.37
Road Density	m/ha	11.92	1.03	0.10-24.49
COMPLEXITY*				
Coastline Length				
500 m	m/ha	6.32	0.46	2.52-11.47
1 km	m/ha	12.46	0.64	6.85-18.69
2 km	m/ha	27.89	1.76	11.85-44.84
Sinuosity				
500 m	—	3.29	0.37	1.18-8.35
1 km	—	2.73	0.26	1.24-6.76
2 km	—	2.65	0.20	1.25-5.67
Fractal Dimension				
500 m	—	1.18	0.02	1.03-1.42
1 km	—	1.16	0.02	1.03-1.29
2 km	—	1.16	0.01	1.04-1.28

and within the surrounding (1-km) context of the wet meadows was forests, accounting for 53.0% and 70.5%, respectively (Table 12). In terms of the shoreline complexity, the shorelines ranged from nearly straight-line (i.e. sinuosity and fractal dimension near 1.0) to very convoluted (e.g. sinuosity 44.84 and fractal dimension 1.42) (Table 12).

Three PERIMETER variables were included in the significant model in 1997, explaining 18.1 % of the variation in snail distributions after accounting for within-patch habitat characteristics (Table 13). Non-forested openings was the only significant variable although the number of interfaces with other patches and adjacency to cattail marsh were included in the significant model (Table 14). The first canonical axis represented the increasing proportion of adjacent non-forested openings and the second axis was correlated with the number of interfaces and increasing cattail (Figure 15, Table 14). *Aplexa elongata* was highly correlated with the increasing proportion of non-forested openings and all other species were only moderately associated with these axes (Figure 15).

In the 1997 CONTEXT variable group, the proportion of forests was highly intercorrelated with the other variables and was removed from the analyses. The full model included three variables explaining 18.9% of the species data. The proportion of non-forested openings and bulrush marsh in the 1-km surrounding the wet meadow were significant variables (Tables 13 and 14). The first axis of the CCA corresponded to an increasing proportion of non-forested openings whereas the second axis was a gradient from bulrush marsh to inland emergent wetlands (Figure 16, Table 14). *Amnicola walkeri* and *A. elongata* were associated with wet meadows situated in a context with increasing non-forested openings whereas *Bithynia tentaculata* was associated with

Table 13. Results of canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows in 1997.

	Axes				Σ canonical	Total	% Variance	1st axis		All axes	
	1	2	3	4	eigenvalues	inertia	explained	F-ratio	P	F-ratio	P
PERIMETER 1997					0.114	0.630	18.1	2.881	0.030	2.251	0.010
Eigenvalues	0.065	0.028	0.022	—[1]							
Species-environment correlations	0.846	0.804	0.836	—							
Cumulative percentage variance											
of species data	10.3	14.7	18.1	—							
of species-environment correlation	56.6	81.0	100.0	—							
CONTEXT 1997					0.119	0.630	18.9	2.929	0.075	2.422	0.010
Eigenvalues	0.066	0.033	0.020	—							
Species-environment correlations	0.887	0.867	0.700	—							
Cumulative percentage variance											
of species data	10.5	15.7	18.9	—							
of species-environment correlation	55.0	82.8	100.0	—							
COMPLEXITY 1997					0.132	0.599	22.0	2.999	0.095	3.178	0.010
Eigenvalues	0.069	0.035	0.028	—							
Species-environment correlations	0.842	0.909	0.795	—							
Cumulative percentage variance											
of species data	11.5	17.3	22.0	—							
of species-environment correlation	52.0	79.0	100.0	—							

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1. Only three variables were included in model.

Table 14. Interset correlations of environmental variables with CCA axes in 1997 for all variables included in significant model. Significant variables (P<0.10) are indicated by **bold type**.

Variable	Interset Correlations Axis 1	Axis 2	Axis 3	Axis 4
PERIMETER 1997				
% Non-Forested Openings	0.716	-0.009	0.446	—[1]
# of interfaces with other patches	-0.044	0.738	-0.329	—
% Cattail Marsh	-0.211	0.672	0.410	—
CONTEXT 1997				
% Non-Forested Openings	0.745	0.276	0.308	—
% Bulrush Marsh	0.253	-0.736	-0.311	—
% Inland Emergent Wetlands	-0.032	0.684	-0.430	—
COMPLEXITY 1997				
Sinuosity - 500 m	-0.660	0.565	-0.011	—
Sinuosity - 2 km	-0.527	-0.096	-0.615	—
Fractal Dimension - 1 km	-0.009	0.457	-0.687	—

1. With three variables only three canonical axes are produced.

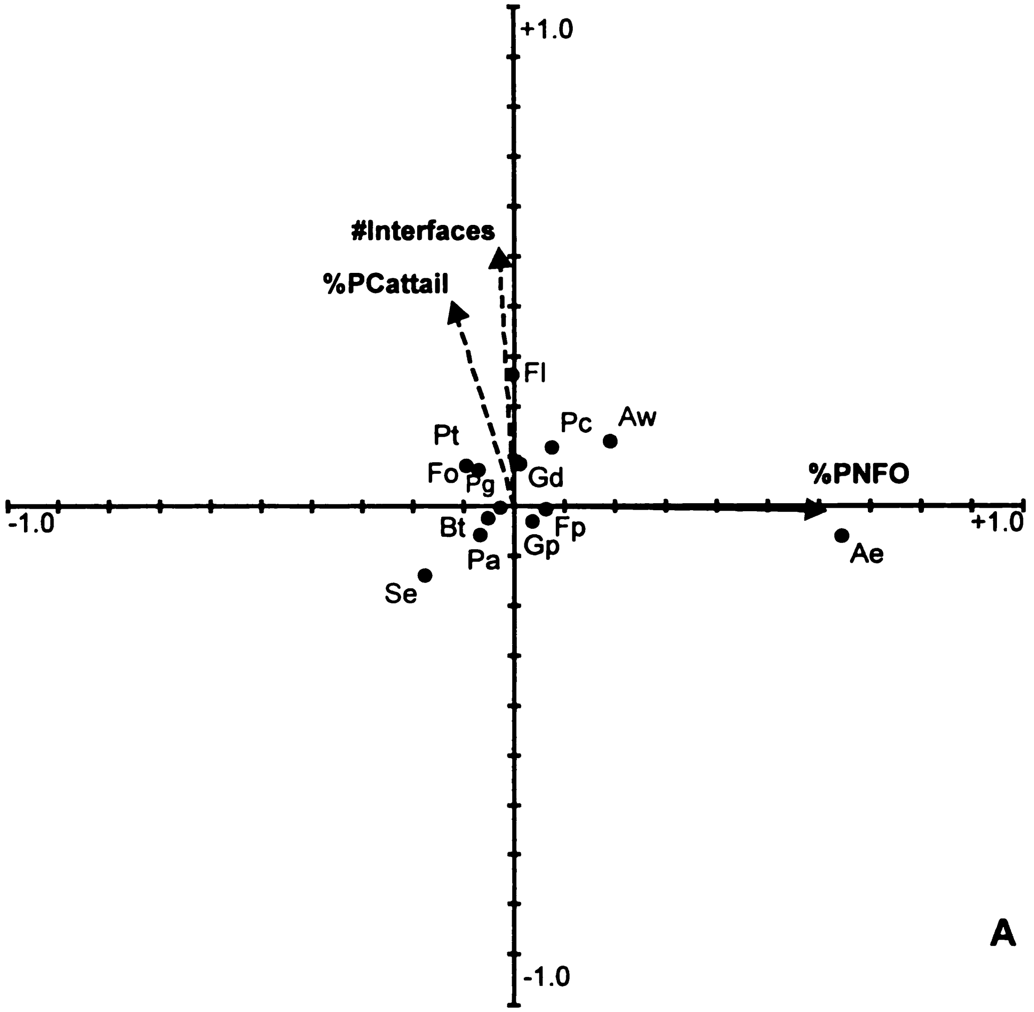


Figure 15. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 PERIMETER variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted landscape variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Landscape variable abbreviations as in Table 11, species labels as in Table 2, and sites labels as in Table 1.

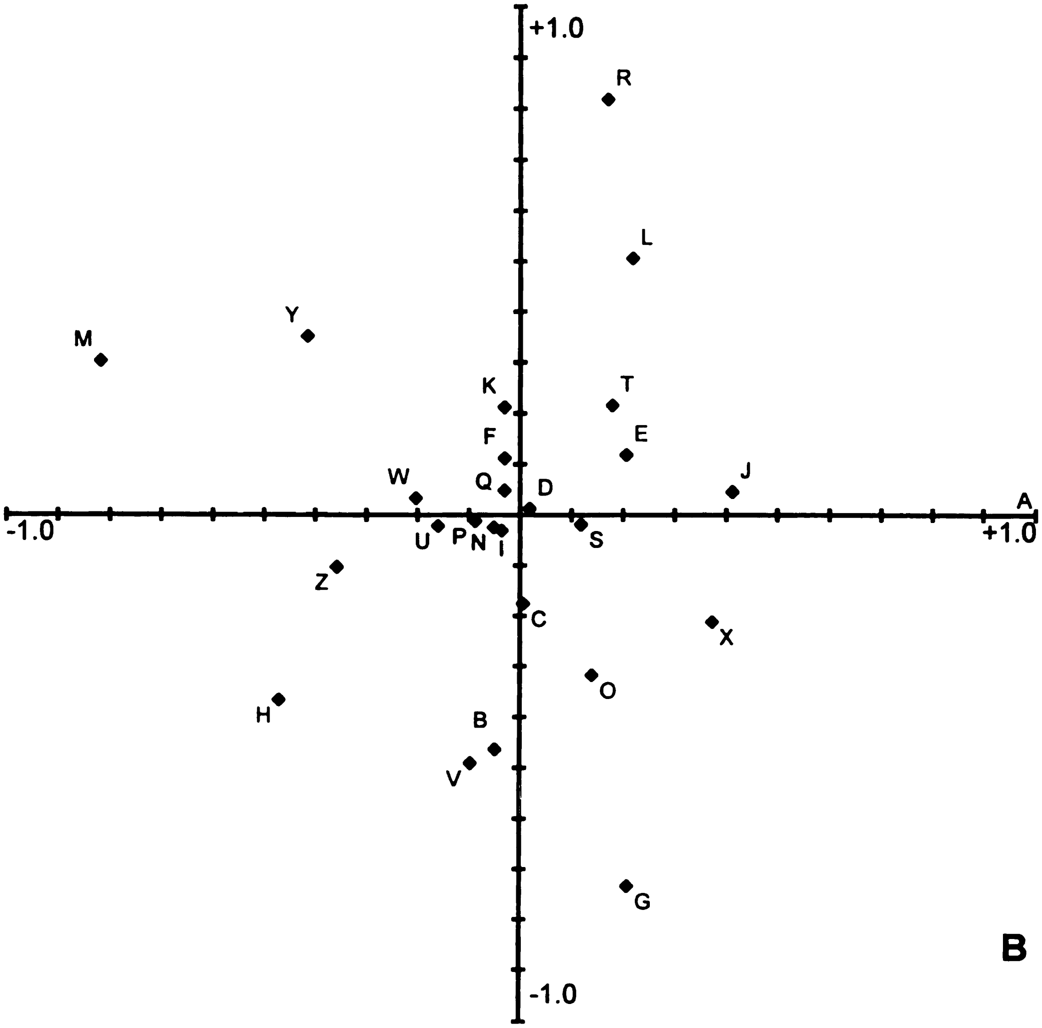


Figure 15. Continued.

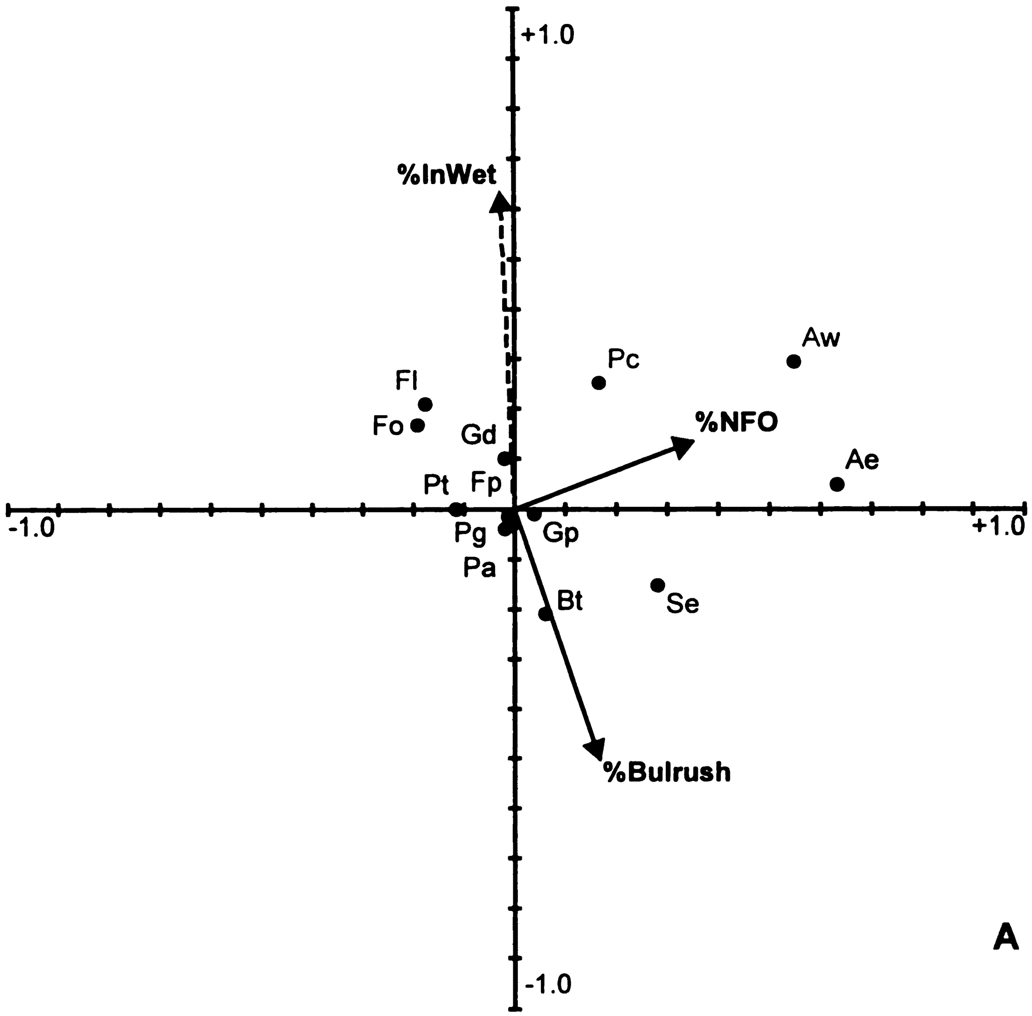


Figure 16. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 CONTEXT variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted landscape variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Landscape variable abbreviations as in Table 11, species labels as in Table 2, and sites labels as in Table 1.

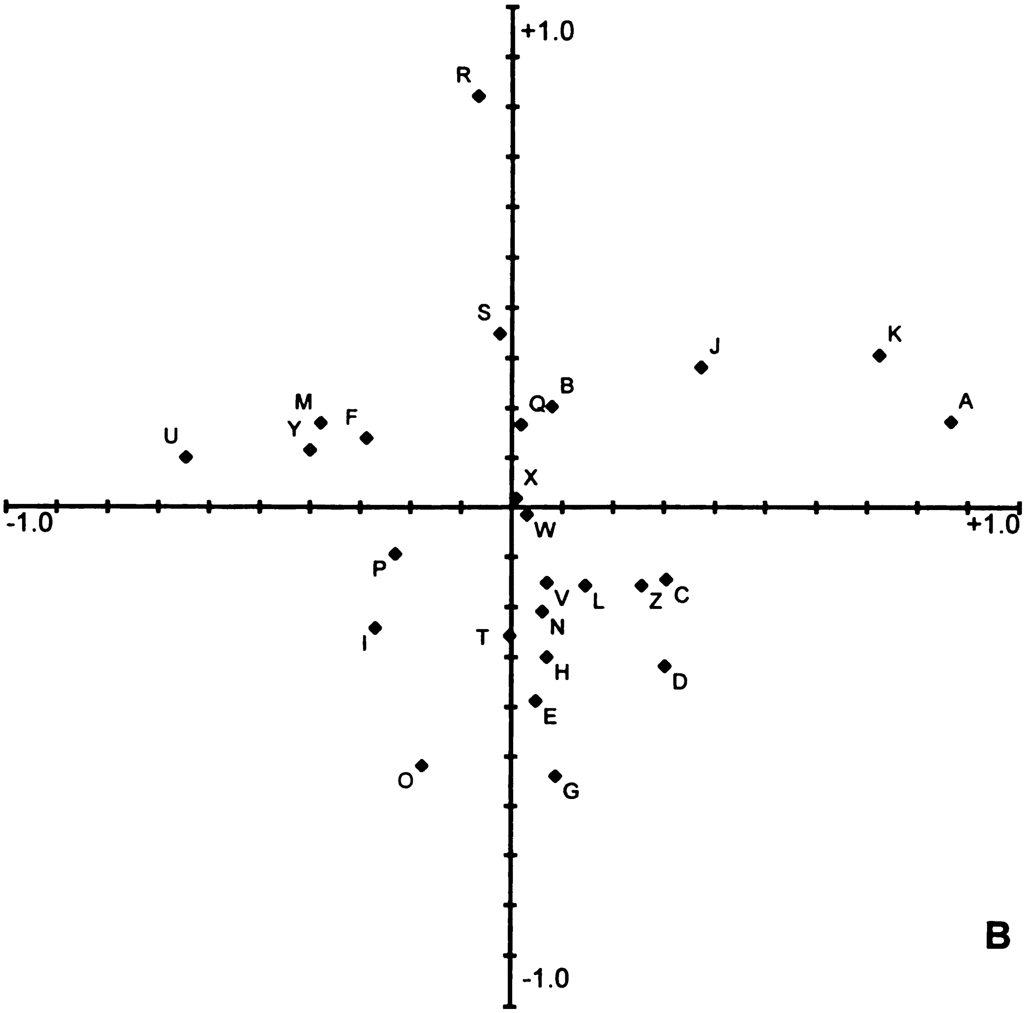


Figure 16. Continued.

increasing bulrush marsh and *Stagnicola elodes* was intermediate with both bulrush marshes and non-forested openings (Figure 16).

Significant variables at all three scales were included in the 1997 COMPLEXITY model and explained 22.0% of the variation in species patterns (Table 13). Axis 1 was correlated with the sinuosity of the shoreline at the 500-m and 2-km scales and axis 2 was correlated with the 500-m sinuosity and 1-km fractal dimension (Figure 17, Table 14). *Aplexa elongata* and *A. walkeri* were clearly associated with less complex, straighter shorelines, whereas *Ferrissia parallela, Planorbella trivolvis*, and *Fossaria obrussa* were associated with more complex, convoluted shorelines (Figure 17).

In 1998, seven variables were included in the PERIMETER model, combining to explain 43.1% of the variation in species data (Table 15). The variable, number of patches, was removed due to high multicollinearity. As in 1997, the proportion of adjacent non-forested openings was significant and included in a gradient with increasing bulrush on the opposite end (Figure 18, Table 16). Cattail marsh was the other significant variable and was highly correlated with the second axis (Table 16). *Aplexa elongata* was associated with increasing non-forested openings whereas *F. parallela* and *Promenetus exacuous* were correlated with increasing bulrush marsh (Figure 18). *Bithynia tentaculata* and *Planorbella campanulata* were negatively associated with cattail marsh whereas *F. obrussa*, *P. trivolvis*, and *Gyraulus crista* were all positively associated with cattail and several other variables, including % urban (Figure 18).

The proportion of bulrush marsh was the only significant variable in the 1998 CONTEXT group along with three additional variables in the model. Together they explained 30.2% of the variation in snail distributions (Tables 15 and 16). The first axis

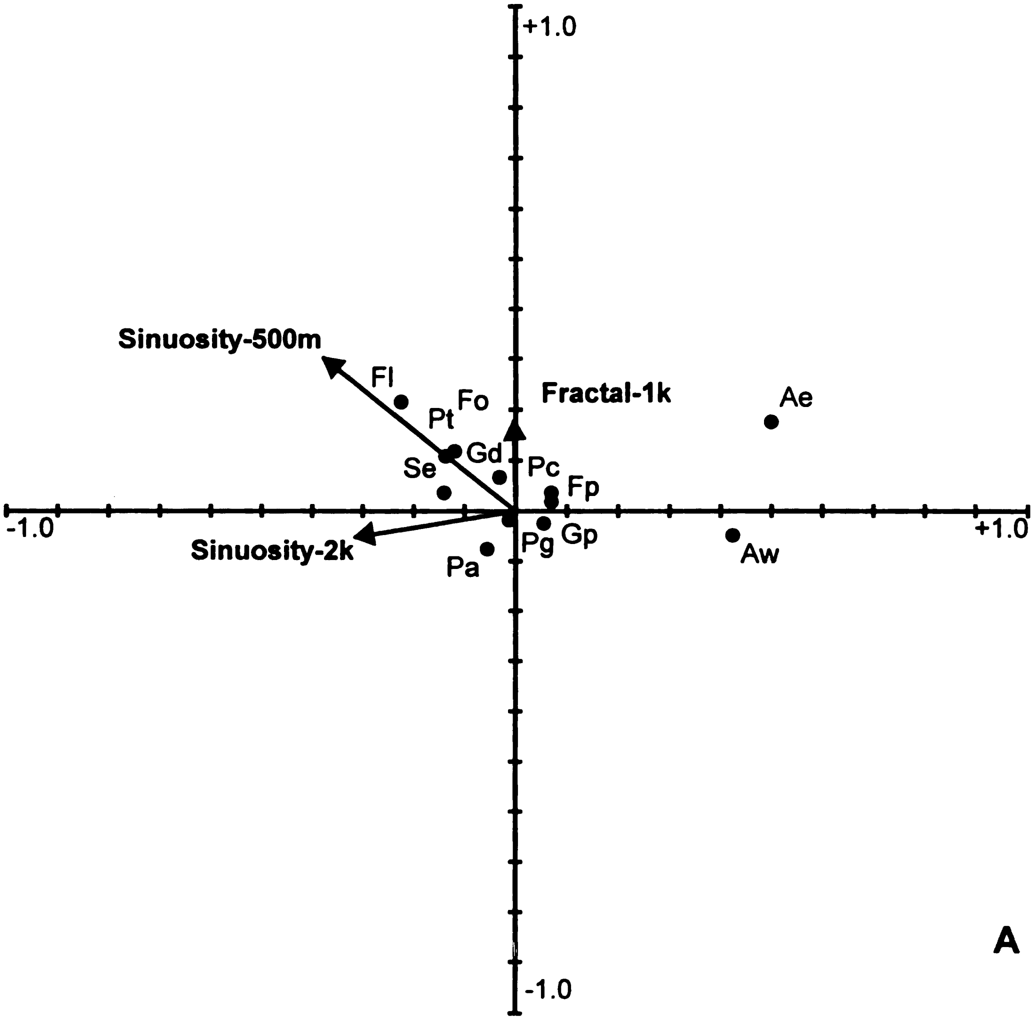


Figure 17. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1997 COMPLEXITY variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted landscape variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Landscape variable abbreviations as in Table 11, species labels as in Table 2, and sites labels as in Table 1.

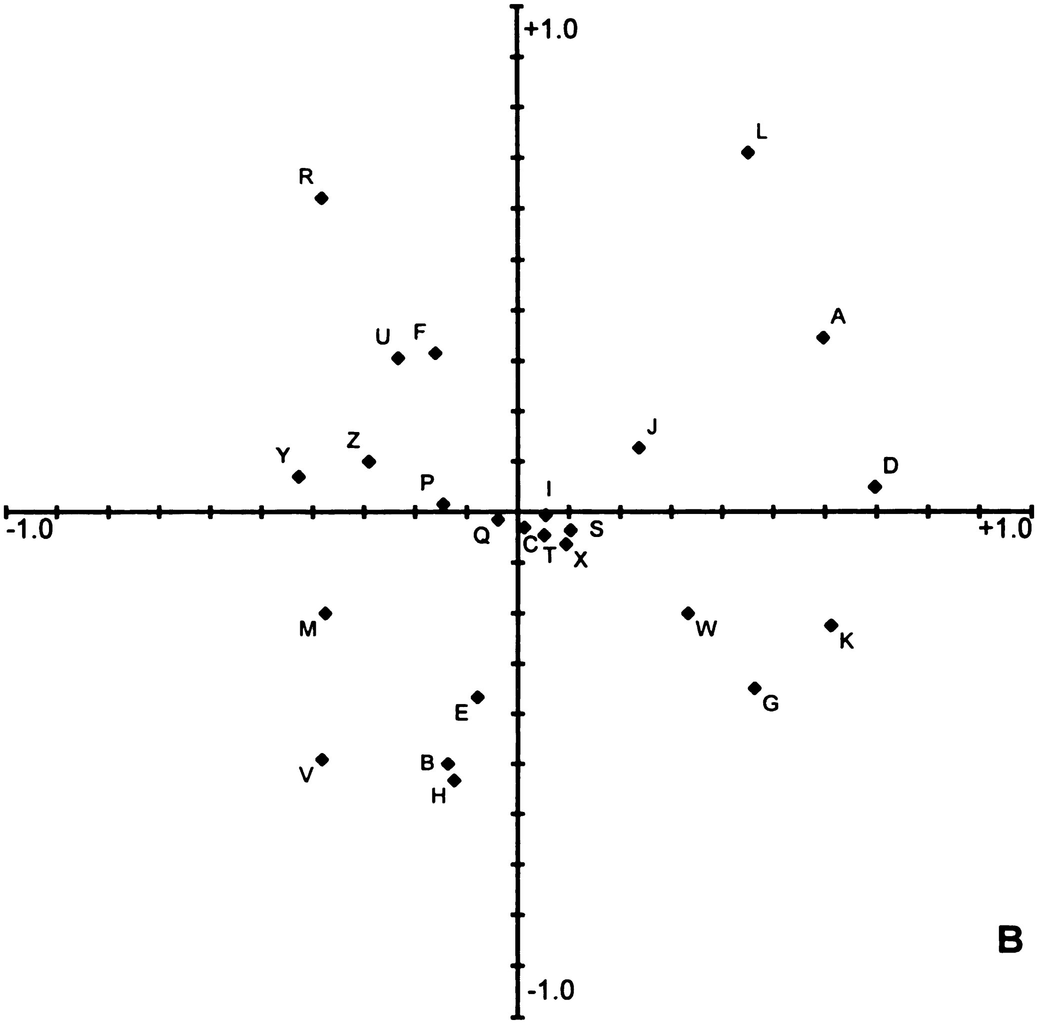


Figure 17. Continued.

Table 15. Results of canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows in 1998.

	Axes				Σ canonical	Total	% Variance	1st axis		All axes	
	1	2	3	4	eigenvalues	inertia	explained	F-ratio	P	F-ratio	P
PERIMETER 1998					0.320	0.742	43.1	2.490	0.055	1.624	0.025
Eigenvalues	0.136	0.094	0.035	0.027							
Species-environment correlations	0.977	0.927	0.829	0.777							
Cumulative percentage variance											
of species data	18.3	31.0	35.7	39.3							
of species-environment correlation	42.4	71.7	82.6	91.1							
CONTEXT 1998					0.224	0.742	30.2	2.517	0.100	1.905	0.020
Eigenvalues	0.104	0.066	0.039	0.014							
Species-environment correlations	0.908	0.884	0.813	0.696							
Cumulative percentage variance											
of species data	14.0	22.9	28.2	30.1							
of species-environment correlation	46.5	75.9	93.5	100.0							
COMPLEXITY 1998											
No significant model											

Table 16. Interset correlations of environmental variables with CCA axes in 1998 for all variables included in significant model. Significant variables (P<0.10) are indicated by **bold type**.

	Interset Correlations			
Variable	Axis 1	Axis 2	Axis 3	Axis 4
PERIMETER 1998				
% Non-Forested Openings	0.845	0.078	0.069	-0.028
% Bulrush Marsh	-0.374	0.127	-0.087	-0.049
% Cattail Marsh	0.261	-0.708	-0.310	-0.311
# of adjacent patch types	0.082	-0.479	0.287	0.247
# of interfaces with other patches	-0.027	-0.495	0.269	-0.138
% Urban	-0.065	-0.330	0.292	0.450
% Forests	-0.118	0.204	-0.298	-0.544
CONTEXT 1998				
% Bulrush Marsh	0.597	0.591	-0.044	-0.239
% Non-Forested Openings	-0.318	0.463	0.271	0.488
% Forested Wetlands	0.566	0.099	0.599	-0.164
% Urban	0.241	-0.037	-0.476	0.532
COMPLEXITY 1998				
No significant model				

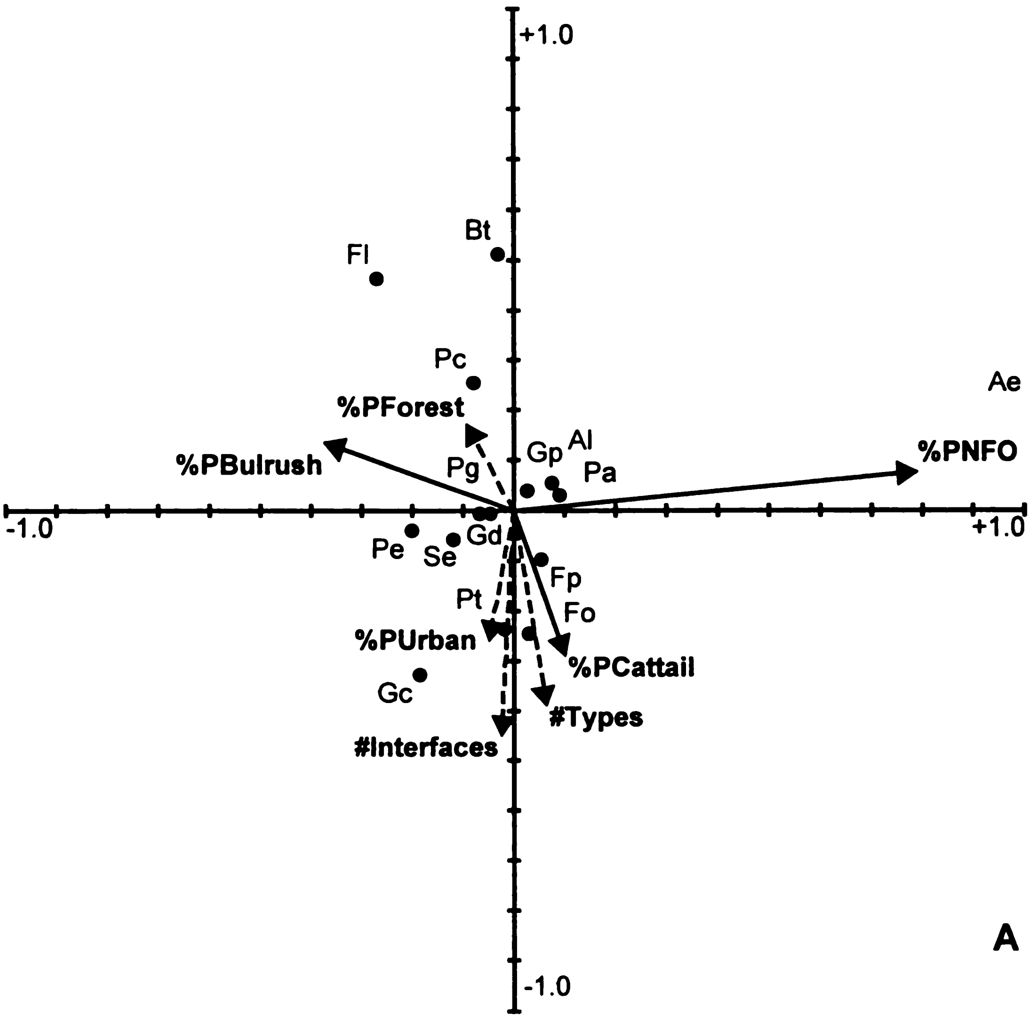


Figure 18. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1998 PERIMETER variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted landscape variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Landscape variable abbreviations as in Table 11, species labels as in Table 2, and sites labels as in Table 1.

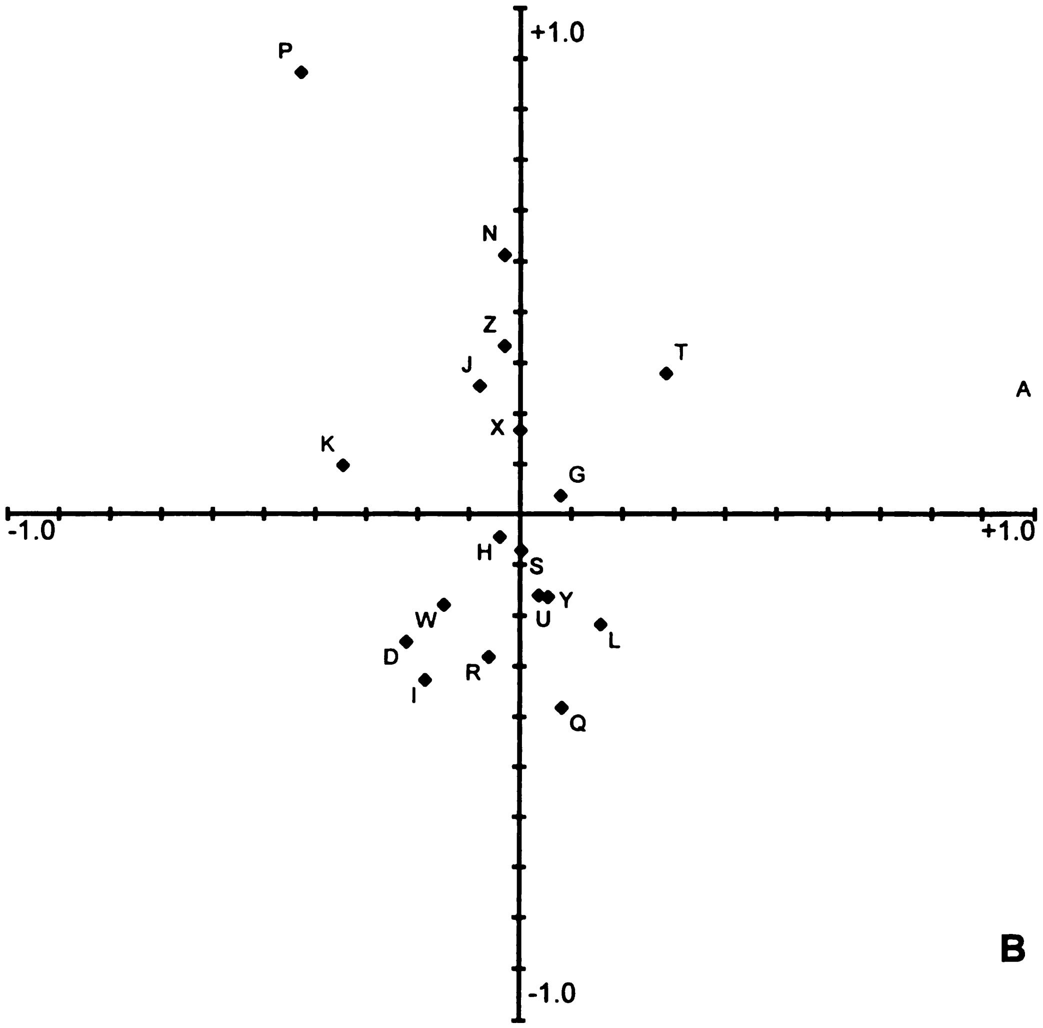


Figure 18. Continued.

was positively correlated with bulrush and forested wetlands and the second with bulrush and non-forested openings (Figure 19, Table 16). Snails positively associated with the first axis were *F. parallela* and *B. tentaculata* whereas *A. elongata* and *P. trivolvis* were negatively associated. *Aplexa elongata* was associated with non-forested openings (Figure 19).

There was no significant model for shoreline COMPLEXITY in 1998. Two wet meadows were not included in the COMPLEXITY analyses because of their location on islands, which prevented the calculation of sinuosity fractal dimension. Thus, in the partial CCA, only the PERIMETER and CONTEXT variable groups were included.

In 1997, partial CCA indicated that both PERIMETER and CONTEXT explained an approximately equal percentage of the variation in the snail data and also shared a large proportion of variance explained. Combined, they explained 28.9% of the variation in the snail data above and beyond that which was explained by within-patch habitat characteristics (Figure 20). In 1998, a greater overall proportion (62.7%) of the variance was explained by PERIMETER and CONTEXT (Figure 21) beyond that of the within-patch characteristics. The PERIMETER variable group explained the majority of the variation, although 10.6% of the variation explained was shared by both groups (Figure 21).

DISCUSSION

Snail distribution and abundance patterns are influenced by many different factors that vary with the scale being examined (Lodge et al. 1987). Among these are water chemistry, habitat diversity, and plant community composition (e.g. Aho 1966, Harman

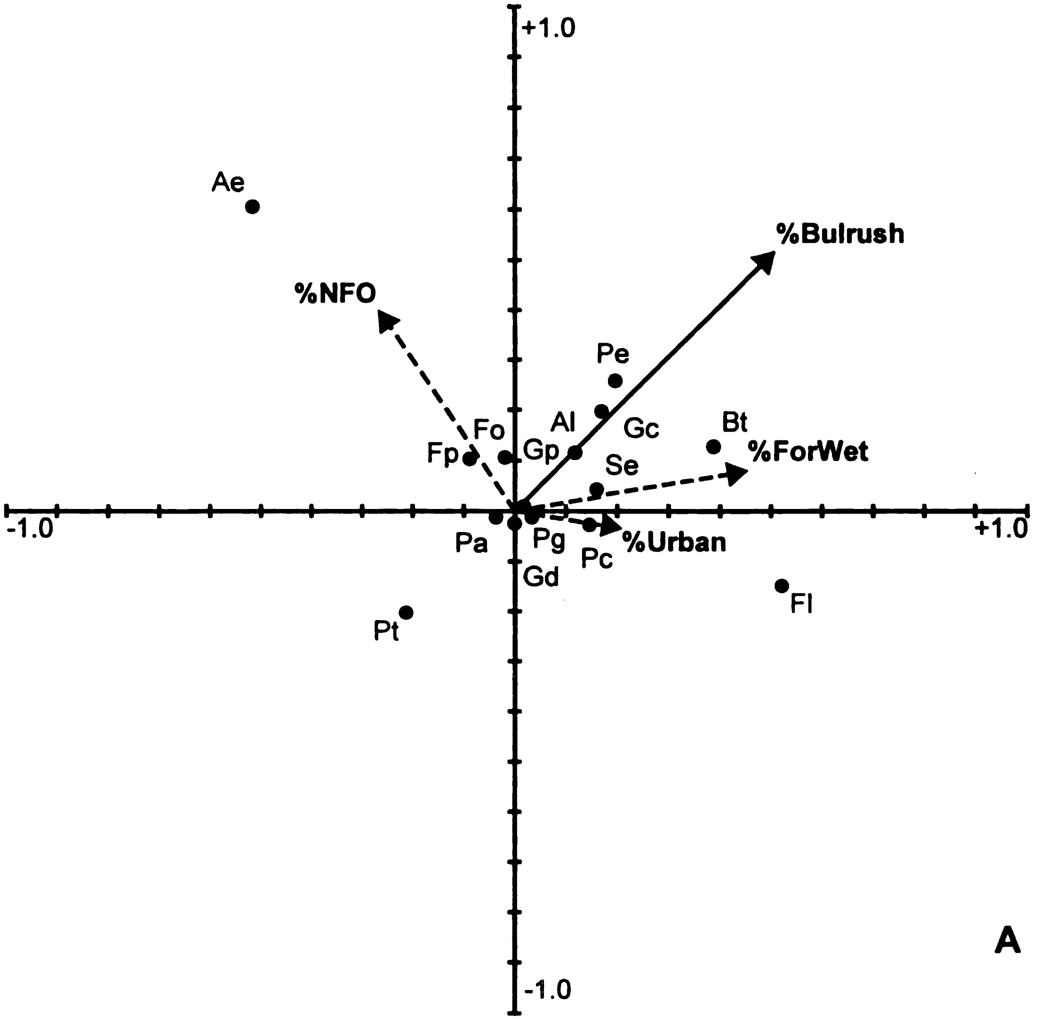
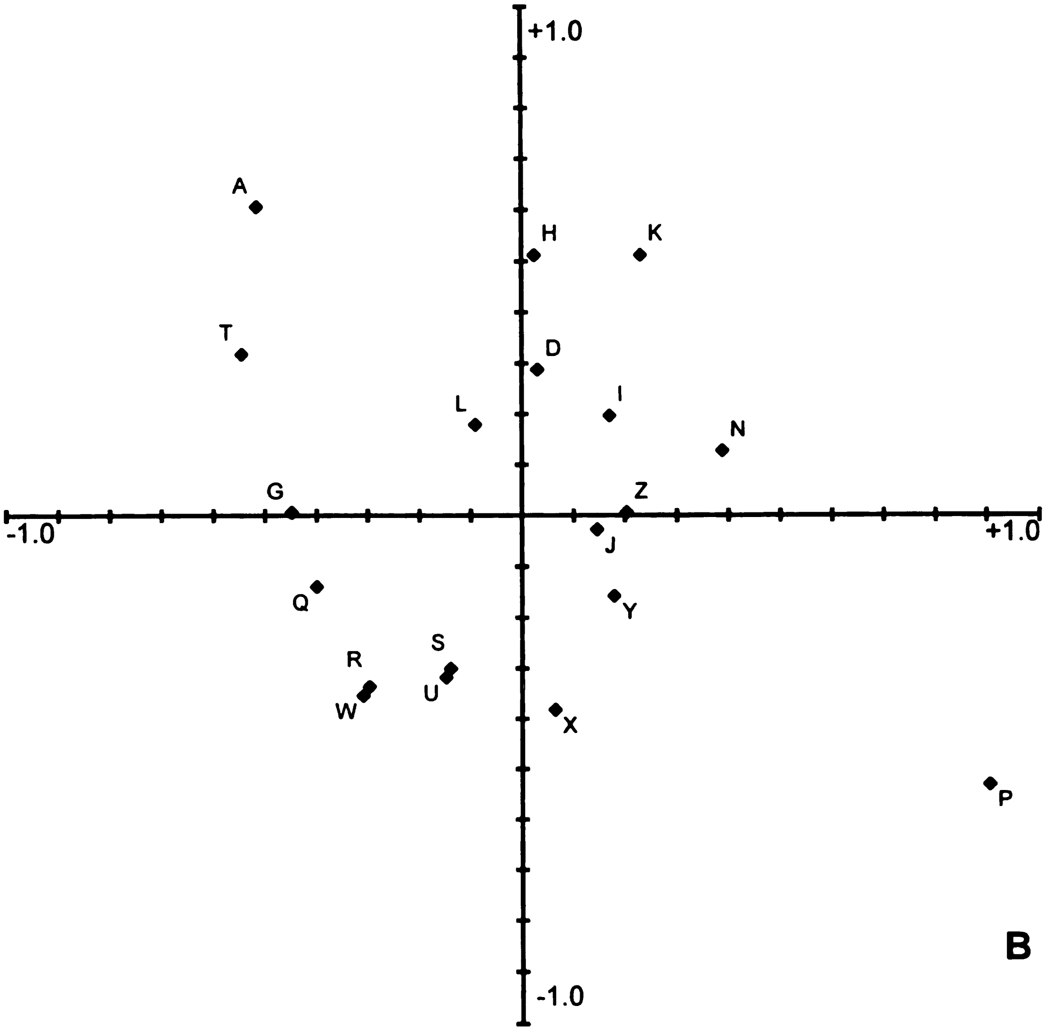


Figure 19. Canonical correspondence analysis of aquatic snails in northern Lake Huron coastal wet meadows using the 1998 CONTEXT variable group as explanatory variables: (A) species-environmental biplot (B) sites-environmental biplot. All plotted landscape variables were included in a significant model; those with solid arrows were significant variables and dashed arrows indicate non-significant variables. Species and sites scores are adjusted to scale = 0.3. Landscape variable abbreviations as in Table 11, species labels as in Table 2, and sites labels as in Table 1.



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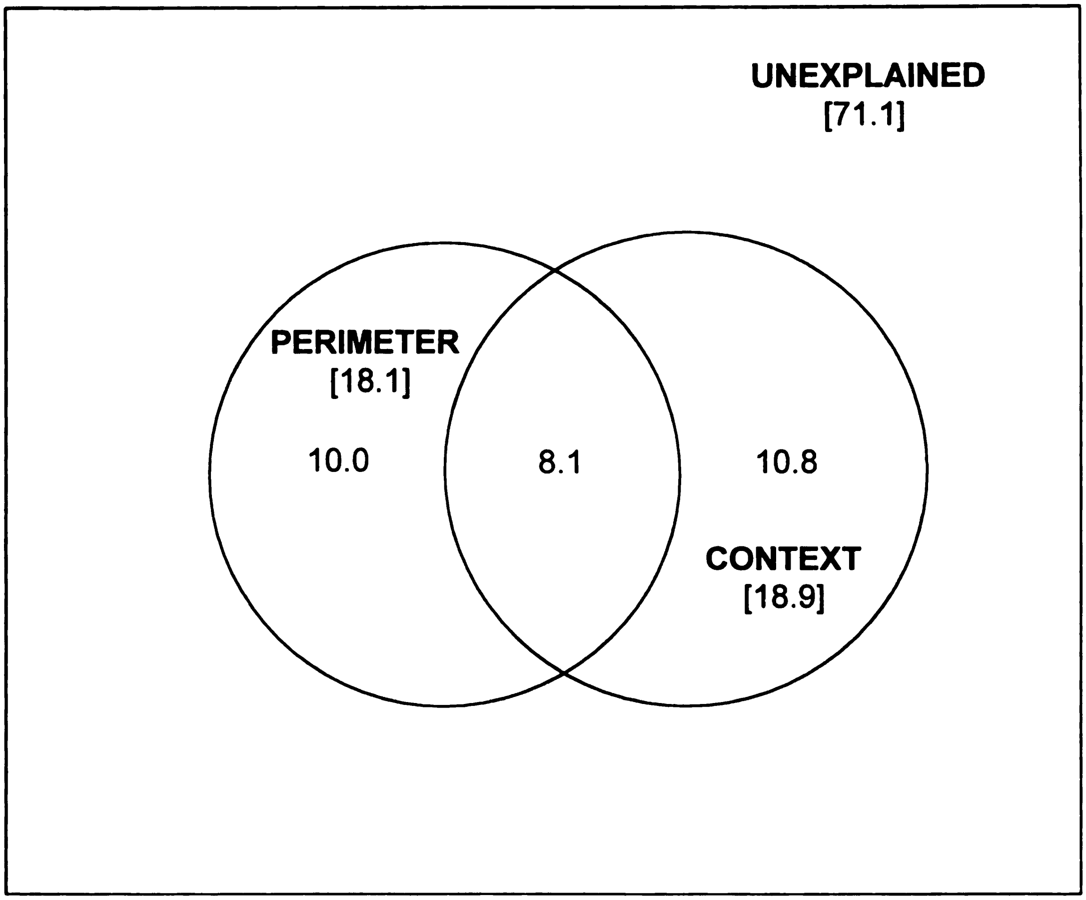

Figure 20. Venn diagram of the CCA variance partitioning of 1997 species data among two variable groups. Total variance explained by a variable group is enclosed in [ ] and represented by the size of the circle. Variance shared by variable groups is indicated in the appropriate intersections. Variance explained is calculated as the sum of all canonical eigenvalues for a particular analysis divided by the total inertia.

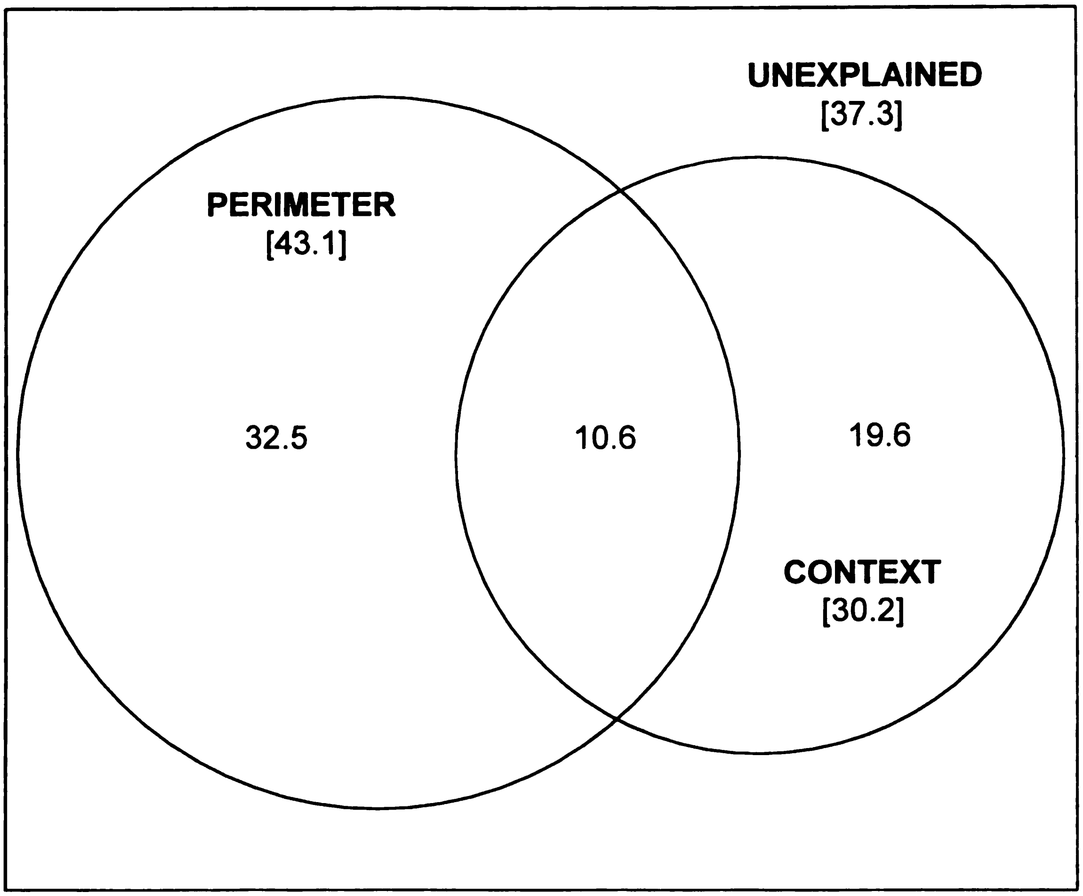

Figure 21. Venn diagram of the CCA variance partitioning of 1998 species data among two variable groups. Total variance explained by a variable group is enclosed in [ ] and represented by the size of the circle. Variance shared by variable groups is indicated in the appropriate intersections. Variance explained is calculated as the sum of all canonical eigenvalues for a particular analysis divided by the total inertia.

1972, Pip 1978, Brönmark 1985). These characteristics of a water body are in turn affected by their position in the surrounding landscape due to regional and local differences in topography, groundwater inputs, and soil conditions (Kratz et al. 1997). Lewis and Magnuson (2000) demonstrated that lake snail assemblages were influenced by the spatial pattern of lakes in Wisconsin. The present study provides evidence that snail communities of northern Lake Huron coastal wet meadows also respond to characteristics at the landscape scale.

Landscape Context and Snail Associations

Because I examined the landscape variables and snail distributions after accounting for variations in the snail community due to within-wet meadow (i.e. within-patch) characteristics, the associations identified were responses at the landscape scale. Snail communities in wet meadows were influenced by adjacent patch characteristics (PERIMETER) as well as the characteristics of a broader area (CONTEXT) surrounding the wet meadow (Figures 22 and 23). It was not surprising that a substantial percentage of the variation in the snail communities was shared by both the immediate as well as the broader context of the wet meadows (Figures 20 and 21). The majority of snail associations with landscape features involved the less common species and therefore these associations must be interpreted with caution (see *Chapter One: Discussion, Patterns in Common and Uncommon Species*). However, the patterns observed are consistent and interpretable allowing conclusions to be made (ter Braak and Verdonschot 1995). Because this is one of the first studies to examine snail-landscape associations, these conclusions should not imply causal mechanisms, but should be regarded as a starting point to future investigations and to experiments that involve more rigorous

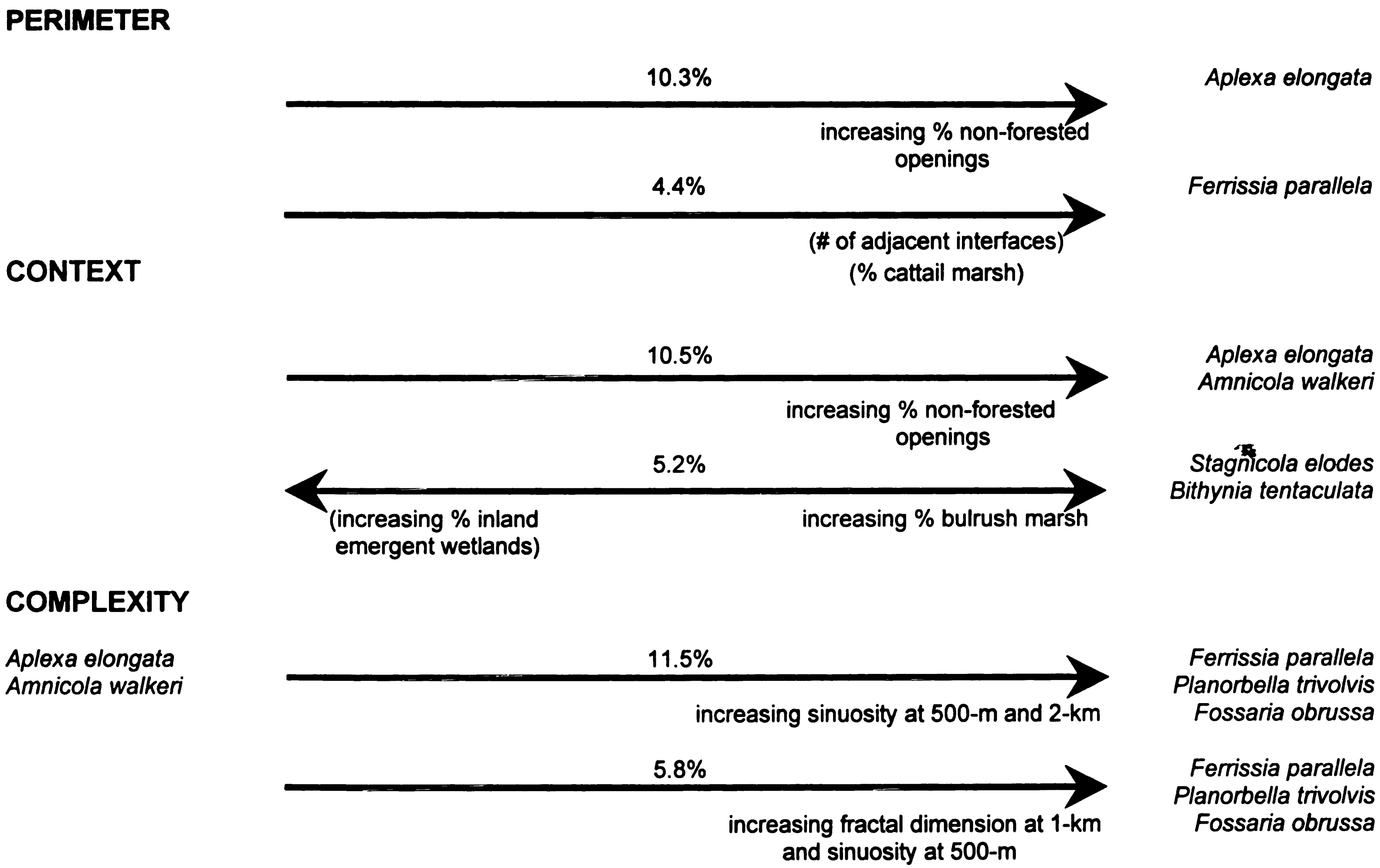

Figure 22. Summary of the 1997 snail-environment relationships using CCA for each of three environmental variable groups. Arrows represent environmental gradients for canonical axes with percentage of the species data explained above. Significant variables correlated with each axis are listed below; correlated, nonsignificant variable are in ( ). Snail species associated with each gradient are listed in the corresponding direction.

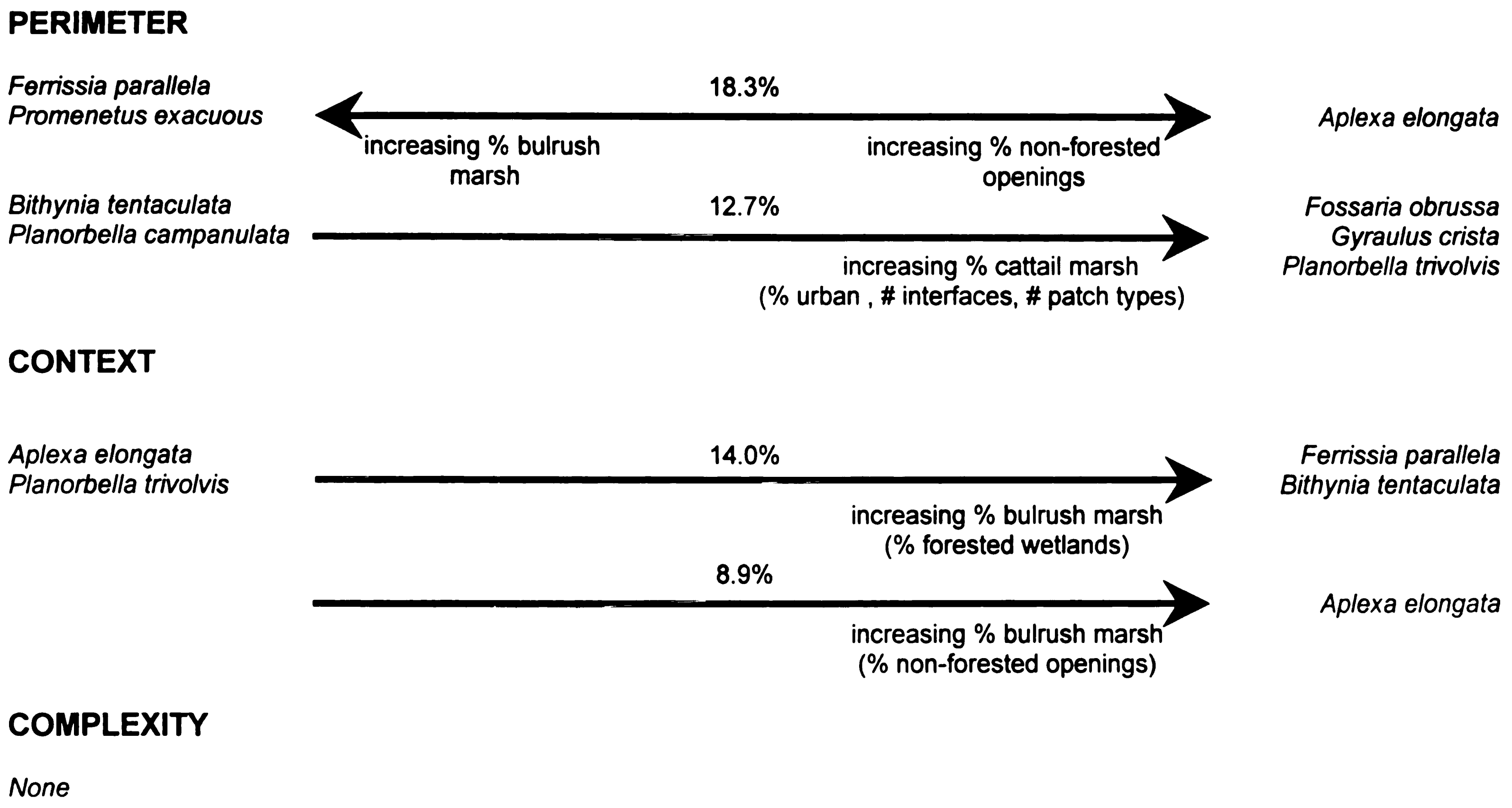

Figure 23. Summary of the 1998 snail-environment relationships using CCA for each of three environmental variable groups. Arrows represent environmental gradients for canonical axes with percentage of the species data explained above. Significant variables correlated with each axis are listed below; correlated, nonsignificant variable are in ( ). Snail species associated with each gradient are listed in the corresponding direction.

testing of specific hypotheses.

The most common landscape characteristic and the one that explained the most variance in the CCA models was non-forested openings, either immediately adjacent to the wet meadow or within a 1-km area around the wet meadow. In the GIS classification scheme used (Table 10), non-forest openings were primarily upland grassy and/or shrubby areas. Thus, wet meadows adjacent to non-forest openings were essentially wet meadows that graded into grasslands as the elevation increased and the water saturation levels decreased. The grass uplands may act as a buffer between the terrestrial and aquatic habitats, limiting nutrient or other inputs that may affect the wet meadows and the snail communities (Karr and Schlosser 1978, Krieger and Klarer 1991, Crosbie and Chow-Fraser 1999). Snails found in wet meadows associated with increasing non-forested openings included *Aplexa elongata* and *Amnicola walkeri* (Figures 22 and 23).

Second in frequency of occurrence in the CCA models was the proportion of bulrush marsh. Similar to the buffering capabilities of adjacent non-forested openings, bulrush marsh, which was commonly adjacent but in deeper water than the wet meadows (Figure 1), probably acts as a buffer to the open waters of Lake Huron. Marsh vegetation reduces the velocity of incoming waves (Leonard and Luther 1995) and this may have significant effects on the communities of some organisms (Cardinale et al. 1997). The reduction in water flow into the wet meadow may settle out suspended solids creating clearer water conditions in wet meadows adjacent to extensive bulrush marshes or may allow for greater development of the wet meadow region. Differences in water quality may directly affect the snail communities or indirectly affect them through some related mechanism such as changes in the periphyton used for food (Russel-Hunter 1978).

Snails showed varying associations with the proportion of bulrush marsh. *Stagnicola elodes, Ferrissia parallela, Bithynia tentaculata* and *Promenetus exacuous* were positively associated with bulrush whereas *A. elongata* and *Planorbella trivolvis* were negatively associated. *Bithynia tentaculata* and *P. exacuous*, were most commonly linked with more densely vegetated habitats and therefore the positive association with bulrush was likely associated with the greater development of the wet meadow region allowed by the presence of the bulrush marsh. On the other hand, *S. elodes* and especially *F. parallela* were often found on bulrush stems (Clarke 1981). The bulrush marsh may act as a source for the dispersal of these snails into the adjacent wet meadows. *Aplexa elongata* was generally found in habitats with high vegetation density (Clarke 1981, *Chapter One*) so the negative relationship with bulrush marsh (which would favor greater wave forces reaching the wet meadow allowing less vegetation development) was unexpected. However, the sites at which *A. elongata* was common and abundant included Pontchartrain 1 and 2, both of which have wet meadows protected from the open waters of Lake Huron by a sandy ridge (see Table 1).

The proportion of cattail marsh was the final significant variable in the CCA models. *Fossaria obrussa, Gyraulus crista*, and *P. trivolvis* were positively associated with wet meadows adjacent to cattail marshes. The presence of cattail marshes is generally a sign of disturbance and/or increased nutrient loadings (Galatowitsch et al. 2000) and these snail species are usually associated with heavily vegetated, eutrophic wetlands (Clarke 1981, Burch and Jung 1992). Thus, this association appears to be another example of the adjacency pattern reflecting a source for the dispersal of these snails into the wet meadow. Additionally, cattail marshes are very productive (Mitsch and Gosselink 1993) and there may be a transfer of detritus and other nutrients to the wet meadow that influences these snail species.

A number of other landscape variables were included in significant models although they were not significant by themselves. These generally included factors related to number of patch types or interfaces with other patches, and suggested that the interconnectivity of wetlands with the surrounding environment was a factor in structuring the snail community. A loss of the diversity of surrounding patches may, therefore, lead to changes in the wet meadow snail community, and this suggests that caution is needed to prevent additional anthropogenic changes to the northern Lake Huron shoreline. Although the proportion of urban patches was included in one model, surprisingly the density of roads in the area, which are known to affect many aquatic communities (Trombulak and Frissell 2000), did not seem to strongly affect the snail community.

Shoreline Complexity

The complexity or convolutedness of the shoreline in 1997 was significantly associated with many of the same species as above. This was likely due to effects of shoreline shape on the development of the different patch types (Kent and Wong 1982). For example, more complex shorelines may permit greater wetland development because of protection from Lake Huron waves and storm surges.

Significant COMPLEXITY variables included sinuosity and fractal dimension at all three of the measured scales. Although fractal dimension is theoretically independent (i.e. self-similar) of the *measurement* scale, it was only significantly associated with the snail community at the 1-km scale. This was likely an artifact of the *sampling* scale and may reflect differences in the processes related to the convolutedness (Forman 1995). Sinuosity was significant at the 500-m and 2-km scales.

Three species of snails were positively associated with sinuosity. *Fossaria obrussa* and *P. trivolvis* were characteristic of densely vegetated wet meadows and *F. parallela* with bulrush marshes that would be expected to develop in a convoluted bay protected from intense wave action and storm surges coming off of Lake Huron. *Aplexa elongata* and *Amnicola walkeri* were associated with "straighter" shorelines that were directly impacted by the open waters of Lake Huron. The wet meadows in which they were found were created and protected by sandy ridges produced by the wave action present on these stretches of shore and that are rare in the protected bays.

In 1998, there was no significant model for COMPLEXITY. The major environmental change from 1997 to 1998 was a significant decline in water levels (USACE 2000) suggesting that it was a factor in the annual change. It is possible that a drawdown event may affect the wetlands in complex shorelines differently than those in straighter shorelines and thereby affect the snail community. These changes may have added additional variation to the data that made detection of a significant model in the already noisy data impossible.

Conclusions

In conclusion, this study has shown that patterns of landscape context (associations with non-forested openings, bulrush and cattail marshes) and shoreline complexity exist in coastal wet meadow snail communities. However, I must reiterate that the determination of cause and effect was beyond the scope of this study and explicitly designed studies are needed to establish the mechanisms behind the observed patterns. Future efforts should be targeted towards identifying other landscape effects and/or confirming those found, and towards the determination of causal mechanisms.

CHAPTER THREE

INFLUENCE OF WATER LEVEL FLUCTUATIONS ON COASTAL WET MEADOW SNAIL COMMUNITIES

INTRODUCTION

In coastal wetlands of the Laurentian Great Lakes, water level fluctuations occur over short-term, seasonal, and multi-annual time scales (Keough et al. 1999). Short-term fluctuations include seiches and storm surges that may vary from less than an hour to several hours with amplitudes of tens of centimeters. Seasonal fluctuations often include mid-summer peaks that are about 30 cm higher than winter lows (Keough et al. 1999). Multi-annual water level fluctuations vary in periodicity and amplitude from year to year depending on regional climatic factors (Bedford 1992). Multi-annual water levels may vary over a range of almost 2 m (Kelley et al. 1984, Keough et al. 1999).

Water level fluctuations strongly affect structure and function of Great Lakes wetlands (Burton 1985, Keough et al. 1999). Previous studies have documented changes in community characteristics and species occurrences for wetland plants (Keddy and Reznicek 1985, 1986, Edsall et al. 1988), fish (Liston and Chubb 1985), and birds (McNicholl 1985). Invertebrates, including aquatic snails, are understudied (Krieger 1992). It has been suggested that they show a lagged response to the changing plant communities (Gathman et al. 1999).

Patterns in freshwater snail distributions have been explained on the basis of water chemistry (Dussart 1976, 1979, McKillop 1985, Økland 1983), and especially the concentration of calcium (Macan 1950, Aho 1966, Økland 1983, Rooke and Mackie 1984, McKillop 1985). Others have used the theory of island biogeography to explain snail distributions in lakes by treating lakes as islands within the mainland (Lassen 1975, Aho 1978a,b, Browne 1981). These studies have focused on variables such as area and isolation (Jokinen 1983, Brönmark 1985), position within the landscape (Lewis and

Magnuson 2000), and the role of habitat variability and disturbance on the snail community (Brönmark 1985, Lodge and Kelly 1985). Lodge et al. (1987) synthesized these ideas into a conceptual model to explain the distribution of freshwater snails over various scales. Wellborn et al. (1996) proposed a similar model for freshwater communities in general. Both models stressed the importance of hydroperiods along a gradient from temporary ponds to permanent lakes. Lodge et al. (1987) suggested that in temporary habitats with similar chemistry, habitat availability and disturbance (e.g. periodic drying) were the most important structuring forces for snail communities.

Great Lakes coastal wetland habitats do not fall neatly into the gradient from temporary ponds to permanent lakes described in the conceptual models of Lodge et al. (1987) and Wellborn et al. (1996). Coastal wetlands often occur along a continuum of habitats, from higher elevation shrub and wet meadow zones (Figure 1), which often lack standing water, to deeper, permanently flooded emergent marshes (Minc 1996). Connectivity of wetlands along this continuum allows mobile aquatic animals to seek refuge in the emergent marsh during low water levels. During high water levels, mobile aquatic animals may quickly move back into the newly flooded habitat in the wet meadow. Behavioral responses (e.g. movement towards and dispersal from refuge) may be more important to mobile species whereas physiological (e.g. desiccation resistance) adaptations are more likely to be of importance for more sessile organisms found in wet meadows.

Movement patterns and desiccation resistance are well known for many marine intertidal snails subjected to daily tidal fluctuations (Levings and Garrity 1983, Marchetti and Geller 1987, Chapman and Underwood 1996). Freshwater snails in non-coastal temporary habitats exhibit behaviors and resistance to desiccation that enable them to survive seasonal dry periods (Jokinen 1978, Brown 1979, Cantrell 1981, Betterton et al. 1988, Vera et al. 1995) with desiccation resistance probably being the most important determinant of species occurrence (Lodge et al. 1987). In coastal wetlands, however, the continuum from permanent to temporary marsh suggests that species that are mobile may be able to survive and compete with species that are poor dispersers but are highly resistant to desiccation.

The water levels in coastal wetlands of northern Lake Huron declined 28 cm from 1997 to 1998 (USACE 2000) providing a natural experiment to examine the responses of the snail community. In this study, I used multiple regression analyses to examine the role of spatial and short-term variation in water levels in structuring the aquatic snail communities. Specifically, I tested six different explanatory water level variables to determine how well they predicted the occurrence of snails in these wetlands. I also contrasted changes in coastal wet meadow snail communities where water level declines left the sites dry, to sites where water levels decreased but the sites remained flooded, and to sites where the water levels remained constant between years. Finally, I used two laboratory experiments to examine the proximate behavioral response of snails to water level decreases and their desiccation resistance as two possible mechanisms influencing the observed patterns in community structure.

METHODS

Study Area

I sampled 26 distinct coastal wet meadows along a 60 km length of the northern

Lake Huron shoreline in Michigan's Upper Peninsula (Mackinac and Chippewa counties) (Figure 2). The wet meadows all were located within 500 m of the shoreline and water levels were influenced by Lake Huron water levels (Table 1). The vegetation was predominantly hummock-forming grasses (*Calamagrostis canadensis*) and sedges (*Carex stricta*, *C. aquatilis*, and *C. latifolia*) with low densities of bulrush (primarily *Scirpus acutus*) and cattail (primarily *Typha angustifolia*). The substrate was muck or mucky-peat, covered by dense layers of the previous season's grass and sedge leaves, and provided a structurally complex habitat (along with the hummock structure) in which most snails were found. Some sites also contained a shrub zone including *Salix* spp., *Myrica gale*, and *Alnus rugosa*. A more detailed description is in *Chapter One: Methods, Study Area.*

Snail Sampling

Transects running perpendicular to the Lake Huron shoreline were established in each wet meadow and divided into 50 m sections. The number of sections sampled in each wet meadow ranged from 1 to 3 depending on the size of the wet meadow and whether the sections contained standing water deep enough to sample with a dip net (~10 cm) (Table 1). Snails were collected using timed D-frame aquatic dip net samples (Brown 1979). A more detailed description of this sampling protocol is provided in *Chapter One: Methods, Snail Collection.*

Sections that were dry (lacked standing water over >50% of the area) in 1998 (Table 17) were sampled by removing five round cores (20 cm diameter, 15 cm deep) from each dry section using a plastic bucket with the bottom removed and the edge serrated. Samples were collected from depressions between hummocks making sure to maintain the sediments and detritus layer intact. After collection, cores were returned to the lab, placed separately in buckets and 5 liters of non-chlorinated well water were added to each. After being flooded for 2 d, water and detritus were poured off and rinsed twice through a 500-μm sieve. The contents of the sieve and any snails observed were preserved in 95% ethanol to which Rose Bengal stain had been added. In the laboratory, snails in the preserved samples were sorted from the detritus, identified to species, and enumerated (empty shells were not included).

Water Level Measurements

Four 50-m radii were established at right angles to one another from the center of each section. Every 10 m along these radii, the water depth between hummocks was measured using a marked, metal rod (nearest 1 cm), for a total of 20 measurements per section (see Figure 3). Mean, maximum, minimum and range of depth were calculated for each section from these 20 measurements. Variation, in addition to the range, was quantified as the coefficient of variation (hereafter referred to as the spatial CV), which is a relative standard deviation based on the mean.

Because water levels in these coastal wet meadows vary not only spatially, but also temporally because of fluctuations in Lake Huron levels and rainfall events, a temporal CV was also calculated. Temporal CV was calculated using depth measurements taken approximately 1 week apart, 4 times during June of each year. Each of these measurements was the mean of 2 depths measured at the start and end of the transect in each section.

Multiple Regression Analyses

All six water level explanatory variables (mean, maximum, minimum, range, spatial CV, and temporal CV) were used in regression models as predictors of the snail community. Because lake levels declined in 1998, analyses were conducted separately for data from 1997 and 1998. All statistical analyses were conducted using SYSTAT software (SPSS 1999).

Snail variables. Species richness was calculated as the number of different species in each section. I calculated total abundance as the number of all individuals of all species collected in a section. I also calculated the abundance of each of the common species (i.e. found in at least 2/3 of all sections sampled). Presence/absence was determined for less common species (found in >10%, but <2/3 of the sections). Species found in fewer than 10% of the sections were not included in analyses.

Regression models. Stepwise multiple *linear* regression was used to examine significant water level predictors for total abundance, richness, and individual species abundances. An F-to-stay=0.15 was used to establish an initial set of water level predictors and models containing each possible subset of this initial set were then assessed. Criteria included overall significance of the model ($\alpha<0.10$), significant *t*-values for each predictor variable ($\alpha<0.10$), and all assumptions of regression (e.g. normality of residuals and constant variance) had to be satisfied. Outliers (>3 S.D.) and points with high leverage (>0.5) were removed and the model reassessed. Models that explained the highest amount of variance (R^2) and met these criteria were kept.

Stepwise multiple *logistic* regression was used to test presence/absence of species.

Again, an F-to-stay=0.15 was used and models containing each subset were assessed. Criteria included overall significance of the model and significant *t*-ratios for each predictor variable ($\alpha<0.10$). Additionally, each model passed the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989). Models meeting these criteria that explained the highest amount of variance (McFadden's ρ^2) were kept.

Annual Comparisons

Mean depths were calculated from the water level measurements for each section and sections divided into three classes: (1) 'Dry' sections were those that lacked standing water in 1998; (2) 'Lower' sections contained standing water in both years but were shallower in 1998; and (3) 'Same' sections in which the water levels were approximately equal in 1997 and 1998 (Table 17). Each section was treated as an independent observation since snails were assumed to respond independently to the differences found over the 50 m distance.

Because Dry sections could not be sampled using the same method in 1997 and 1998, the abundance of snails could not be compared directly. For these sections, the presence/absence of each species was calculated and the proportions between years compared using the Fisher exact test. This test has no statistic, and instead directly calculates a P-value using a 2×2 contingency table (year and presence/absence) (Zar 1999). The abundance of snails in the Lower and Same sections were compared using the Wilcoxon signed ranks test. This non-parametric test was used because the data did not meet the assumption of normality. Statistical tests were computed using SYSTAT software (SPSS 1999) using an *a priori* $\alpha<0.10$. This more liberal value was used

Table 17. Comparison of the sampling effort in wet meadows of the northern Lake Huron shoreline from 1997 to 1998, and the classification of water level changes. See text for details.

Site label	Wet meadow	1997 Net[1]	1997 Core[2]	1998 Net	1998 Core	Classification Dry	Classification Lower	Classification Same
A	Pontchartrain 1	2	—	1	—	0	0	1
B	Pontchartrain 2	3	—	0	—	—	—	—
C	St. Martin's	2	—	0	—	—	—	—
D	Carpenter 1	2	—	1	1	1	0	0
E	Carpenter 2	1	—	0	1	1	0	0
F	Search 1	2	—	0	—	—	—	—
G	Search 2	1	—	1	—	0	1	0
H	Mismer	3	—	2	2	2	1	0
I	Hessel 1	2	—	1	1	1	1	0
J	Hessel 2	2	—	2	—	0	2	0
K	Hessel 3	2	—	1	1	1	1	0
L	Mackinac	3	—	1	2	2	1	0
M	Rudd	3	—	0	2	2	0	0
N	Flowers	3	—	2	—	0	1	0
O	Hill Island	1	—	0	—	—	—	—
P	Lakeside	2	—	1	—	0	1	0
Q	Port Dolomite	3	—	3	—	0	0	3
R	Prentiss	3	—	2	1	1	2	0
S	Scotty	3	—	3	—	0	3	0
T	Seymour 1	1	—	1	—	0	1	0
U	Seymour 2	3	—	2	—	0	2	0
V	Seymour 3	3	—	0	3	3	0	0
W	Sweets 1	3	—	3	1	1	2	0
X	Sweets 2	3	—	3	—	0	3	0
Y	Sweets 3	2	—	2	—	0	1	1
Z	Sweets 4	1	—	1	—	0	1	0
	Totals	59	0	33	15	15	24	5

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1. Number of sections sampled with a D-frame aquatic dip net as described in *Methods*.
2. Number of sections lacking standing water that were sampled with a coring device as described in *Methods*.

because of the variability inherent in field observations, and to maintain an acceptable Type II error rate. To protect against inflated Type I error rates, I corrected for multiple comparisons within test families (the 3 tests for each species) (Hochberg 1988).

Laboratory Experiments

Species Selection. The species used in the experiments were selected based on 4 criteria: (1) familial relationships, (2) frequency of occurrence in the wet meadows, (3) presence or absence of an operculum (i.e. Prosobranchia or Pulmonata), and (4) primary habitat preferences (Table 18). Representatives of four families were used to examine whether responses were affected or constrained by phylogenetic relationships. Because I was attempting to explain species occurrence patterns, I also selected species that were widespread in the coastal wet meadows as well as those restricted to only a few sites in the area (see Table 3). The presence of an operculum that covers the apertural opening when the snail retracts into its shell was used because it may confer additional resistance to desiccation (Gibson 1970). I also selected one species (*Amnicola limosa*) because it was primarily considered a permanent water inhabitant rather than a resident of the more temporary wet meadows (Clarke 1973, 1981). The other species were either shallow water inhabitants or generalists across a wide variety of habitats (see references in Burch and Jung 1992).

Experiment I: Snail Movement. Six experimental chambers were prepared by arranging sand in plastic containers to provide a 3-tiered system (Figure 24). The sand provided an even drainage of water through chambers to the drain spouts. A simulated natural substrate, consisting of sieved (1 mm) organic sediment from a nearby wetland, was placed on top of the sand to a regular depth of approximately 3 cm. The sieving of

Table 18. Criteria for selecting snail species used in laboratory experiments.

Species	Family	Frequency of Occurrence[1]	Operculum	Habitat Preference[2]	Movement Chamber Density
Physa gyrina (Say)	Physidae	Very common	No	S, D, P, T	120
Aplexa elongata (Say)	Physidae	Uncommon	No	S, T	120
Planorbula armigera (Say)	Planorbidae	Very common	No	S, P	120
Planorbella trivolvis (Say)	Planorbidae	Common	No	S, D, P	30
Gyraulus deflectus (Say)	Planorbidae	Very common	No	S, D, P	120
Gyraulus parvus (Say)	Planorbidae	Very common	No	S, D, P	240
Bithynia tentaculata (L.)	Bithyniidae	Uncommon	Yes	S, D, P	—[3]
Amnicola limosa (Say)	Hydrobiidae	Uncommon	Yes	D, P	—

1. Frequency of occurrence in the study area only
2. S = shallow, D = deep, P = permanent, T = temporary
3. Species were not used in the snail movement experiment

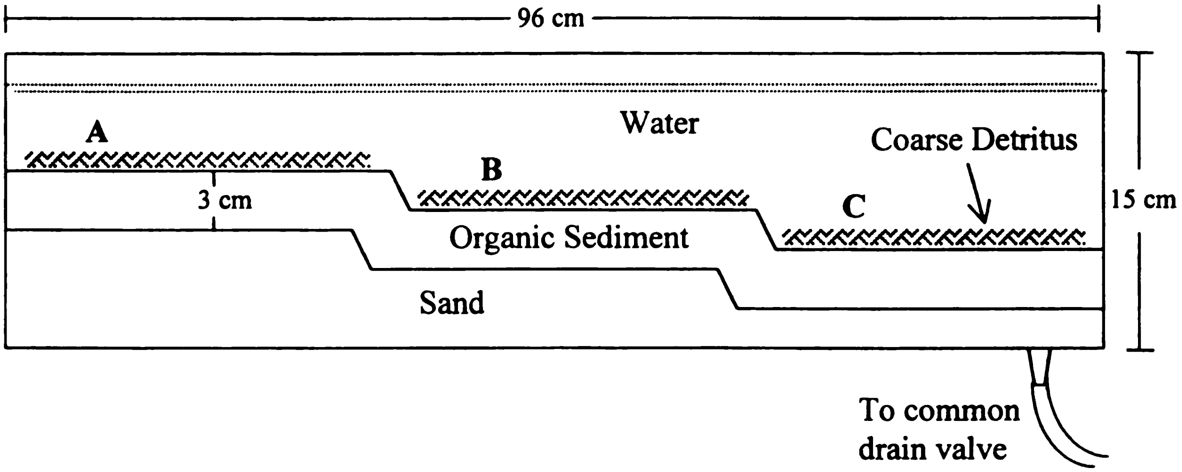

Figure 24. Diagram of the side view of one chamber in the Snail Movement experiment showing the arrangement of sand, sediment and water producing 3 tiers: shallow (**A**), medium (**B**), and deep (**C**). Initial water depth was adjusted so that water level was 4 cm above detritus. The drains of all 6 chambers were connected to one common valve used to maintain the same, constant reduction in water level. Width=42 cm.

the substrate ensured that no snails were present except the experimental animals. On top of this was placed equal amounts of coarse detritus (primarily dead *Carex* spp. leaves with snails removed) to provide a complex structure representative of the natural habitat and to provide a microbially-rich biofilm food source. Water from Lake Huron was added to each chamber to cover the shallowest tier to a depth of 4 cm. Water and substrate in the chambers were allowed to settle for 24 h before snails were added to them.

Each focal snail species was added to individual chambers (equal numbers on each tier) on 4 June 1999, in numbers corresponding to the size of each species and in the approximate densities found in the wet meadows from which they were collected (Table 18). Snails were allowed to acclimate to the experimental chambers for one week. Starting 11 June 1999, the water was slowly and continuously drained from the chambers at a constant rate resulting in a lowering of water levels by approximately 5 cm/wk. The experimental chambers were maintained outdoors in semi-shade to provide the natural diel temperature fluctuations (max 21.9±4.1 C, min 12.5±3.7 C, mean±1 S.D.) and light:dark photoperiod (~15:9). By day 24, the experimental chambers had been completely drained, and the experiment was concluded.

The detritus in each tier was carefully searched and the number of snails in each tier was recorded and all snails were removed by hand or by sieving the substrate. The chi-square goodness of fit test was used to test whether the final distribution of snails was different from random (i.e. different than the original, equal numbers of snails in each tier) using an *a priori* $\alpha < 0.05$.

Experiment II: Desiccation Resistance. The desiccation resistance of seven species of snails (unfortunately enough *Gyraulus deflectus* adults were not able to be collected at the beginning of the experiment) was determined by exposing them to extended lengths of time without water. I used a 7x3 factorial design (N=3), sampling (without replacement) the seven species at three different time periods (2, 7 and 12 wks). Each experimental chamber was a 500 ml cylindrical container (12 cm height) filled with 5 cm sieved (1 mm) organic sediment covered by 5 cm of water. Only 1 species was added to a chamber so a total of 63 chambers was required (7 species × 3 wks × 3 replicates). Snails were added to the chambers as follows [species and (#/container)]: *P. gyrina* (5), *A. elongata* (8), *G. parvus* (12), *P. armigera* (8), *P. trivolvis* (2), *B. tentaculata* (5), and *A.limosa* (12). These numbers were based on snail size (for example, two *P. trivolvis* at 20mm each versus 12 *G. parvus* at 4 mm each) to maximize sample size without overcrowding the chambers. The snails were acclimated to the chambers for 3 days after which small pin holes were drilled in the bottom of each chamber to drain the water slowly, allowing the snails a short time to react (possibly bury themselves, over-hydrate, etc.) before experiencing the dry conditions. Thirty-six hours after the draining began, all containers were void of standing water. All snails were assumed to still be alive at this point in time (week 0). Experimental containers were maintained at room temperature and humidity.

Survival was measured after 2, 7 and 12 weeks by removing the snails from the experimental containers and placing them in aquaria filled with water. Most surviving snails began moving in <1 hr. Snails were assumed to be dead if they did not move by the end of 24 hr; no additional snails began moving after more than 24 hr. SYSTAT (SPSS 1999) statistical software was used to perform a two-way ANOVA to test for the main effects of species and time and their interaction (wk 0 was not included in analyses since the snails were all assumed to be alive, but were not actually sampled). Data were arcsine transformed prior to analyses in order to meet normality assumptions (Zar 1999). Tukey HSD tests were used for post hoc analyses of significant effects.

RESULTS

A total of 35,537 individuals of 19 species of aquatic snails were collected in dip net samples 1997 and 1998 (Table 2). *Physa gyrina* and *Gyraulus parvus* were the most common species (frequency of occurrence) in both 1997 and 1998 along with *G. deflectus* in 1998. Likewise, *P. gyrina* and *G. parvus* were the most abundant snails in 1997 whereas in 1998, *G. parvus* and *G. deflectus* were most abundant (Table 3).

Physa gyrina and *Fossaria parva* declined significantly from 1997 to 1998 (paired $t=2.28$, $df=29$, $P<0.05$ and paired $t=2.26$, $df=29$, $P<0.05$, respectively). *Planorbula armigera* and *G. deflectus* both increased in abundance from 1997 to 1998 (paired $t=2.92$, $df=29$, $P<0.01$ and paired $t=3.71$, $df=29$, $P<0.01$). Species richness per section was similar in both years, ranging from 3-8 in 1997 and 3-11 in 1998. However, abundance of all snails collected per section varied dramatically (Table 3).

The dominant species in these coastal wet meadows, based on frequency of occurrence and abundance, were *P. gyrina*, *G. parvus*, *P. armigera*, *F. parva*, *G. deflectus*, and *Planorbella trivolvis*. The remaining species (see Table 3) were encountered infrequently and in low abundance in the wet meadows.

Multiple Regression Analyses

Mean water levels dropped approximately 15.8 cm from 1997 to 1998 resulting in 26 sections that were sampled in 1997 but were dry or too shallow to sample with D-frame dip nets in 1998 (Table 19). Thus, in 1998 only 33 sections were analyzed, compared to 59 in 1997.

Because the six variables all were based on the water level variation in the wet meadows, they were interrelated (Figures 25 and 26). The majority of pairs had an r^2 of less than 50%, and many were influenced by extreme values. The most highly correlated were mean and maximum depth, mean and minimum depth, and maximum and range of depth. Maximum and range of depth were especially correlated in 1998 because the low water levels caused many section to have dry areas (minimum depth = 0), which made the maximum depth equal to the range of depth. When these variables were included in the regression models, models including related variables were also examined to ensure that the best predictor was being entered.

Regression Models. Species richness, total abundance, and a total of 11 species met the criteria for inclusion in the regression modeling (see pages 108-109). At least one water level variable was a significant predictor in 7 of 11 species as well as richness and total abundance during at least one year (Table 20). The data were variable (see Figures 27 and 28 for examples of the variability), and the variance explained by the models (R^2) ranged from 6 to 32%.

Mean depth was the most commonly selected variable in the models. As mean depth increased, the abundance of *F. parva* and *G. deflectus* increased, as well as species

Table 19. Mean, standard deviation, and range of the water level variables and snail species richness and abundance variables. N=59 in 1997, N=33 in 1998.

	Mean ± S.D.		Range for all sections	
Variable[1]	1997	1998	1997	1998
Depth	28.9 ± 13.1	13.1 ± 7.7	5.1 - 57.8	0.0 - 26.1
Min	10.4 ± 12.1	1.2 ± 2.8	0.0 - 40.0	0.0 - 9.0
Max	52.1 ± 27.1	38.3 ± 28.2	11.0 - 151.0	10.0 - 120.0
Range	41.6 ± 24.1	37.1 ± 28.1	11.0 - 126.0	9.0 - 120.0
sCV	48.7 ± 36.2	106.4 ± 72.5	8.4 - 236.0	27.1 - 292.6
tCV	31.6 ± 26.6	21.9 ± 20.0	5.3 - 125.4	4.1 - 94.2
Richness	5.4 ± 1.2	5.9 ± 1.5	3 - 8	3 - 11
Abundance	345.9 ± 260.4	472.5 ± 341.9	5 - 1107	19 - 1257

1. Depth = mean depth (cm), Min = minimum depth (cm), Max = maximum water depth (cm), Range = range of water depth (cm), sCV = spatial coefficient of variation, tCV = temporal coefficient of variation, Richness = number of snail species, Abundance = total abundance/section of snails collected.

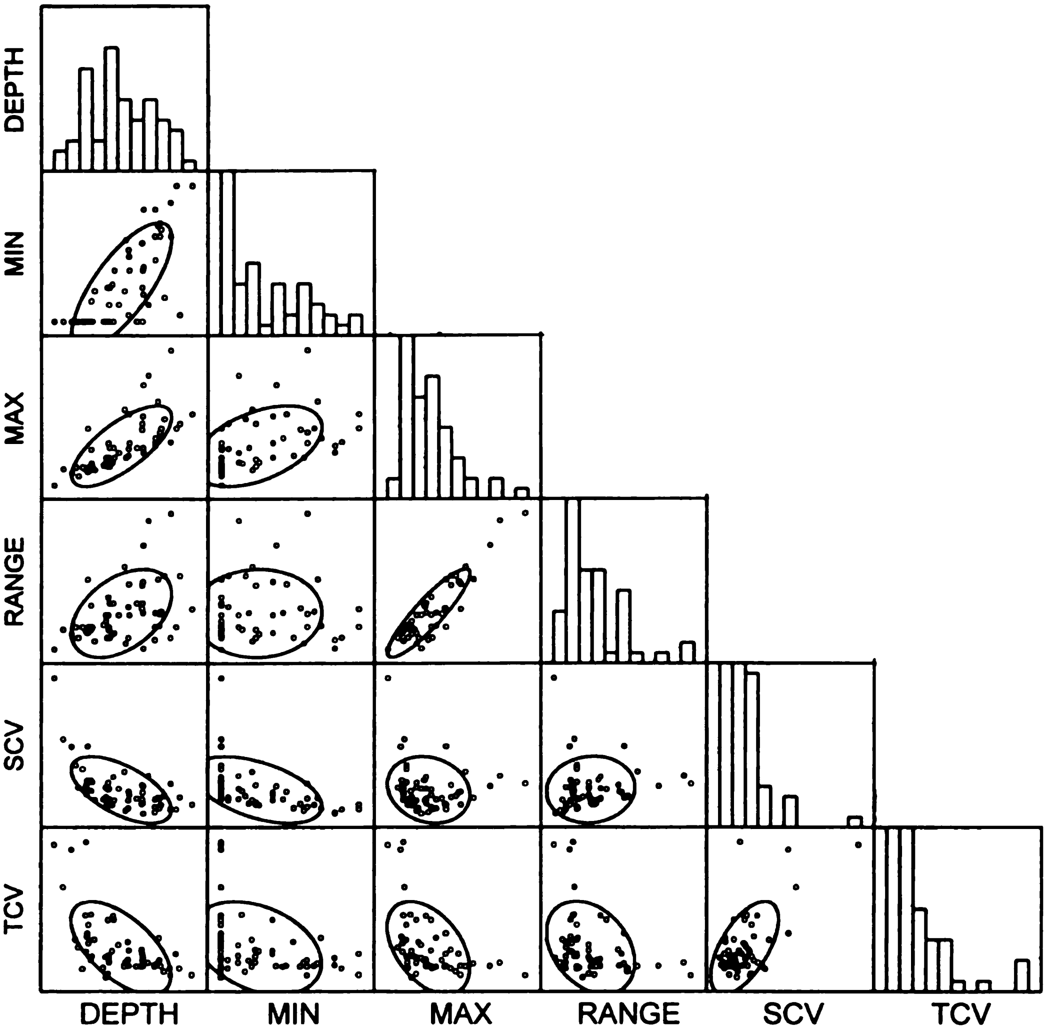

Figure 25. Scatterplot matrix of the 6 water level explanatory variables used in the regression analyses for 1997. Ellipses are 68% confidence intervals (±1 S.D. around x and y axes), N=59. Histograms are shown on the diagonal for each variable. Values in each graph are r^2 values that includes all points, but note the presence of extreme values that would influence this value in many variable pairs. Axes labels are explained in the footnote for Table 19.

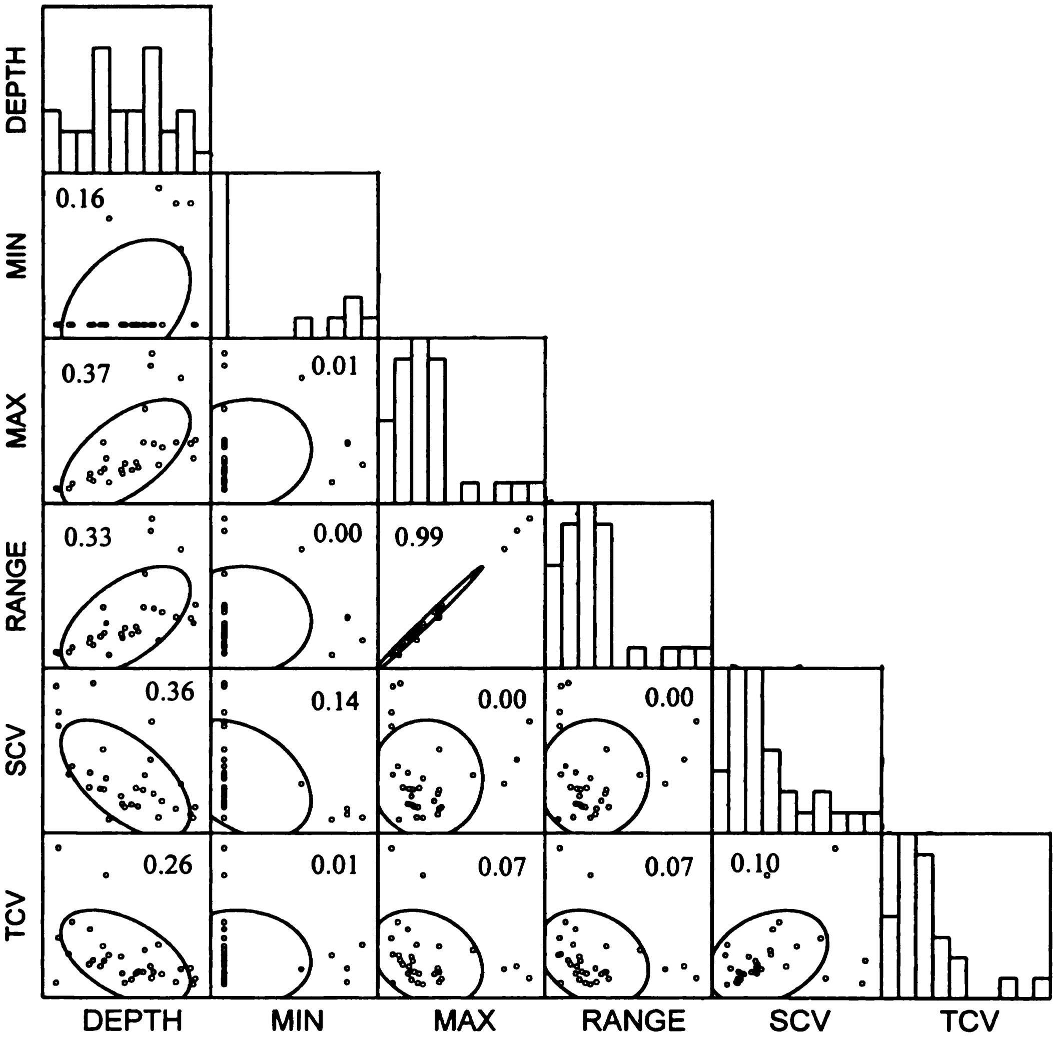

Figure 26. Scatterplot matrix of the 6 water level explanatory variables used in the regression analyses for 1998. Ellipses are 68% confidence intervals (±1 S.D. around x and y axes), N=33. Histograms are shown on the diagonal for each variable. Values in each graph are r^2 values that includes all points, but note the presence of extreme values that would influence this value in many variable pairs. Axes labels are explained in the footnote for Table 19.

Table 20. Results of stepwise multiple regression on species richness and abundance, and presence/absence variables of snails in northern Lake Huron coastal wet meadows.

Variable	Predictors in model	R^2
Richness		
1997	(+) Mean depth	0.09[1]
1998	–[2]	–
Total Abundance		
1997	–	–
1998 (log)[3]	(-) Spatial CV	0.32
	Species Abundance	
Fossaria parva		
1997	(+) Range of depth, (+) Temporal CV	0.16
1998 (log)	(+) Mean depth, (+) Temporal CV	0.20
Gyraulus deflectus		
1997 (log)	(+) Mean depth, (+) Spatial CV, (-) Range of depth	0.22
1998	(+) Mean depth	0.20
Gyraulus parvus		
1997	–	–
1998	–	–
Planorbula armigera		
1997	–	–
1998	–	–
Physa gyrina		
1997 (log)	(-) Mean depth, (+) Minimum depth	0.22
1998	–	–
	Presence/Absence	
Aplexa elongata		
1997	(+) Temporal CV	0.09
Amnicola limosa		
1998	(+) Minimum depth	0.11

Table 20. Continued.

Variable	Predictors in model	R^2
Fossaria obrussa		
1997	(+) Maximum depth, (+) Temporal CV	0.21
Ferrissia parallela		
1998	–	–
Planorbella trivolvis		
1997	(+) Minimum depth	0.06
1998	(-) Spatial CV	0.16
Stagnicola elodes		
1998	–	–

1. Values are the coefficient of determination for richness and abundance variables and McFadden's ρ^2 for presence/absence variables.
2. A '–' indicates there was no significant predictors in the model (P>0.10).
3. Indicates that variables were log transformed to meet regression assumptions.

richness (Figures 27 and 28). *Physa gyrina* decreased in response to increasing mean depth (Table 21).

Minimum depth, spatial CV and temporal CV were significant predictors for 3 species each (Table 21). As minimum depth increased, *P. gyrina*, *A. limosa*, and *P. trivolvis* became more common. *Gyraulua deflectus* increased in abundance in sections with higher spatial CV whereas *P. trivolvis* was less common, and total abundance of all species was lower. *Fossaria parva* and *F. obrussa* as well as *A. elongata* were more common in sections with high values for temporal CV (Table 21).

Fossaria obrussa was the only species positively associated with maximum depth and no species were negatively associated. *Fossaria obrussa* increased as the range of depth increased, whereas *G. deflectus* was negatively associated with range of depth (Table 21).

Annual Comparisons

A subset of 44 sections was analyzed for additional annual comparisons of the snail community. The omitted 15 sections were primarily dry sections for which cores were not accessible. Fifteen of these 44 sections were dry in 1998 and 24 of the 44 sections had significantly lower water levels in 1998 (paired t=3.24, df=23, P<0.01) with a decline in these sections of approximately 27 cm (Table 22). The depths in 5 sections were found to remain constant from 1997 to 1998 (paired t=-0.47, df=4, P=0.665) (Table 22).

Nineteen species of aquatic snails were collected from the flooded wet meadows in 1997 and 1998 (see Table 2), and 9 species were collected in cores from dry sections in 1998 (Table 23). The 9 species collected in the dry sections were the most frequently

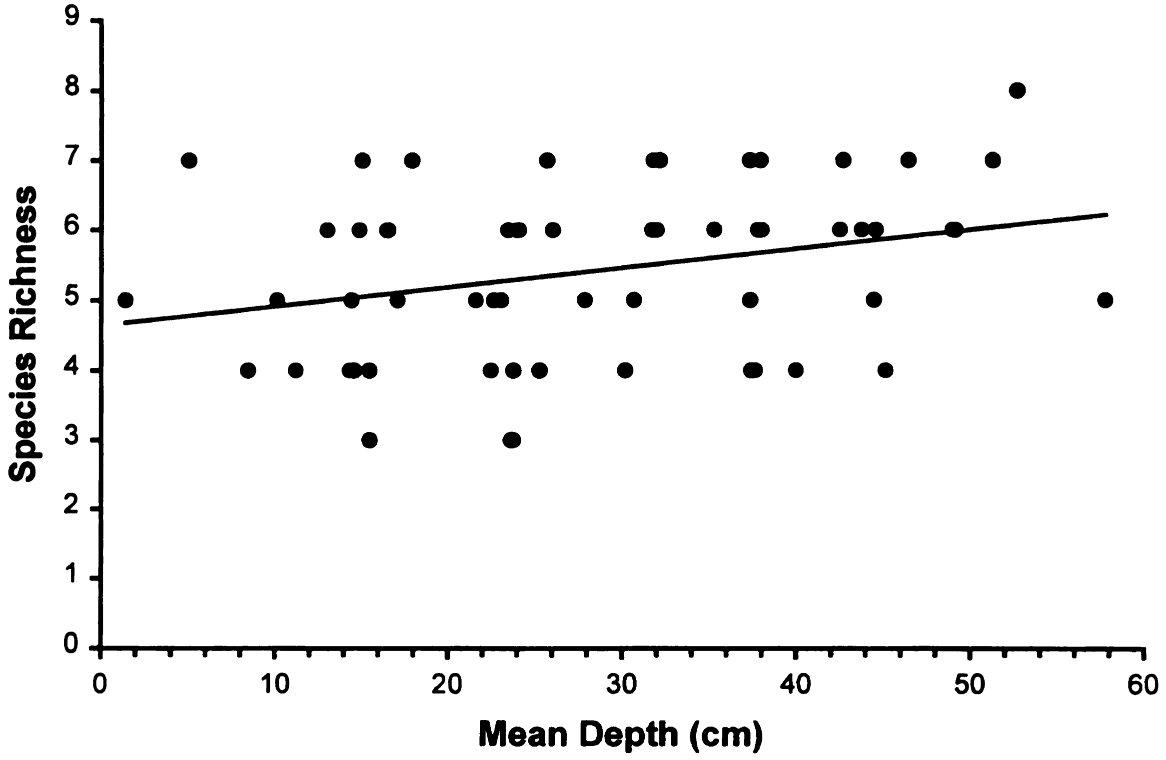

Figure 27. Species richness (S) – Depth curve for snails in coastal wet meadows of the northern Lake Huron shoreline during 1997. N = 59. The line represents the significant ($P<0.05$) linear model, $S = 0.027(\text{Depth}) + 4.642$, $R^2 = 0.09$.

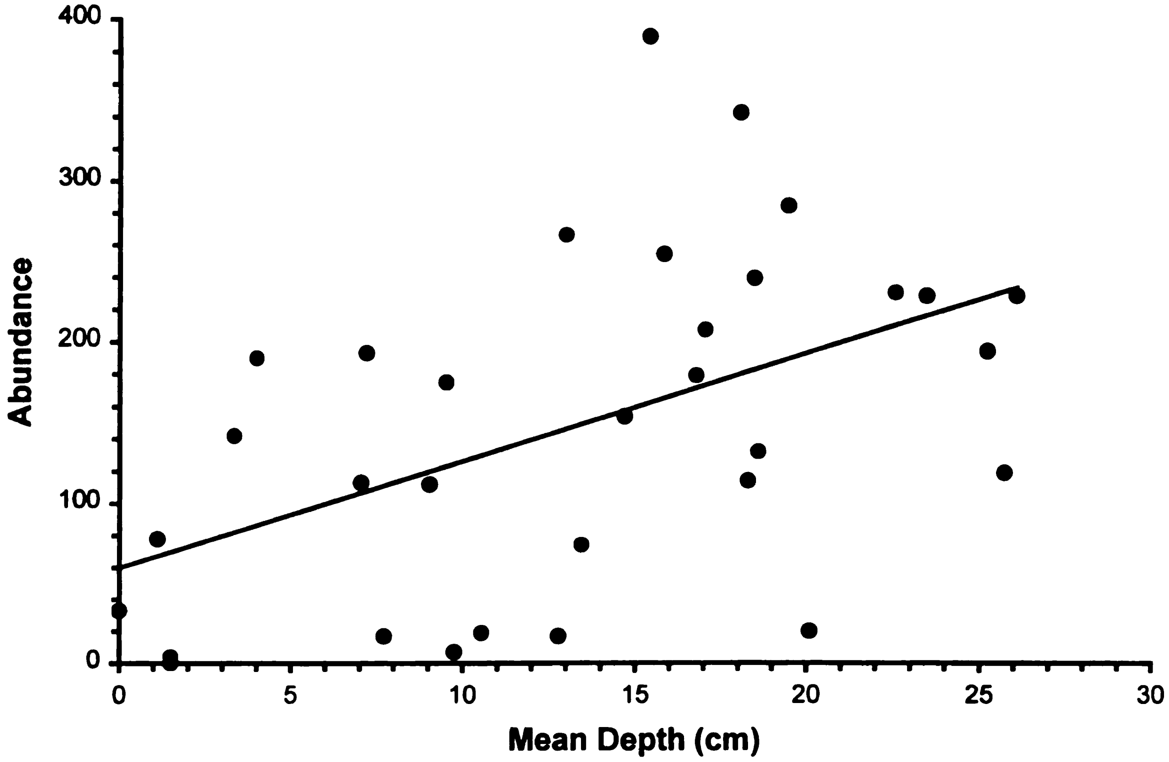

Figure 28. Abundance – Depth curve for *Gyraulus deflectus* in coastal wet meadows of the northern Lake Huron shoreline during 1998. $N = 33$. The line represents the significant ($P<0.05$) linear model, Abundance = 6.240(Depth) + 64.244, $R^2 = 0.20$.

Table 21. Variables exhibiting negative and positive relationships to the six predictors used in the regression modeling.

Negative (-)	Predictor	Positive (+)
Physa gyrina (1997)	Mean depth	*Fossaria parva* (1998) *Gyraulus deflectus* (1997, 1998) Richness (1997)
–	Minimum depth	*Physa gyrina* (1997) *Amnicola limosa* (1998)[1] *Planorbella trivolvis* (1997)
–	Maximum depth	*Fossaria obrussa* (1997)[1]
Gyraulus deflectus (1997)	Range of depth	*Fossaria parva* (1997)
Planorbella trivolvis (1998) Total Abundance (1998)	Spatial CV	*Gyraulus deflectus* (1997)
–	Temporal CV	*Fossaria parva* (1997, 1998) *Aplexa elongata* (1997)[1] *Fossaria obrussa* (1997)[1]

1. Only examined in one year.

Table 22. Mean depth, range and standard deviation for three classifications of coastal wet meadow sections in 1997 and 1998. N = number of sections.

		Mean ± S.D.		Range	
Class	N	1997	1998	1997	1998
Dry	15	21.9 ± 8.3	–[1]	10.2 - 37.4	–
Lower	24	40.2 ± 9.8	13.6 ± 6.9	14.4 - 57.8	1.1 - 26.1
Same	5	10.3 ± 6.8	9.6 ± 6.8	1.4 - 17.1	1.5 - 17.1

[1] Sections did not have standing water.

Table 23. List of species collected in cores from dry sections in 1998 and their mean abundance/section when flooded in 1997.

Species	1997 Abundance
Physa gyrina	130.6
Aplexa elongata	5.0
Gyraulus deflectus	40.3
Gyraulus parvus	90.7
Planorbula armigera	60.3
Planorbella trivolvis	4.2
Planorbella campanulata	0.7
Fossaria obrussa	2.7
Fossaria parva	9.6

occurring species in 1997, and were used in the remaining analyses. Sample sizes for the other species were too small to be reliably tested.

'Dry' Sections. The frequency of occurrence of live snails in Dry sections was significantly less in 1998 than it had been in 1997 only for *Physa gyrina* (Figure 29). All other species showed no significant change (P>0.10 corrected) in frequency from 1997 to 1998 (Figure 29, Table 24).

'Lower' Sections. Planorbula armigera and *Gyraulus deflectus* both increased in abundance in wet meadow sections where water levels declined from 1997 to 1998, but did not dry out, whereas *Fossaria parva* declined (Figure 30 and Table 24).

'Same' Sections. Physa gyrina was the only species to show a response in wet meadows that remained constant in depth from 1997 to 1998; it decreased in abundance (Figure 30 and Table 24). No other species showed significant differences between years (Figure 30 and Table 24).

Laboratory Experiments

Experiment I: Snail Movement. Snail movement patterns of individual species varied widely in response to the reduction in water levels. *Planorbula armigera* and *Planorbella trivolvis* were found more often in the shallow tier, *Physa gyrina* was found significantly more often in the deep tier, and the remaining species showed random distributions among the tiers (Table 25). The percentage of snails that were completely buried at the end of the experiment ranged from 2.5% of *Gyraulus deflectus* to 43.3% of *P. trivolvis* (Table 25).

Experiment II: Desiccation Resistance. Some individuals of all species tested, except for *Amnicola limosa*, were able to survive for the 12 week length of the

Table 24. Results of statistical analyses comparing snail abundance and presence/absence between 1997 and 1998 in three classes of wet meadows. **Bold** P-values are significant at $\alpha<0.10$ after correction for multiple tests.

	Wet Meadow Class				
	Dry	Lower		Same	
	Fisher exact P-value	Wilcoxon *Z*	P-value	Wilcoxon *Z*	P-value
Physa gyrina	**<0.001 (-)**[1]	-1.50	0.133	-2.02	**0.043**
Planorbula armigera	1.000 (nc)	2.68	**0.007**	0.94	0.345
Planorbella trivolvis	0.224 (-)	-1.12	0.262	0.00	1.000
Gyraulus deflectus	0.066 (-)	3.83	**<0.001**	0.40	0.686
Gyraulus parvus	0.483 (-)	-0.39	0.700	-0.68	0.498
Aplexa elongata	1.000 (-)	-1.00	0.317	-1.00	0.317
Planorbella campanulata	0.483 (-)	-1.00	0.317	–[2]	–[2]
Fossaria obrussa	1.000 (-)	0.41	0.680	-1.34	0.180
Fossaria parva	0.651 (+)	-2.42	**0.016**	-0.40	0.686

1. Direction of change from 1997 to 1998.
2. *Planorbella campanulata* was not found in these sections.

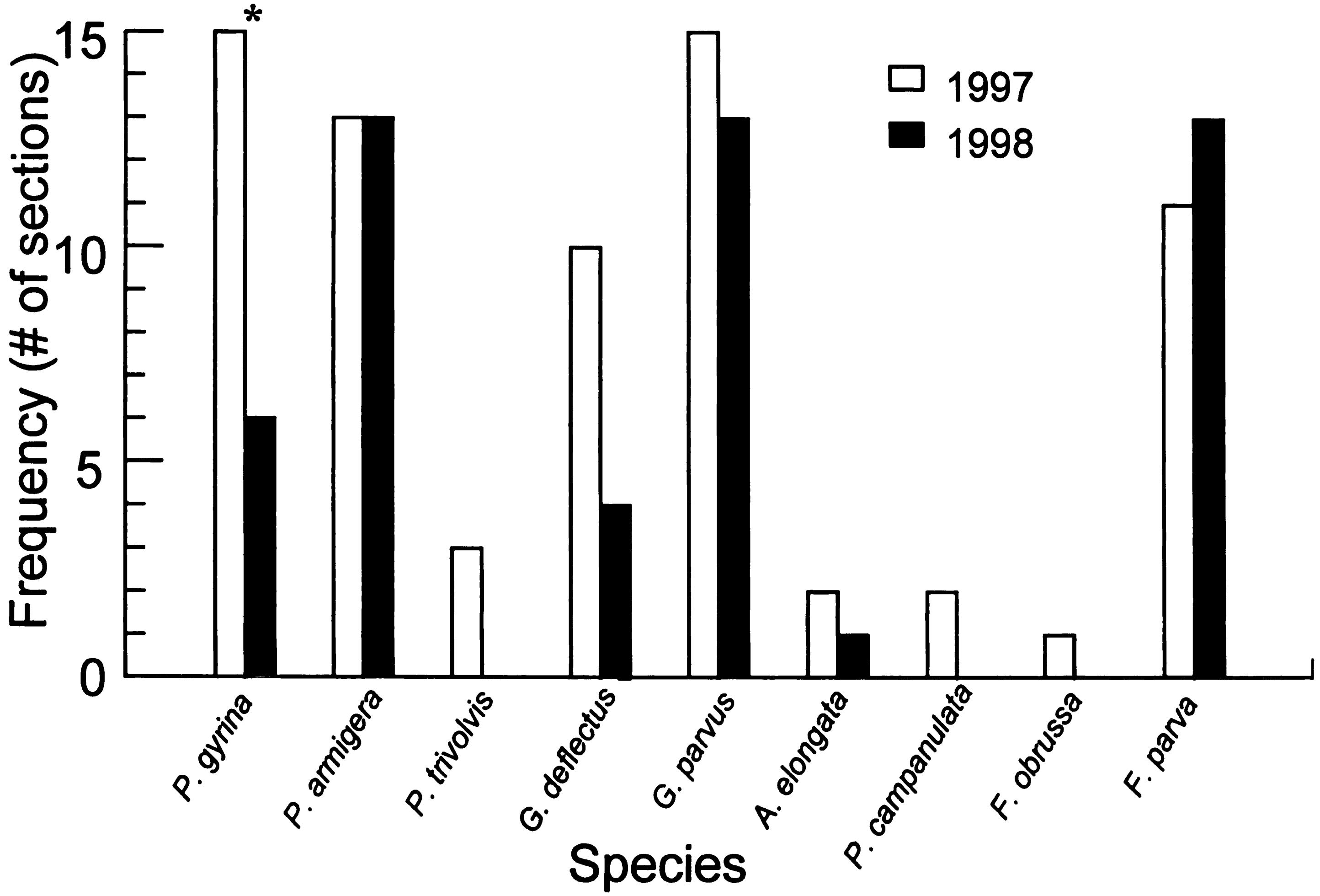

Figure 29. Number of sections (out of 15 that were dry in 1998) in which living snails were present in 1997 (wet, sampled by dip nets) and 1998 (dry, sampled by cores). '*' indicate significant differences between years (P<0.10).

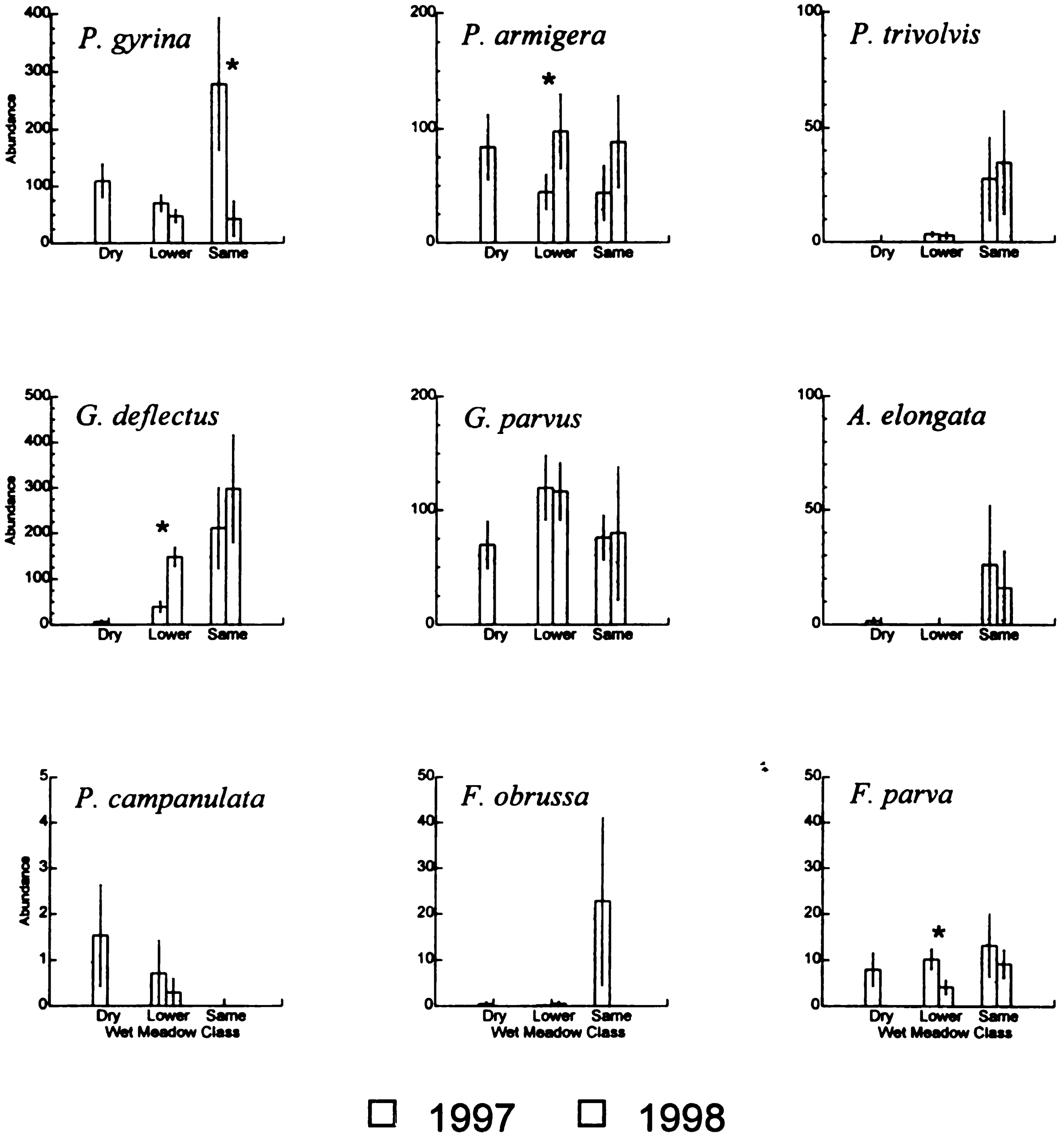

Figure 30. Mean abundance of snails from three classes of coastal wet meadows in 1997 and 1998. 'Dry' wet meadows were flooded in 1997 and dry in 1998 (results not shown here because of different sampling methods), N=15; 'Lower' wet meadows were flooded in both years, but shallower in 1998, N=24; and 'Same' wet meadows were the same depth in both 1997 and 1998, N=5. Error bars are ± 1 S.E.M. '*' indicates a significant different between years (P<0.10). Note differences in scaling of the vertical axes.

Table 25. The number of snails in each tier at the end of the Snail Movement experiment. χ^2 values are from the chi-square goodness of fit test, DF=2. The total number of each species is also the number at the beginning of the experiment.

		Tier					
Species	Total	Shallow	Medium	Deep	χ^2	P	% Buried
P. gyrina	120	9	34	77	59.15	<0.001	27.5
A. elongata	120	36	48	36	2.40	0.301	10.8
P. armigera	120	68	33	19	31.85	<0.001	35.8
P. trivolvis	30	25	3	2	33.80	<0.001	43.3
G. deflectus	120	36	47	37	1.85	0.397	2.5
G. parvus	240	83	64	93	5.43	0.066	12.9

experiment, and this percentage ranged from 3 to 93% (Figure 31). There was a significant species effect (Table 26) and post hoc tests revealed three significantly different survival patterns. (1) *Aplexa elongata* and *Gyraulus parvus* had a large decrease in survivorship at 2 weeks and then a slow decline through week 12, whereas (2) *Physa gyrina*, *Planorbula armigera*, *Planorbella trivolvis*, and *Bithynia tentaculata* maintained a relatively high survival rate throughout the experiment; (3) *Amnicola limosa* did not survive for even 2 weeks (Figure 31). There was also a significant time effect (Table 26) and post hoc tests indicated an overall significant decline in survivorship between weeks 2 and 12.

Individuals in the desiccation experiment were not identified as buried or visible on the surface when determining if they were alive at the end of each time period. However, a comparison of the percentage surviving at week 12 (Figure 31) in the desiccation experiment with the percentage of snails buried (Table 25) in the snail movement experiment shows a positive correlation (Figure 32). Species with higher burial rates in Experiment I tended to be the same species that exhibited better survival in Experiment II.

DISCUSSION

With an average decline of >15 cm in 1 year, extensive changes occurred in the coastal wet meadows of northern Lake Huron from 1997 to 1998. Significant results in all 3 approaches to examining water level effects on snails in coastal wet meadows suggested water levels were important. Here, I first discuss the water level fluctuations used in the regression analyses and annual comparison, and then examine the proximate responses of the snails to water level declines shown in the laboratory experiments.

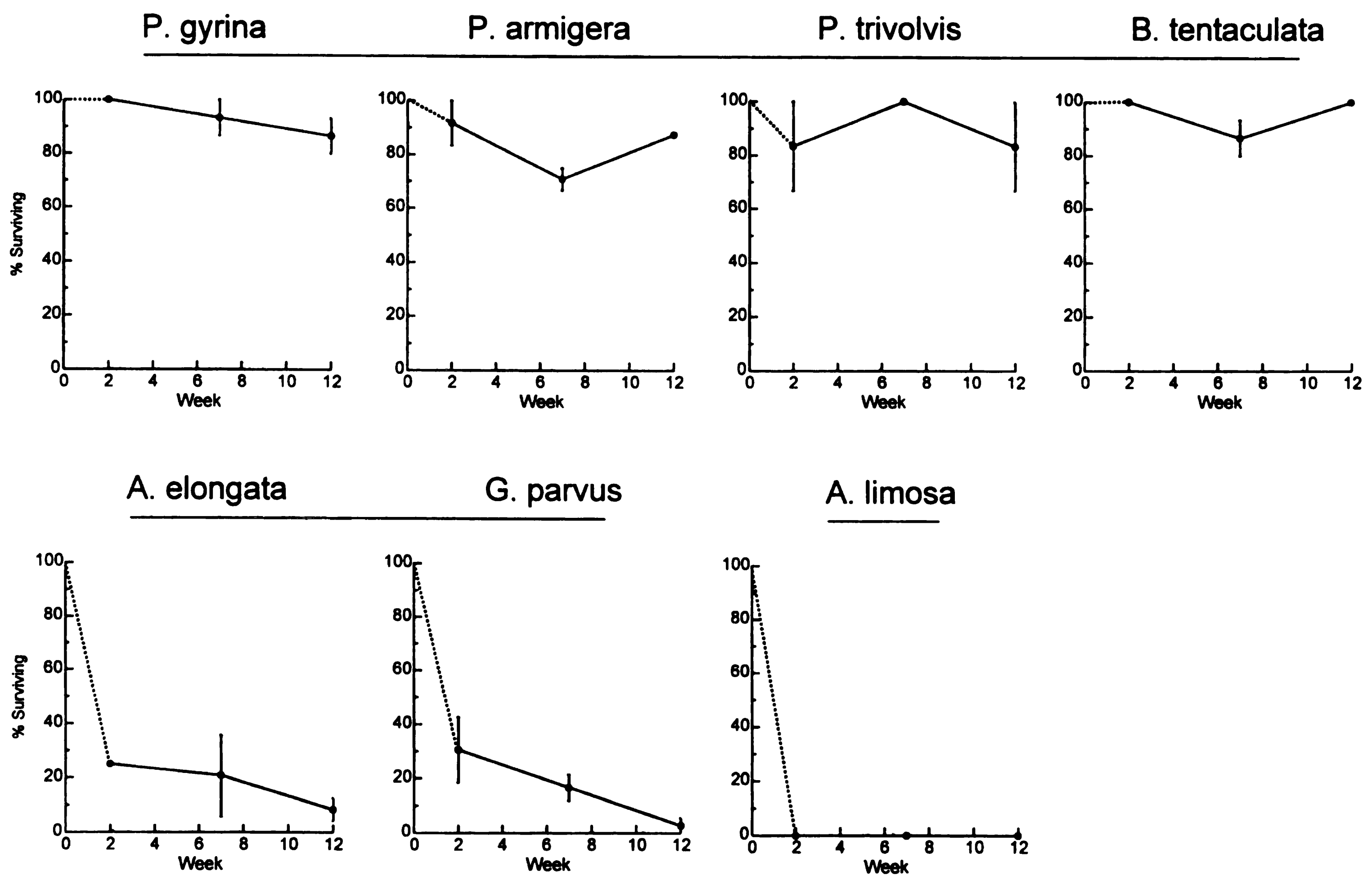

Figure 31. Desiccation survival curves of 7 species of snails. The dashed lines in each graph indicate that all snails were assumed to be alive at week 0. Species names not connected by a common line are significantly different (Tukey HSD, P < 0.05). Error bars are ± 1 SEM.

Table 26. Two-way ANOVA of snail survival in the desiccation resistance experiment.

Source of Variation	ss	df	ms	F	P
Species	20.677	6	3.446	70.515	<0.001
Time	0.353	2	0.176	3.609	0.036
Species * Time	0.812	12	0.068	1.385	0.211
Error	2.053	42	0.049		

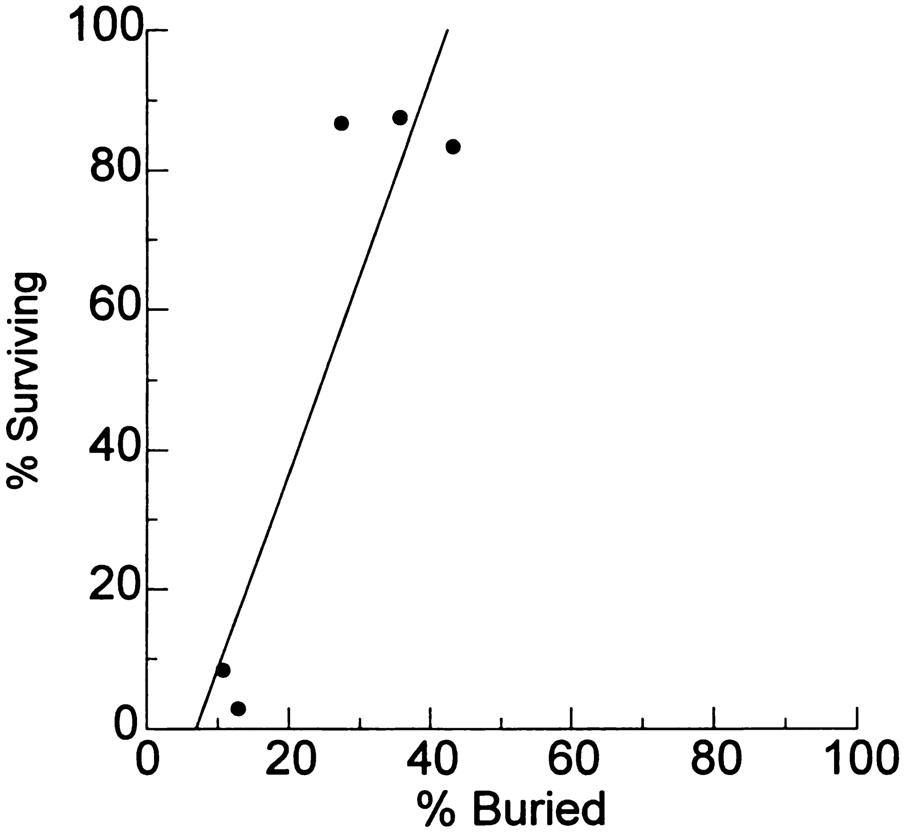

Figure 32. Correlation of the percentage of snails buried in experiment I with the percentage surviving in experiment II (r = 0.91, N=5, P = 0.03).

Finally, I combine the results of all 3 approaches in examining responses of individual species to water level fluctuations in the coastal wet meadows and the overall effect it has on the snail community.

Water Level Fluctuations

I used 6 explanatory water level variables in the regression analyses. Mean, minimum, and maximum depths all related directly to the depth of water in the wet meadow although each represented a slightly different aspect of the habitat. Minimum depth reflected the shallowest parts of the wet meadow. Sections with shallow minimum depths were those that were likely to dry out completely when Lake Huron water levels were low (e.g. in 1998 - classified as 'dry' in the annual comparison), but would be wet during high water years (e.g. 1997). In 1998, these dry sections were moist or saturated (presumably from rainfall and/or groundwater inputs), and after periods of heavy rain, some depressions among the hummocks contained very shallow puddles. These sections were probably similar conceptually to traditional temporary ponds in general models (Lodge et al. 1987, Wellborn et al. 1996). Sections with deeper minimum depths were likely to remain permanently flooded in all but the lowest water levels, and were significantly shallower in 1998 (classified as 'lower' in the annual comparison). The rapid decline in water levels observed during this study was likely too rapid for major changes to occur in the plant community, except for some opportunistic annuals (Keddy and Reznicek 1985). Thus, the changes observed in the wet meadow snail community were probably direct responses to the drawdown event, rather than indirect effects from plant community shifts.

The significance of maximum depth was more difficult to assess. In this study, deeper maximum depths represented sections that were more lakeward and bordered the more sparsely vegetated, emergent marsh (Minc and Albert 1998). Mean depth was conceptually a combination of minimum and maximum depths and reflected the overall water level in the section.

Range of depth and spatial CV were both measures of spatial variability in water levels within a section. Range of depth was a good indicator of the extremes in depths within a section but gave little indication of the evenness of the depth and could be influenced by a small number of extreme depths. Spatial CV incorporated the variation in depth relative to the mean and was less influenced by extreme values. Low spatial CVs indicated a more uniform depth throughout the section.

Temporal CV was a measure of the variation in water levels over time. Temporal CVs in this study were not indicators of seasonal and multi-annual fluctuations in water levels that occur in Great Lakes coastal wetlands (Bedford 1992, Keough et al. 1999), but rather represented the magnitude of water fluctuations in the 1-month immediately prior to sampling. Low temporal CVs indicated a tighter connection to the hydrology of Lake Huron, and higher CVs indicated sections that were less connected to Lake Huron, which includes those isolated by naturally formed dune ridges as well as anthropogenic impoundment (e.g. road building). The water levels fluctuated more over time because these semi-isolated wetlands were more strongly influenced by rainfall patterns/droughts.

In comparison to the short-term water level changes above, in 5 sections, water levels did not change significantly from 1997 to 1998 (classified as ‘same’ in the annual comparison). Two of these sections occurred in wet meadows partially isolated hydrologically from Lake Huron by small dune ridges, and were probably influenced by rainfall. The other 3 sections were in a wet meadow separated from Lake Huron by a road, but connected via a culvert and with a stream running through it.

Experiment I: Movement Patterns

The behavioral responses of freshwater snails to declining water levels have been examined in several studies of temporary pond habitats. In these populations, the snails must be able to resist desiccation to survive from one season to the next. The movement patterns that were often exhibited have been interpreted as an adaptive mechanism to increase the probability of successfully resisting desiccation by finding more suitable microhabitats, either in shallower or in deeper habitats. Jokinen (1978) and Brown (1979) found that adult *Stagnicola elodes* did not react to changing water levels, but that juveniles did, by moving out of the drying pond to the surrounding mud (i.e. toward shallow areas). Betterton et al. (1988) suggested that the opposite pattern (i.e. moving toward deeper water) may also be advantageous in two other species, *Bulinus rohlfsi* and *B. globosus*. They were both observed to move to the bottom of the drying ponds before aestivation, and there was no apparent difference in the movement of adults and juveniles, although older snails did survive better after reviving (Betterton et al. 1988).

Overall, my results mirror these studies; some species moved to shallow areas and others followed the receding water (Table 25). In environments with fluctuating water levels, moving away from the receding water to shallow, dry areas as *Planorbella trivolvis* and *Planorbula armigera* did in the current study may have several benefits. First, premature revival from aestivation, e.g. after a single, early rainfall (Betterton et al. 1988), may be prevented. A second possible advantage is escaping predation. In temporary ponds, the falling water levels would decrease the suitable habitat available, and confine the snails into small areas of high densities, making them vulnerable to both aquatic and terrestrial predators. Supporting this, both *P. trivolvis* and *P. armigera* exhibited the greatest percentage of burying behavior (Table 25), a response that may decrease predation rates.

These explanations for moving to shallow areas may be important for temporary ponds, but do not entirely explain the behavior in coastal wet meadows where a permanent refuge is available if the snails would follow the receding water. It is possible that these behaviors are advantageous, even in coastal wet meadows, because of the heterogeneity within the wetlands. Isolated pools may act like non-coastal temporary ponds even though at a larger scale, the wetland is contiguous with a permanent water environment. Thus, the behaviors that are advantageous to snail populations in temporary ponds may also be advantageous to those in coastal wet meadows.

Physa gyrina was the only species to move with the water as it declined and most were found in the deepest tier (Table 25). Clampitt (1974) found a maximum dispersal rate of approximately 7 m in 24 h for the closely related congener *P. integra*. This rate by itself would be sufficient to move to refuge in the coastal wetlands. In addition, as the water flows out of the wetlands during frequent seiches, snails may float with the current, either attached to the surface film or buoyed by air bubbles in their shells (BEK: pers. obs.). The combination of these behaviors suggested that directed movement following the water is a viable, adaptive response by *P. gyrina* to falling water levels.

The remaining species tested (*Aplexa elongata*, *Gyraulus parvus*, *Gyraulus deflectus*) did not show any significant direction to their movement, indicating that they may not respond behaviorally to declining water levels. It was possible that rather than moving in preparation for aestivation (as done by *P. trivolvis* and *P. armigera*), they were preparing physiologically by increasing the hydration of their tissues (Arad 1990). They apparently did not use burying as a behavior to increase survival after aestivation as they showed the lowest burial rate (Table 25).

Experiment II: Desiccation Resistance

Freshwater snails from non-coastal temporary habitats were frequently observed to resist desiccation for various lengths of time until more favorable conditions returned (Jokinen 1978, Brown 1979, Betterton et al. 1988). In the present study, six of seven species were able to survive at least 12 weeks of desiccation.

The four species that showed the highest survival rate (Figure 31) were a diverse group phylogenetically. *Physa gyrina*, *Planorbula armigera*, and *Planorbella trivolvis* were pulmonates from two different families whereas *Bithynia tentaculata* was a prosobranch. Desiccation resistance in *B. tentaculata* was probably enhanced by the presence of the thick, calcareous operculum characteristic of the family, and a tendency to bury in the substrate. The presence of an operculum did not guarantee resistance, as the only other operculate snail in the study, *Amnicola limosa*, did not even survive two weeks (Figure 31).

It was not clear why the three pulmonates should show such high survival rates. It may be a function of physiological tolerance of high hemolymph osmolality resulting from water loss, or of other behavioral adaptations for reducing water loss. Adaptations to resist desiccation may include retaining water in the mantle cavity (Blinn 1964), creating a soil and mucus plug covering the apertural opening (Parashar and Rao 1998), or burying in the sediment or other moist habitat (Jokinen 1978, Thomas and McClintock

1996). They were observed to bury quite frequently in the present study (Table 25).

Gallo et al. (1984) found that *Planorbella trivolvis* survived <5 d at low relative humidity (12-14%) and <40 d at high humidity (96-98%). Clampitt (1970) found 51% of *Physa gyrina* surviving after 12 days of desiccation (humidity not indicated). In contrast, I found a much longer survival time (at least 84 d). The difference in results may be because Gallo et al. (1984) maintained the snails in moist paper towel (they were simulating shipping conditions) and Clampitt (1970) in dry dishes, rather than in a substrate in which the snails could burrow, as was the case in the present study. This emphasizes the importance of behavioral adaptations to increase desiccation resistance, and should be taken into consideration when making comparisons of desiccation resistance among studies with different methods. Additionally, for some species, there was limited evidence that populations from temporary habitats were able to survive longer periods of desiccation than populations from permanent habitats (Olivier 1956).

Some individuals of *Aplexa elongata* and *Gyraulus parvus* were able to survive 12 weeks of desiccation but with a much lower rate (Figure 31). Why there was such a difference between these species (both pulmonates) and the other three pulmonates was unclear, but it may be due to behavioral adaptations (i.e. reduced burying rates, Table 25) rather than major physiological differences.

Snail Responses

Species richness was significantly related to increasing mean depths in 1997 but there were no predictors in 1998 (Table 20). The deeper water levels recorded in 1997 allowed snails that were normally associated with the deeper, more permanent habitat of the emergent marsh (i.e. bulrush marsh) to occur in the wet meadow regions. Thus, in

1998 when the water levels receded, and these species were not found in as many wet meadows, on average, there was a decline in species richness in relationship to depth.

Total abundance of snails was related to decreasing water level spatial variability in the wet meadows in 1998 (Table 20). Sections with low spatial variation (i.e. more uniform depth) may have had higher abundances because of the more stable water levels.

Physa gyrina. The negative association in 1997 with mean depth, and a positive association with minimum depth, suggested that *P. gyrina* was most abundant in shallower sections, but only those that were likely to remain flooded. Thus, in the annual comparison, *P. gyrina* was found less frequently in the Dry sections (Table 20). This pattern was consistent with behavioral and physiological results that showed high desiccation resistance and active movement to deeper water (Figure 31, Table 25). In some sections, the snails may have been able to move out of shallow sections with the receding water because of sparser vegetation or shorter distances to permanent water (Clampitt [1974] observed a very similar congener to move up to 7 m in 24 hr). This directed movement would result in relatively few individuals aestivating in the shallow sections (<8% remained in the dry sections during the experiment, Table 25). Because of the decreased density, few snails would be collected and a significant decline (Figure 29) would be expected. Instead, they could be found in permanently flooded, shallow sections as in this study. They were apparently not as common in deeper water, perhaps because of increased predation risk from fish (Turner 1996). *Physa gyrina* were thin-shelled which made them especially vulnerable to fish predation (Sadzikowski and Wallace 1976, Mittelbach 1984).

Abundance of *P. gyrina* was not significantly predicted by any of the water level variables in 1998. Because of the lower water levels in 1998 (Table 19), the sampled sections were those that were deeper in 1997. Since *P. gyrina* was found in shallower sections in 1997, it was not surprising that they were less common in 1998. Life history characteristics of *P. gyrina* suggest that they have a high reproductive rate (Brown 1979) that may allow them to recover after one or more generations, and become the most abundant species once again, as it was in 1997.

I found *P. gyrina* to be the most common and abundant species overall (see Table 2) which was consistent with other studies which have found that where *P. gyrina* occurs, it was often the most abundant (Clarke 1981). For example, McKillop (1985) found it at all sites sampled and in the highest abundances in southeastern Manitoba, Canada, and Pip (1985, 1987) found it to be the most common species in her sites in central Canada.

Fossaria parva. *Fossaria parva*, in both 1997 and 1998, was significantly predicted by higher temporal CV (Table 20). It was also predicted by increasing range of depth (1997) and mean depth (1998). These results suggested that *F. parva* was more commonly found in sections that were less connected to Lake Huron (positive temporal CV) and that were more likely to remain permanently flooded (positive range and mean depths). The behavioral response and desiccation resistance of *F. parva* were not studied, but these results suggested that it probably would not move in response to changing water levels, and it probably has a low desiccation resistance. These attributes may explain the significant decrease in abundance from 1997 to 1998 as water levels dropped and *F. parva* was not able to respond (Table 2).

Previous researchers have reported *F. parva* to be amphibious, occurring above the water line or at the edges of large, permanent water bodies (Baker 1928, Laursen et al.

1992). My results agreed with this; that *F. parva* was found in more permanent sections of coastal wet meadows. However, I could not distinguish where in the water column the individuals were when collected. It was possible that even in these deeper sections, they were amphibious and occupied the water's edge, occurring at the upper edges of hummocks.

Gyraulus deflectus. In both 1997 and 1998, *G. deflectus* was associated with deeper mean depths. In those deeper sections in 1997, it was also predicted by a narrow range of depths and increased spatial CV (Table 20). In the behavioral experiments, *G. deflectus* did not react to changing water levels (Table 25), a result consistent with a species found in deeper water where fluctuating water levels would not be as important. These results supported those of Pip (1985) who also reported that *G. deflectus* was found in habitats where seasonal variation was reduced, and of Clarke (1981) who reported that it was found in permanent habitats.

Gyraulus deflectus had significantly higher abundances per section in 1998 compared to 1997 (Table 2). This result was primarily due to the increase observed in sections that had lower water levels in 1998 (Figure 30). This may have been a delayed response to the high water levels in 1997. Since *G. deflectus* was found in deeper water, the lower water levels in 1997 may have been conducive to high recruitment which manifested itself in the 1998 population. Supporting this conclusion that the population increase was a lagged response, in sections that remained the Same in 1998, abundance remained at high levels and did not significantly change from 1997 (Figure 30).

I followed the nomenclature of Burch and Jung (1992) and counted both hirsute (*G. hirsutus*) and non-hirsute forms as one species, *G. deflectus*. Both forms were present in the sampled coastal wet meadows.

Gyraulus parvus. *Gyraulus parvus* did not move in response to changing water levels and had a low tolerance for desiccation (Table 25, Figure 31). The abundance of *G. parvus* remained the same in 1997 and 1998 (no significant difference, Table 2), there was no difference in Lower and Same sections (Figure 30), *G. parvus* was common in cores from Dry sections (Figure 29), and there were no predictors in either year (Table 20). This was also consistent with the behavioral response, but its low desiccation resistance suggested that *G. parvus* should be more common in deeper, permanent water. It was very clear that *G. parvus* populations were not affected by water level changes in the coastal wet meadows. *G. parvus* was a very small species (3-5 mm) and may be able to remain in shallower sections, despite the possibility of desiccation, because the periodic pooling in shallow depressions after rainfall was enough for these species to survive dry periods during drawdown events (i.e. because they are not actually exposed to a desiccating environment).

Planorbula armigera. There were no significant water level predictors of *P. armigera* abundance in the current study. In contrast, in laboratory experiments, *P. armigera* were highly desiccation resistant and moved to shallower regions in response to falling water levels (Table 25, Figure 31). Those results suggested that water levels may be important for this species and that it should be found in shallower, more variable sections. In the current study, *P. armigera* did increase in abundance from 1997 to 1998 (Table 2), was more abundant in Lower sections (Figure 30), and was found in cores in all Dry sections (Figure 29). This pattern was similar to that for *G. deflectus* and a lagged response in population increase from 1997 to 1998 may also be responsible for the observed changes.

Previous reports for the habitat of *P. armigera* varied widely. Pip (1985) found it more commonly in rivers (>2 m deep) whereas Clarke (1981) reported it from stagnant and heavily vegetated habitats. Coastal wet meadows, although more dynamic than stagnant, are similar to Clarke's description of the habitat requirements.

Planorbella trivolvis. The occurrence of *P. trivolvis* was explained by increasing minimum depth in 1997 and decreasing spatial CV in 1998 (Table 20). These both reflected deeper, more stable water levels. In contrast, the behavior experiments suggested that perhaps *P. trivolvis,* was adapted to more variable, shallower environments since they moved towards shallower water (Table 25), could resist desiccation for extended periods of time (Figure 31), and were more likely to bury themselves (Table 25). Because *P. trivolvis* was more likely to remain in deeper sections of the wet meadows, these responses may instead serve to decrease predation risk.

Planorbella trivolvis was often found on the bottom substrate, which was usually mucky, rather than on the vegetation as were the majority of other species (Boerger 1975, Burch and Jung 1992). In the coastal wet meadows such habitat was more common in the deeper sections where vegetation was less dense and the bottom was less covered by decaying vegetation (BEK: pers. obs.). Clarke (1981) reported that it was usually found in permanent water habitats.

Aplexa elongata. *Aplexa elongata* occurrence was predicted by high temporal CVs (Table 20) which indicated that populations of *A. elongata* were found in sections that were variable over time and that may have hydrology separated from Lake Huron. Hydrology that is less dependent on Lake Huron may show increased temporal variability due to variability in rainfall. Although not quantified, I observed water level changes that corresponded to heavy rainfall and short drought periods during regular visits to wet meadows where *A. elongata* was common. Desiccation studies showed that it was not very resistant to drying out and moved little in response to decreasing water levels (Table 25, Figure 31). Other researchers have found *A. elongata* in temporary habitats that dry seasonally (Baker 1928). The positive association with temporal CV suggested it could be found in temporary habitats, but the low desiccation resistance of the individuals in the current study required more permanent water levels. It was possible that the coastal wet meadows in which *A. elongata* were found generally had permanently standing water, from rainfall, regardless of the water level fluctuations of Lake Huron, and it was possible that in years with drought conditions and low water levels of Lake Huron, that these sections would dry out completely causing populations of *A. elongata* to become locally extirpated.

Fossaria obrussa. *Fossaria obrussa*, similar to *A. elongata*, was found in sections with a positive temporal CV (maybe influenced by rainfall) that remained permanently flooded (positive maximum depth) (Table 20). Previous studies suggested that *F. obrussa* was found in similar habitats and locations (at water's edge) to *F. parva* (Baker 1928, Laursen et al. 1992).

Amnicola limosa. Behavioral responses were not examined for *A. limosa* but it was found to be extremely susceptible to desiccation with no individuals surviving over 2 weeks (Figure 31). Those results suggested that *A. limosa* should be found in deeper, permanently flooded wet meadows. In the current study, it was associated with increasing minimum depths (Table 20) which supports the laboratory observations. These observations are also consistent with other researchers that reported *A. limosa* was a resident of permanent lakes and rivers (Clarke 1973, Pip 1985).

Ferrissia parallela. There were no significant water level predictors for *F. parallela*, the only ancylid (freshwater limpet) found in the current study. There are few reports of habitat preferences for *F. parallela* but Burch and Jung (1992) reported it from quiet waters (shallow lakes, ponds and ditches) in northern Michigan and Clarke (1981) stated that it was often found attached to cattail (*Typha* sp.) and bulrush (*Scirpus* sp.) stems, which was consistent with personal observations in the coastal marshes. The lack of response to water levels and its rarity in the wet meadows supported its primary habitat as a deeper water species (bulrush and cattail are found in deeper water).

Stagnicola elodes. Stagnicola elodes had no significant water level predictors in the current study. It was known to be very adaptable species, found in a range of habitats from temporary woodland ponds to more permanent water bodies (Clarke 1981, Laursen et al. 1992). The low frequency and abundance in the current study could reflect the temporary nature of this species in the coastal wet meadows and it may be more common in the deeper, emergent marsh. Because of its known adaptability, it was unclear why it should not also be able to flourish in the more variable and temporary wet meadows.

Conclusions

The objective of this study was to examine the role of water level, independent of other environmental characteristics, in structuring the snail communities in coastal wet meadows. As suggested by their responses in laboratory experiments, the occurrence of snails in coastal wet meadows can be partially explained by the six variables examined. Mean depth was the most common predictor, explaining in part, four snail variables. Variation in the water levels spatially, as well as through time, were significant predictors for three snail variables each. Increasing minimum depth also explained three snail variables. Finally, range of depth was a significant predictor for two variables and increasing maximum depth for one snail variable. Although significant, the variables examined in this study only explained a small amount of the variance in the snail data. However, these results suggested that in part, the response to water levels by coastal wet meadow snails was based on relatively simple and immediate responses made by the snails.

CONCLUSIONS

My research has confirmed the complex nature of factors affecting the distribution and abundance of aquatic snails, and suggested that many factors operating at different scales (see Lodge et al. 1987) combined to determine snail community structure. As the first comprehensive study of aquatic snails in Great Lakes coastal wet meadows, I have identified several consistent variables that were associated with one or more snail species, although the causal mechanisms of many remain unconfirmed. Here I synthesize the results of research examining within-patch and surrounding landscape characteristics and the effects of water level changes, by presenting a conceptual model describing the identified determinants of snail community structure. It is hoped that this model will provide a guide for further research aimed at investigating the mechanisms behind the observed patterns.

The Model

The conceptual model (Figure 33) was based on water depth as the single most important factor affecting snail distributions. Many of the factors in the model were directly or indirectly related to water depth. For example, bulrush marsh was associated with deeper water, whereas shrubs and hummocks were more common in shallower depths. In many cases, snail community associations with water depth were an indirect result of the water depth affecting the physical habitat, and a presumed differential response by snail species to the physical habitat. In addition to the indirect effects, some snails responded directly to changing water levels in laboratory experiments.

In order to describe the factors affecting the snail community structure, I separated the apparent depth gradient into three relative categories: deep, shallow and

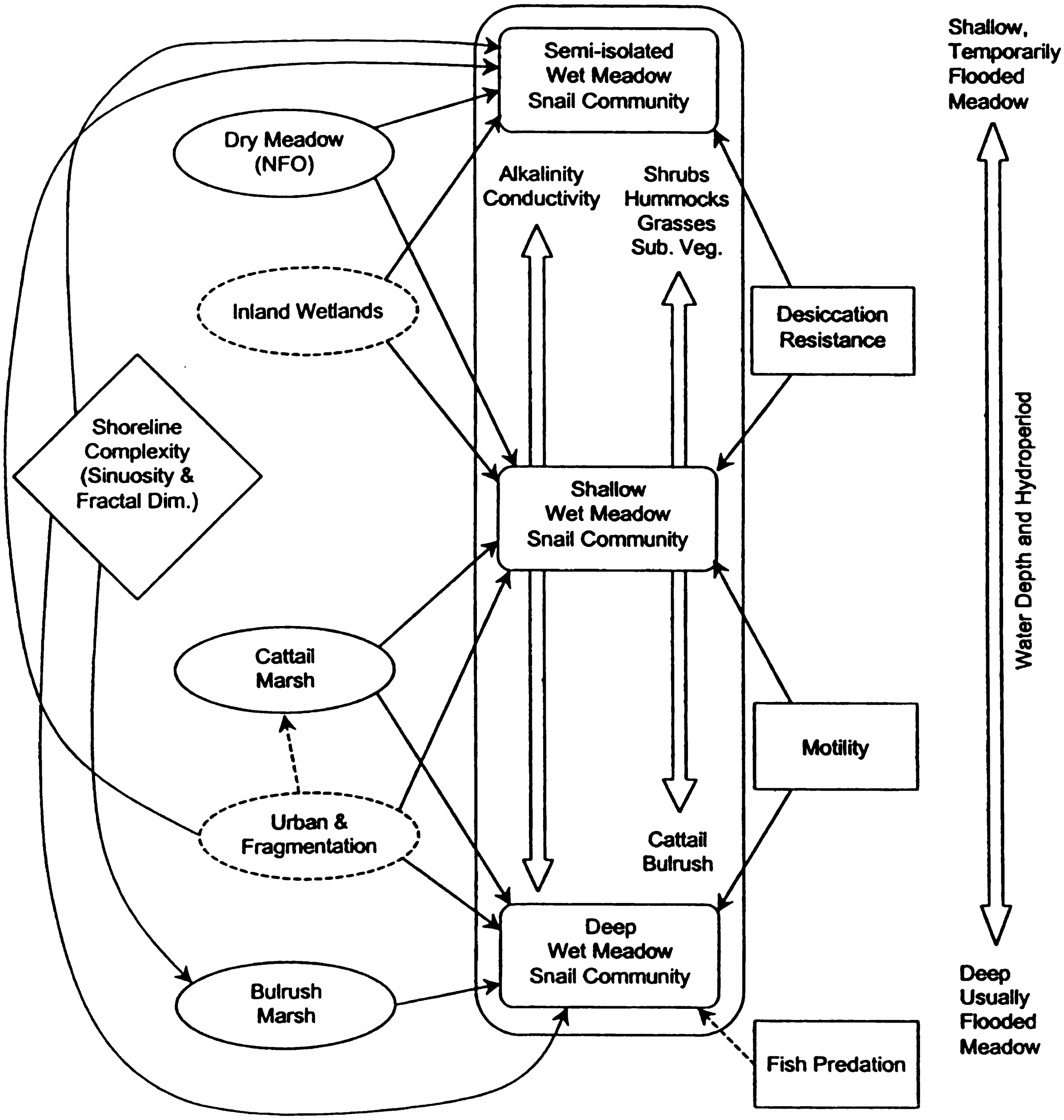

Figure 33. Conceptual model of the determinants of snail community structure in a Great Lakes coastal wet meadow complex (large box). Block arrows indicate chemical, structural, and plant gradients within a wet meadow gradient. Solid arrows are significant associations observed in the present study whereas dotted arrows are weaker or implied associations.

semi-isolated wet meadow snail communities (Figure 33). However, it is important to realize that these categories represent a continuum, rather than discrete changes in the snail community. Based on my results, I assigned the snails and their relative abundance to each wet meadow category (Table 27, Figure 34).

Deep Wet Meadow Snail Community

The deep wet meadow snail community was influenced by its proximity to the open water of Lake Huron and the deeper emergent marsh vegetation, especially bulrush (*Scirpus* spp.) (Figure 33). In all but the most extreme cases, it would remain permanently flooded. Snails common to this area were those that were intolerant of desiccation in experiments and in cores examined from dry sections of wet meadows (Figure 34).

Within-patch characteristics of the deep wet meadow included lower alkalinity and conductivity when compared to shallower depths. These values of the deep wet meadow were expected to be closer to the values of the open water in Lake Huron because of increased mixing, and previous studies suggested that this may affect the invertebrate community (Cardinale et al. 1997, 1998). The deep wet meadow also included a higher frequency of bulrush relative to shallower depths. *Ferrissia parallela* and *Stagnicola elodes* showed a significant association with the bulrush, most likely as a preferred substrate for attachment (Clarke 1981). It is possible that decaying bulrush enriched the detrital base and could have affected other snail species (Brown 1982).

Bulrush and cattail marshes adjacent to and nearby the wet meadows were associated with the snail community structure (Figure 33). Testing the mechanism for this association was beyond the scope of the present study, but three hypothesized

Table 27. Great Lakes coastal wet meadow snail community structure in three categories of wet meadows. N = combined number of snails collected in 1997 and 1998. '*' = uncommon, '**' = common, and '***' = very common.

Species	N	Wet Meadow Category			"Habitat Preference"
		Semi-isolated	Shallow	Deep	
Pulmonata					
Physidae					
Physa gyrina	9520	**	***	*	Shallow and semi-isolated wet meadows
Aplexa elongata	377	***	*		Semi-isolated wet meadows
Planorbidae					
Gyraulus deflectus	7831	**	***	***	Generalist, more connected wet meadows
Gyraulus parvus	9446	**	**	**	Generalist, no preference
Gyraulus cristus	1		*		Too few data for definite preference
Planorbula armigera	6603	***	***	**	Generalist, shallow and semi-isolated meadows
Planorbella trivolvis	506		**		Shallow wet meadows
Planorbella campanulata	49	*	*		Shallow and semi-isolated wet meadows
Promenetus exacuous	42			*	Deep, uncommon in wet meadows
Lymnaeidae					
Stagnicola elodes	13			*	Deep, uncommon in wet meadows
Fossaria obrussa	171	*	*	*	Generalist
Fossaria parva	755	*	**	*	Generalist, frequent in low abundance
Acella haldemani	1			*	Too few data for definite preference
Ancylidae					
Ferrissia parallela	27			*	Deep, uncommon in wet meadows
Prosobranchia					
Hydrobiidae					
Amnicola limosa	33			*	Deep, uncommon in wet meadows
Amnicola walkeri	4	*			Too few data for definite preference
Pyrgulopsis lustricus	2		*		Too few data for definite preference
Bithyniidae					
Bithynia tentaculata	154	*	**		Shallow, uncommon in wet meadows
Valvatidae					
Valvata tricarinata	2			*	Too few data for definite preference

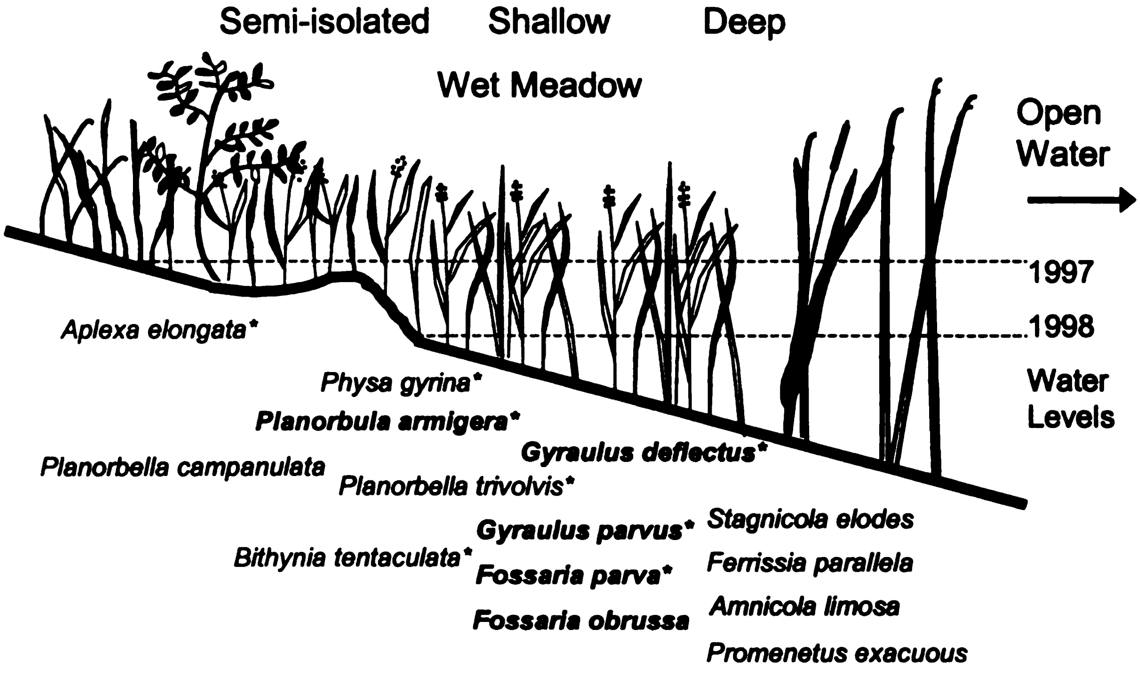

Figure 34. Schematic cross-section of a coastal wetland along the northern Lake Huron shoreline showing the three wet meadow snail communities (semi-isolated, shallow and deep) described in a conceptual model (Figure 33). Relative placement of snail species follows Table 27; species in **bold type** are generalists. Species with '*' are able to tolerate drying as water levels decline (see Figures 29 and 31). Approximate water levels are indicated for 1997 and 1998.

mechanisms may be postulated. Bulrush and cattail marshes may have provided a source of snail species (e.g. *F. parallela*) that were not as commonly found on wet meadow vegetation. The bulrush and cattail marshes may have limited the wave action from Lake Huron, preventing thorough mixing and altering water chemistry (see Cardinale et al. 1997) and/or the wet meadow vegetation characteristics. Finally, larger fish from the deeper emergent marsh may have selectively preyed on susceptible snail species that were found in the deep wet meadow.

The location of the wet meadow within coves or sheltered bays (i.e. high sinuosity or fractal dimension) decreases the hydraulic effects of Lake Huron and generally allows for greater wetland development (Keough et al. 1999). Therefore shoreline complexity may have affected snail community structure both directly by affecting the development of wet meadow characteristics, and indirectly by the development of bulrush marshes and its effects as described above.

When Lake Huron water levels decline, as was the case from 1997 to 1998, snail motility may play a role in structuring the snail community (Figure 33). Species such as *Physa gyrina* were able to move with the declining water levels from the shallower wet meadows. Snails that may have initially been more common in shallow depths could become more abundant in the deeper wet meadow as the lake levels decline.

Shallow Wet Meadow Snail Community

The shallow wet meadow region lies between the terrestrial environment and the permanently flooded deep wet meadow. In some years all or part of the shallow wet meadow may dry out from seasonal or longer-term water level declines.

Higher alkalinity and conductivity levels in the shallow wet meadows probably resulted from the decreased volume of water, lower dilution of salts from the limestone/dolomite bedrock and higher evapotranspiration rates, combined with limited mixing with Lake Huron water. *Aplexa elongata* and *Fossaria obrussa* were the only two species closely associated with increasing alkalinity (and the correlated calcium levels) and conductivity in 1997 and there were no associations in 1998. As Lodge et al. (1987) points out, water chemistry was not likely to influence snail distributions within regions. The alkalinity (calcium) levels present in the shallow wet meadow were well above the threshold level for limiting snail presence/absence. Therefore the higher levels in the shallow wet meadow more likely affected snail abundance rather than distribution.

There was an association between several snail species and the higher density and frequency of grasses, hummocks, submersed vegetation and shrubs that were found in the shallow wet meadows. Hypothesized mechanisms for these observations included the increased diversity of specific plant-snail associations or an increased surface area for growth of the microbially-rich biofilm (see Brown and Lodge 1993). The structurally complex habitat coupled with the shallower water levels may also have reduced the rates of predation from larger predators such as fish. Additionally, the structural complexity and the resulting shading and temperature differences may have affected the biofilm community, oxygen availability and snail growth rates.

Adjacent landscape features associated with the snail community were cattail marshes and non-forested openings (e.g. dry, upland meadows). The mechanisms behind the cattail marsh association were probably similar to those discussed above for the deep wet meadows. The positive association of dry meadows with the snail community may be affected by the buffering effects from nearby terrestrial systems (Karr and Schlosser

1978). The exact nature of the interface between the terrestrial systems and the shallow wet meadows deserves more research.

Because the shallow wet meadow snail community may be exposed to short- or long-term desiccation events caused by seasonal or annual changes in water level, interspecific differences in motility and behavioral or physiological mechanisms for resisting desiccation may have affected snail community structure (Figure 34). Some species (e.g. *P. gyrina*) may move to deeper water as the water levels decrease, whereas others may have been able to resist desiccation for long periods of time (at least 12 weeks in laboratory experiments and longer from cores taken in dry wet meadows). When water levels rise again, the snail community will be dominated by desiccation-resistant species (Figure 34) until others can re-colonize from adjacent habitats. Nearby inland wetlands (forested and emergent marshes) were included in two models, possibly reflecting their role as sources for re-colonization. Investigations of these source communities and their spatial relationship with specific wet meadows may further help to elucidate their role in the re-colonization of coastal wet meadows after desiccation events.

Semi-Isolated Wet Meadow Snail Community

The semi-isolated wet meadow category includes wet meadows that were partially separated from adjacent wetlands and Lake Huron. The separation may have been from natural causes such as sand ridge formation in exposed, simple shorelines (Figure 33) or from anthropogenic influences such as roads (see Table 1). My results and observations suggested that because of their decreased connectivity with Lake Huron, these wet meadows experienced greater water level fluctuations due to rainfall and a potentially increased likelihood of drying out during drought periods. However, I did not design my study to address these mechanisms directly and specific investigations into the hydrological link between rainfall and water levels in many of these wet meadows may provide new insights.

The snail community in these semi-isolated wet meadows was influenced by many of the same factors as the shallow wet meadow community (Figure 33). However, because of their limited connectivity to the deeper wet meadow and Lake Huron, they were probably more affected by their interface with the terrestrial environment, and the effects of periodic drawdowns (Figure 34). The snail community was composed of snails with high desiccation resistance or with the ability to disperse rapidly into the wet meadows following a desiccation event.

Human Influences on Great Lakes Coastal Wet Meadows

Because of increased use and development along the northern Lake Huron shoreline and the number of roads that were located adjacent to or through coastal wetlands, their impact on the wetland flora and fauna was of special concern. My results suggested that at the current time, these impacts were having limited or no effect on the aquatic snail community. Two areas of potential concern for future investigations were highlighted by my research: the hydrologic isolation of wet meadows by road construction and the impacts of fragmentation of wetlands by continued development.

Approximately half of the wet meadows examined in the present study were situated adjacent to or were bisected by a road. Wet meadows bisected by roads may have experienced altered hydrological regimes as they became isolated from Lake Huron. As discussed above, isolation influenced the snail community structure by increasing the abundance of species that could tolerate desiccation and changes in the water chemistry and vegetation. However, a direct examination of roads in the surrounding landscape context showed no negative (or positive) associations with roads. Because of the change in hydrology, roads have been inferred to affect many aquatic communities (see Trombulak and Frissell 2000). Therefore continued monitoring of wet meadows adjacent to roads is important to document any impacts that do occur.

A suite of variables that indicated human disturbance was included in a statistically significant model in 1998 (see *Chapter Two*). The variables included increasing cattail marsh, urban contexts, number of patch interfaces and patch types. Development along the northern Lake Huron shoreline consisted largely of the building of new homes and vacation properties. The development of these urban patches within the more contiguous shoreline increased the fragmentation (Forman 1995) of both aquatic and terrestrial systems (indicated by the increased number of patch interfaces). Also, cattail marshes may increase after human disturbances and introduction of nutrients such as those produced by improperly located septic systems (Mitsch and Gosselink 1993).

Overall, my results indicated the importance of both the within-patch characteristics of coastal wet meadows as well as their surrounding context. The structure and vegetation within a wet meadow had the greatest effect on the snail community structure with a minor role for water chemistry. Wet meadows within larger wetland complexes that included adjacent bulrush and cattail marshes and that were buffered on the terrestrial side by meadows also had more diverse snail communities. Maintaining this context will be important as the northern Lake Huron shoreline continues to be developed for human use.

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