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ABIOTIC AND BIOTIC INFLUENCES ON AQUATIC INVERTEBRATE COMMUNITY STRUCTURE IN A LAKE HURON COASTAL WETLAND

By

Joseph Paul Gathman

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ABSTRACT

ABIOTIC AND BIOTIC INFLUENCES ON AQUATIC INVERTEBRATE COMMUNITY STRUCTURE IN A LAKE HURON COASTAL WETLAND

By

Joseph Paul Gathman

Shoreline wetlands of large lakes are ecotones between terrestrial and aquatic systems, and many ecological characteristics (e.g. water chemistry, vegetation) vary along the lake-to-upland elevation gradient in these systems. In Great Lakes coastal wetlands, this variation is enhanced by annual and multi-annual changes in water level. Aquatic animal communities are likely to respond to this spatial variation in habitat conditions, but few studies have sought such faunal variation or its causes. In this study I collected animal community data along the elevation gradient in a northern Lake Huron coastal wetland over a 3-year period during which the water level changed dramatically.

Replicate samples were collected along the slope at 10 cm elevation intervals, covering a 60 cm elevation range in a ~120 m horizontal distance. In the first year, multivariate analysis revealed that animal community composition varied gradually with elevation, and seasonal changes appeared to result from up-slope migrations of some animal taxa. During the second year water levels were over 30 cm higher, and in the third year water level dropped back toward initial levels. Most insect taxa were able to respond rapidly to these changes, while many non-insects migrated more slowly. These differences led to increasing invertebrate densities and changes in community composition at different points on the gradient, and led to a loss of wetland diversity, as many rare taxa declined and generalist animals thrived. Flooding duration was signficantly correlated with densities of the most common invertebrate taxa.

Because predator densities also varied over the gradient, I ran field experiments to determine whether they (small fish and larval dragonflies) partly caused the observed faunal differences over space and time. Fish reduced invertebrate densities, favoring certain generalist taxa, while dragonfly effects were less dramatic. Taxon-specific effects suggested that predation can prevent some prey taxa from occurring at gradient points where predators are dense. Results led to a conceptual model of temporal and spatial shifts in flooding and predation controlling animal community composition in coastal wetlands.

To my wife, Denise

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TABLE OF CONTENTS

CHAPTER 3

BIOTIC CONTROLS IN AN ABIOTICALLY-VARIABLE HABITAT: EXPERIMENTS ON THE EFFECT OF PREDATORS ON A GREAT LAKES COASTAL WETLAND AQUATIC INVERTEBRATE COMMUNITY 98

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Great Lakes coastal wetlands have received relatively little research attention, despite their recognized importance as breeding and feeding habitats for fish (Brazner 1997, Jude and Pappas 1992, Liston and Chubb 1986), waterfowl (Prince et al. 1992), and migrating songbirds (D. Ewert, pers. comm.). This oversight may be because these systems "fall through the cracks", not fitting into the traditional definitions of wetland or lake habitats. However, a special symposium (Prince and D'Itri 1985) and a 1992 special issue of the Journal of Great Lakes Research each focused on Great Lakes coastal wetlands, indicating a growing recognition of the need for more research on these systems. While all components of these wetlands require much more work, Krieger (1992) noted that invertebrate communities in particular had been almost completely ignored. These communities are especially diverse and inhabit spatially-complex habitats compared to non-wetland Great Lakes communities, and are likely affected by a variety of environmental factors such as water chemistry gradients, lake connectivity, wave exposure, and predators (reviewed in Gathman et al. 1999). In the last two decades, invertebrates in a few coastal wetlands have received attention (e.g. Duffy and Batterson 1987, McLaughlin and Harris 1990, Brady 1992, Brady and Burton 1995, Cardinale et al. 1997), but most other sites have remained unstudied.

Great Lakes coastal wetlands are like other wetlands in many respects, but their position at the interface between uplands and large lakes subjects them to a unique suite of water movements and water-level changes that appear to determine many biotic characteristics. These hydrologic factors include waves from the open lakes and large ships, storm surges, multi-annual and annual water level changes resulting from climatic variation, and short-term seiche-induced changes. Coastal wetlands only develop where shoreline morphology offers at least partial protection from the direct force of waves and storm surges. Maynard and Wilcox (1997) classified Great Lakes coastal wetland types based on shoreline form and, implicitly, exposure to waves. The turbulent mixing caused by waves can affect factors that influence benthic invertebrates such as vegetation, substrate structure (Cole and Weigman 1983) and water chemistry (Suzuki et al. 1995, Cardinale et al. 1997). Unlike wave-induced turbulence, water-level changes affect all lake-connected coastal wetlands and are important in determining vegetation zonation (Minc 1996) and wetland area (Burton 1985), though their effects on aquatic animals have not been determined.

Over 50% of pre-settlement coastal wetlands of the Great Lakes have been lost to human uses with losses of the more vulnerable habitats, such as wet meadows, approaching 100% in certain areas (Brazner 1997, Comer et al. 1995, Jaworski and Raphael 1978). The Les Cheneaux Islands area in Northern Lake Huron (the location of the present study) has largely escaped this fate so far, so it is one of the few remaining Great Lakes shoreline regions with a wealth of coastal wetland acreage that has been left mostly intact. However, other than fairly recent vegetation surveys (Albert et al. 1987, Minc 1996), no formal studies including Les Cheneaux coastal wetlands have been published. This is unfortunate because wetlands in this region are currently threatened by increased commercial and residential shoreline development, higher human population density, more inshore boat traffic, and invasions of several exotic plant and animal species.

In the studies presented here, I focused on the ecotonal nature of a northern Lake Huron coastal wetland, emphasizing animal community variation along a continuum from a relatively-deep emergent marsh "lake-like" habitat to a wet meadow "wetland-like" habitat at the wetland-upland border. In Chapter 1, I test the hypothesis that animal assemblages vary significantly and gradually along this continuum, and argue that variation in flooding regimes is probably the most important influence on the gradient in community composition. I also present evidence that animal movements along the gradient are important, but that many animal taxa move very little, so community composition along the gradient varies over the course of a summer season.

In Chapter 2, I focus on a natural "experiment" in flood-regime alteration. A substantial increase in Lake Huron water level in the second year of the study presented an opportunity to study the effects of a change from temporary to year-round flooding in the wet meadow, while positions of vegetation zones changed little. Animal changes in the wet meadow community were much greater than in lower-elevation wetland zones, so I again argue for the importance of flooding regime and animal movements. However, it was also apparent that recent flooding history was important, as invertebrate assemblages varied depending on how long a given wetland area had been flooded.

During the three years of water-level change, I also observed changes in distributions of the major aquatic predators in the wetland. Because these changes co-occurred with invertebrate community changes, I sought to determine whether variation in predation pressure may have been an important factor contributing to the observed community changes. Chapter 3 describes the results of field experiments in which I manipulated predators in mesocosms to observe their effects on their prey. I examine the results in light of observations presented in previous chapters, and then suggest a modification of a literature-derived conceptual model of abiotic and biotic factors determining aquatic invertebrate community structure. Finally, I conclude with a summary of all results and their implications.

Chapter 1

FAUNAL VARIATION ALONG A FLOODING REGIME GRADIENT IN A LAKE HURON COASTAL WETLAND: AQUATIC COMMUNITY STRUCTURE AND SEASONAL CHANGES

INTRODUCTION

Coastal wetlands are important habitats for many game and forage fish (Jude and Pappas 1992), waterfowl (Prince et al. 1992), and migrating songbirds (D. Ewert, The Nature Conservancy, Michigan Chapter, pers. comm.), but losses of coastal wetland acreage have been large (Brazner 1997, Comer et al. 1995, Jaworski and Raphael 1978). Despite the importance of these systems, advances in knowledge of Great Lakes coastal wetlands have not kept pace with studies of many other wetland types (Krieger 1992). Similarly, work on the ecology of invertebrates and fish in wetlands has lagged behind achievements in areas such as hydrology and vegetation dynamics (Batzer and Wissinger 1996), so knowledge of coastal wetland fish and invertebrate ecology is based on the work of only a few authors. Krieger (1992) cited only two studies (Duffy and Batterson 1987, McLaughlin and Harris 1990) from the upper Great Lakes in his review of coastal wetland invertebrate ecology , but at least one wetland in Saginaw Bay has received considerable attention since that time (Brady and Burton 1995, Cardinale et al. 1998).

Given the paucity of studies on coastal wetland fauna, we know very little about the most basic environmental influences on these communities. However, it is becoming apparent that some coastal wetland processes vary spatially along the substrate-elevation gradient from the upland/wetland boundary down to the lower wetland interface with deeper pelagic waters. Such factors as water quality (Cardinale et al. 1998) and vegetation (Minc 1996) vary along this gradient, and may influence animal communities. However, these factors are ultimately controlled by hydrologic factors (water depth, water movements, and flooding regime), so any faunal variation along the gradient is likely to be caused by hydrologic variation, at least indirectly.

Hydrology in coastal wetlands is dynamic and very influential on wetland structure. As in most wetlands, coastal vegetation occurs in distinct zones along elevation gradients in response to spatial variation in flooding regimes and soil moisture (Mitsch and Gosselink 1993, Minc 1996). Many Great Lakes coastal flooding regimes show a distinct spatial pattern, progressing from permanently-flooded lower elevations to temporarily-flooded high-elevation zones (reviewed in Gathman et al. 1999). The occurrence of temporary flooding regimes in these high zones is ensured by a fairly predictable seasonal pattern in lake levels. The annual cycle begins with low water levels in mid-winter, which rise through the spring as snow-melt water and spring rains run into the lakes. The highest annual levels are observed in mid-summer, when reduced precipitation and high evaporation and transpiration combine to cause a net water loss and water levels begin their autumn decline. As the water rises, it floods progressively higher-elevation wetland area, and as it falls, these areas are drained. The resulting wetland flooding-regime gradient was of particular interest to Krieger (1992), who called for researchers to look for invertebrate community variation along the gradient, because he expected community composition to vary in direct response to variation in flood duration found there.

Many authors agree that water level fluctuations (flooding regime) are key structuring features of wetlands (Wiggins et al. 1980, Williams 1987, Krieger 1992, Mitsch and Gosselink 1993, Schneider and Frost 1996), and may even be the most influential factor (Batzer and Wissinger 1996). Water depth, water and sediment temperatures (Williams 1987), plant communities (Voights 1976, Zedler 1981), and detritus quality (Nelson et al. 1990, Barlocher et al. 1978) are all strongly influenced by flooding regime, and may influence wetland fauna. Other potential influences on fauna, such as turbidity and conductivity, are likely to be affected by evaporation and, conversely, by dilution from water inputs (Williams 1987). Furthermore, aquatic animals are directly affected by the habitat area increases and reductions resulting from water fluctuations (Williams 1987, Wiggins et al. 1980).

Whether through direct or indirect mechanisms, flooding regime is important in determining wetland animal communities. Wiggins et al. (1980) found that temporary pools were inhabited by a distinct assemblage of macroinvertebrates which was less diverse than that of permanent waters. They categorized the genera of this assemblage according to life history adaptations to temporary aquatic environments, such as drought resistance and active dispersal, which permanent-water animals apparently lacked. Similarly, Williams (1987) found "relatively little overlap" in species between temporary and permanent waters.

Collinson et al. (1995), Jeffries (1994) and Hanson and Swanson (1989) found that invertebrate species assemblages varied with flooding regime, and these and other studies (e.g. Bataille and Baldassarre 1993, Neckles et al. 1990) found community composition differences even at higher taxonomic levels. These apparent higher-taxa habitat preferences were consistent across several studies, suggesting habitat constraints imposed by body plan or other relatively-immutable similarities among related species. For example, microcrustaceans, Hydracarina, Coleoptera, migrant Hemiptera, Gastropoda, and certain families of Diptera were particularly abundant in temporary ponds, while Porifera, most Megaloptera, and many families of Plecoptera, Odonata, and Trichoptera were excluded from these systems.

While a distinction between fauna of isolated permanent and temporary waters is well supported, such a distinction has not been sought in coastal wetlands which consist of permanent and temporary zones that are directly connected. If flooding regime is an important controlling factor in these systems, it is reasonable to expect that the fauna of higher-elevation temporary zones differs from that found in permanent emergent marsh zones. On the other hand, the relative ease of migration between these broadly-connected zones may preclude strong faunal differences, so investigation of this possible spatial difference in communities is needed.

In this study, I examined the invertebrate and fish community along a flooding-regime gradient in a single summer season. Rising water levels in the study site caused progressively later inundation in successively higher-elevation wetland zones, in contrast to low elevations, which were flooded throughout the year. I hypothesized that the faunal community would gradually and unidirectionally vary from low to high elevations as a result of differences in life-history and behavioral adaptations to temporary water conditions. Further, I expected that animal taxa initially found at low elevations would migrate up-slope as the advancing water line made available newly re-flooded habitat.

I tested the following hypotheses: 1. the community can be described as a multivariate faunal "gradient" corresponding more to elevation (hence, flooding regime) than to specific water depths; 2. the gradient deteriorates over the season as immigrating fauna mix into the temporary-zone community; 3. the community varies gradually from low elevation to high, rather than in discrete steps corresponding to plant zones.

METHODS

Study site

The study area was located on the northern shore of Lake Huron in Mackinac Bay, which was immediately east of Hessel, Michigan (Figure 1.1). A two-lane, paved rural highway formed the northern upland border of the site. The site was characteristic of wetlands in the area, with a diverse plant community exhibiting typical wetland vegetation zonation (Figure 1.2). Starting from the open water, this zonation began with a deep-marsh community dominated by hardstem bulrush (*Scirpus acutus*) and interspersed with yellow water lily (*Nuphar* sp.), pickerelweed (*Pontedaria* sp.), arrowhead (*Sagittaria* sp.), and a variety of submergent plants. Moving up-slope the deep-marsh community gave way to a transition zone, which consisted of a dense band of cattail (mostly *Typha* *angustifolia*) and spike rush (*Eleocharis smallii*) richly interspersed with species from adjacent zones. This zone was relatively narrow and was succeeded by wet meadow at higher elevations. The wet meadow was dominated by several sedge species of the genus *Carex* (especially *C. lasiocarpa* and *C. aquatilis*), and included a diverse assemblage of graminoid and broad-leaved facultative wetland plants. Finally, at the upper edge of the wetland, several shrub and grass species were abundant among the sedges, which were dominated by *C. stricta*, a hummock-forming sedge.

Sample collection and processing

In May, 1996, I established five replicate transects in the site running from high-elevation wet meadow down to permanently-flooded emergent marsh (Figure 1.3). I selected transect positions that were approximately evenly spaced, while avoiding either of two small streams running through the site from upland to lake. Water depth was not a reliable elevation measure because seiche activity caused constant water level fluctuations over a range of several cm, and because the wet meadow was not yet flooded. Instead, I used a laser level for elevation measurements, establishing six sampling stations on each transect at 10 cm elevation intervals so that a range of six flooding-regime zones would be sampled (Figure 1.2). Stations were numbered 1 through 6, from highest-elevation to lowest. The highest stations, 1 and 2, were in the wet meadow, while 3 and 4 were in the cattail-dominated transition zone, and 5 and 6 were in the deep emergent marsh. Transect 4 was different from the others in that it ran through a break in the cattail stand, so the plant community around Station 3 was sedge-dominated wet meadow, and that around Station 4 was a bulrush-dominated deep marsh community.

Transect lengths, from Station 1 to Station 6, averaged 120 m, with inter-station distances averaging 24 m. Because stations were selected based on elevation, horizontal distances between them varied. In the transition/cattail zone, where substrate slopes were relatively steep, sample stations were closer together than elsewhwere (average ~13 m between Stations 3 and 4, all transects). I also installed a staff gauge at Station 6 of the middle transect to monitor seasonal water-level changes, using the Station 6 substrate as a benchmark of 0 cm depth.

To sample animals, I used activity traps made from 2 L plastic bottles placed horizontally in the water on the substrate. These traps were constructed by cutting the bottom off one bottle, then cutting the top off a second bottle and inserting it, narrow end first, into the open bottom of the other bottle and securing the two pieces with staples. The result was a funnel (created by the inserted, inverted top) leading into the bottle, with a screw-on cap at the opposite end of the bottle for trap emptying. I placed traps ten meters from each sample station, in a perpendicular direction from the transect and always on the same side. Traps were held in place by flagged dowels that passed through plastic loops (made from cable ties attached to the trap sides) and into the ground. After 24 hours I emptied the traps to prevent specimen deterioration, and re-set them in the same location. After a second 24-hour period I collected the traps, poured the contents through a 250 μm mesh sieve, euthanized fish in MS-222, and preserved all specimens in 95% ethanol.

Data collection and analysis

To identify invertebrates, I used Merritt and Cummins (1996), Pennak (1989), and taxon-specific keys for lower taxonomic levels, when appropriate. Fish identification followed Hubbs and Lagler (1967). I identified fish to species and invertebrates to the lowest taxonomic level possible with a dissecting scope. I attempted to identify invertebrates to the genus level, but this was not possible or feasible in many cases because the majority of individuals were very immature, lacking some key characters. For each sample, I counted all individuals of each taxon, then calculated the relative abundance of each taxon as a proportion of all animals in the sample. Data were decidedly non-normal and heteroscedastic because of a high frequency of zero counts. This problem appeared to be an artifact of the sampling method because many traps with fish and other predators in them may have suffered from high predation losses, and because activity traps are a "passive" sampling method that depends on voluntary trap entry. The data could not be transformed to meet the assumptions of parametric statistical methods, so I used methods with less-restrictive assumptions, as described below.

Gradient analyses

To determine whether whole communities varied gradually over the elevation gradient, I combined data from all months and from all five replicate samples at each elevation (for a total of 6 multivariate observations, 1 per elevation), then conducted correspondance analysis (CA) on the multivariate data set using SAS software, procedure CORRESP. I chose this ordination method because: 1. it was designed for gradient analysis of count data; 2. it assumes unimodal (rather than monotonic) distributions of taxa along environmental gradients; 3. it is not constrained by assumptions of multivariate normality; and 4. it allows simultaneous analyses of locations (elevations) and taxa. I examined the resulting two-dimensional plot, looking for a numerical ordering of elevations along the first axis, which would indicate a community gradient corresponding to the elevation gradient. Next, I plotted the positions of individual taxa in the two-dimensional display, and examined the diagnostic measures from the CA output. These measures summarize the roles played by each taxon and each elevation in each CA dimension, so each taxon and elevation are assigned a set of diagnostics for every dimension. The number of dimensions is 1 less than the number of elevations or taxa, whichever is lower. In this case, there were 6 elevations (much fewer than the number of taxa), so there were 5 CA dimensions. The "Partial Contribution" measure in SAS corresponds to Greenacre's (1984) "CRT", and represents how much a taxon or elevation contributed to the total inertia of the dimension, i.e. the degree to which variation in that taxon or elevation corresponded to variation in the dimension. The "Squared Cosine" in

SAS corresponds to Greenacre's "COR", and represents how much of the variation within a taxon or elevation was represented in the dimension, i.e. the degree to which a taxon's or elevation's variation is accounted for in the dimension.

I also ran correspondance analyses on two other aggregations of the data. First, I separated all data by month, and aggregated the five replicate samples at each elevation within each month (6 multivariate observations per analysis). Analyses of these individual data sets resulted in separate ordinations for each month from May through August, which allowed me to determine whether a faunal gradient occurred during individual months. Second, I aggregated samples from the entire summer by water depth, regardless of elevation, so May's Station 4 samples were grouped with June's Station 2 samples, and Station 1 samples from July and August because all of these were taken in water approximately 10 cm deep. The resulting ordination of depth groups allowed assessment of whether these groups were numerically ordered along the first axis, suggesting a strong community response to water depth changes.

To explore distributions of individual taxa and their temporal changes, I examined all data graphically, plotting taxa abundances and relative abundances against elevation, depth, and plant zone for individual months and for all months combined. I then tested whether taxa abundances significantly varied by elevation (station), water depth, plant zone, and month. Because the data could not be effectively transformed, as explained above, I could not reliably use regression analysis to examine animal distributions along the elevation gradient, as is common in direct gradient analysis. Given the data structure, I usually used the non-parametric Kruskal-Wallis test followed by a graphical examination of taxon abundances by each independent variable that produced a significant result. Only a few variables (e.g. total abundance) could be effectively transformed to meet assumptions and allow the use of parametric methods. I used 90% α levels as the standard for hypothesis tests because of the above-mentioned high within-group variances.

To examine animal distribution changes over the sampling period, I calculated mean elevation-gradient positions for all taxa during each month. This involved a weighted averaging method in which I calculated the following for each taxon on each transect:

$$GP = \frac{\sum_{i=1}^{6} i \times N_i}{\sum_{i=1}^{6} N_i};$$

where GP=gradient position, i=sample station number, and N_i=total abundance of the taxon at station i. The resulting "gradient position" was the abundance-weighted mean elevation (using sample station number as an arbitrary elevation index) where the taxon in question occurred. The integer values used for sample station identifications served as effective elevation indicators because the physical gradient that they depicted was measured in equal intervals of elevation rather than horizontal distance. Performing GP calculation for each transect resulted in five replicate mean gradient positions (1 per transect) for each taxon. I then used simple linear regression of gradient positions vs. month (thus 5 replicates per month for four months) to determine whether the gradient position for each taxon changed unidirectionally over the course of the sampling season.

RESULTS

Water level changes and wetland flooding

In early May, when I first set transect positions and the depth gauge, the water line was near the upper edge of the transition zone, where I placed Station 3 on each transect. This water level corresponded to an initial reading of 30 cm on the Station 6 gauge, so Station 5 was under 20 cm of water and Station 4 had a depth of around 10 cm, the operational limit for the activity traps. These depths were approximate averages, but continual seiche activity caused constant depth fluctuations. Seiche amplitudes were usually only a few cm except after storms, and depth changes were subtle and undetectable to the casual observer.

The water level increased fairly rapidly through June, rising nearly 20 cm and allowing trap placement at Stations 3 and 2 during the sampling period late that month (Figure 1.2). By the same time in July, the water had risen an additional 10+ cm, flooding Station 1, and stayed at that level through the August sampling period. The August flooding of Station 1 was not predicted because, on average, Lake Huron levels peak in late July and begin to drop shortly thereafter. The maintenance of high water flooded the wet meadow longer than expected, and presaged higher water levels in subsequent years.

Multivariate analysis: ordination by elevation

Correspondance analyis of the combined data from the six sampling stations resulted in a numerical ordering of the stations in two-dimensional ordination space (Figure 1.4). The combined inertias of the first two axes exceeded 69% of total inertia, indicating that the two-dimensional display represented 69% of the total variance in the data set that was accounted for by the analysis. The relative plotted positions of elevations were nearly identical whether family-level data were used or genera were substituted for family data when available. The numerical ordering of elevations indicated a gradual shift in community composition from the upper wet meadow (Station 1) through successively lower stations, to the deep emergent marsh at Station 6. Stations 3 and 4, in the cattail/transition zone, were relatively close together, indicating relatively greater similarity between samples collected at transition zone stations than between any other two stations.

A subset of the animal taxa collected contributed the most inertia to the creation of the first two ordination axes, as indicated by relatively high "partial contribution" parameters in the SAS CA output. The first axis primarily represented a distinction between the two wet meadow stations and Station 6 at the opposite end of the transects.

Three groups of taxa contributed most (contribution index > 0 in SAS output) to first-axis inertia. The first group consisted of several taxa that were strongly associated with the wet meadow stations, especially *Ilybius* (the dominant Dytiscidae beetle genus), early-instar Libellulidae dragonfly nymphs, Isopoda, Sphaeriidae clams, Planorbidae snails, and Nematoda. The second group included taxa that were strongly associated with the deep marsh throughout the season: larvae of *Trianodes* (the dominant Leptoceridae caddisfly genus), *Hyalella* (the dominant amphipod genus), young-of-year *Amia calva* (bowfin), and *Bufo* tadpoles (which only occurred in the early summer). Finally, the microcrustaceans and Chironomidae contributed to the axis because of their high abundances. These groups were somewhat more widespread over the gradient, but still showed associations with certain elevations. Chironomidae, Cladocera, and Copepoda abundances peaked in the lower wet meadow/upper transition zone (Stations 2 and 3), while ostracods were most abundant in the upper deep marsh (Station 5).

The second axis caused the "arch effect", a familiar phenomenon in correspondance analysis that arose as a mathematical artifact of the occurrence of several taxa that dominated the middle of the gradient but tended not to occur at either end. In this study, these shared taxa were more abundant below the gradient middle, hence the asymmetric arch evident in Figure 1.4. These taxa contributed strongly to the second axis inertia and included the mayfly *Caenis*, the hydroptilid caddisfly *Oxyethira*, the corixid bug *Palmacorixa*, and the Lepidoptera in general. In most cases, plotted positions of the genera contributing strongly to these axes were very near the positions of their confamilial relatives, for example, the position of *Palmacorixa* was generally indicative of the position of all Corixidae genera sampled, even though they were not identified as strong contributors to the axis inertia (not having a contribution index > 0 in SAS output). However, more variety in gradient position occurred at and above the family level. For example, the Odonata families Libellulidae, Aeschnidae, and Coenagrionidae were associated with progressively lower parts of the gradient.

Figure 1.4 includes the names of those taxa that were best represented in the first two ordination axes, as measured by the "squared cosine" parameters associated with each taxon in the SAS CA output. I included all taxa with a summed two-dimension squared cosine value greater than 0.5, indicating that over 50% of the variation in that taxon was accounted for in the two-dimensional plot. Correspondance analysis plots commonly include points for "sites" and "species", or stations and taxa in this case. I replaced taxa points with taxa names because actual measured distances between taxa and elevation positions cannot be interpreted directly in correspondance analysis. Consequently, the proximity of taxa positions to elevation positions should be interpreted as general correspondances between them, rather than quantitative associations. However, plotted taxa positions relative to the "arch" can indicate habitat specificity vs. generality. For example, the fact that the plotted position of Chironomidae was in the interior of the arch suggested that it was more generally distributed on the gradient because it was relatively close to several elevation points. Conversely, taxa that were found outside the arch or past its ends usually corresponded strongly to the nearest elevation point.

Multivariate analysis: Ordination by depth

The ordination of all samples grouped by water depth did not result in a numerical ordering of samples along the first axis (Figure 1.5). Instead, the axis primarily represented a distinction between two broods of tadpoles that appeared at different depths during the summer. These groups may have been influential because they occurred at high abundances, but these data were also used in the elevation ordination and did not have as strong an influence. By contrast, the second dimension produced a near-complete numerical ordering of communities at successively greater depths, although the 60-cm depth occurred in the middle of the axis. This axis contrasted a group of shallow-water taxa (e.g. Limnephilidae, Sphaeriidae, Hirudinea, Nematoda, *Umbra limi*, *Agabus*, Isopoda, *Ilybius*, Chironomidae, Copepoda) with fewer deeper-water associates that tended to occur at higher abundance (Ostracoda, *Amia calva*, *Bufo* tadpoles).

Multivariate analysis: Monthly changes in ordination

The analysis of the May data resulted in an ordination by elevation along the first axis (Figure 1.6a), though this is not remarkable because only three elevations were included in the ordination (because low water precluded sampling higher elevations). Nonetheless, the taxonomic groups that contributed most to the May ordination comprised communities that were somewhat indicative of patterns seen later in the season. The upper end of the reduced May gradient was characterized by Dytiscidae, Chironomidae, Gastropoda, and Collembola, all of which became abundant in the wet meadow later in the year. Meanwhile, the lower-station communities consisted largely of Amphipoda, Corixidae, Hydracarina, and Ostracoda, all of which remained dominant at low elevations through the season. Also, the May communities included several taxa that apparently were early-season specialists, rarely or never appearing in later samples. These included Iowa darters (*Etheostoma exile*), very large leeches, an unidentified Limnephilidae caddisfly genus, and the Metropodidae mayfly genus *Siphloplecton*, all of which occurred in the highest-elevation (Station 4) May samples.

The June data included samples from five elevations because the water level had risen almost 20 cm between the end of May and late June. The multivariate analysis of these data also resulted in a numerical ordering by elevation along the first dimension, but Station 2, representing the newly flooded wet meadow, appeared far to the right of the other points, suggesting strong dissimilarity between the community at this elevation and the others (Figure 1.6b). The first axis, not surprisingly, was most strongly influenced by a group of taxa that only appeared in the wet meadow: larvae of the small dragonfly *Sympetrum* (Odonata: Libellulidae) and biting midges *Serromyia* and *Forcipomyia* (Diptera: Ceratopogonidae), the exotic prosobranch snail *Bithynia*, and several unidentified fly larvae (Diptera: Brachycera). Also influential were several taxa associated with the wet meadow in the overall ordination (e.g. *Ilybius*, Planorbidae).

The July and August analyses produced quite different results from the others. No numerical ordination by elevation was apparent in the July plot's first dimension, which was primarily determined by a distinction between discontiguous elevations dominated by Cladocera and those dominated by a combination of Chironomidae, Copepoda, and Naididae worms. The second dimension, however, was largely determined by a distinction between Station 1 and Stations 4 and 6 (based on partial contributions to inertia), suggesting a partial ordination by elevation (Figure 1.6c). The taxa contributing most to this axis were positioned at opposite ends of the plot, and were dominated by the wet meadow (at one end) and deep marsh (at the other) associates identified in the overall ordination.

The August plot included the elevation-based gradient, but in two separate parts along the first two axes (Figure 1.6d). The first axis was determined by a distinction between Stations 1 and 2 (wet meadow) and Station 3. The strongly contributing taxa consisted of established wet meadow residents, and several taxa that apparently became abundant there later in the season (e.g. Sphaeriidae, Copepoda, Isotomidae, *Physa*, *Umbra limi*). Meanwhile, the second axis was driven by a distinction between Station 3 and Station 6, with the intervening elevations ordered numerically between them. As in the overall ordination, Leptoceridae, Corixidae, and Amphipoda were influential deep marsh taxa, and young-of-year *Micropterus salmoides*, the Branchobdellida (crayfish parasitoids), and Ephydridae fly larvae were also influential at low elevations. Station 3 was strongly characterized by Cladocera, which influenced both axes.

Univariate analysis: Abundance differences among stations, plant zones, and depths

I followed the multivariate analyses with univariate analyses of individual taxa (Table 1.1). Kruskal-Wallis comparisons of abundances of individal taxa at different elevations tended to confirm correspondance analysis results. The majority of analyses performed on family-level (and higher) data indicated significant inequality of abundances along the gradient. However, significant differences were not found for many individual genera and less-common families, probably because these occurred at low abundances (including many zero counts) so statistical tests could not detect differences that may have existed. I also used Kruskal-Wallis tests to compare taxa abundances among water depths and vegetation zones, comparing p-values from these tests to each other and to those from tests among elevations. While this is not a true statistical test of the relative importance of environmental variables, lower p-values suggest lower probabilities that random chance produced apparent animal associations with these variables. For example, Table 1.1 shows that the Anisoptera abundance difference among elevations produced a lower p-value ($p<0.01$) than its difference among vegetation zones or depths (both $0.05<p<0.001$), so the probabity that only random chance produced the elevation difference was lower than in the vegetation and depth tests. However, this method is qualitative and weak compared to parametric variance-partitioning approaches, especially with such inter-correlated environmental variables, so p-value differences among the three analyses for any given taxon are only indicators of potential differences among these variables as causative factors.

Only a few taxa showed strong associations with water depths but not with elevation or vegetation zones (Table 1.1). These included Caenidae mayflies (and Ephemeroptera in general), which occurred in low numbers at low elevations in May and proceeded to increase in abundance at progressively higher elevations over time, remaining consistently most abundant at 40 cm depth ($p<0.01$). Damselfly larva (Odonata: Coenagrionidae) abundances were greatest at 40-60 cm depths ($p<0.05$) and were not significantly related to elevation ($p>0.1$), and only weakly related to the deep marsh plant zone ($0.1>p>0.5$). Three caddisfly taxa were most associated with water depth: *Oxyethira* (Hydroptilidae, 30-50 cm depths), *Trianodes* (Leptoceridae, 40-50 cm depths), and Polycentropodidae (50 cm depth). The Collembola in general, and Isotomidae in particular were most associated with the two lowest depths, which was consistent with their importance in the wet meadow community. Oligochaetes tended to concentrate in deeper water, with highest abundances at the 60 and 40 cm depths.

Qualitative distinctions between animal-vegetation and animal-elevation associations were complicated by the fact that any taxon with a high association with a single station would have a *de facto* association with a plant zone. Thus, I considered vegetation to be a more important factor only in cases in which the p-value from the vegetation test was lower than the value from the elevation test, though this decision rule is qualitative and somewhat arbitrary. The majority of taxa that appeared to correspond with wet meadow vegetation included several genera of Dytiscidae beetles, Haliplidae beetles, various Diptera (e.g. three Ceratopogonidae taxa, Culicidae, unidentified Brachycera), Isotomidae springtails, the Phryganeidae caddisfly *Fabria*, and Bithyniidae snails. Ephemeroptera, some Hemiptera, and Hydroptilidae caddisflies were most associated with the transition zone, and amphipods, damselflies (Coenagrionidae), and the Leptoceridae caddisfly *Trianodes* were primarily found in the deep marsh zone.

Animal taxa could be generally classified according to four distribution types: wet meadow specialists, mid-to-lower gradient generalists, deep marsh specialists, and generalists. Representative gradient profiles of each type are shown in Figure 1.7. The wet meadow specialists were those taxa that were almost exclusively found on the upper half of the gradient, especially Stations 1 and 2. Lower gradient generalists tended to occur broadly among Stations 3 through 6, especially at Stations 4 and 5. Deep marsh specialists were always concentrated at Station 5 or 6, or both, while generalists occurred broadly over the gradient. This last group is of interest because it mostly consisted of higher taxonomic levels. Had identification been taken to lower levels, greater gradient specificity would likely have been observed.

Univariate analysis: Temporal changes in gradient positions

Several taxa apparently migrated up-slope over the summer (e.g. Isopoda, Figure 1.8). Mean gradient positions (weighted averages) for each taxon during each month are listed in Table 1.2, along with significance levels of linear regressions of these positions on the independent variable "month". Regressions were based on raw numbers per trap effort (averaged in Table 1.3), but taxa were not collected on every transect in every month, so the number of data used in regressions varied widely from taxon to taxon. Table 1.2 only includes those taxa that occurred during at least two months and on enough transects to perform regression. Results of regressions of rare taxa should only be accepted conditionally, and emphasis should be placed on regressions of the more common taxa and higher taxonomic groupings.

The regression results suggested three patterns: early wet meadow colonists which only appeared at high elevations (shallow water), migrators which showed a significant trend of decreasing gradient position (increasing elevation) over time, and non-migrators which remained at middle or low elevations (deeper water) through the summer. The earliest wet meadow colonists were dominated by mites, copepods, certain biting midge genera (Ceratopogonidae: *Serromyia* and *Forcipomyia*), various Cladocera, Planorbidae snails, and Dytiscidae beetles (each taxon comprising at least 10% of samples), all of which appeared to migrate from lower elevations. Later in the season, wet meadow stations were increasingly dominated by Chironomidae, Libellulidae dragonfly larvae, Isopoda, leeches, and Collembola. These groups apparently migrated more slowly or, in the case of insects, up-slope dispersal was temporally limited to oviposition by flying adults during a certain period of the summer. Those groups that only appeared in the wet meadow, showing no evidence of migrating from lower elevations, included Dytiscidae larvae, Culicidae, Sphaeriidae, Bithyniidae, and Nematoda.

The majority of the remaining taxa were limited to lower elevations (deeper water), showing little tendency to migrate to higher elevations. Among these were a few taxa whose distributions widened, including higher elevations, but remained centered on lower elevations (e.g. Caenidae, Leptoceridae, most Hemiptera, Ostracoda). All other groups were more narrowly associated with mid-elevation stations (e.g. Mesoveliidae, Aeschnidae, *Oecetis*, Naididae) or the low end of the gradient (e.g. Corixidae, Coenagrionidae, *Trianodes*, Amphipoda). One or more individuals of most taxa occurred at most elevations (so presence-absence analysis would be ineffective), suggesting that the spatial variation with elevation was a true gradient.

Univariate analyses: Microcrustaceans and fish

Although macrofauna were the primary focus of the study, microcrustaceans collectively comprised the largest proportions of animals in most samples, so I included them in the multivariate analyses described above and I also analyzed their distributions with univariate tests. Certain spatial and temporal trends were apparent among these animals (Figure 1.9), even though they were not identified further than the level of Ostracoda, Copepoda (almost exclusively Cyclopoida), and Cladocera. Copepoda were early wet meadow colonizers and remained most abundant there throughout the season. They comprised a large proportion (17-28%) of Station 1 and 2 samples ($p<0.05$ relative abundance), showing a strong association with wet meadow zone samples ($p<0.05$, raw <u>and</u> relative abundances). They showed a significant ($p<0.001$) up-slope migratory trend because of their immediate strong presence at newly-flooded wetland elevations. Overall copepod abundance subtly rose until July, and then began to decline ($p<0.05$), possibly because water level had stabilized by then.

Ostracoda were consistently most abundant at low elevations, peaking at Station 5 ($p<0.001$), though they also showed an up-slope migratory trend ($p<0.05$) as small numbers appeared at higher elevations through the season. Because of their high abundances at Stations 5 and 6, ostracods were strongly associated with the deep marsh zone ($p<0.01$). Their significant difference among depth classes ($p<0.05$) was an anomaly resulting from a very high abundance in June at Station 6, and did not represent a consistent association with the 50 cm depth. In contrast to ostracods, the Cladocera gradient position was dynamic, showing a significant ($p<0.05$) up-slope migratory trend as they became more abundant in the wet meadow samples from June to July. A significant increase in abundance over the summer ($p<0.01$) led to high numbers at Station 3 in August, which was an important influence in the August CA ordination, as mentioned above.

The fish assemblage varied over the elevation gradient also (Table 1.1). Density ($p<0.1$) and taxa richness were highest at Station 4. Of 86 fish caught in all months, 38 were caught at Station 4, representing 7 of the 10 species. The most common species in the wet meadow and the wetland as a whole was mudminnow (*Umbra limi*) comprising 34% (29 fish) of all fish caught, 15 of 18 (83%) caught at Station 2, and the only fish caught at Station 1. Iowa darters (*Etheostoma exile*) were quite common in May, presumably in the shallows to spawn, while few fish of any species were caught in June, and total numbers caught increased in July and August as young-of-year mudminnows, largemouth bass (*Micropterus salmoides*), bowfin (*Amia calva*), and yellow perch (*Perca flavescens*) became abundant. Brook stickleback were caught in all months, mostly at Station 4. These figures do not include a brood of very young bowfin (*Amia calva* ~2-3 cm) that occurred in two June deep marsh traps at high densities (20 and 56 fish per trap), or 7 unidentified larvae caught at Stations 2 and 3 in July.

DISCUSSION

My first hypothesis was that ordination of the total data set would result in a numerical ordering of sampling stations along the first axis. Because there are 6! possible sequences of the 6 stations, the probability of random chance producing the hypothesized order is 1 in 720, or a probability of ~0.00139. Thus, the ordinations of the total data set and of the May and June data are consistent with the hypothesis that a community gradient occurs corresponding to the elevation gradient. The fact that ordinations produced similar results regardless of taxonomic level suggested that the community gradient was a major phenomenon relating to adaptations in body form found at high taxonomic levels, at least in some of the taxa sampled. Had all animals been identified to genus, or at least family, the gradient structure may have been further enhanced. However, the fact that I used some relatively high taxonomic levels must be recognized as a limitation on full interpretation of the results.

My second hypothesis, that the community gradient would deteriorate over time, was supported by the fact that the July and August ordinations did not result in a numeric ordering of all stations in Dimension 1. Instead, the July ordination suggested a re-shuffling of some members of communities at different elevations. One reason the six stations were plotted in seemingly random positions is that high-level taxonomic groups defined communities in July while specific groups that I identified to lower levels were migrating up-slope, homogenizing the communites at different elevations. Greater taxonomic resolution may have revealed a numerical ordination in July, although it would not change the fact that changes were occurring in the gradient structure as many taxa shifted along the elevation gradient. Insects may have been particularly influential in rearranging ordination plots because they could emerge as adults at low elevations and oviposit at higher points, skipping the intervening elevations. This could create community discontinuities as long as pre-emergent larvae and newly-hatched larvae are present at discontiguous elevations at the same time.

The August ordination contained evidence of the community gradient re-asserting itself, though in a somewhat different form. The wet meadow community still included most early (June) constituents, but also included the newer immigrants (e.g. isopods, Physidae snails) from lower elevations. I had anticipated that communities would progressively homogenize, causing the gradient to break down by August, but this did not occur, in part because certain taxa apparently did not move up gradient from their low and mid-elevation positions. The distinction between taxa that migrated and those that remained "true" to their position on the gradient may be an important piece of evidence in any attempt to understand what factors caused the community gradient.

Combining the classifications by distribution type and by gradient position regression results, I can assign most taxa collected to one of 4 categories: early wet meadow colonists (dominating wet meadow elevations as soon as they are flooded), wet meadow immigrants (migrating up-slope from lower elevations), mid-gradient generalists (occurring broadly, especially across Stations 3 through 5), and low-elevation specialists (with peak abundances always at Stations 5 and 6). The early wet meadow colonists included those taxa that only appeared in the wet meadow. Larvae of Dytiscidae beetles and Culicidae (mosquitoes) appeared later in the season at high elevations, apparently as a result of mid-season oviposition by adults in the newly-flooded wet meadow. However, the Sphaeriidae, Bithyniidae, and Nematoda are non-insects that were likely to have been present in the soil/detritus matrix prior to flooding. It is possible that even when surface water is not present in the wet meadow, the underlying substrate remains wet enough to allow these organisms to survive non-flooded periods.

Those taxa that appeared to migrate to higher elevations over time probably used different mechanisms to do so. Some probably were "true" migrators, in that individuals crawled (e.g. Isopoda, Planorbidae, Physidae) or swam (e.g. Dytiscidae and Hydrophilidae beetles, mudminnows, leeches) to higher elevations. Insects, as described above, are capable of migrating through emergence as adults and subsequent oviposition at new locations. This mechanism probably explains the gradient position shift of the Libellulidae dragonflies, Chironomidae (midges), and Caenidae mayflies. It is also possible that some animals may have been carried up-slope during the occasional storm surges that can temporarily raise coastal water levels and batter shorelines with high-energy waves. Such surges have been observed in the study site (S. Riffell, pers. comm.), but whether they move large numbers of invertebrates shoreward has not been studied. Another complication in interpreting mechanisms of these apparent migrations is the lack of taxonomic specificity in this study. Usually-speciose taxa (e.g. Chironomidae) may have shown gradient position shifts because different species occupied different positions at different times, but these dynamics would be indistinguishable from true upslope migrations without more detailed taxonomic work.

Meanwhile, many taxa that should be capable of relatively rapid migration did not become abundant up-slope. These included fast swimmers such as Corixidae bugs, Amphipoda, and most fish species. Also, many insects did not show position shifts, despite the fact that they were obviously emerging and ovipositing during the summer, as evidenced by the appearance of early instars in later months. These included most Trichoptera, the Coenagrionidae, and some Hemiptera. Reasons for these failures to migrate cannot be determined from these data, but there are several possibilities, including "active" mechanisms of habitat selection and "passive" mechanisms of habitat exclusion, as discussed below.

It may seem contradictory that the ordination including all months produced such an obvious numeric ordering of elevations, while the July and August ordinations did not. The explanation probably lies in the fact that community compositions at low elevations remained relatively constant while higher elevations changed. Also, though high-elevation communities changed, they still remained different from low-elevation communities. In June the wet meadow community was strongly different from lower elevations, but as it changed in later months, more taxa were added to the community rather than replacing early colonists. Some of these appeared to migrate from lower elevations, but some (e.g. Dytiscidae and Culicidae larvae) appeared for the first time in June and August, and only at high elevations. The result was an accumulation of taxa at higher elevations so overall taxa richness was highest at high elevations (Figure 1.10).

In contrast to the ordination by elevation, the ordination by depth did not produce a numerical ordering of communities at adjacent depths, suggesting that entire assemblages did not move up-slope as water level rose even though many individual taxa did. Water depth and substrate elevation are strongly correlated so distinguishing the effects of these two factors on fauna is difficult. Variance-partitioning methods could not be used because the data could not be made to meet the assumptions of normality and homoscedasticity. The method used here, comparing two ordinations, has the advantages of being relatively assumption-free, and of comparing entire communities rather than testing taxa individually.

Possible causal factors

It is unlikely that a single causal factor was most responsible for all the animal distributions observed in this study. Distinguishing among the various candidate causal factors is further complicated by the inter-correlation of so many coastal wetland environmental parameters. The data collected in this study did not allow for a robust statistical distinction among causal factors, and I do not suggest that the analyses presented here do any more than provide some clues to the relative influences of elevation, vegetation, and depth on animal distributions.

My initial hypotheses were driven by an expectation that flooding regime variation would be directly responsible for most faunal variation, causing animals to sort themselves into a temporary wetland community and a permanent wetland community at opposite ends of the gradient. The gradation of community composition between these two extremes was expected to comprise the community gradient that was revealed through correspondance analysis. This expectation is supported by the fact that the majority of taxa most associated with the wet meadow have been identified as common residents of temporary waters in other studies (see Introduction for review): snails, beetles, mites, midges (Chironomidae), mosquitoes, and copepods. Those groups generally considered to be excluded from temporary waters were generally not common in the wet meadow in this study: mayflies, caddisflies, amphipods, and most dragonfly/damselfly (Odonata) taxa.

Despite the above suggestion that drought-tolerance is an important determinant of coastal wet meadow fauna, it is also possible that water quality factors were very influential, as suggested by Cardinale et al. (1998). Dissolved oxygen is one such factor that may have been important. The dominance of the wetland fish community by mudminnows suggests that hypoxia is common in the shallows because these fish can avoid oxygen stress by gulping air at the surface. Many invertebrates are affected adversely by low dissolved oxygen levels (Merritt and Cummins 1996), and a large proportion of the wet meadow inhabitants in this study were taxa equipped with air-breathing mechanisms (pulmonate snails, diving beetles, mosquitoes) or were taxa that are known to have species with hypoxia tolerance (Chironomidae). It is also possible that the variation in fish species over the gradient, possibly caused by dissolved oxygen variation, caused a gradient of constantly-varying predation pressures. Invertebrate predators also varied over the gradient, so the complex spatial and temporal variation in the assemblage of predators could be important influences on the remainder of the invertebrate community.

Plant community types are used in many wetland delineation and classification schemes (e.g. Cowardin et al. 1979), and have been the focus of several studies of wetland invertebrates (reviewed in Batzer and Wissinger 1996). I initially hypothesized that vegetation zonation would not be an important influence on invertebrate communities because it may be more important as a human-perceived classification than an environmental factor influencing aquatic animals. This is not to say that plant community composition is unimportant to animals, but that the division of the wetland continuum into zones is not likely to be recognized by animal communities. In this case, I applied this hypothesis specifically to my division of the wetland vegetation into three zones, based primarily on the dominance of cattails in the middle of the transects, with very different communities on either side. Transect 4 lacked cattails so Stations 3 and 4 were classified as wet meadow and deep marsh respectively. If animals responded strongly to these plant community differences, or to their associated detritus differences, I expected that sampling stations in similar vegetation zones would occur relatively near each other in ordination plots. This did not occur in any plots, except that Stations 3 and 4 were relatively close to each other in the ordination of the entire data set. This may indicate high similarity among animal communities in the transition zone, or it may simply reflect the fact that these two stations were horizontally closer to each other than to other stations because of the steeper substrate slope in the transition zone.

Despite the lack of strong evidence for animal community association with vegetation zones, several individual taxa were strongly associated with plant zones. In at least one case this may be explained by food preference: the Leptoceridae caddisfly *Trianodes* feeds on soft live plant tissues, so this genus would be expected to remain in the deep marsh zone where submergent and floating-leaved plants were abundant. In most other cases, possible reasons are less apparent, yet vegetation zonation cannot be dismissed as an important environmental factor for at least some invertebrates. The taxa most likely to have been influenced by vegetation were probably those that were significantly associated with vegetation zones and also did not appear to migrate across zone boundaries. Some of these (e.g. Haliplidae, Corixidae, Amphipoda, Sphaeriidae, Gastropoda) may have been influenced by vegetation-associated food variables such as detritus type and periphyton availability, but others (e.g. Dytiscidae, Ceratopogonidae, Coenagrionidae) were predators, so the non-animal food base was not a likely direct influence on them.

Some animals may have been influenced by plant structural complexity. Complexity of submergent plant surfaces directly affects invertebrate colonists (Krecker 1939), but emergent plant stems rarely support high abundances of epiphytic animals (Batzer and Wissinger 1996). However, the degree of habitat complexity created by emergent plants can affect invertebrate abundances (Batzer and Resh 1992) and provide refuge for fishes (Werner and Hall 1988). Further, invertebrates can benefit from reduced fish predation efficiency in areas of high plant structural complexity (Gilinsky 1984). I did not measure structural complexity, but related sampling (Gathman and Keas 1999) indicated that emergent stem density decreased, and submergent plant coverage increased, with lower elevations (greater depth), so variations in spatial structure occurred along the gradient and may have influenced animals. Nonetheless, the ready migration and broad distributions across zone boundaries observed in so many taxa in this study mitigate against any suggestion of a strong role of vegetation zonation in defining the community gradient.

I used multivariate analysis to determine whether entire communities were strongly associated with depth ranges. The fact that such associations were not evident was not because animals did not follow rising water up-slope, but because various groups responded in different ways to the rising water. As a result, the situation was more complicated than my initial hypotheses anticipated. Communities changed over time as some taxa migrated and others expanded their ranges, all doing so at different rates against the backdrop of the more spatially-stable groups. Depth was not a good indicator of community composition, but the increasing area flooded over the season that resulted from water level rise allowed many animals to move to new habitats. The failure of some taxa to move up-slope may have resulted from any of the habitat variables suggested above, or may have resulted from taxonomically-differential mortality along the elevation gradient. The fact that abundances of predators (e.g. fishes, Odonata) varied spatially suggested that predation pressures may have varied over the gradient, possibly limiting the abilities of some taxa to occupy some habitats.

This movement, which appeared to differ among taxa, was probably a very important factor determining community composition along the elevation gradient. For example, some taxa may have been able to survive the de-watered period in the substrate, while others were able to migrate into the wet meadow when it became flooded, though some did so more quickly than others. Still other taxa did not appear to migrate, remaining at the low-elevation end of the gradient. However, factors other than direct migration and dispersal movements may have produced the appearance of movement, or lack thereof. For example, some low-elevation taxa may have engaged in up-slope range-expansion movements, but encountered high mortality in higher-elevation habitats, precluding their successful establishment there. Whatever the causes, this difference in apparent migration and dispersal responses to changing water level was an important determinant of community composition at successively higher points on the gradient.

Despite the seasonal changes resulting from migrations, the correspondance analysis results clearly indicated a gradual variation in community composition along the wetland elevation gradient in the study site. The numerical ordination of sampling stations along the first axis indicated that the main component of community variation in this wetland site was strongly related to substrate elevation, either directly or indirectly. Thus, the different environmental conditions at different elevations appeared to create a spatial distinction in habitats that was important to animals in the wetland. What could not be clearly determined from this study is what proximate factors were responsible for the variation observed. However, the observation of the pattern is a necessary first step toward understanding coastal wetland animal community structure.

Table 1.1. Significant differences in abundances of taxa among sample stations, plant zones, and depths; monthly and all months combined (Kruskal-Wallis test; * 0.1>p>0.05, ** 0.05>p>0.01, *** p<0.01).

Independent variable:	Station					Plant zone					Depth
TAXON \ Month:	ALL	May	Jun	Jul	Aug	ALL	May	Jun	Jul	Aug	ALL
Coleoptera	***			***		***			***	**	***
Dytiscidae	***			***	*	***		**	***	**	***
Dytiscidae adult	***			***		***		**	***	*	***
Laccophilus											
Ilybius	***			**		***			***		
Rhantus						***			*		**
Hygrotus						***					
Agabus	***					***			*		
Uvarus											
Hydroporus											
Dytiscus	***			*		*					
Coptotomus											
unident. Dytisc.							*				
Dytiscidae larvae	**					***			**		
Dytiscus						***			**		
Hydroporus											
Agabus											
Gyrinidae - *Gyrinus*											
Haliplidae - *Haliplus*						*					
Hydrophilidae				*					*	*	
Tropisternus				*					*		
Laccobius											
Helochares											
Curculionidae - *Lixus*											
Scirtidae	***			*		*					
Diptera	***			**		***			*		
Ceratopogonidae						*		**			
Serromyia						*					
Forcipomyia											
Atrichopogon						**					
Bezzia/Palpomyia				*		**			*		
Culicoides											
unident. Cerat.								**			
Chironomidae	***			*		***	*				
Ephydridae											
Sciomyzidae											
Culicidae	*					**					
Culex	*										
Anopheles											
Dixidae											
Brachycera						**				**	
Ephemeroptera					**	*			**	*	***
Baetidae			*								**
Metropodidae - *Siphloplecton*											

Table 1.1 (cont'd).

	Independent variable:	Station					Plant zone					Depth
TAXON \	Month:	ALL	May	Jun	Jul	Aug	ALL	May	Jun	Jul	Aug	ALL
Ephemeroptera -	cont'd											
Caenidae -	*Caenis*	**				**					*	***
unident. Ephem.												
Hemiptera							**					*
Belostomatidae												
Corixidae		***			*		***			***		**
Corix. adult		***				***	***			*	*	*
Hesperocorixa												
Sigara							**					
Palmacorixa		***		*			*					**
unident. Corix.										*		
Corix. larvae							**			**		*
Saldidae												
Mesoveliidae												
Nepidae												
Veliidae							*					
unident. Hemipt.												
Lepidoptera												
Pyralidae												
Parapoynx												
other Pyral.												
other Lepidopt.												
Odonata		***	*	*								
Anisoptera		***	*			**	**					**
Aeshnidae												
Libellulidae		***					***					**
Leucorrhinia		**				**						
Sympetrum												
immature Libel.		***				***	***			**	*	*
Coenagrionidae					***		*			*		**
Telebasis												
Homoptera		*					***			*		
Trichoptera						***			**		***	**
Hydroptilidae						*	*				***	
Oxyethira						**	*				***	*
immature Hydropt.												
Leptoceridae				*					**			
Trianodes		*		**			**		**			**
Oecetis												
Mystacides												
Limnephilidae									**			
Phryganeidae							*				*	
Polycentropodidae												**
Collembola		**		*			**			**	*	**
Sminthuridae												

Table 1.1 (cont'd).

	Independent variable:	**Station**					**Plant zone**					**Depth**
**TAXON **	**Month:**	**ALL**	**May**	**Jun**	**Jul**	**Aug**	**ALL**	**May**	**Jun**	**Jul**	**Aug**	**ALL**
Collembola -	**cont'd**											
Isotomidae				*			*				*	*
Poduridae												
other Collembola				*						*		
Hymenoptera												
Thysanoptera												
Amphipoda		**	**				**			*		
Gammaridae							*					
Hyalellidae		*	**				**					
Crangonyctidae							*			*		
Asellidae		**					***				***	
Cambaridae	*Orconectes*											
Argulus					*						**	
Hirudinea		**	***			*	*	**	*			**
Oligochaeta			*								*	**
Lumbriculidae												
Naididae			*								*	*
Tubificidae												
other Oligo.												
Branchiobdellida												
Mollusca		***				**	***				**	
Sphaeriidae		***			*		***			**	*	
Gastropoda		**				**	**				**	
Bithyniidae		**					***				*	
Lymnaeidae												
Physidae												
Planorbidae		**		*			**			*		**
Succineidae												
ACARI					*							
NEMATODA		***			*		***	*		*		***
TURBELLARIA												
CLADOCERA						*						*
OSTRACODA		***			**	*	***			***	*	**
COPEPODA							**					
HYDRIDAE		**										
FISH		*	**					***				
Etheostoma exile								*				
Ameiurus nebulosus		**										
Umbra limi						**		*				
Culaea inconstans					*			**				
Amia calva												*
Pungitius pungitius												
Gasterosteus aculeatus												
Cyprinidae												
Micropterus salmoides												**
Perca flavescens												

Table 1.1 (cont'd).

Independent variable:	Station					Plant zone					Depth
TAXON \ Month:	ALL	May	Jun	Jul	Aug	ALL	May	Jun	Jul	Aug	ALL
fish larvae	*			*							
tadpole											
Bufo tadpole											
Rana tadpole						**					
unknown tadpole			*								**
# taxa per trap	***	**			**	***					
Total abundance					*					**	

Table 1.2. Mean gradient positions (weighted averages) of each taxon over all months and for each month, and results from regressions of positions against month.

	Mean Gradient Position					Regression		
Taxon	All Months	May	Jun	Jul	Aug	slope	p-value	n
Coleoptera	2.32	4.33	2.98	1.94	2.11	-0.717	0.001	18
Dytiscidae	2.21	4.00	2.90	1.96	1.98	-0.625	0.004	17
Dytiscidae adult	2.22	4.00	2.90	1.99	2.05	-0.598	0.006	17
Ilybius	2.19	n.a.	3.00	2.23	2.21	-0.360	0.297	13
Rhantus	2.19	n.a.	2.67	1.67	n.a.	-1.000	0.101	6
Hygrotus	2.25	n.a.	3.50	1.50	1.50	-1.000	0.076	6
Agabus	1.41	n.a.	3.00	1.33	1.00	-1.000	0.111	5
Dytiscidae larvae	2.08	n.a.	n.a.	1.80	2.30	0.500	0.300	4
Haliplidae	2.88	n.a.	3.50	1.00	3.00	-0.250	0.879	3
Hydrophilidae	3.00	5.00	n.a.	3.00	1.75	-1.083	0.001	5
Diptera	3.22	4.58	3.66	2.67	3.32	-0.456	0.013	19
Ceratopogonidae	3.19	4.50	3.07	3.49	2.96	-0.364	0.212	13
Atrichopogon	1.81	n.a.	3.00	1.50	n.a.	-1.500	0.330	3
Chironomidae	3.26	4.33	3.83	2.70	3.37	-0.373	0.053	19
Culicidae	1.88	n.a.	n.a.	2.17	2.00	-0.167	0.868	4
Brachycera	2.81	n.a.	3.89	3.13	1.83	-1.028	0.124	9
Ephemeroptera	3.73	5.17	5.00	4.50	3.52	-0.552	<0.001	13
Caenidae	3.66	5.00	5.00	4.83	3.52	-0.616	0.008	11
Hemiptera	4.43	5.56	4.17	4.32	3.83	-0.479	0.002	19
Belostomatidae	4.33	n.a.	n.a.	6.00	3.50	-2.500	0.812	3
Corixidae	4.76	5.56	4.32	4.97	4.63	-0.191	0.287	18
Corixidae adult	5.08	5.56	4.38	5.00	6.00	0.151	0.493	15
Corixidae larvae	4.38	5.00	4.08	4.58	4.26	-0.074	0.760	12
Mesoveliidae	3.46	n.a.	3.75	2.30	n.a.	-1.540	0.154	6
Nepidae	3.69	n.a.	4.00	n.a.	3.50	-0.250	0.667	3
Veliidae	2.33	n.a.	n.a.	3.00	1.67	-1.330	0.219	5
Odonata	3.26	4.83	4.25	3.33	2.95	-0.654	0.005	17
Anisoptera	3.02	4.83	4.00	3.05	2.49	-0.790	0.001	16
Aeshnidae	4.22	4.50	n.a.	3.33	n.a.	-0.583	0.133	5
Libellulidae	2.88	5.00	3.50	2.89	2.49	-0.765	0.005	14
Coenagrionidae	4.41	n.a.	5.00	4.83	4.54	-0.250	0.567	9
Trichoptera	4.46	4.17	4.80	4.33	3.98	-0.198	0.326	15
Leptoceridae	5.01	5.00	5.03	4.00	3.87	-0.500	0.079	10
Trianodes	5.32	5.00	5.42	4.00	6.00	0.086	0.796	8
Oecetis	4.60	n.a.	5.00	n.a.	3.50	-0.750	0.312	4
Limnephilidae	3.48	4.00	2.50	3.00	6.00	0.731	0.337	5
Collembola	2.93	4.25	3.39	2.08	1.25	-1.054	0.001	12
Sminthuridae	3.55	4.25	4.00	2.50	n.a.	-0.897	0.118	6
Isotomidae	2.76	4.00	3.00	3.50	1.25	-0.798	0.042	7
Hymenoptera	3.80	n.a.	n.a.	4.50	2.00	-2.500	0.312	3
Amphipoda	4.47	4.63	4.32	4.21	4.59	-0.025	0.844	19
Hyalellidae	4.48	4.63	4.32	4.17	4.73	0.010	0.943	19
Asellidae	2.41	5.00	4.00	2.88	2.07	-0.972	0.096	9
Cambaridae	4.76	n.a.	4.50	n.a.	6.00	0.750	0.333	3

Table 1.2 (cont'd).

	Mean Gradient Position					Regression		
Taxon	All Months	May	Jun	Jul	Aug	slope	p-value	n
Naididae	4.08	4.83	3.50	3.87	3.70	-0.278	0.275	16
Mollusca	3.10	4.67	4.07	3.05	2.64	-0.712	<0.001	18
Sphaeriidae	1.63	n.a.	n.a.	1.37	2.35	0.483	0.266	7
Gastropoda	3.35	4.67	4.07	3.31	2.73	-0.660	<0.001	18
Bithyniidae	1.81	n.a.	2.00	n.a.	1.67	-0.167	0.667	4
Lymnaeidae	3.18	5.00	3.30	2.98	3.33	-0.255	0.587	14
Physidae	3.95	4.50	4.73	3.68	3.16	-0.592	0.040	16
Planorbidae	3.02	5.00	4.03	3.00	2.89	-0.647	0.003	16
Succineidae	3.71	n.a.	n.a.	3.67	4.00	0.330	0.800	4
Acari	3.81	4.77	3.93	2.88	3.94	-0.356	0.066	20
Nematoda	2.75	4.00	2.58	1.40	2.36	-0.438	0.225	11
Turbellaria	3.50	n.a.	n.a.	2.00	3.11	1.111	0.652	4
Claodocera	3.72	5.00	4.20	3.62	3.58	-0.456	0.025	18
Ostracoda	4.71	4.88	4.68	4.70	3.81	0.321	0.021	20
Copepoda	3.54	4.99	3.75	3.42	2.97	-0.640	<0.001	20
Hydridae	2.75	n.a.	n.a.	3.81	2.00	-1.806	0.206	7
All Fish	4.39	4.13	4.55	3.98	3.25	-0.326	0.075	18
Etheostoma exile	4.23	4.14	4.00	n.a.	n.a.	-0.143	0.667	3
Umbra limi	2.90	4.00	n.a.	3.92	2.54	-0.592	0.117	9
Culaea inconstans	3.67	4.00	3.00	4.50	3.00	0.008	0.984	8
Amia calva	5.16	n.a.	4.90	5.00	5.00	0.062	0.922	6
Micropterus salmoides	4.33	n.a.	n.a.	4.00	4.25	0.250	0.904	5

Table 1.3. Mean abundances of taxa by month and sampling station.

	MONTH:	May			June					July						August					
	STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \	DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
Coleoptera		0.8	0.4	0.0	1.4	1.4	1.2	0.2	0.0	5.8	5.8	2.0	0.6	0.2	0.0	1.8	2.2	1.4	0.6	0.2	0.4
Dytiscidae		0.8	0.0	0.0	1.4	1.2	1.0	0.0	0.0	5.2	5.8	1.6	0.6	0.2	0.0	1.6	1.6	0.8	0.6	0.2	0.2
Dytiscidae adult		0.8	0.0	0.0	1.4	1.2	1.0	0.0	0.0	4.6	5.4	1.4	0.6	0.2	0.0	1.4	1.2	0.4	0.4	0.2	0.2
Laccophilus		0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ilybius		0.0	0.0	0.0	0.8	0.2	0.2	0.0	0.0	2.8	4.0	1.4	0.4	0.2	0.0	0.8	1.0	0.4	0.4	0.2	0.2
Rhantus		0.0	0.0	0.0	0.4	0.5	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hygrotus		0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0
Agabus		0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Uvarus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydroporus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dytiscus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coptotomus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
unident. Dytisc.		0.4	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dytiscidae larvae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	0.2	0.0	0.0	0.0	0.2	0.4	0.4	0.2	0.0	0.0
Dytiscus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydroporus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0
Agabus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.2	0.0	0.0
Gyrinidae -	*Gyrinus*	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Haliplidae -	*Haliplus*	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0
Hydrophilidae		0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0
Tropisternus		0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Laccobius		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Helochares		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Curculionidae -	*Lixus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Scirtidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera		6.8	1.2	0.4	3.2	4.8	3.1	0.5	1.6	11.2	3.0	3.6	4.6	1.8	2.4	5.2	9.0	10.4	7.6	2.4	7.0
Ceratopogonidae		1.2	0.4	0.0	2.3	0.7	0.5	0.0	0.6	0.8	0.2	0.2	0.8	0.2	0.2	0.0	0.6	1.0	0.4	0.0	0.0
Serromyia		0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 1.3 (cont'd).

	MONTH:	May			June					July						August					
	STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \	DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
Forcipomyia		0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atrichopogon		0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bezzia/Palp.		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Culicoides		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.8	0.4	0.0	0.0
unident. Cerat.		1.2	0.4	0.0	1.8	0.5	0.5	0.0	0.6	0.2	0.0	0.2	0.4	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae		5.6	0.8	0.0	0.5	4.1	2.4	0.2	0.5	8.6	2.0	2.8	3.6	1.4	2.0	4.8	7.8	9.2	7.2	2.4	6.8
Ephydridae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Sciomyzidae		0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Culicidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Culex		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anopheles		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Dixidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Brachycera		0.0	0.0	0.0	0.4	0.0	0.2	0.2	0.5	1.2	0.4	0.0	0.2	0.2	0.2	0.4	0.2	0.2	0.0	0.0	0.0
Ephemeroptera		0.0	1.2	0.4	0.0	0.0	0.2	0.0	0.2	0.0	0.4	0.4	0.8	1.0	1.0	0.0	3.2	8.0	8.4	1.2	0.8
Bactidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metropodidae -	*Siphloplecton*	0.0	0.8	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caenidae -	*Caenis*	0.0	0.4	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.4	0.6	0.6	1.0	0.0	3.2	8.0	8.4	1.2	0.8
unident. Ephem.		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera		0.0	3.6	2.4	0.4	3.0	2.4	1.4	1.6	0.2	1.0	0.4	1.6	0.8	1.8	0.4	0.2	1.0	1.6	0.6	1.2
Belostomatidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.2	0.0	0.0
Corixidae		0.0	3.6	2.4	0.4	1.5	1.4	0.5	1.6	0.0	0.6	0.2	0.6	0.8	1.4	0.0	0.2	0.4	1.2	0.6	1.2
Corix. adult		0.0	3.2	2.4	0.4	0.7	0.2	0.2	1.1	0.0	0.2	0.0	0.4	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.6
Hesperocorixa		0.0	0.8	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sigara		0.0	2.4	1.2	0.0	0.0	0.0	0.0	0.5	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Palmacorixa		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2
unident. Corix.		0.0	0.0	0.0	0.4	0.7	0.2	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.2
Corix. larvae		0.0	0.4	0.0	0.0	0.8	1.2	0.2	0.5	0.0	0.4	0.2	0.2	0.8	0.8	0.0	0.2	0.4	1.2	0.6	0.6
Saldidae		0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 1.3 (cont'd).

MONTH:	May			June					July						August					
STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \ DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
Mesoveliidae	0.0	0.0	0.0	0.0	1.4	0.7	0.4	0.0	0.2	0.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nepidae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Veliidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.2	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.0
unident. Hemipt.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.2	0.2	0.0
Pyralidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Parapoynx	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
other Pyral.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cosmopterigydae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
other Lepidopt.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Odonata	0.4	1.6	0.0	0.4	0.0	0.0	0.7	0.0	0.6	3.2	2.4	3.0	1.6	0.0	0.4	4.4	1.8	1.4	0.8	0.6
Anisoptera	0.4	1.6	0.0	0.4	0.0	0.0	0.5	0.0	0.6	3.2	2.4	2.6	0.8	0.0	0.4	4.0	1.4	0.8	0.2	0.0
Aeshnidae	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Libellulidae	0.0	0.8	0.0	0.4	0.0	0.0	0.2	0.0	0.6	3.0	2.0	2.4	0.8	0.0	0.4	4.0	1.4	0.8	0.2	0.0
Leucorrhinia	0.0	0.8	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sympetrum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	2.0	0.6	0.0	0.2	0.2	0.0	0.0	0.2	0.0
immature Libell.	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.6	2.8	1.4	0.2	0.0	0.0	0.2	3.8	1.4	0.8	0.0	0.0
other imm. Anisopt.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coenagrionidae	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.0	0.4	0.4	0.6	0.6	0.6
Telebasis	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
immature Coenag.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.0	0.4	0.4	0.6	0.6	0.6
Homoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Trichoptera	1.2	0.4	0.0	0.9	0.7	1.0	1.9	5.2	0.0	0.0	0.2	0.4	0.0	0.2	0.2	0.0	3.6	2.4	1.8	0.8
Hydroptilidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	1.6	1.0	0.2
Oxyethira	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	1.6	1.0	0.0
immature Hydropt.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2
Leptoceridae	0.0	0.4	0.0	0.5	0.2	1.0	1.9	4.8	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.8	0.2	0.4	0.4
Trianodes	0.0	0.4	0.0	0.0	0.2	0.7	1.7	3.8	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2

Table 1.3 (cont'd).

MONTH:	May			June					July						August					
STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \ DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
Branchiobdellida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.4
Mollusca	0.8	0.8	0.4	1.9	2.2	3.7	4.0	1.2	4.4	3.6	2.0	4.8	1.0	2.0	6.8	6.6	3.4	2.4	2.0	0.6
Sphaeriidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	1.2	0.2	0.0	0.0	0.0	3.0	0.8	0.0	0.0	0.4	0.2
Gastropoda	0.8	0.8	0.4	1.9	2.2	3.7	4.0	1.2	2.2	2.4	1.8	4.8	1.0	2.0	3.8	5.8	3.4	2.4	1.6	0.4
Bithyniidae	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0
Lymnaeidae	0.0	0.4	0.0	1.0	1.4	0.2	0.5	0.0	0.4	0.4	0.6	0.2	0.0	0.4	0.2	0.4	0.2	0.2	0.0	0.2
Physidae	0.4	0.4	0.0	0.0	0.0	2.7	1.4	1.0	0.6	0.6	0.2	2.2	0.8	1.4	1.0	1.4	0.2	0.6	0.6	0.2
Planorbidae	0.4	0.0	0.4	0.7	0.8	0.7	2.1	0.2	1.2	1.4	0.8	2.0	0.2	0.2	2.4	3.4	2.6	1.4	0.8	0.0
Succineidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.4	0.2	0.2	0.0
Acari	2.0	1.6	0.8	3.4	5.8	5.0	3.5	5.4	2.8	3.8	2.0	0.8	1.6	2.2	1.2	1.8	0.6	4.8	1.4	1.8
Nematoda	2.8	0.0	0.0	0.6	1.4	0.0	0.0	0.0	1.2	0.2	0.0	0.2	0.0	0.0	1.0	0.2	0.0	0.4	0.0	0.0
Turbellaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.6	0.4	0.0
Cladocera	0.4	2.0	0.8	4.0	4.4	6.7	1.2	10.8	14.2	37.8	22.0	12.6	29.2	21.0	2.6	8.0	39.4	27.6	6.2	18.0
Ostracoda	7.2	16.4	1.6	1.6	37.9	29.7	43.4	75.6	0.8	0.8	2.8	6.8	3.6	16.0	1.6	4.2	6.8	10.2	6.4	4.8
Copepodae	9.2	9.2	2.8	6.2	9.8	7.0	3.6	9.6	19.8	11.8	6.8	3.4	12.0	16.6	12.4	10.2	4.0	9.4	4.8	3.2
Hydridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.6	0.2	0.0	0.6	0.4	0.2	0.0	0.2	0.0	0.0
Fish:	4.0	0.0	0.8	0.0	1.9	0.5	11.7	4.6	0.0	1.2	0.8	1.2	0.8	0.6	0.2	2.8	1.2	2.0	0.6	0.6
Etheostoma exile	2.8	0.0	0.4	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ameiurus nebulosus	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Umbra limi	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.6	0.2	0.0	0.2	2.6	0.8	0.0	0.4	0.2
Culaea inconstans	0.8	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.2	0.2	0.0	0.0	0.2	0.0	0.0	0.0
Amia calva	0.0	0.0	0.0	0.0	0.8	0.0	11.7	4.3	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0
Pungitius pungitius	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gasterosteus aculeatus	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyprinidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Micropterus salmoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.4	0.0	0.4
Perca flavescens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	1.6	0.0	0.0

Table 1.3 (cont'd).

	MONTH:	May			June					July						August					
	STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \	DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
Oecetis		0.0	0.0	0.0	0.2	0.0	0.2	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.2
Mystacides		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
immature Lept.		0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0
Limnephilidae		0.8	0.0	0.0	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Phryganeidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.6	0.0	0.0
Polycentropodidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
immature Trich.		0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Collembola		1.2	0.4	0.0	0.0	0.7	0.7	0.0	0.0	0.8	1.2	0.0	0.4	0.0	0.2	0.6	0.2	0.0	0.0	0.0	0.0
Sminthuridae		0.8	0.4	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isotomidae		0.4	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.2	0.6	0.2	0.0	0.0	0.0	0.0
Poduridae		0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
other Collembola		0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hymenoptera		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Thysanoptera		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Orthoptera	*Tetrigidae*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Amphipoda		4.8	7.2	0.0	0.0	2.4	7.7	1.0	3.0	0.0	1.0	0.8	3.0	1.6	1.8	0.4	0.2	1.4	2.6	0.6	4.4
Gammaridae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Hyalellidae		4.8	6.8	0.0	0.0	2.4	7.7	1.0	3.0	0.0	1.0	0.8	2.4	1.2	1.8	0.4	0.2	1.0	2.6	0.6	4.4
Crangonyctidae		0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asellidae		0.0	0.4	0.0	0.0	0.0	0.2	0.0	0.0	0.8	0.4	0.0	0.2	0.0	0.2	1.6	1.4	0.2	0.2	0.2	0.2
Cambaridae	*Orconectes*	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Argulus		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.2	0.6	0.2	1.2	0.4	0.0	0.4	0.2
Hirudinea		2.8	0.0	0.0	0.6	0.5	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.4	0.0	0.0	0.0	0.0
Oligochaeta		0.4	2.0	0.0	0.4	0.0	0.5	0.2	0.0	2.8	1.6	1.8	5.2	2.6	8.6	1.2	1.2	5.6	3.8	2.8	2.4
Lumbriculidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Naididae		0.4	2.0	0.0	0.4	0.0	0.5	0.2	0.0	1.6	1.0	1.2	3.8	0.6	6.4	1.2	1.2	5.6	3.8	2.6	2.4
Tubificidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
other Oligo.		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.4	0.6	1.4	2.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0

Table 1.3 (cont'd).

	MONTH:	May			June					July						August					
	STATION:	4	5	6	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
TAXON \	DEPTH:	10	20	30	10	20	30	40	50	10	20	30	40	50	60	10	20	30	40	50	60
larvae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
tadpole		0.0	0.0	80.0	0.0	0.4	1.9	0.5	38.8	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bufo tadpole		0.0	0.0	80.0	0.0	0.0	1.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rana tadpole		0.0	0.0	0.0	0.0	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
unknown tadpole		0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bufo adult		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rana adult		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
		7.6	8.0	3.0	8.4	9.2	12.2	9.0	7.6	15.2	15.2	12.4	15.8	12.0	12.2	13.2	16.4	14.6	15.0	12.2	11.2
# taxa per trap																					
Total abundance		45.6	48.4	90.4	25.4	77.4	72.5	74.3	157.9	68.0	77.4	48.8	51.6	58.4	76.2	39.6	58.2	89.8	86.4	33.2	47.6

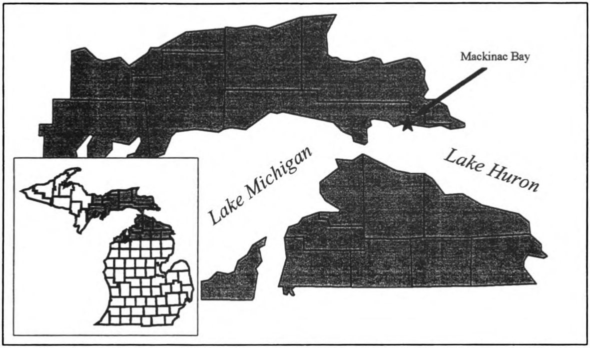


Figure 1.1. Study site location

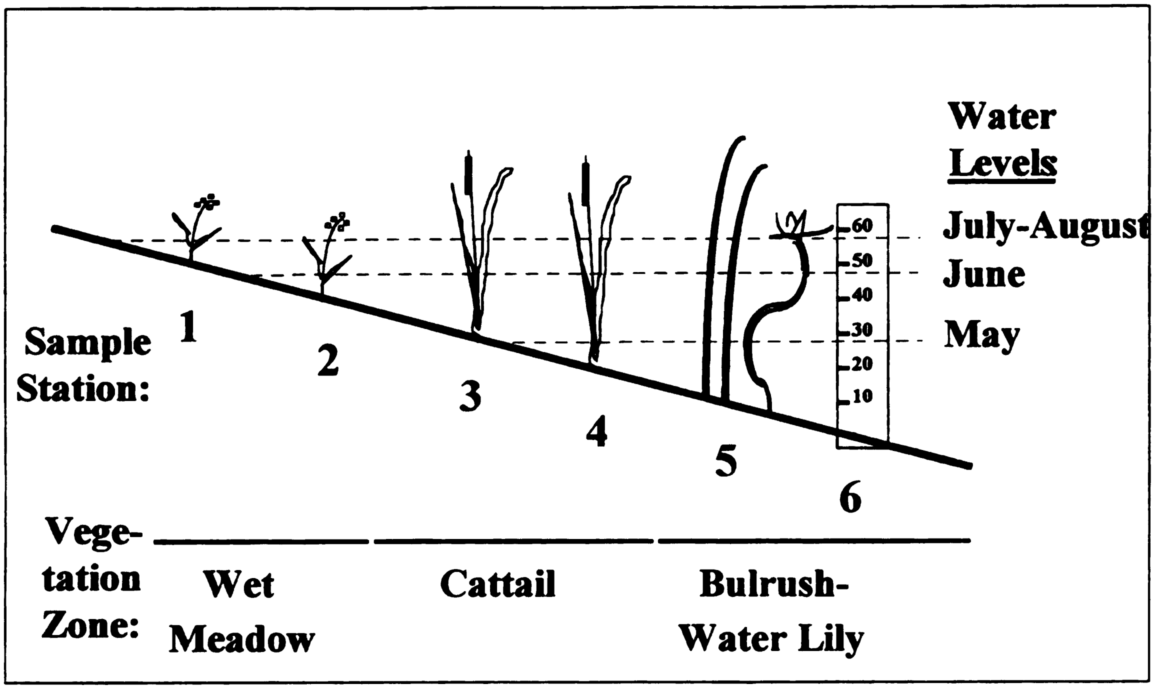


Figure 1.2. Schematic cross-section through a sample transect, showing vegetation zonation and monthly water levels in 1996 at Mackinac Bay.

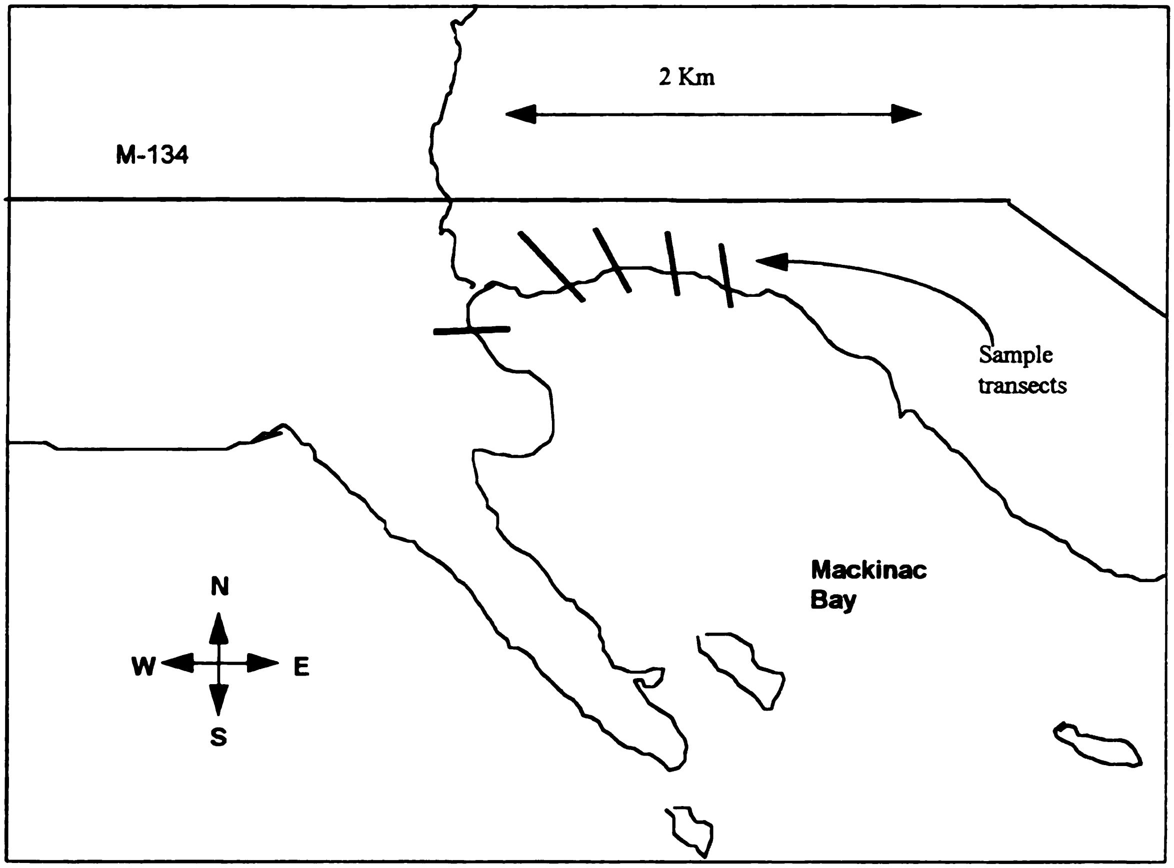


Figure 1.3. Overhead view of Mackinac Bay and transect placement.

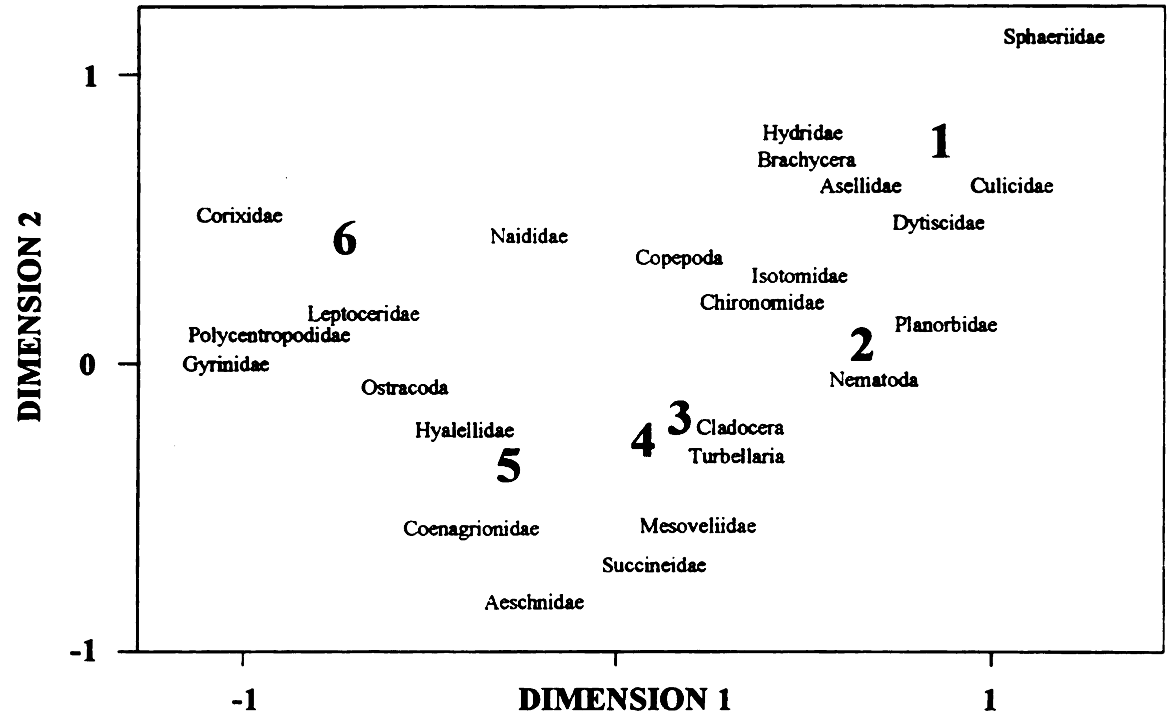


Figure 1.4. Correspondance analysis ordination (representing >69% of total inertia) of invertebrate communities at six elevation stations during summer (May-August), 1996, including positions of all taxa with combined two-dimensional squared-cosine values greater than 0.5.

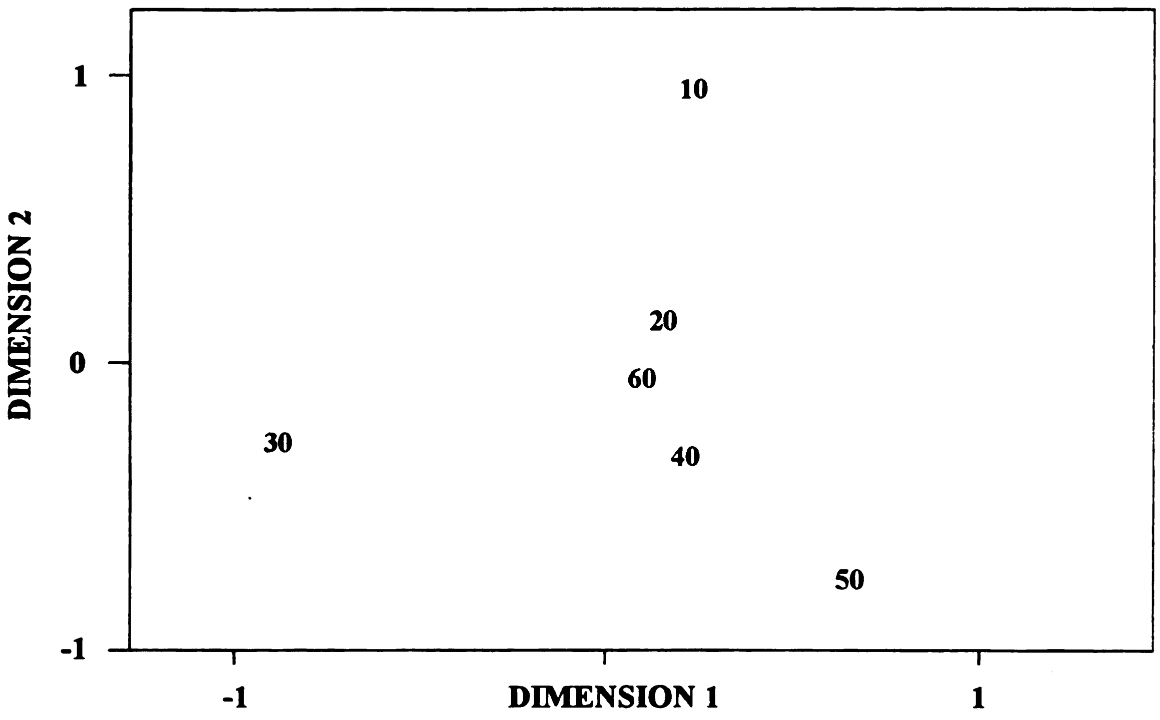


Figure 1.5. Correspondance analysis ordination (representing >71% of total inertia) of invertebrate communities at six water depths during summer (May-August), 1996.

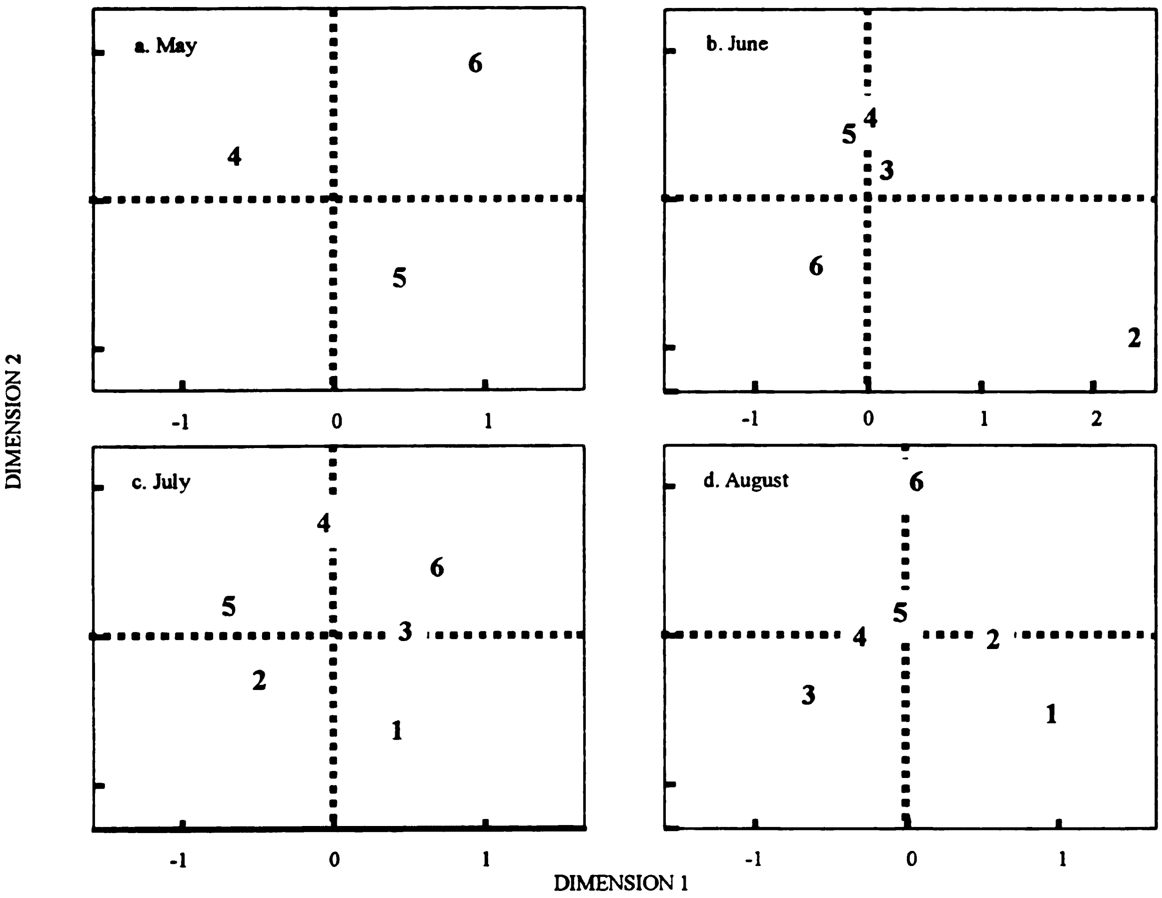


Figure 1.6. Correspondance analysis ordinations of invertebrate communities at six elevations during each of four months (May-August), 1996.

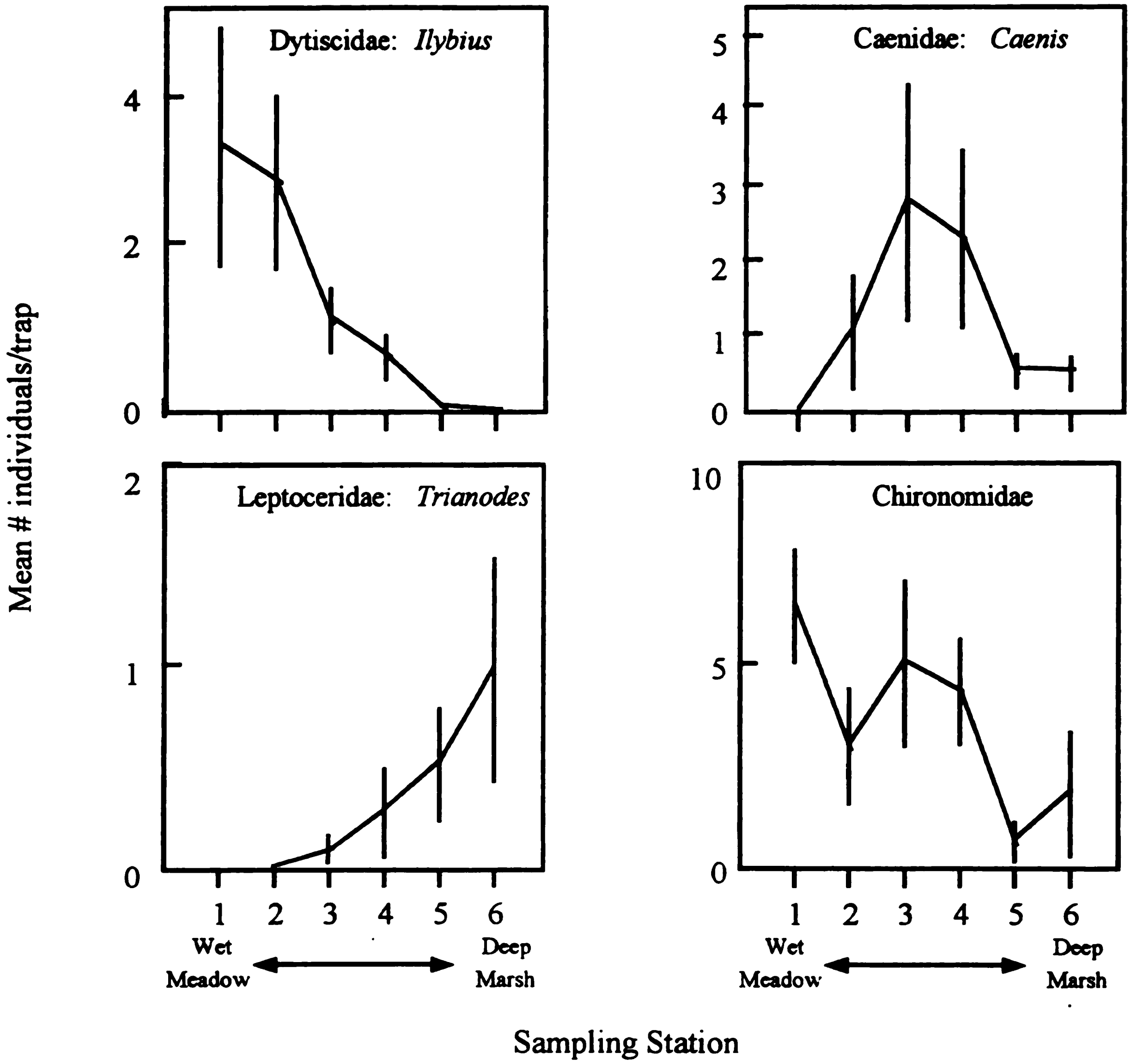


Figure 1.7. Gradient distribution profiles of representative high-, mid-, and low-gradient associated genera (*Ilybius*, *Caenis*, and *Trianodes*, respectively), and a higher taxon (Chironomidae) with a more general distribution, during summer (May through August), 1996 (means with standard errors).

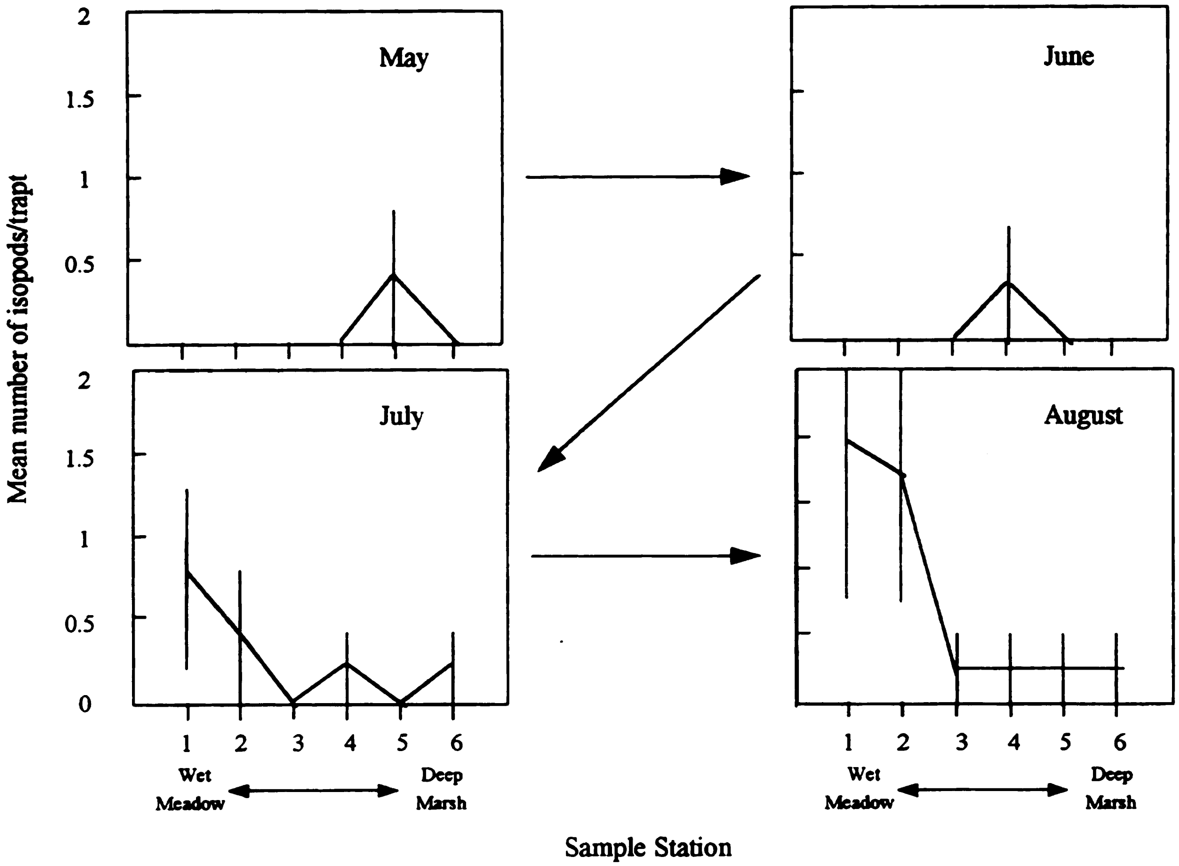


Figure 1.8. Comparison of gradient distributions of Isopoda: *Caecidotea* during each month (May through August) of summer, 1996 (means with standard errors).

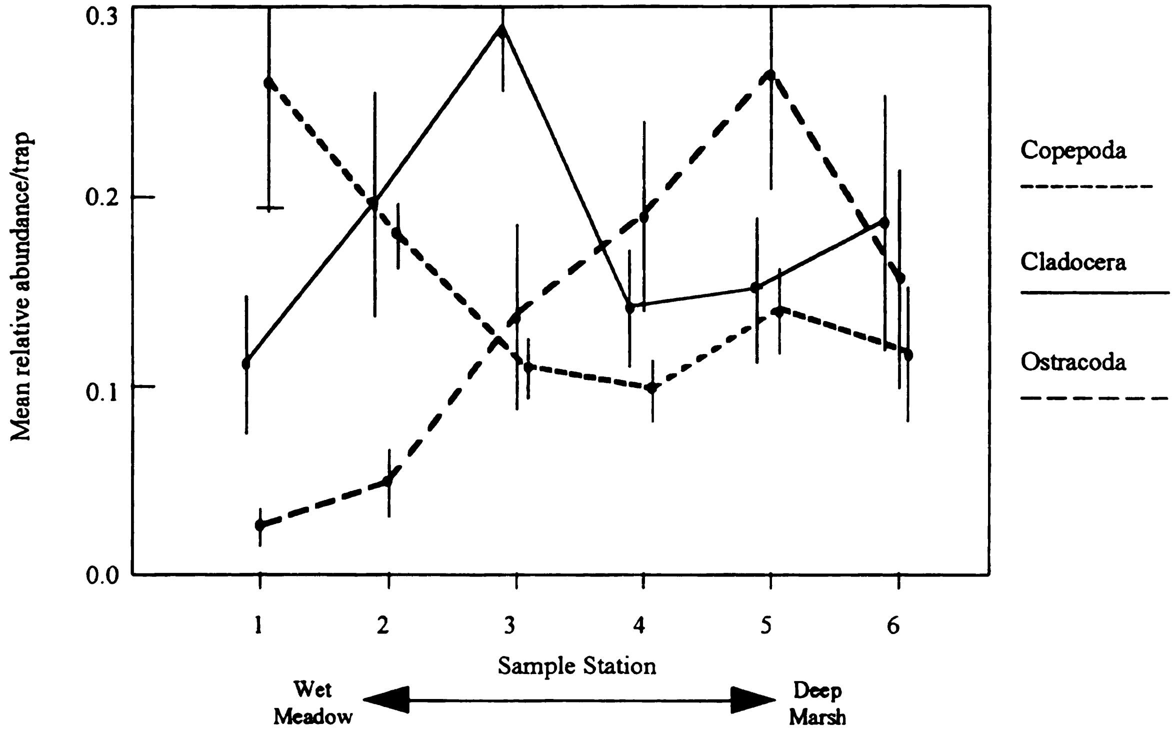


Figure 1.9. Gradient distribution profiles of microcrustaceans during summer (May through August), 1996 (means with standard errors).

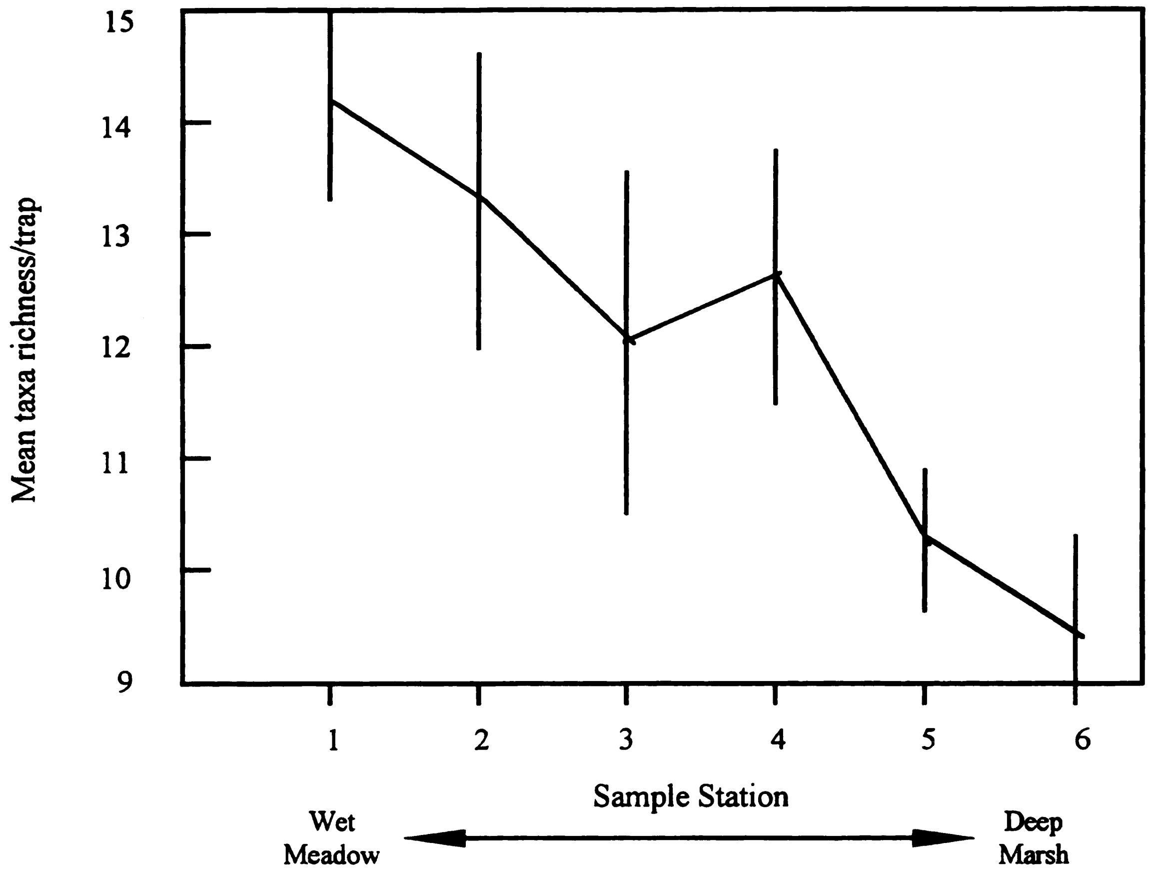


Figure 1.10. Variation in taxa richness (means and standard errors) across the elevation gradient over all months (May through August) of summer, 1996.

Chapter 2

IMPACTS OF HIGH WATER LEVELS ON THE BIOTA OF A LAKE HURON COASTAL WETLAND: RESULTS OF A NATURAL EXPERIMENT

INTRODUCTION

Great Lakes water levels fluctuate on several time scales, including fairly predictable seasonal cycles, and erratic long-term cycles that are determined by regional climatic variation. On average, the level of Lake Huron rises approximately 25 cm from midwinter to midsummer each year, falling again through autumn and early winter (Prince and Burton 1996). This cycle, combined with gentle substrate slopes, creates a gradient of hydrologic conditions in coastal wetlands: from permanently-flooded deep emergent marsh to progressively higher zones that are flooded for shorter durations as the water line moves slowly up, and then down, the slope (Krieger 1992, also see Figure 2.1). Animal communities gradually vary in composition along this gradient (Chapter 1), possibly because of differences among taxonomic groups' adaptations to temporary flooding. Drought-resistant taxa appear to comprise the majority of the communities at higher elevations, while those groups without such adaptations are progressively more abundant at lower elevations. Further, some taxa migrate up the gradient as the duration of seasonal flooding lengthens, though some conspicuously do not.

Determining the causes of animal community variation along the elevation gradient is difficult because most environmental factors that may affect aquatic animals co-vary with the gradient. While variation in flooding regime is one likely cause of faunal variation, correlated variables such as plant community composition (Voights 1976, Zedler 1981), detritus composition and quality (Barlocher et al. 1978, Nelson et al. 1990), water quality (Cardinale et al. 1997), and predator assemblages (Wellborn et al. 1996) may also affect fish and aquatic invertebrates. The influences of some of these factors may be distinguishable through controlled experimentation, but the effects of other factors are more difficult to separate from each other.

The above description of flooding regime gradients in coastal wetlands is overly simple because it does not incorporate the effects of year-to-year lake level changes. Amplitudes, durations, and directions of these long-term changes are unpredictable, but they can be equal to or greater than seasonal changes (Figure 2.2). Rising water levels cause permanent flooding in previously temporary zones, and falling water levels reverse this effect. Even relatively small changes can flood or drain large areas of the shallow-sloped coastal wetlands, and these flooding changes are known to cause plant community changes over time (Burton 1985). However, effects of such hydrologic change on wetland fish and invertebrates have not been well studied.

Aquatic fauna differ among isolated wetlands with different flooding regimes (e.g. permanent, semi-permanent, seasonal, temporary, ephemeral; Williams 1987, Batzer and Wissinger 1996), so changes in coastal wetland flooding may be expected to change animal communities. The apparently-distinct communities at high elevations (Chapter 1) should change when these areas are subjected to year-round flooding, rather than the usual seasonal inundation pattern. Some members of these distinct communities may even be temporarily lost where up-slope migration is impeded by human shoreline development. Also, hydrologic variability may be an important determinant of long-term survival of animal species, especially if it increases in the future, as predicted by some global climate change models (Mortsch 1998). Animals that cannot adjust to high-amplitude and/or short-period water level change will probably give way increasingly to a lower-diversity community of generalists, as is typical of temporary waters (Wiggins et al. 1980).

From late 1996 to early 1998 Lake Huron's water level rose abruptly and then fell, creating a high-water year (1997) between two lower-water years and dramatically altering coastal wetland hydrologic conditions. During this period, high-elevation wet meadow communities switched from temporary flooding (4 months or less) to year-round flooding and back again, so faunal changes in response to a flooding-regime change could be studied. Also, plant communities did not change dramatically during this period, and the vegetation zonation pattern along the elevation gradient remained the same, offering an opportunity to determine whether animal distributions changed horizontally along the gradient or whether they remained in the elevation/plant zones where they had previously been most abundant. Thus, at least temporarily, many variables directly associated with vegetation zonation and those associated with water level were de-coupled.

In this study I hypothesized that if flooding regime differences among wetland zones are very important faunal structuring forces, as is argued in the previous chapter, dramatic alteration in flooding from year to year should alter the animal communities most in coastal wetland zones that experienced the greatest change in flooding regime, particuarly the high-elevation wet meadow. Meanwhile, deep marsh communities that were flooded continuously throughout the study period would change little. On the other hand, if vegetation zonation and associated variables (e.g. detritus characteristics, shading, etc.), which respond more slowly to hydrologic changes, are of key importance to animal communities, then these communities should show relatively little change in spatial distribution among zones when water levels change.

METHODS

The study site was the same northern Lake Huron coastal wetland, with the same sampling transects used in the 1996 analysis described in Chapter 1. In 1997, I observed a substantial water level rise in the wetland, which was the impetus for this study. Water levels changed over the three years (1996-1998) of the study as follows (also see Figure 2.3). In Year 1 (1996) the water line was at the upper edge of the cattail/transition zone in early May. I considered this an "average" year, because cattail plants are generally considered an indicator of the long-term average water level, and later examination of NOAA data indicated that the rise from January to May was just over half the total rise for the year. Year 2 (1997) was the high-water year. By May of that year, the water level was at least 30 cm higher than it had been one year earlier, resulting in year-round flooding of the wet meadow zone. Because the high water reached much farther into the wet meadow than in Year 1, I added an additional high-elevation sample station (Station 0) to each transect. The water peaked in late July and then began a multi-year general decline. In May of Year 3 (1998) the water line was approximately intermediate between the May levels of the previous two years. After a relatively brief rise, the level peaked in June and declined slowly for the rest of the year. Under these conditions the upper wet meadow only remained flooded until late June so Station 0 samples could not be taken after that month. By the August sampling period there was just enough water at Station 2 sites to allow sampling.

Sampling procedures

To estimate relative fish abundances at different elevations among years, I continued the activity trap sampling described in Chapter 1. However, for invertebrate samples I used a Wilding-type stovepipe sampler to collect quantitative substrate/water-column samples. This method was a measure of a standardized subset of invertebrates found on and above a known surface area of wetland substrate, so it could be used to estimate invertebrate density differences among sample stations and time periods. I collected this type of sample from even-numbered sampling stations resulting in one sample from each vegetation zone (wet meadow, transition, bulrush) on each transect (thus five replicates per zone), during each sampling period (once monthly during June, July, and August of 1996 through 1998). Because the water level was high in the second year of the study, I established, and sampled, an additional station (Station 0) at an elevation 10 cm higher than the previously-highest station (Station 1) of each transect.

The sampling method consisted of forcing one end of a metal stovepipe-like tube (14.5-cm diam.) into the substrate to enclose 165.1 cm^2 of substrate with its overlying water. Large detritus and any attached animals were scooped out of the cylinder by hand and placed in a sieve-bottom bucket (250 μm mesh). The water in the cylinder was then stirred to suspend fine particulate matter and small animals, and the cylinder contents were pumped into the bucket using a plastic manual transfer pump. The pump was very inexpensive and commonly available in stores, and consisted of a hand-squeezed bulb atop a one-way valve assembly with incurrent and excurrent tubes. I standardized the volume of sampled material by squeezing the bulb 100 times per sampler placement.

Sample sites were selected at a random distance from 5 to 15 meters from each sampling station, perpendicular to the transect and always on the same side. From the randomly-selected location, I collected three stovepipe samples at one-meter intervals, combining the three in the sieve bucket to reduce the effects of small-scale spatial variations on the data. I rinsed all material in the sieve bucket to remove small particles, then transferred the bucket contents to a one-quart canning jar. Upon returning from the field site each evening, I drained excess water from each jar and preserved the contents in 95% ethanol with Rose Bengal dye to stain animal tissues for easier lab sorting.

Each sample was processed as follows. First, all sample material was rinsed through a 1-cm mesh to remove large detritus that would interfere with the subsampling procedure. The sample was washed through a 500 μm mesh sieve and two random one-sixth subsamples were collected and combined, so a total of one-third of each sample was selected for further processing. The subsampling device was a ray-finned divider that fit into a standard sieve and consisted of six plastic dividers radially arranged and glued together at the center. The device "cut" the sample into six equal-sized "pie" pieces in the sieve. To do this, I placed the sieve in a tub of water deep enough to submerge the sample but shallow enough that the top edge of the sieve was above the water surface. I then agitated the sample with a stirring rod for two minutes, and placed the subsampler in the sieve, twisting the device as I slowly lowered it to keep sample material suspended. Once the divider was lowered to the mesh surface, I removed the sieve from the water and the randomly-selected "wedges" were easily removed from the sieve with a rinse bottle. All invertebrates were picked from each subsample under 10X magnification and retained for identification.

I also collected plant community data from each sampling station, though I did not begin this sampling until the second year. For the first year I was able to use data from a single transect that were collected as part of a related study, but for the next two years I collected data from all stations on all transects. Plant sampling was performed as follows. Three 0.5m X 0.5m quadrats were selected at random angles and distances (1 to 20 m) from each sampling station. Stems of each emergent species in the quadrat were counted and percent areal coverage of each submergent species was visually estimated.

Data collection and analysis

Invertebrates were identified according to Merritt and Cummins (1996), Pennak (1989), and taxon-specific keys for lower taxonomic levels, when appropriate. Fish identification followed Hubbs and Lagler (1967). I identified fish to species and invertebrates to the lowest taxonomic level possible using a dissecting microscope, and counted individuals in each taxon. This resulted in different levels of taxonomic resolution, so subsequent comparisons of taxa richness and Shannon-Weiner taxa diversity may not have fully reflected differences at the genus level. After data entry, I used correspondance analysis to examine and display among-year changes in invertebrate communities at different elevations. First I aggregated the monthly data from each station during each year resulting in 10 data records (3 sampling stations during each of three years, plus the additional high wet meadow station in Year 2). I used the CORRESP procedure in SAS to simultaneously ordinate the ten samples, and plotted the samples in two-dimensional ordination space to examine changes in community similarities among years.

To explore changes in abundances of individual invertebrate taxa, I first examined data distributions and decided to use a ln(x+1) transformation to normalize the data and equalize variances. I initially used a two-way ANOVA approach (with Transect as a "blocking" factor, and Year and Sampling Station as main effects) to analyze differences in abundances and relative abundances of all taxa, total abundance, and taxa richness. However, the Year X Station interaction term was significant ($p<0.05$) in almost all cases, so I analyzed data from each station separately. I used individual paired t-tests to analyze differences in observations matched by transect and month from Year 1 to Year 2, and then from Year 2 to Year 3. This approach accounted for the effects of repeated measures from the same transects, and accounted for differences among months without including them in the analysis. The three-year sequence of events, then, was treated as two separate natural experiments.

After the "experiment" analysis, I analyzed data records from all stations and sampling periods with multiple regression to explore likely causes of the changes observed in response variables. The response variables tested included total invertebrate abundance, total insect abundance, and abundances of the most abundant taxa. Independent variables used in the regressions (both complete and stepwise) included sampling station, water depth, month, time since first re-flooded, plant stem density, % cover of submergent plants, dragonfly larva density, and fish catch per unit effort. The "time since re-flooded" variable was a sum of all non-winter months of continuous flooding since the last time the sample location had been "dry" (not flooded). For low-elevation sampling stations, the last "dry" time was inferred from NOAA water-level records. I ran regressions with and without the vegetation variables because I lacked vegetation data for all records, so the with-vegetation regressions had to be based on fewer data records. I examined the residuals from regressions on untransformed data and decided to re-run the analyses on ln(x+1) transformations of the dependent variables.

RESULTS

Changes in total invertebrate density

The absolute density of invertebrates almost tripled over the three-year period (Figure 2.4), from nearly 15,000 animals/m^2 (~253/sample for all 1996 samples) to over 41,500 (~705/sample for all 1998 samples), averaged over all stations ($p<0.001$, ANOVA on log-transformed abundances). Density was highest in the deep marsh initially (Table 2.1), but rates of increase were higher at higher points on the gradient, so that by 1998 densities in the wet meadow and transition zone equalled or exceeded that in the deep marsh (Figure 2.5). The greatest increase (~375%) occurred in the wet meadow, with a higher rate of increase in the first period (~181%, 1996-97) than in the second (~69%, 1997-98). On the other hand, density increase in the transition zone and deep marsh were higher in the second period. The transition zone density increased ~30% and ~220% in the first and second periods, respectively; deep marsh density rose ~20% and ~73% in these periods. To test whether invertebrate density growth approached exponential rates at each station, I log-transformed the total abundance data and ran simple linear regressions of log(density+1) against sampling time (June through August of each year, or nine sample times). The data fit a linear function well at each station ($p<0.001$) with an r^2 as high as 0.64 at Station 4, indicating that the invertebrate density increase approximated an exponential growth curve.

Community composition changes along the elevation gradient

The correspondance analysis (CA) plot (2-dimensional inertia 56.74% of total) illustrated changes in communities among years and stations as distances between their plotted positions (Figure 2.6). The positions of the wet meadow, transition zone, and deep marsh communities in 1996 indicated the community gradient ordered along the first ordination axis. The 1997 communities at these stations, plus the added "hummock" station in the high wet meadow, also were ordered along the first axis but two differences were evident. First, the total 1997 gradient, even with the additional station, was shorter than the 1996 gradient, indicating less variability from end to end in 1997 than in 1996. Second, the 1997 gradient was oriented differently along the second axis than the 1996 gradient, indicating partial changes in community composition among years. The 1998 gradient was the shortest of the three, indicating a substantial homogenization of communities from deep marsh to wet meadow. Yet, the orientation of the gradient was roughly parallel to the 1996 gradient, indicating a partial return to community compositions characteristic of the first year of the study (Figure 2.7). The greatest magnitudes of community change (represented by arrows in Figure 2.6) occurred in the wet meadow community during both periods.

Examination of the partial contributions to inertia for each axis (from the SAS output, as explained in Chapter 1) revealed that the taxa contributing most to the first axis (contribution index > 1) were from two groups: those that were most associated with the highest points on the gradient during the first two years (and subsequently decreased in relative abundances), as opposed to those that were more generally distributed and increased in relative abundance at most stations over time (discussed in detail below). The first group could be split into two subgroups that contributed to the second axis, which represented among-year differences at the highest-elevation stations. These sub-groups were those that were most characteristic of the wet meadow community in 1996 (and 1998 to a lesser extent) vs. those that became more abundant in the wet meadow and hummock communities in 1997, at the expense of the first sub-group.

Overall, the greatest spatial heterogeneity in community composition (ordination axis 1) occurred in 1996, indicated by the gradient length in the CA plot (Figures 2.6 and 2.7). Over the three-year period, wet meadow communities became more like lower-elevation communities, whose ordination positions changed little. This loss of gradient variation was a result of lowered relative abundances of many taxa that characterized the wet meadow community initially, and the increasing dominance of a few groups that had been initially abundant only at lower elevations, but became more generally distributed (as described below). Secondary variation (represented by the second ordination axis) apparently consisted of differences between wet meadow communities under high water and low water conditions.

Diversity: Richness and equitability

Shannon-Wiener taxa diversity differed both spatially and temporally (Table 2.2). These differences indicated variation in taxa identified to various taxonomic levels: genus in most cases, but also higher taxa that were difficult to identify further at low magnification. I present these data as indicators of diversity differences, though they may not fully reflect differences in species or genus diversity. Initially, diversity was greatest in the wet meadow, but after a decline at all stations in 1997, diversity in the deep marsh recovered while it continued to decrease at other stations. This resulted in a reversal of the diversity spatial trend: from highest diversity in the wet meadow in 1996 to highest diversity in the deep marsh in 1998 (Figure 2.8). The greatest diversity loss (from 3.02 in 1996 to 2.20 in 1998) occurred in the wet meadow, while deep marsh diversity changed much less. Transition zone diversity decreased most from 1996 to 1997 (2.71 to 2.17) and very little after that. The hummock zone had the highest diversity of all stations (2.63) in 1997, and dropped to 2.45 in 1998, though this number only represents a single month's data.

These diversity differences reflected spatial and temporal differences in the two components of diversity: richness and equitability. Taxa richness decreased among the wet meadow, transition zone, and deep marsh communities from 1996 to 1997 partly because several taxa associated with the higher elevations in 1996 did not occur in 1997 samples, or were only found at the newly-established "hummock" stations. Richness rebounded partially in 1998 as some of these taxa returned to lower elevations (Figure 2.9). On the other hand, equitability decreased throughout the study period. This was primarily the result of increases in community dominance by a few taxa, especially isopods (mostly *Caecidotea*), midge larvae (Chironomidae), Caenidae mayflies (all *Caenis*) and, to a lesser extent, amphipods (mostly *Hyallela*). Increasing dominance by these groups was typical of communities at all stations, with Chironomidae reaching their highest relative abundances in 1997 and the other three groups generally increasing in abundance and relative abundance at all stations over the whole study period (Figure 2.10).

Community composition variation: Individual taxa

Community compositions varied among stations and years (Table 2.3). In general, Chironomidae larvae numerically dominated all stations in 1996, but Caenidae mayfly larvae and Isopoda grew in relative abundance all along the gradient over time (Table 2.4). The increase of these two groups proceeded from lower to higher stations, though Caenidae increased at higher elevations sooner than isopods. Amphipods showed a similar trend to isopods, though they increased less and remained most abundant at Station 6 (deep marsh) at all times.

The wet meadow community changed most dramatically and somewhat differently during both periods (1996-1997 and 1997-1998). While isopods and amphipods increased in importance over the whole period, other changes occurred that made the 1997 high-water wet meadow community relatively distinct (as was indicated by the ordination plot, discussed above). Several taxa "invaded" the wet meadow in 1997, only to decrease in abundance again as water fell in 1998. These changes were accompanied by decreases in abundance of several taxa that were characteristic of the 1996 wet meadow community. For example, Nematoda worms, Oribatei soil mites, Harpacticoida copepods, Limnephilidae caddisfly larvae, Ceratopogonidae fly larvae, Sphaeriidae clams, and Dytiscidae diving beetles all decreased in wet meadow relative abundance in 1997, and most of them returned to higher abundances the following year (Table 2.4). Taken collectively, all taxa that were most abundant at Station 2 in 1996 were significantly less abundant (p=0.002) among all stations in 1997, though many of these groups occurred at the newly-flooded Station 0. Conversely, these taxa collectively increased (p<0.001) over all stations (but predominantly at Station 2) from 1997 to 1998.

Shifts in spatial position of peak taxa abundances among years

Abundances of taxa generally peaked at single sampling stations, but these peaks changed position on the gradient from year to year for most taxa (Table 2.5). Four peak-shift categories could be distinguished, and they corresponded to the spatiotemporal relative abundance changes summarized in Table 2.4. The most common pattern was seen in about one-third of the taxa and consisted of up-slope peak shifts in 1997 when water was high, followed by down-slope shifts during the declining water levels of 1998. Groups showing this pattern included many insect taxa, most microcrustaceans, some snails, and water mites. Some of these taxa shifted from low parts of the gradient to higher elevations, and back again, while certain others (e.g. Dytiscidae, most Ceratopogonidae genera) were wet meadow associated taxa that shifted to the hummock stations when water was high and returned to the lower wet meadow the following year.

Other peak shift patterns included taxa that progressively moved to higher elevations through the entire study period, particularly those that shifted from the wet meadow to the hummock zone and stayed there (e.g. *Libellula*, *Planorbula*, *Haliplus*, an unidentified Limnephilidae genus, Harpacticoida, Isotomidae, Oribatei, Nematoda) or disappeared completely from the samples over time (e.g. Ceratopogonidae: *Forcipomyia* and *Atrichopogon*, Sminthuridae). A different, and very important, pattern was shown by the Pericarida crustaceans (Isopoda and Amphipoda): they increased in relative abundance at all stations, as mentioned above, but nonetheless remained abundant at the lowest elevations during all years. A few other taxa showed this pattern of stable abundance peaks in the transition zone and deep marsh (though not expanding up-gradient as did the Peracarida): limpets (Ancylidae), Libellulidae: *Leucorrhinia* dragonfly nymphs, Chrysomelidae beetles, Polycentropodidae caddisflies, and non-*Stylaria* Naididae worms.

A few taxa showed anomalous patterns. Brachycera initially (1996) peaked in the wet meadow, then in the deep marsh in 1997 and 1998; Leptoceridae caddisflies showed two disconnected abundance peaks in 1997 (in wet meadow and deep marsh); Sphaeriidae were always most abundant at high elevations, but consistently showed a secondary peak in the deep marsh. In each case it is likely that these discontinuities represented different distributions of distinct, but unidentified, genera within the higher taxonomic category. Bithyniidae snails and Oribatei soil mites remained most abundant in the lower wet meadow (Station 2) communities during all years, but the Bithyniidae were only common on the western-most transects, suggesting a localized population within the site. Hydrobiidae snails and Corduliidae dragonfly nymphs, on the other hand, were not present in 1996 samples, then peaked in the deep marsh and transition zone during 1997 and 1998, respectively, suggesting that they were migrating up-slope from elevatons that were lower than the deep marsh stations.

Fish distributions

In 1996 most fish caught were mudminnows (*Umbra limi*), especially in the wet meadow. Juvenile largemouth bass (*Micropterus salmoides*), bowfin (*Amia calva*), and yellow perch (*Perca flavescens*) occasionally occurred there, but were more common in the transition zone. Brown bullhead (*Ictalurus nebulosus*) were only caught in the deep marsh. I observed common carp (*Cyprinus carpio*) breeding activity in the deep marsh and into the transition zone, but dense vegetation and shallow water (<20 cm) prevented their invading the wet meadow that year.

Wet meadow and transition zone fish densities were apparently lower in 1997 than in 1996 (Figure 2.10), though this is somewhat misleading. Because the activity traps used for fish sampling were size limited, any fish that could not fit through the opening

(~23 mm inner diameter) were not sampled. Other fish sampling with large fyke nets (conducted as part of a related study) indicated that larger fish (e.g. yearling bowfin, pumpkinseed, bullhead) were present in the wet meadow in 1997. However, mudminnows (the most common species) of all sizes were small enough to fit into the traps, and they were less abundant in 1997 than in 1996, but increased again in 1998 ($p=0.014$, Kruskal-Wallis test). Juvenile bowfin, bullhead, and bass extended their range far into the wet meadow in 1997 where they had been rare in 1996.

In 1998, the initial water level was about as high as the 1996 peak. The fish assemblage resembled the 1996 assemblage in composition and spatial distribution, except that juvenile pumpkinseed were much more abundant ($p=0.009$ Wilcoxon rank-sum test), and mudminnows were concentrated in the transition zone rather than the wet meadow. As water level fell, fish were apparently forced to move further down-gradient until only small mudminnows were present in the wet meadow. Densities, however, remained lower than in 1996.

Regression analyses of possible causal factors

Multiple regression analysis revealed that total invertebrate density was significantly associated with duration of flooding ($p<0.001$) largely because of increased densities of the most abundant taxa: isopods ($p<0.001$), Caenidae mayfly larvae ($p<0.001$), Chironomidae ($p=0.016$), amphipods ($p=0.011$), and snails ($p=0.01$). However, flooding duration was not a significant influence on the abundances of Dytiscidae beetle larvae, Ceratopogonidae larvae, or microcrustaceans, all of which were inversely associated with water depth ($p<0.05$), which was consistent with their tendency to peak at high elevations. Trichoptera as a group were not associated with flooding time, but were inversely associated with water depth. A small minority of taxa were weakly ($0.1>p>0.05$) associated with emergent stem density, submergent plant coverage, and densities of the dominant predators (fish and dragonfly larvae). However, none of these factors consistently influenced dependent variables, with both positive and negative relationships occurring, and some factors being included or excluded (during stepwise regression) depending on which data transformations and aggregations were used.

Plant community changes

This study was partly based on the idea that plant communities changed little while water levels were changing. Data collected on Mackinac Bay plant communities in this study, and on several nearby wetlands in a related study (Gathman and Keas 1999), revealed that vegetation zones did not change position on the elevation gradient during the study period. I defined wet meadow communities as those that were numerically-dominated by sedges (*Carex*) and which included grasses, shrubs, and a characteristic assemblage of facultative wetland plants (e.g. *Campanula aparanoides*, *Lysimachia thyrsiflora*, *Iris versicolor*, etc.). Deep marsh communities were characterized by a very different assemblage of emergent plants (*Scirpus acutus*, *Pontedaria cordata*, *Sagittaria* sp., etc.) as well as floating-leaved and submergent species. The transition zone community was characterized by dense growths of cattails (*Typha angustifolia* and *T. latifolia*). Over all 3 years, plant communities surrounding my sampling stations remained in the same categories, although some changes occurred among individual species.

These relatively few vegetation changes could be summarized as follows. First, in the transition zone and wet meadow, emergent stem density decreased progressively over the 3-year period, and submergent plant coverage increased under high water (decreasing again when water-level was falling). As described above, I included stem density and submergent coverage in regression analyses and found that they were not significantly associated with most invertebrate abundances. Second, many rarer wet meadow plant species disappeared or declined under high water, and most did not return immediately the next year. Third, plant community composition shifts under high water were the opposite of hypothesized shifts (i.e. the transition zone became more similar to the wet meadow rather than the deep marsh, etc.). This occurred in part because distributions of certain flooding-tolerant sedge species (*Carex aquatilis* and *C. lasiocarpa*) spread down-slope from the lower wet meadow into the transition zone and upper deep marsh.

DISCUSSION

I used correspondance analysis to determine whether community composition at each station shifted from year to year according to the following expectations. Under high water conditions, the wet meadow community should become more like transition zone and deep marsh communities, and the transition zone community should become more like the deep marsh community. If flooding regime differences are very important structuring factors, then the most change should be seen in the wet meadow community, where flooding regime changed the most from 1996 to 1997. The magnitude of change should be less in transition zone communities, while deep marsh communities should not change.

These hypotheses were generally supported by the data. The plotted position of the wet meadow community in 1997 was far to the left of the 1996 wet meadow position, and very near most of the other plotted points. This indicated a relatively large change in community composition that strongly increased the similarity between the wet meadow community and communities at lower elevations. Also, the loss of diversity was greatest in the wet meadow because many taxa that were dominant there in 1996 decreased in abundance in 1997, while a smaller number of taxa originally from lower elevations became more abundant. Shifts along the second CA axis reflected this turnover in dominant taxa. The greatest difference between communities in this second dimension was between the 1996 wet meadow and the hummock zone in 1997, indicating that the wet meadow changes reached far up the gradient because the water level was high long enough to allow many taxa to migrate many tens of meters across the wetland.

In general, the 1996-1997 changes can be described as up-slope distribution shifts or expansions of most taxa, though these shifts occurred at different rates among taxa.

The 1997-1998 changes, on the other hand, were more varied. While many taxa reversed their previous responses by shifting back down-slope, many others apparently did not. Some of the initially characteristic taxa of the wet meadow that appeared to find a high-water refuge in the hummock zone failed to return to the lower wet meadow stations when the water level was dropping. These tended to be rare taxa and non-insects, while those that readily reversed their shifts were insects. The taxa that most influenced community composition changes (isopods, mayflies, midges, and amphipods) showed different patterns from those described above. Midge larvae numerically dominated communities at all stations in 1996, but gave way to mayflies and isopods as their numbers increased dramatically. By 1998, when many taxa were returning to lower elevations, isopods, mayflies and amphipods continued to increase at all stations, including the wet meadow.

Vegetation zonation must not have played a strong direct role in determining invertebrate community composition in this study. Invertebrate distributions shifted along the elevation gradient despite the lack of similar shifts in plant zones. In fact, the down-slope spread of two very abundant sedge species was an unexpected shift in the opposite direction to shifts observed in invertebrates. Nonetheless, the observed changes in plant community structure cannot be fully dismissed as influences on invertebrates. The literature does not suggest that changes in emergent species composition are likely to strongly affect invertebrates, although detritus produced by different species may have some affects because it can vary in food quality (Batzer and Wissinger 1996). Also, the observed wet meadow reduction in emergent stem density and increase in submergent plant coverage probably had some impact on some invertebrates: submergent plants provide colonizable surfaces and complex structure for invertebrates, and lower emergent stem density allows greater light penetration, which may have increased water and substrate temperatures and enhanced algal growth. If these factors affected invertebrates, the effects were too weak to be detected by most of the regression analyses described above.

The water level changes observed in Mackinac Bay from 1996 through 1998, and resulting biotic changes, are best understood when placed in their historical context. The lake level had been quite low the year before I began sampling (Figure 2.2), so in 1996 the wet meadow was flooded for the first time in two years. The transition zone had been only seasonally flooded the previous year and even the deep marsh had experienced very low winter water levels, so it was probably subjected to deep substrate freezing and ice scour. As a result, initial invertebrate densities were very low, probably because all zones were recovering from the effects of low water conditions. The wet meadow community, however, was probably the most adversely affected by the previous year because only a minority of invertebrate taxa can survive dormancy in non-flooded soil for over a year (Williams 1987).

The 1996 dominance of midges was probably a result of their aerial dispersal and short generation time which make them rapid colonizers of newly-flooded areas. The other taxa dominating the 1996 wet meadow (e.g. pulmonate snails, Sphaeriidae clams, beetles, etc., copepods) were also either rapid re-colonizers, or were groups with adaptations for tolerating de-watered periods by estivating in the detritus/soil substrate. Subsequent increases in abundances of other taxa resulted from slower re-colonization of the wetland from lower elevations. These other taxa, including isopods, amphipods, mayflies, most caddisflies, and others, were all groups typically restricted to permanent waters.

Possible causal mechanisms

While the gradient distributions of most animal taxa were clearly affected by water level changes, the actual mechanisms driving these changes were less clear. The rapid changes in animal distributions among years suggested that plant zone characteristics were not very important determinants of gradient positions, but certain other questions remain to be answered: Why did many deep marsh taxa fail to occupy the wet meadow until the water level rose in Year 2? Why did the initial wet meadow taxa decline in 1997? Why did isopods, mayflies, and amphipods remain abundant in the wet meadow in 1998 even though they had not been there in 1996 under similar flooding conditions?

It seems likely that the initial distinctions (in 1996) between deep marsh and wet meadow communities were partly caused by differences in life history adaptations to temporary flooding because the wet meadow community consisted of common temporary-water inhabitants (as identified by Williams 1987). This hypothesis is further supported by the fact that the wet meadow had not been flooded the previous year, so the "drought" period in the wet meadow had lasted through an entire summer season. Had the water level followed the average annual pattern, falling back to the transition zone in late 1996 and rising the next spring, a similar pattern would likely have been observed in 1997. Presumably, any animals without drought-tolerance or avoidance mechanisms that migrated into the wet meadow would not survive the de-watered period. However, the water did not drop in late 1996 and many taxa did appear to migrate into the wet meadow (Chapter 1) that year. They may have simply been continuing an up-slope migration that had begun a year earlier, although quite a few taxa did not show this pattern.

Perhaps these non-migrating taxa were responding to water chemistry gradients, as Cardinale et al. (1997) observed in a Saginaw Bay coastal wetland. Gradients in dissolved oxygen, conductivity, and pH were detected in 1998 in Mackinac Bay in a related study (Gathman and Keas 1999) and showed evidence of changing with water level changes. In particular, dissolved oxygen decreased from supersaturation in the deep marsh to hypoxic conditions in the wet meadow, but this gradient moved up-slope and down-slope as water levels rose and fell with oscillating seiches. There was a direct correlation between water level changes of ~10 cm in the wet meadow and dissolved oxygen levels, so it is likely that under the very high water conditions of 1997, wet meadow dissolved oxygen levels were considerably higher than in 1996 or 1998.

Dissolved oxygen or other water chemistry variables may have been important to some invertebrate taxa. The 1996 wet meadow community consisted of taxa that were not only drought-tolerant, but also had low-oxygen adaptations such as the ability to breathe atmospheric oxygen (pulmonate snails, diving beetles), high-efficiency gas exchange mechanisms (cases in Limnephilidae caddisfly larvae), or high surface-area to volume ratios (Chironomidae, Nematoda, Copepoda). However, similar statements could be made about most lower-elevation taxa as well. Using "Tolerance" values from the Hilsenhoff Biotic Index (Hilsenhoff 1988) as a measure of low dissolved-oxygen adaptation, none of the invertebrate taxa collected were strongly intolerant (Tolerance below 3), and the few that could be considered moderately intolerant were not restricted to the deep marsh. Aeschnidae dragonfly larvae (Tolerance value 3) were common in the wet meadow in 1998, and Limnephilidae caddisfly larvae were characteristic of the wet meadow despite having the same tolerance value as the other caddisfly families sampled (Tolerance value 4). On the other hand, the damselfly larvae (Coenagrionidae) and amphipods (mostly Talitridae) had high tolerance (Tolerance value 8) but nonetheless were rare at high elevations in 1996. The dominant taxa showed even less evidence of oxygen limitation. As the wet meadow water levels fell to <10cm in 1998, isopods, amphipods, and Caenidae mayflies remained very active and abundant, even in small isolated depressions high in the wet meadow where dissolved oxygen levels were below the reliable detection limits of the instrument used. However, many other taxa did not remain or survive in these environments. Overall, then, it seems unlikely that dissolved oxygen was a strong limiting factor, except at extremely low levels for some taxa.

It is possible that dissolved oxygen played a different role in regulating invertebrate communities. If it varied spatially and temporally as argued above, it may have determined fish community compositions, which could, in turn, affect invertebrate communities through predation. The dominance of mudminnows at higher elevations indicated a probable dissolved oxygen limitation on most fish because mudminnows can occupy low-oxygen habitats by "breathing" air at the surface. This spatial variation in fish species may have imposed spatially-variable predation pressures on invertebrates, though such differences in feeding preferences among these fish species are little known. Fish density, on the other hand, is considered to be a strong influence on wetland invertebrate communities (Batzer and Wissinger 1996, Wellborn et al. 1996). Wet meadow small fish densities decreased over the study period, coinciding with increased invertebrate density. These reduced fish densities may have resulted from the invasion of the wet meadow by piscivorous fish under high-water conditions, as suggested by data on distributions of larger fish (Gathman and Keas 1999). Based on the multiple regression results, fish density did not appear to be an important influence on invertebrate abundances, but the obvious variations in fish communities in this study cannot be dismissed as partial determinants of invertebrate faunal composition.

Dragonfly larvae may have imposed important predation pressures also, though attempts to experimentally determine whether invertebrate predators can structure invertebrate prey communities have produced mixed results (Wellborn et al. 1996). Although the increase in mean wet meadow dragonfly larva density was non-significant from 1996 to 1997, all of these larvae collected in 1996 were late-season new hatchlings which were probably too small eat larger macroinvertebrates such as isopods. Excluding immature larvae, dragonfly larva density increased in the wet meadow from 0 in 1996 to 1.23 per sample in 1997 ($p=0.014$), and up to 1.71 per sample in 1998 ($p=0.034$). However, while wet meadow dragonfly larval density was highest in 1998, these were all mature larvae that showed evidence of reduced development rates, which suggests reduced feeding. In previous years dragonfly nymphs emerged as adults in July, but in 1998, 40 dragonfly nymphs in wet meadow enclosures (in a related experiment) failed to develop to the emergent adult stage by late July, and even in early September mature larvae were very common in the wet meadow. Relatively few dragonfly larvae collected in 1998 were early-instar hatchlings (Figure 2.12), and none of these were collected from the wet meadow, suggesting that dragonfly development was stunted. Thus, it appeared that the effective dragonfly larva density (in terms of predation pressure) was highest in the wet meadow in 1997, which may have contributed to the decreased abundances of many taxa characteristic of the low-water wet meadow.

It may seem contradictory to discuss possible predation effects after regression analyses suggested little association between invertebrate prey and the most abundant predators. However, the regression analysis was a weak test of predation effects, in part because the fish abundance data used were based on a passive trapping method which did not measure actual fish density. These data were probably reliable measures of relative fish abundance differences among sample stations on average, but they had high within-group variability with many zero counts, even at elevations with relatively high total fish catches over all transects. Because fish predation is generally considered to be an important community structuring force (Wellborn et al. 1996), and because large invertebrate density increases coincided with reduced fish density in most cases in this study, further study involving controlled experimentation is called for.

The large invertebrate density increases that I observed were not always associated with reduced fish abundance. The transition zone and deep marsh density increases from 1997 to 1998 coincided with increases in fish numbers so any explanation of invertebrate density must include factors other than predation mortality. The general density increases over the study period may have occurred because invertebrate communities were recovering from previous low-water conditions, so perhaps relative rates of increase at different times and places were better indicators of possible mechanisms. Initial wet meadow densities were quite low, and subsequent increases may have resulted from a combination of up-slope immigration, reproduction in the "new" habitat, and reduced fish predation. I did not study reproduction, so I cannot evaluate whether recruitment varied over space or time. It is possible that the wet meadow, with its large and relatively-untouched detritus food source, was a very favorable habitat for reproduction. Also, as emergent plants became less dense over time, reduced shading probably led to higher water temperatures, which would favor invertebrate growth.

The largest single density increase occurred in the transition zone from 1997 to 1998, when fish numbers were relatively high, so recruitment and/or immigration must have been quite high there. Immigration is a likely explanation for this large density increase, because the wet meadow was draining in 1998 and many invertebrates could have been moving down-slope, merging into the "resident" community. As in the transition zone, the deep marsh density increase from 1997 to 1998 was higher than in the previous period, and a similar down-slope invertebrate concentration may have been responsible. However, the deep marsh increase was dwarfed by that observed in the transition zone, so perhaps the transition zone was a more favorable habitat. Fish numbers were relatively high in both zones, but higher plant and coarse detritus density may have made the transition zone a predation refuge. Again, I did not study reproduction, so I cannot determine whether reproduction was particularly high in the 1998 transition zone, but the speculations on food source and temperature in the wet meadow, noted above, probably do not apply to these other zones.

Dispersal mechanisms and immigration rates

The initial goal of this study was to separate the effects of flooding changes from vegetation zone characteristics by analyzing spatial distribution changes along the coastal wetland elevation gradient. However, the data suggest that differences in dispersal mechanisms among the non-drought-tolerant taxa are very important in determining community differences over space and time. Jeffries (1994) discussed the importance of invertebrate dispersal in flood-variable wetlands, but was studying separate pools without surface water connections. In coastal wetlands such as Mackinac Bay, areas with different flooding conditions are connected by surface water allowing animals without aerial life stages to invade usually-temporary zones when water is high.

The main changes related to water level variations in Mackinac Bay appeared to result from dispersal differences. Many taxa shifted their gradient positions up-slope when water rose, and down-slope when it fell. Most of these taxa were insects with aerial adult dispersal stages, so they were able to respond quickly to spatial environmental changes. Meanwhile, non-insects tended to move up-slope during high water, but were less able to return back down-slope the following year, so many animals were probably left "stranded" at high elevations, where they would not be able to survive the loss of surface water. These patterns were equally important in determining the distributions of the dominant taxa. Chironomidae, which are rapid colonizers, initially dominated all elevations, and dominated the wet meadow and newly-flooded hummock zone in 1997. Caenidae mayflies, also aerial dispersers, dominated the transition zone in 1997 and became abundant at higher elevations as well. The more slowly-dispersing isopods and amphipods, however, became progressively more abundant at successively higher elevations, with isopods eventually overtaking all other taxa in relative abundance at all elevations. They were able to do this because water level was almost constantly rising from late 1996 until mid 1997, and even in 1998 the wet meadow was initially flooded all the way up to the hummock zone.

While many taxa, mostly non-insects, were unable to respond to the dropping water levels in 1998, isopods and amphipods remained abundant at lower elevations because, rather than shifting their gradient positions, they were able to simply expand their ranges while remaining very abundant at low elevations. Thus, although many individual isopods and amphipods were undoubtedly "stranded", many more remained at lower elevations. Other taxa did not fare as well. As mentioned above, dragonfly larvae in the wet meadow appeared to develop slowly in 1998, and I found large numbers of dead and dying individuals in very shallow water in the wet meadow that year.

Implications

Water level fluctuations may be important ecosystem regulators in coastal wetlands. This study suggests that temporary high-water episodes cause increased invertebrate production, which may lead to increased detritus processing and may provide a very large food source for fish and avian invertivores. While fewer small fish were present to exploit the high-water wet meadow prey, larger fish may have gained from increases in densities of larger invertebrates. Dragonfly larvae densities were high in 1997, and may have provided an important food source for intermediate-sized fish (too large for activity trap sampling, but too small to eat other fish). Also, related sampling (unpublished data) indicated that crayfish densities increased over the three year period, providing food for large fish.

Falling water levels may have different effects. The high wet meadow invertebrate densities in 1998 probably led to high mortality as the wet meadow drained and many animals died. These animals were probably easy prey for predators and scavengers, and may have led to an important export of energy and material from the wetland to terrestrial communities. At the low end of the elevation gradient, dropping water levels force more animals into smaller wetland areas, where they probably face competition and increased vulnerability to predators. I can only speculate that this would lead to lower production in the following year.

Constant water-level variation seems to be the norm in coastal wetlands, so short-term high or low water conditions are common. However, if changed water-level conditions last for several years, the spatial positions of vegetation zones shift in the direction of the water line, so the complete wetland vegetation gradient is re-established at a new elevation range (Burton 1985). Animals would be expected to adjust to the new habitat position, but this study suggests that they may do so in a time-lagged fashion, with a succession of colonists (e.g. midges, mayflies, isopods) establishing populations consecutively. This constant "catching up" by the invertebrate community may limit total invertebrate production at a level below the maximum possible under stable conditions, keeping long-term material and energy flows in dynamic equilibrium determined by water levels.

Aquatic invertebrate populations in coastal wetlands can only persist if they are adapted to water level changes, but the changes observed in this study were unusual. Figure 2.2 illustrates the 20-year history of water level changes in northern Lake Huron, showing that water levels can rise or fall relatively quickly, but these changes are usually sustained for several years. Examination of the 100-year data record indicates that a rapid water level rise followed immediately by an equivalent drop is historically unusual. In the present case, this series of events led to decreased invertebrate diversity because a few highly-adaptable generalist taxa became dominant. If such rapid water level changes increase in frequency under changing climate conditions, they could lead to sustained diversity loss in coastal wetlands.

Diversity loss could be exacerbated where human shoreline development interferes with up-slope migrations of biota, as is common in many Great Lakes wetlands. Road embankments, seawalls, dikes, and residential development interrupt the gently-sloping wetland substrate, so when water rises, high-elevation temporarily-flooded zones are eliminated. This study suggests that many taxa rely on this marginal zone as a refuge during high-water conditions, so loss of this habitat could eliminate these invertebrates from coastal wetlands. The dynamic hydrology of Great Lakes coastal wetlands leads to variablity in aquatic animal communities on fairly small spatial and temporal scales. Further research is needed to determine specific community-regulating mechanisms, but it may be more useful to develop a method to functionally classify invertebrates according to their dispersal capabilities, which could be used to predict their vulnerabilities to habitat alteration. In the meantime, human activities that interrupt the upland-to-lake elevation gradients in the few remaining intact coastal wetlands should be prevented to maintain diversity in these little-studied systems.

Table 2.1. Mean invertebrate abundance (#/m^2) over all months and transects at each station during each year.

Year	Station 0	Station2	Station 4	Station 6
1996	n.a.	2931.0	5734.9	6697.7
1997	6933.9	8242.0	7388.1	8011.9
1998	5510.8*	13,940.5	23,623.8	13,898.1

*Only June samples were collected.

Table 2.2. Shannon-Wiener diversity at each station during each year, based on averages of taxa relative abundances over all months and transects.

Year	Station 0	Station2	Station 4	Station 6
1996	n.a.	3.02	2.71	2.50
1997	2.60	2.30	2.17	2.28
1998	2.45*	2.20	2.14	2.54

*Only June samples were collected.

Table 2.3. Top ten most abundant taxa (ranked by relative abundance) at each sampling station during each year.

1996		1997		1998	
STATION 0					
n.a.		Chironomidae	28.13%	Asellidae	26.41%
		Asellidae	14.43%	Chironomidae	17.69%
		Cyclopoida	8.27%	Caenidae	8.82%
		Daphniidae	8.09%	Cyclopoida	5.96%
		Planorbidae	7.46%	Isotomidae	5.85%
		Macrothricidae	4.83%	Planorbidae	4.17%
		Sphaeriidae	3.97%	Ceratopogonidae	3.92%
		Physidae	3.58%	Harpacticoida	3.83%
		Caenidae	3.25%	Sphaeriidae	3.18%
		Chydoridae	2.45%	Libellulidae	2.40%
STATION 2					
Chironomidae	18.56%	Chironomidae	32.20%	Asellidae	36.89%
Cyclopoida	10.15%	Caenidae	17.67%	Caenidae	16.49%
Oribatei	8.05%	Asellidae	15.93%	Chironomidae	15.88%
Planorbidae	6.82%	Planorbidae	5.25%	Amphipoda	7.83%
Sphaeriidae	6.51%	Cyclopoida	4.16%	Cyclopoida	6.12%
Asellidae	5.06%	Daphniidae	4.08%	Isotomidae	1.89%
Ceratopogonidae	4.63%	Physidae	3.33%	Planorbidae	1.68%
Brachycera	4.37%	Naididae	1.77%	Ceratopogonidae	1.32%
Harpacticoida	3.84%	Ostracoda	1.75%	Ostracoda	0.90%
STATION 4					
Chironomidae	28.65%	Chironomidae	32.59%	Caenidae	29.78%
Asellidae	12.48%	Asellidae	24.41%	Asellid	24.22%
Caenidae	12.34%	Caenidae	16.98%	Chironomidae	21.57%
Amphipoda	8.25%	Amphipoda	4.09%	Amphipoda	5.40%
Cyclopoida	4.24%	Planorbidae	2.48%	Cyclopoida	4.06%
Daphniidae	3.04%	Naididae	2.39%	Ostracoda	2.04%
Ceratopogonidae	2.96%	Daphniidae	2.12%	Daphniidae	1.69%
Chydoridae	2.57%	Physidae	1.95%	Macrothricidae	1.46%
Macrothricidae	2.44%	Ostracoda	1.86%	Naididae	1.26%
Ostracoda	2.14%	Cyclopoida	1.76%	Planorbidae	1.03%
STATION 6					
Chironomidae	22.19%	Asellidae	32.77%	Asellidae	26.39%
Asellidae	17.90%	Chironomidae	23.77%	Caenidae	16.29%
Caenidae	16.60%	Caenidae	13.32%	Chironomidae	14.79%
Amphipoda	10.45%	Amphipoda	10.11%	Ostracoda	12.33%
Ostracoda	6.32%	Cyclopoida	3.50%	Amphipoda	9.56%
Cyclopoida	2.88%	Ostracoda	3.45%	Cyclopoida	2.20%
Naididae	2.71%	Naididae	1.85%	Naididae	2.15%
Macrothricidae	2.63%	Sphaeriidae	1.25%	Coenagrionidae	1.88%
Daphniidae	1.80%	Sididae	0.84%	Lymnaidae	1.48%
Ceratopogonidae	1.79%	Planorbidae	0.83%	Ancylidae	1.37%

Table 2.4. Relative abundance changes (increase or decrease) of individual taxa between years at each station, and p-values from paired t-tests.

		Station2		**Station 4**		**Station 6**	
		'96-'97	**'97-'98**	**'96-'97**	**'97-'98**	**'96-'97**	**'97-'98**
Insecta	Ephemeroptera						
	Caenidae	↑ **0.001**	↓ 0.686	↑ 0.087	↑ **0.044**	↓ 0.498	↑ 0.304
	**Baetidae	n.a.	n.a.	n.a.	n.a.	↑ **0.039**	↓ **0.047**
	Diptera						
	Chironomidae	↑ **0.002**	↓ **0.032**	↑ 0.441	↓ 0.054	↑ 0.697	↓ **0.048**
	Ceratopogonidae	↓ **0.003**	↑ 0.069	↓ **0.001**	↑ 0.553	↓ 0.211	↑ 0.449
	**Tipulidae	↓ **0.044**	n.a.	↓ 0.808	↓ 0.334	n.a.	↑ 0.334
	**Dixidae	↓ 0.336	n.a.	n.a.	n.a.	n.a.	n.a.
	**Culicidae	↓ 0.336	↓ 0.334	n.a.	n.a.	n.a.	n.a.
	**Sciomyzidae	↓ n.a.	↑ 0.334	n.a.	n.a.	n.a.	n.a.
	Brachycera	↓ **0.000**	↑ 0.074	↓ 0.406	↓ 0.121	↑ 0.105	↓ 0.910
	Coleoptera						
	Dytiscidae	↓ **0.006**	↑ **0.013**	↓ 0.171	↑ 0.083	↑ 0.334	↓ 0.334
	**Hydrophilidae	↓ 0.336	↑ 0.334	↓ 0.334	↑ 0.334	n.a.	n.a.
	**Scirtidae	↓ 0.336	↑ 0.334	n.a.	n.a.	n.a.	n.a.
	**Gyrinidae	↓ 0.336	↑ 0.334	↓ 0.334	↑ 0.710	↓ 0.164	n.a.
	Chrysomelidae	n.a.	n.a.	↓ 0.168	0.613	↑ 0.182	0.053
	**Haliplidae	↓ 0.336	n.a.	↓ 0.334	n.a.	n.a.	n.a.
	**Lampyridae	↓ 0.166	n.a.	n.a.	n.a.	n.a.	n.a.
	Trichoptera						
	Leptoceridae	↑ **0.022**	↓ **0.029**	↓ 0.065	↓ 0.438	↓ 0.127	↑ 0.554
	Limnephilidae	↓ **0.015**	↓ 0.102	↓ **0.049**	↑ 0.334	n.a.	n.a.
	Phryganeidae	↑ 0.101	↓ 0.087	↓ 0.079	↑ 0.514	↓ 0.214	↓ 0.402
	Polycentropodidae	↑ 0.056	↑ 0.081	↓ 0.238	↑ 0.485	↓ 0.376	↑ 0.146
	Hydroptilidae	↑ **0.016**	↓ **0.008**	↓ 0.123	↑ 0.155	↓ 0.084	↑ **0.034**
	Odonata						
	Aeschnidae	– 0.336	↑ **0.070**	↓ **0.018**	↓ 0.536	↓ 0.392	↑ 0.633
	**Gomphidae	n.a.	n.a.	n.a.	n.a.	n.a.	↑ 0.165
	Libellulidae	↑ 0.842	↓ **0.017**	↓ **0.002**	↑ 0.918	↑ 0.063	↓ 0.215
	Corduliidae	n.a.	↑ 0.334	↑ 0.093	0.684	↑ 0.229	↑ 0.064
	Coenagrionidae	↑ **0.001**	↓ **0.003**	↓ 0.858	↓ 0.488	↓ **0.008**	↑ **0.026**
	**Lestidae	n.a.	↑ 0.334	↑ 0.334	↓ 0.334	– 0.334	n.a.
	Hemiptera						
	Corixidae	↑ **0.045**	↓ **0.045**	↓ 0.953	↓ 0.803	↓ 0.140	↓ 0.154
	Veliidae	↓ 0.454	↑ **0.040**	↓ 0.334	↑ **0.022**	n.a.	n.a.
	Mesoveliidae	n.a.	↑ 0.334	↓ 0.152	n.a.	↓ 0.373	↑ 0.766
	**Gerridae	n.a.	↑ 0.165	n.a.	↑ 0.334	n.a.	n.a.
	**Hydrometridae	n.a.	↑ 0.334	n.a.	n.a.	n.a.	n.a.
	Homoptera	↓ **0.001**	↑ 0.181	↓ **0.020**	↑ 0.334	↓ 0.334	n.a.
	**Hymenoptera	↓ 0.180	n.a.	n.a.	↑ 0.166	n.a.	n.a.
	Lepidoptera	↓ 0.082	↑ 0.995	↓ 0.169	n.a.	↑ 0.198	↓ 0.080
	Collembola						
	Isotomidae	↓ **0.001**	↑ **0.012**	↓ 0.086	↑ 0.184	↓ 0.092	↑ 0.324
	Sminthuridae	↓ 0.093	↑ **0.025**	↓ **0.029**	↑ 0.168	n.a.	n.a.
	**Poduridae	↓ 0.194	n.a.	n.a.	n.a.	n.a.	n.a.

Table 2.4 (cont'd).

	Station2		Station 4		Station 6	
	'96-'97	'97-'98	'96-'97	'97-'98	'96-'97	'97-'98
Crustacea						
Isopoda	↑ **0.038**	↑ **0.003**	↑ **0.009**	↓ 0.945	↑ **0.014**	↓ 0.140
Amphipoda	↑ 0.270	↑ **0.003**	↓ 0.057	↑ 0.527	↓ 0.954	↓ 0.801
Cladocera						
Daphniidae	↑ **0.006**	↓ **0.016**	↓ 0.322	↓ 0.568	↓ **0.008**	↑ **0.029**
Sididae	n.a.	n.a.	↓ 0.710	↓ **0.047**	↑ **0.037**	↓ **0.037**
Macrothricidae	↓ 0.191	↓ 0.443	↓ 0.103	↑ 0.232	↓ 0.171	↑ 0.337
Chydoridae	↓ 0.164	↓ **0.080**	↓ 0.068	↓ 0.952	↓ **0.030**	↓ 0.725
**Polyphemidae	↓ 0.376	n.a.	n.a.	n.a.	n.a.	n.a.
Copepoda						
Cyclopoida	↓ **0.020**	↑ 0.146	↓ **0.022**	↑ **0.015**	↑ 0.708	↓ 0.357
Harpacticoida	↓ 0.280	↑ 0.946	↓ 0.236	↓ 0.076	n.a.	↑ 0.334
**Calanoida	n.a.	n.a.	n.a.	n.a.	↑ 0.334	↓ 0.714
Ostracoda	↑ 0.052	↓ 0.269	↓ 0.706	↑ 0.798	↓ 0.184	↑ 0.069
Arachnida						
Hydracarina	↓ 0.800	↓ 0.260	↓ 0.667	↑ 0.835	↓ 0.316	↑ 0.133
Oribatei	↓ **0.006**	↓ 0.794	↓ **0.001**	↑ 0.178	↓ 0.223	↑ 0.334
Halacaridae	↓ **0.004**	↑ **0.022**	↓ 0.075	↑ 0.689	↓ 0.334	n.a.
Araneae	↓ **0.020**	↑ 0.126	↓ 0.283	↑ 0.667	↓ 0.334	↑ 0.164
Annelida						
Oligochaeta						
Naididae	↓ 0.249	↓ 0.070	↑ 0.251	↓ 0.186	↓ 0.494	↑ 0.703
**Tubificidae	↓ 0.336	n.a.	↓ 0.116	n.a.	↓ 0.120	↑ 0.227
Lumbriculidae	↑ **0.034**	↓ **0.035**	↓ 0.268	↓ 0.058	↓ **0.048**	↑ **0.080**
Hirudinea	↑ **0.007**	↓ **0.030**	↑ 0.196	↓ 0.677	↓ 0.252	0.302
Mollusca						
Pelycypoda						
Sphaeriidae	↓ 0.105	↓ **0.030**	↓ 0.906	↓ 0.148	↓ 0.342	↓ 0.944
**Dreissenidae	n.a.	n.a.	n.a.	n.a.	n.a.	↑ 0.344
Gastropoda						
Ancylidae	n.a.	n.a.	↑ 0.334	↑ **0.035**	↑ 0.450	↑ **0.008**
Planorbidae	↓ 0.531	↓ **0.003**	↑ 0.199	↓ 0.223	↓ 0.559	↑ 0.918
Physidae	↑ 0.072	↓ **0.041**	↑ **0.048**	↓ **0.004**	↓ 0.052	↓ 0.858
Succineidae	↓ **0.001**	↑ 0.055	↓ **0.017**	↑ 0.104	↓ 0.165	↑ 0.191
Bithyniidae	↓ 0.336	↑ 0.191	n.a.	↑ 0.189	n.a.	↑ 0.165
**Hydrobiidae	n.a.	n.a.	↑ 0.334	↓ 0.334	↑ 0.084	↓ 0.284
Lymnaidae	↓ 0.111	↑ 0.088	↑ 0.812	↓ 0.370	↓ 0.200	↑ 0.156
Nematoda	↓ 0.075	↓ 0.677	↓ **0.007**	↓ 0.703	↓ 0.051	↑ 0.090
****Platyhelminthes-Turbellaria**	↓ 0.336	↓ 0.334	↓ 0.334	↓ 0.334	↓ 0.334	↓ 0.334
****Cnidaria-Hydrazoa**	↑ 0.336	↓ 0.334	↑ 0.334	↓ 0.334	↓ 0.334	n.a.
Total abundance	↑ **<.001**	↑ **0.001**	↑ 0.175	↑ **<.001**	↑ 0.458	↑ **0.011**
Taxa richness	↓ 0.656	↑ 0.535	↓ **<.001**	↑ **<.001**	↓ **0.015**	↑ 0.068

Table 2.5. Taxa abundance changes (all stations) with paired t-test significances, and peak shifts among years.

		1996-1997		1997-1998		Abundance Peaks*		
		% change	p	% change	p	'96	'97	'98
Insecta	Ephemeroptera							
	Caenidae	**+197.8**	**<.001**	**+212.5**	**<.001**	4-6	2	4
	**Baetidae	+ ***	**0.024**	**-80.2**	**0.044**	-	6	6
	Diptera							
	Chironomidae	**+82.8**	**0.001**	+.241	0.198	4-6	2	4
	Ceratopogonidae	**-72.5**	**<.001**	**+301.3**	**<.001**	2-4	0	2
	**Tipulidae	-77.1	0.055	0.0	1.000	2	4	6
	**Dixidae	-100.0	0.323	-	-	2	-	-
	**Culicidae	+ ***	0.323	-100.0	0.323	-	2	-
	**Sciomyzidae	-	-	+ ***	0.323	-	-	2
	Brachycera	-48.1	0.078	+69.0	0.125	2	0	2
	Coleoptera							
	Dytiscidae	**-100.0**	**0.003**	+ ***	**0.001**	2	0	2
	**Hydrophilidae	-100.0	0.160	+ ***	0.160	2-4	-	2-4
	**Scirtidae	-100.0	0.323	+ ***	0.323	2	0	2
	**Gyrinidae	-73.3	0.268	+1157.1	0.079	6	0	4
	Chrysomelidae	+57.4	0.391	-40.1	0.087	4-6	6	6
	**Haliplidae	-100	0.160	-	-	2-4	0	-
	**Lampyridae	-100.0	0.160	-	-	2	0	-
	Trichoptera							
	Leptoceridae	+44.0	0.364	+25.3	0.660	6	2/6	6
	Limnephilidae	**-91.2**	**0.001**	-57.7	0.433	2	2	0
	Phryganeidae	+8.2	0.659	-9.0	0.844	4-6	2	4
	Polycentropodidae	-26.4	0.356	**+400.0**	**<.001**	4	4	4
	Hydroptilidae	-50.0	0.610	+180.2	0.089	4	2	4
	Odonata							
	Aeschnidae	**-65.3**	**0.037**	**+564.2**	**0.003**	4	4	2
	**Gomphidae	-	-	+ ***	0.160	-	-	6
	Libellulidae	+39.8	0.360	-11.9	0.689	4	2	4
	Corduliidae	**+2757.1**	**0.030**	**+144.5**	**0.020**	4	6	6
	Coenagrionidae	+27.2	0.367	+89.6	0.115	6	2/6	6
	**Lestidae	+528.6	0.481	-50.0	0.759	6	4	2
	Hemiptera							
	Corixidae	+5.0	0.941	-70.3	0.054	6	0-2/6	4-6
	Veliidae	-46.7	0.520	**+4971.4**	**0.002**	4	2	2
	Mesoveliidae	-87.0	0.130	+200	0.462	4	6	2/6
	**Gerridae	-	-	+ ***	0.092	-	-	2
	**Hydrometridae	-	-	+ ***	0.323	-	-	2
	Homoptera	**-100.0**	**<.001**	+ ***	0.092	2	-	2
	**Hymenoptera	-100.0	0.112	+ ***	0.160	2	-	4
	Lepidoptera	+100.0	0.393	-77.3	0.069	2	2	2
	Collembola							
	Isotomidae	**-95.9**	**<.001**	**+6363.6**	**0.001**	2	0-2	0
	Sminthuridae	**-100**	**0.007**	+ ***	**0.001**	4	-	2
	**Poduridae	-100.0	0.160	-	-	2	-	-

Table 2.5 (cont'd).

		1996-1997		1997-1998		Abundance Peaks*		
		% change	p	% change	p	'96	'97	'98
Crustacea	Isopoda	**+142.0**	**<.001**	**+167.6**	**<.001**	6	6	4
	Amphipoda	-16.9	0.818	**+226.9**	**<.001**	6	6	6
	Cladocera							
	Daphniidae	+52.0	0.347	+43.7	0.289	4-6	0	4
	Sididae	+64.7	0.225	-46.5	0.090	4	6	6
	Macrothricidae	**-74.2**	**0.046**	**+391.5**	**0.030**	6	0	4
	Chydoridae	**-55.5**	**0.036**	+78.6	0.162	4	0	4
	**Polyphemidae	-100.0	0.323	-	-	2	-	-
	Copepoda							
	Cyclopoida	+6.3	0.711	**+183.0**	**<.001**	2	0	2
	Harpacticoida	-38.6	0.527	+92.5	0.627	2	0	0
	**Calanoida	+ ***	0.323	0.0	1.000	-	6	6
	Ostracoda	+15.1	0.478	**+154.7**	**<.001**	6	2/6	6
Arachnida								
	Hydracarina	+61.4	0.474	**+121.9**	**0.015**	6	0-6	6
	Oribatei	**-80.9**	**<.001**	**+134.8**	**0.021**	2	2	2
	Halacaridae	**-93.5**	**0.001**	**+1918.2**	**0.004**	2	-	2
Annelida								
	Oligochaeta							
	Naididae	+42.8	0.328	+52.2	0.159	2	6	6
	**Tubificidae	**-100.0**	**0.013**	+ ***	0.199	4-6	-	6
	Lumbriculidae	+48.9	0.250	+22.9	0.183	4	2	0-2
	Hirudinea	+51.9	0.163	+60.8	0.261	6	6	0/4
Mollusca								
	Pelycypoda							
	Sphaeriidae	-21.5	0.228	-4.4	0.883	2	0	0
	**Dreissenidae	-	-	+ ***	0.323	-	-	6
	Gastropoda							
	Ancylidae	+155.8	0.263	**+1103.0**	**<.001**	6	6	6
	Planorbidae	**+124.5**	**0.036**	-.204	0.810	2	0	0-4
	Physidae	+115.8	0.054	-38.9	0.117	6	0	2
	Succineidae	**-93.5**	**<.001**	**+2086.0**	**0.004**	2	0	2
	Bithyniidae	+200.0	0.633	**+1918.2**	**0.024**	-	2	2
	**Hydrobiidae	**+ ***	**0.028**	-57.0	0.345	-	6	4
	Lymnaidae	-24.7	0.281	**+351.1**	**0.043**	2	4	6
Nematoda		**-69.4**	**0.002**	+142.0	0.089	4	2	0
****Platyhelminthes-Turbellaria**		+200.0	0.194	-50.0	0.306	4	2	4
****Cnidaria-Hydrazoa**		+528.6	0.287	-100.0	0.160	6	0-4	-
Total abundance		**+55.8**	**0.001**	**+117.6**	**<.001**			
Taxa richness		**-26.2**	**0.016**	**+25.0**	**0.003**			

* Station(s) where taxon was most abundant: 0=hummock; 2=wet meadow; 4=transition zone; 6=deep marsh.

** Rare taxa (10 or fewer individuals taken in all samples).

*** Increased from zero.

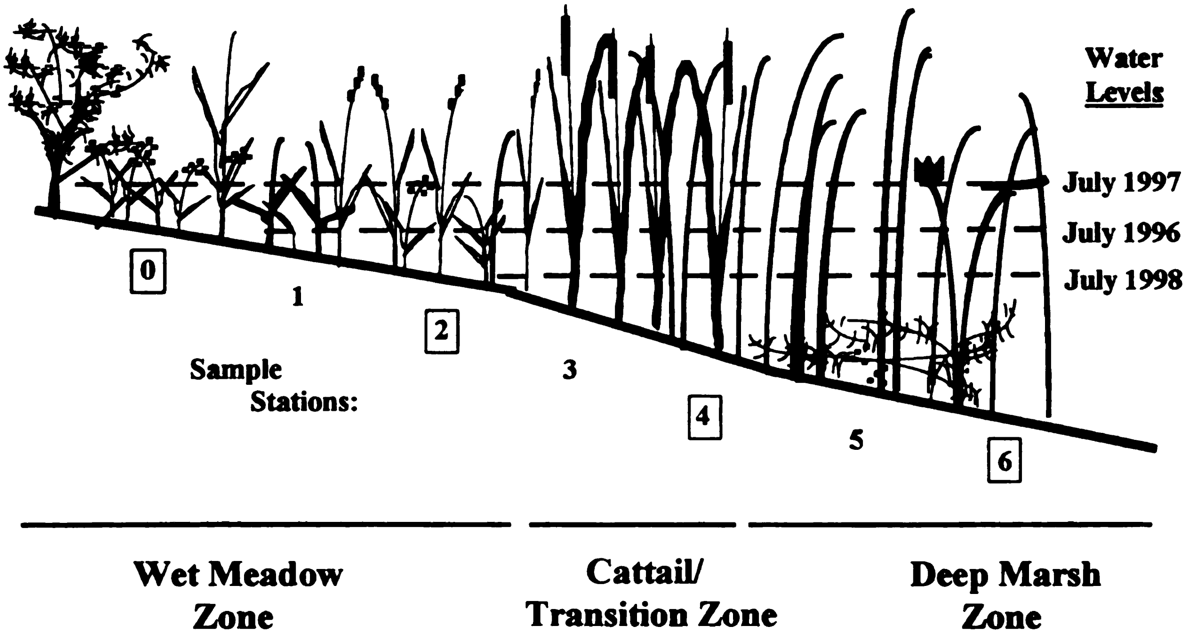


Figure 2.1. Schematic cross-section through representative sample transect in study site.

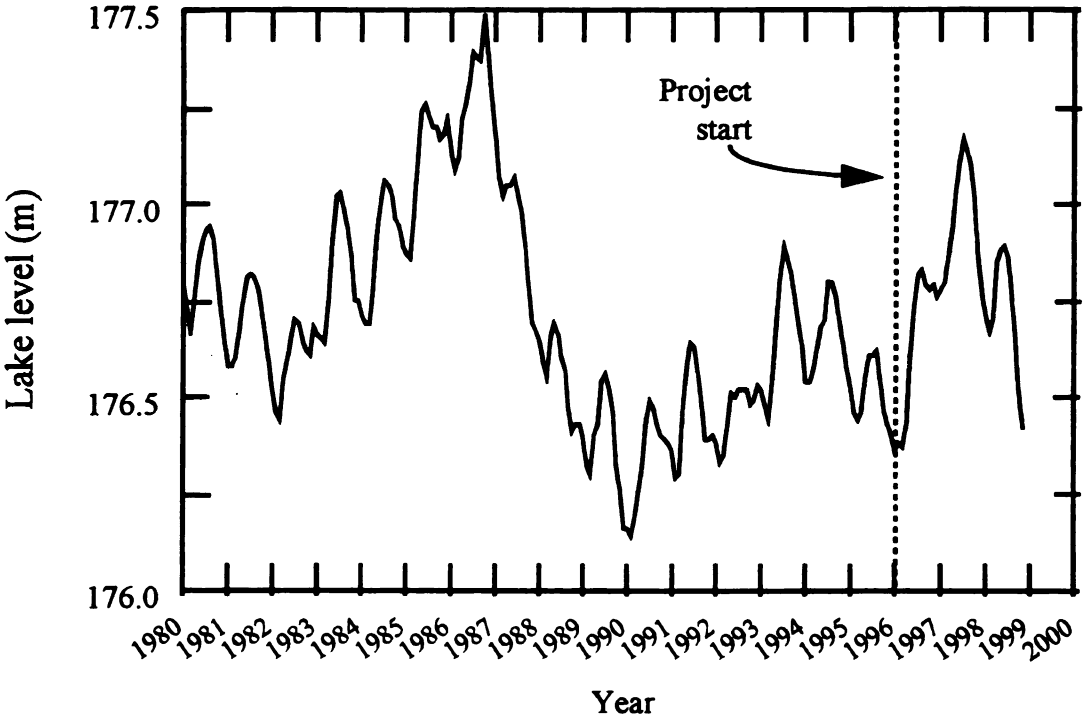
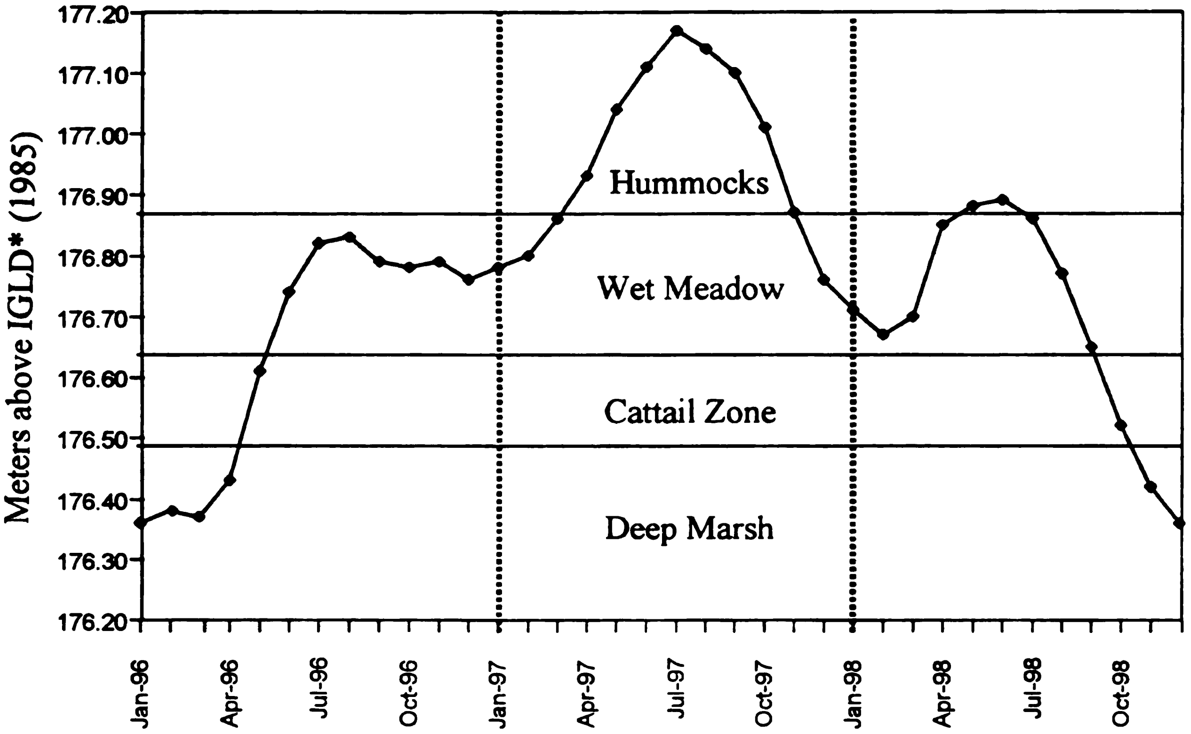
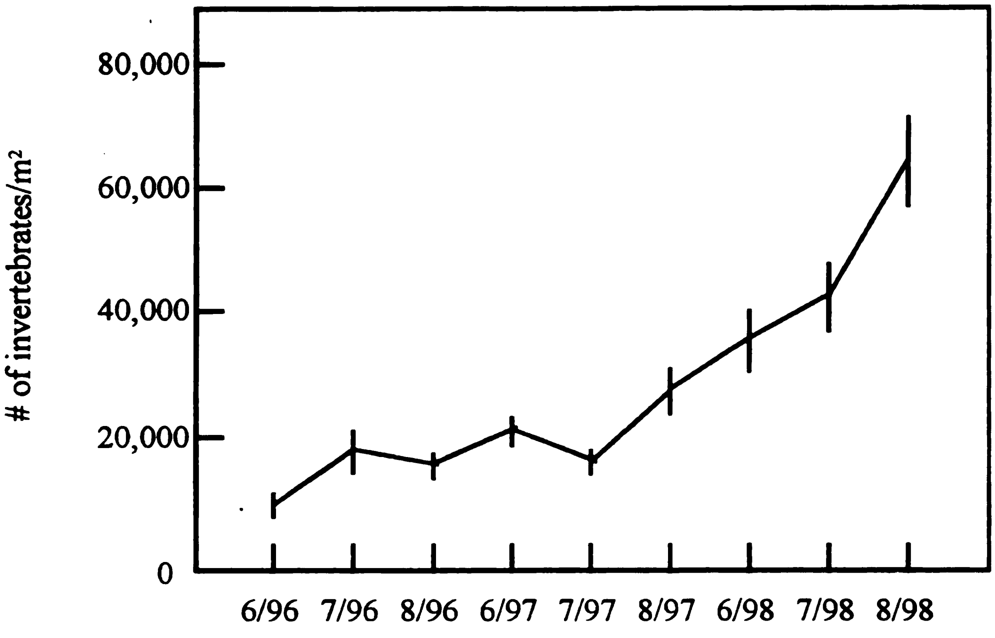


Figure 2.2. Lake Huron monthly average water levels in meters above International Great Lakes Datum, measured at DeTour Village, MI, 1980 through 1998 (Data source: U.S. Department of Commerce, NOAA/NOS, Silver Spring, MD).



*International Great Lakes Datum

Figure 2.3. Water level changes at Mackinac Bay over the study period.



Time (m/yy)

Figure 2.4. Average density of invertebrates among all sample stations, by sampling date (means with standard errors).

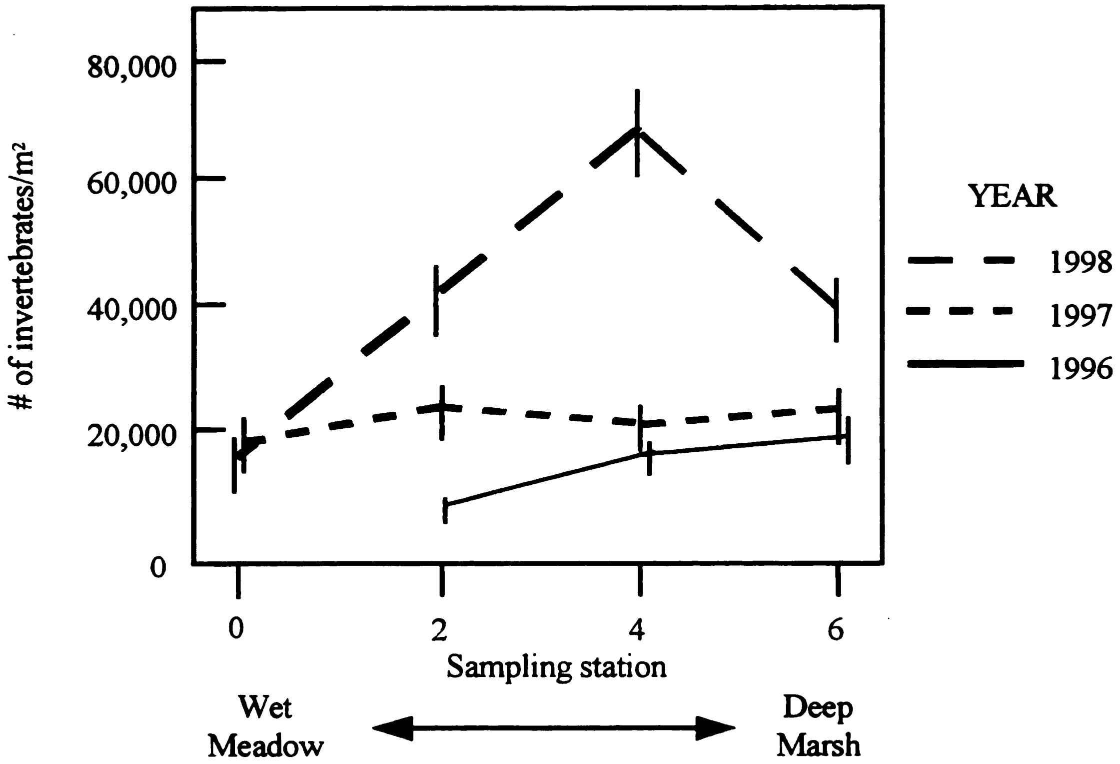


Figure 2.5. Invertebrate density differences among sampling stations, by year (means with standard errors).

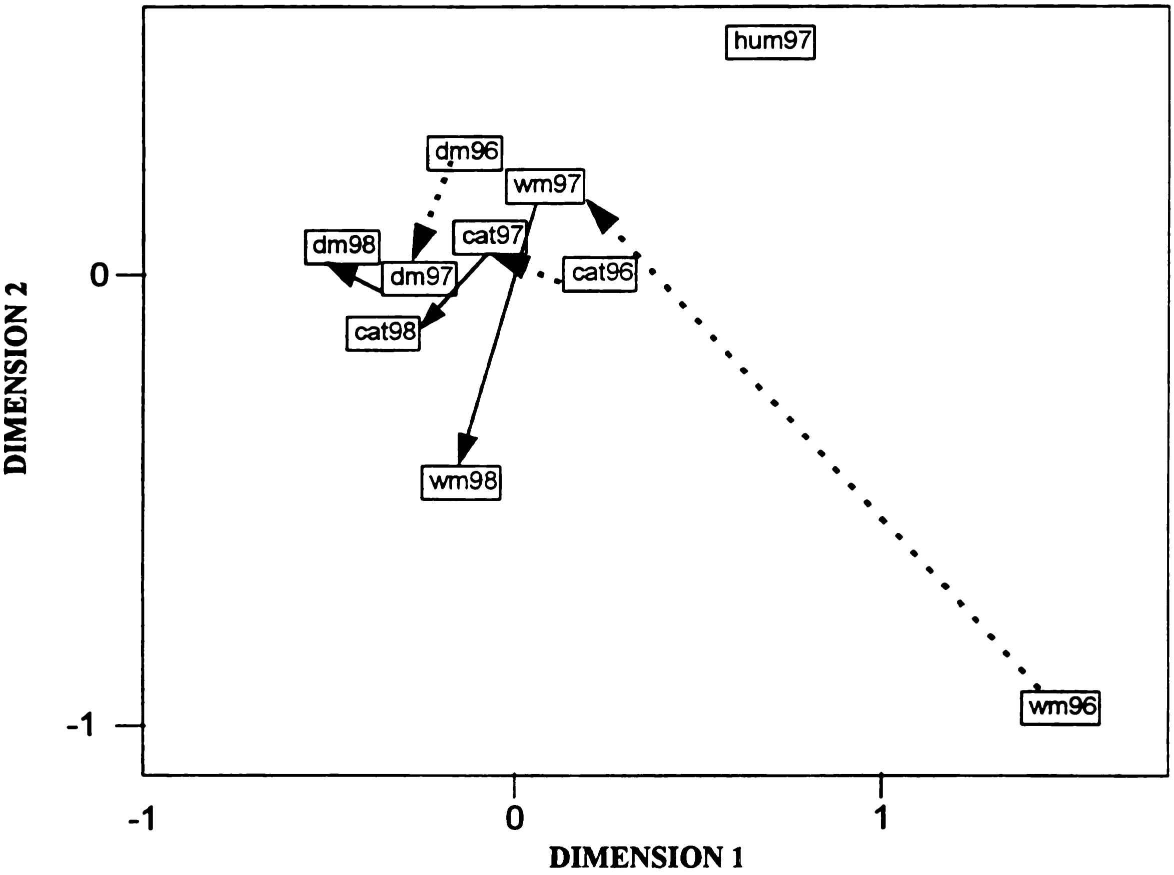


Figure 2.6. Correspondance analysis ordination of communities at each sampling station during each year, with year-to-year shifts indicated by arrows.

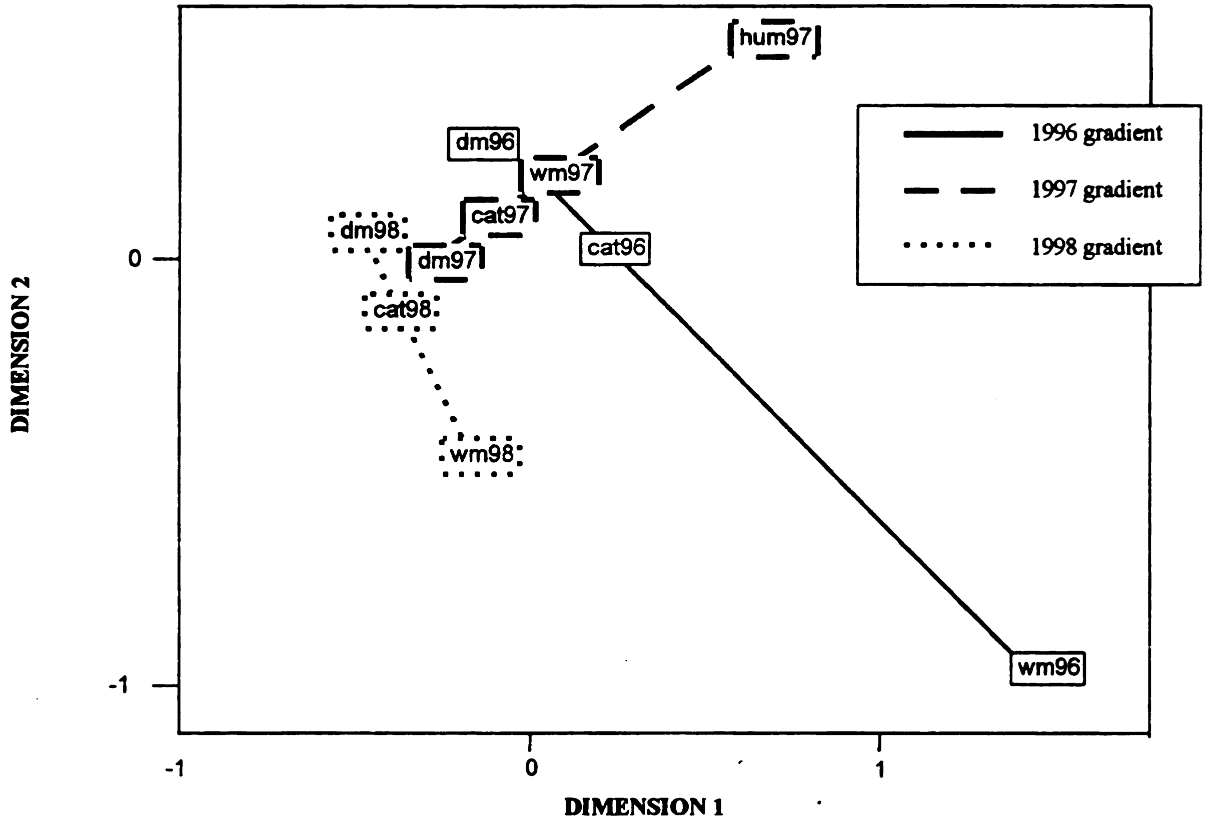


Figure 2.7. Correspondance analysis ordination of invertebrate communities with connecting lines representing community gradients during each year.

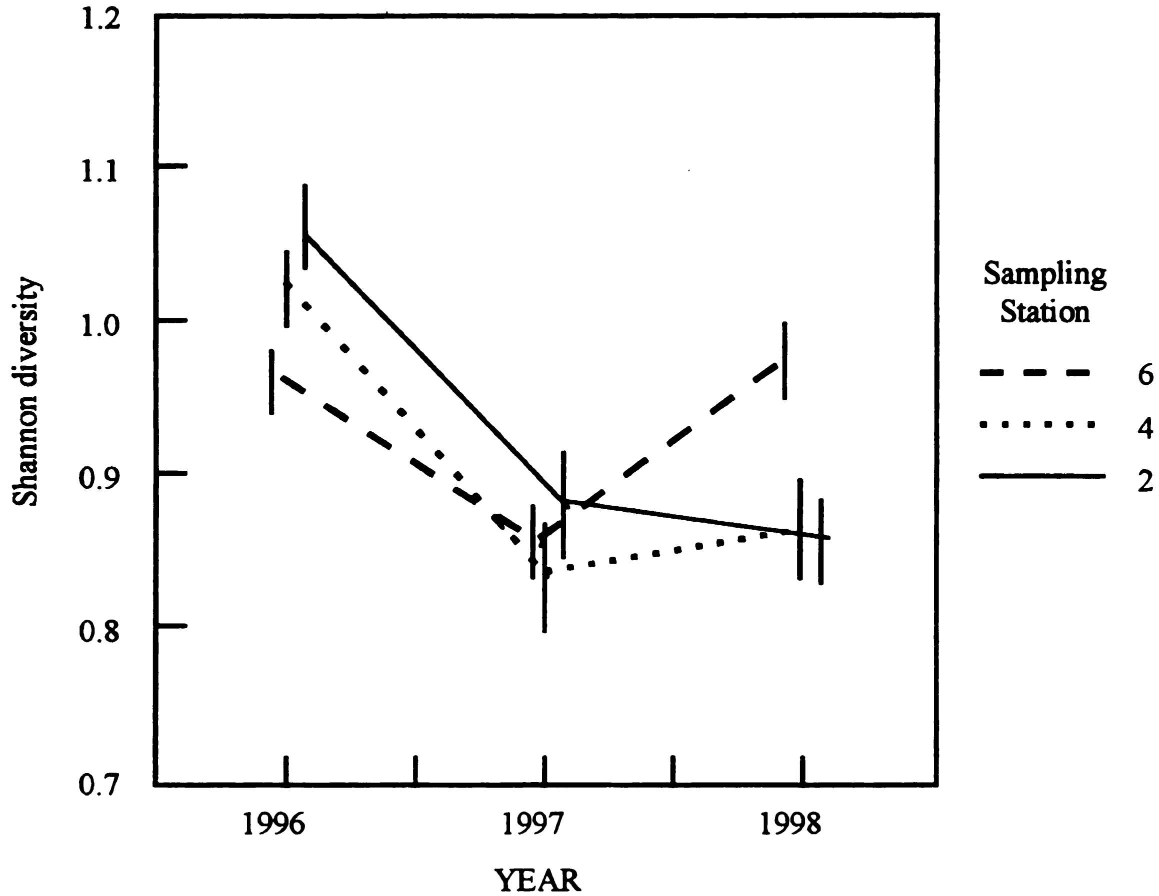


Figure 2.8. Shannon diversity of invertebrate samples at each sampling station, by year (means with standard errors).

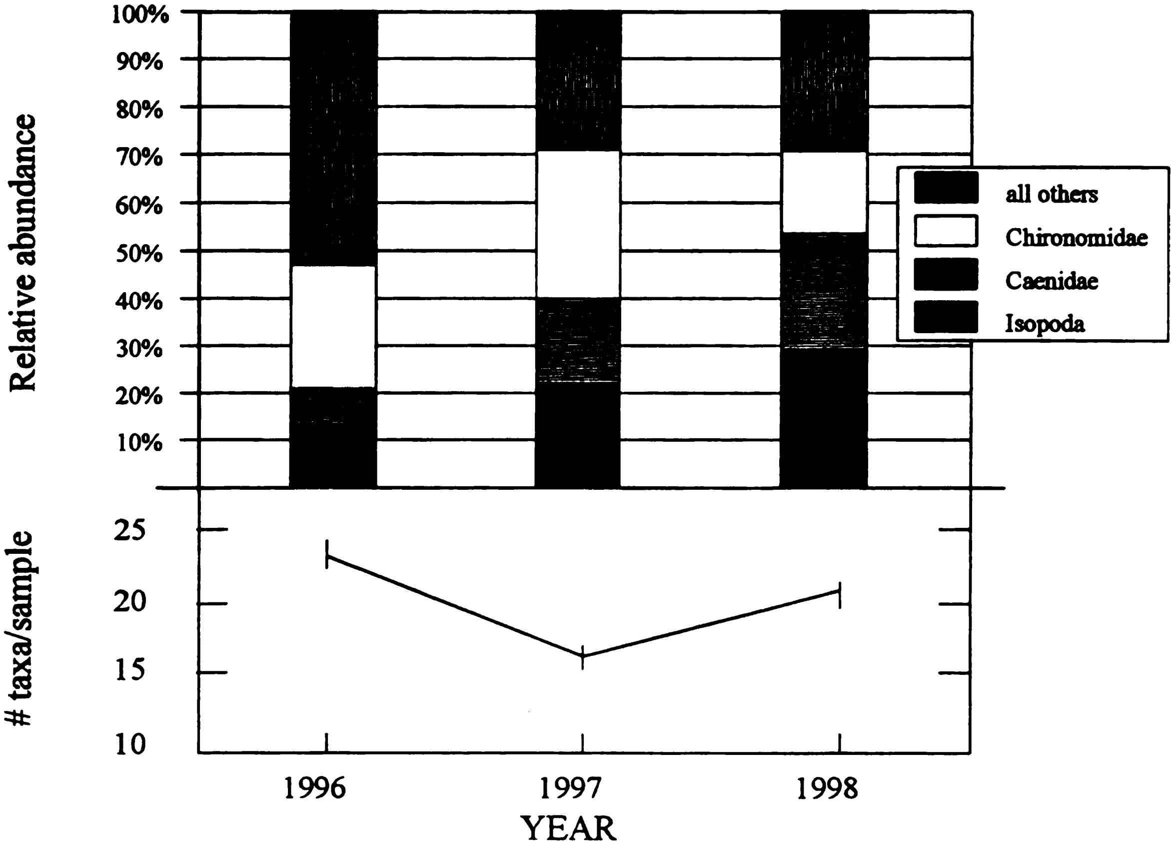
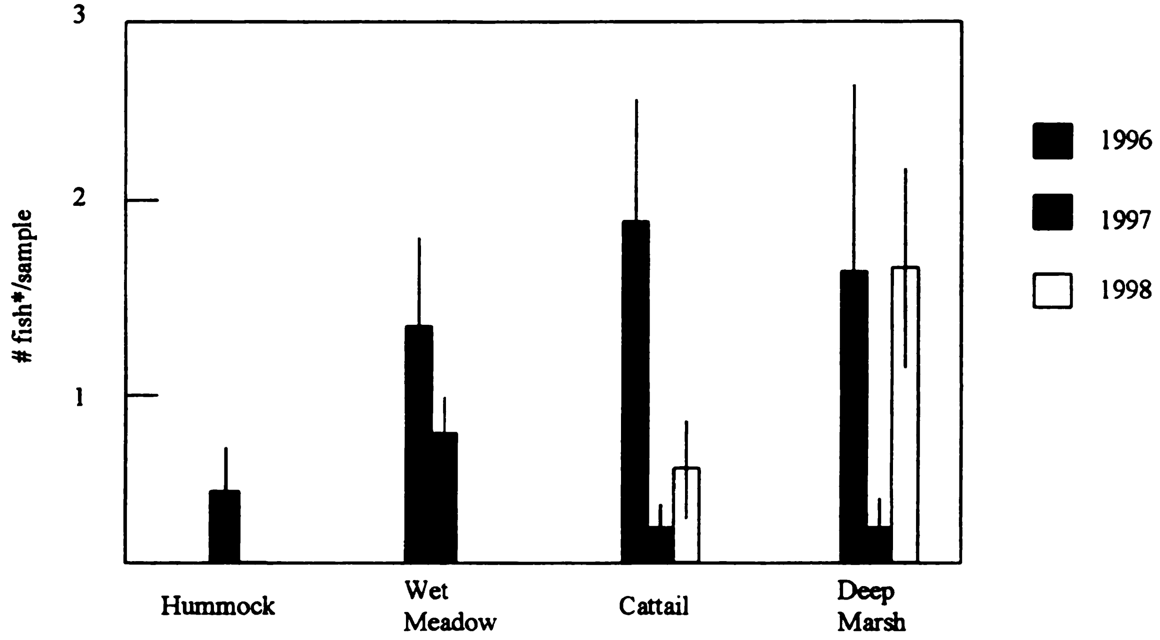


Figure 2.9. Dominant taxa relative abundances, and changes in taxa richness by year (means over all stations, with taxa richness standard errors).



*small fish up to ~50 mm

Figure 2.10. Mean fish catch per unit effort among stations and years (means with standard errors).

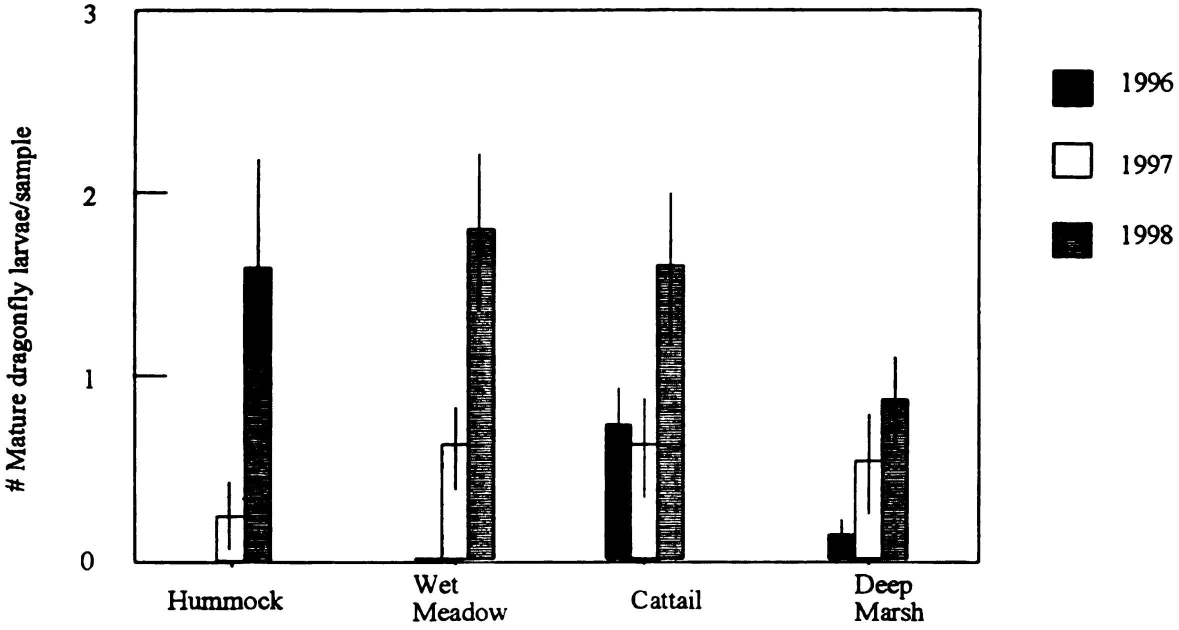


Figure 2.11. Mean densities of mature dragonfly larvae among stations and years (means with standard errors).

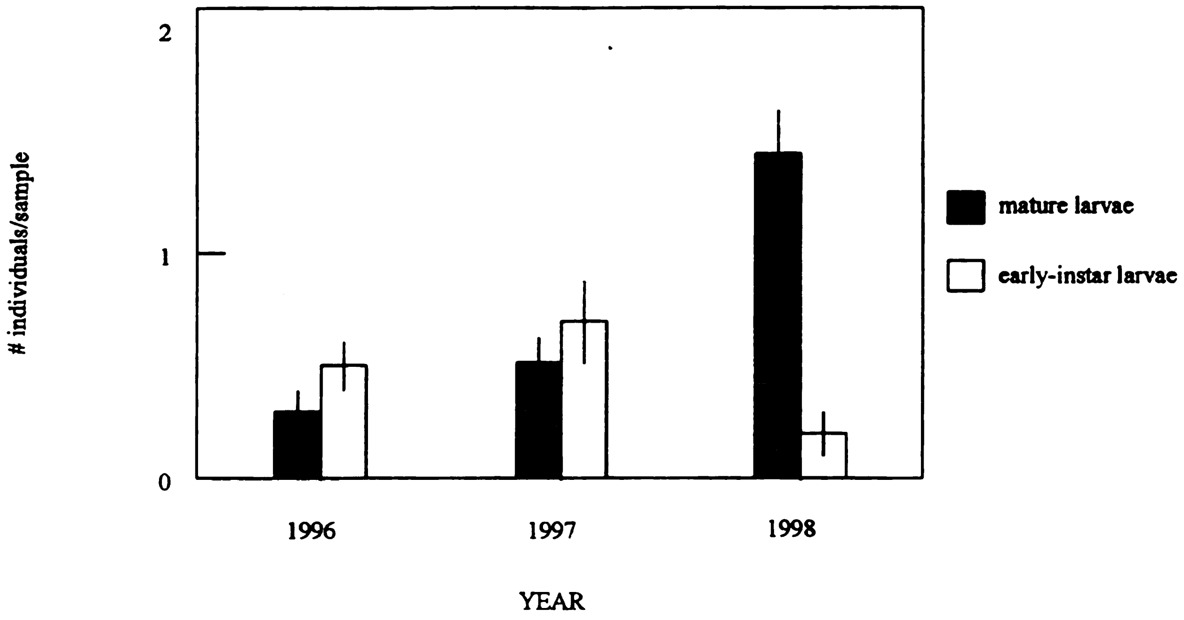


Figure 2.12. Densities of mature and early-instar dragonfly nymphs by year (means with standard errors).

Chapter 3

BIOTIC CONTROLS IN AN ABIOTICALLY-VARIABLE HABITAT: EXPERIMENTS ON THE EFFECTS OF PREDATORS ON A GREAT LAKES COASTAL WETLAND AQUATIC INVERTEBRATE COMMUNITY.

INTRODUCTION

The relative importance of biotic factors in controlling community composition is believed to vary depending on habitat stability, which often depends on flooding regimes in shallow lentic systems (Batzer and Wissinger 1996). When placed on a continuum from permanent to ephemeral flooding, communities in systems that experience permanent or near-permanent flooding are expected to be structured primarily by predation, while systems with more temporary flooding are mostly influenced by the constraints imposed by fluctuating abiotic conditions (Figure 3.1; Wellborn et al. 1996). According to this model, fish are the dominant predators when present, and large invertebrate predators dominate in the absence of fish. In very temporary systems, however, populations of predators cannot become established well enough to become dominant influences on the invertebrate community.

The importance of top-down regulation of invertebrate communities in vegetated shallow waters can vary among and within sites, depending on flooding regimes and vegetation structural complexity, among other factors (reviewed in Batzer and Wissinger 1996). Wetlands with fish usually have lower invertebrate diversity and biomass, but in vegetated lake littoral zones, fish can strongly reduce abundances of some invertebrate taxa and weakly reduce others (Hall et al. 1970, Johnson et al. 1996). When the effects are weak, it may be because of reduced feeding efficiency in structurally-complex vegetation (Gilinsky 1984), or because prey communities are "experienced", hence adapted to their local predator assemblage (Wellborn and Robinson 1991). Invertebrate predator control can also vary, but is apparently not as effective or as general as fish predation. Wissinger and McGrady (1993) were able to demonstrate predation effects of dragonfly larvae in lab experiments, but it has been more difficult to demonstrate strong dragonfly larva effects on invertebrate communities in the field (Johnson et al. 1996). Several studies have shown few or no significant reductions of prey densities by these predators (e.g. Johnson et al.1987), but this may be because high prey turnover balances predation with recruitment (Benke 1976). Prey may also benefit indirectly from dragonfly larva predation on other invertebrate predators (Larson 1990), and fish predation may have similar effects.

The Wellborn et al. (1996) model described above is a useful generalization, but may not apply to all systems. Coastal wetlands of the Great Lakes are characterized by continuous gradients in flooding regimes along elevation gradients from lake to shore (Gathman et al. 1999). High-elevation fringing wet meadows are flooded seasonally as lake levels rise and fall somewhat predictably, so fish and invertebrates from adjacent low-elevation permanent zones have direct aquatic access to these temporary zones. This creates a situation that differs from the model in that the impermanence of flooding does not fully exclude permanent-water predators from wet meadows, and distributions of fish and large invertebrate predators overlap along the elevation gradient (Chapter 1). In such cases, it is difficult to predict whether temporary-water invertebrate communities will be structured by predation pressures from immigrants, or whether the fluctuating abiotic conditions prevent invading predators from regulating communities.

A further complication in coastal wetlands is that distributions of individual fish species vary over the elevation gradient (Cardinale et al. 1997, Gathman and Keas 1999; Chapter 1). Fish cannot be considered a monolithic functional group because they vary in size and feeding preferences ontogenetically (Werner and Hall 1988) and taxonomically. This means that spatial variation in coastal wetland fish assemblages should create spatial variation in predation pressures as well. While many fish predation studies in lake littoral zones have focused on relatively large invertivores such as *Lepomis* spp. (e.g. Bohanan and Johnson 1983, Gilinsky 1984), fewer (e.g. Johnson et al. 1996) have tried to determine the effects of the many small-bodied species, and juveniles of larger species, that are often abundant in the vegetated shallows of lakes and wetlands.

The conceptual model described above includes a version of the "environmental sieve" idea (sensu van der Valk 1981), in which abiotic environmental factors prevent some organisms from occupying more harsh or variable habitats. Conversely, it states that inhabitants of harsh habitats are excluded from more "benign" habitats by biotic interactions (predation and competition). However, in the middle of the harsh-to-benign, or temporary-to-permanent, gradient, both biotic and abiotic factors can be important. This study focused on predation in the middle of the gradient, with a particular focus on how predation, rather than abiotic conditions, may prevent permanent-water taxa from occupying temporary-water wetland zones. I studied predation effects in a coastal wetland in which small fish, especially mudminnows (*Umbra limi*), and dragonfly larvae (families Libellulidae and Aeschnidae) were common in the lower-elevation portions of the temporarily-flooded wet meadow zone. I hoped to determine whether these two different types of predators could significantly influence wet meadow invertebrate community composition by excluding taxa that were characteristic of deeper, more permanent zones

METHODS

Two experiments were run in the Lake Huron coastal wetland described in earlier chapters. Because the lake level was slowly dropping in 1998, I placed mesocosms in the transition zone of the wetland, at a lower elevation than the wet meadow, to ensure that sufficient water depth would be present for the duration of the experiments. The majority of the transition zone was occupied by a dense cattail-dominated plant community, but openings could be found in the band of emergent plants, so I chose one of these as an experiment site to minimize vegetation damage. Both experiments were run for 28 days in late summer, 1998.

Predator assemblage and fish density estimates

The fish and invertebrate predator assemblage varied along the elevation gradient, though only invertebrate predators (mostly Dytiscidae beetle larvae and adults) were common at the highest elevations in the shallowest water (Chapter 2). Below this shallow extreme, the lower wet meadow was dominated by dragonfly larvae and small fish. Mudminnows (*Umbra limi*) and Iowa darters (*Etheostoma exile*) were the most common "resident" species, while juvenile largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), and pumpkinseed (*Lepomis gibbosus*) frequented the wet meadow as well as lower elevations. Just below the wet meadow was the transition zone, dominated by cattail plants. Fish density tended to remain high in this zone, but dragonfly larva density and fish density both tended to decrease with lower elevation (greater depth) where the transition zone plants gave way to an emergent marsh dominated by bulrushes. In this zone, larger piscivores were common, small fish were more sparse, and the most common dragonfly larvae were very sessile, sprawling types (mostly Corduliidae: *Epitheca*).

Previous years' sampling indicated that the wet meadow fish assemblage was dominated numerically by mudminnows (*U. limi*), occurring in three size classes: young-of-year (YOY): ~30 mm mean standard length by late summer; presumed yearlings: ~55 mm mean standard length; larger fish: ~90 mm mean standard length. Gut analyses (unpublished data) indicated that YOY mudminnows fed exclusively on meiofauna, while larger size classes ate macroinvertebrates also. The dragonfly assemblage in the site consisted of several genera of Aeschnidae, Libellulidae, and Corduliidae, distributed differently along the elevation gradient. The lower wet meadow was occupied by *Aeschna* (Aeschnidae), and three genera (Libellulidae: *Libellula*, Corduliidae: *Dorocordulia*, *Somatochlora*) that were morphologically indistinguishable in the field.

To estimate ambient mudminnow densities, I carefully enclosed three areas (~9.3 m^2) of wet meadow using lead-line netting from fish trap nets (Fyke nets). Nets had floats along the top edge and I slowly and quietly worked the weighted lower edge into the bottom detritus so it was flush against the underlying substrate, being careful not to step in the enclosed area. I then distributed twelve activity traps within the enclosure, laying them horizontally on the substrate.

I emptied the traps twice daily until two successive checks resulted in no mudminnows caught in any traps, which occurred within three days in each enclosure. This method probably resulted in a somewhat conservative estimate of mudminnow density because some fish may have fled the sample area before I finished the enclosure. However, previous experience indicated that, when startled, mudminnows tended to hide in detritus rather than flee, so losses due to disturbance during initial net placement were probably relatively low. The procedure was effective in catching individuals of several species other than mudminnows, predominantly young-of-year pumpkinseed, but also including young brown bullhead (*Ameiurus nebulosus*) and bowfin (*Amia calva*). Estimated mean densities based on total numbers of fish removed from the enclosed areas were 1.39 fish/m^2 or 1.02 *U. limi*/m^2.

Experiment 1 design and setup

The first experiment was a 2x2 factorial randomized complete block design with 10 blocks. The two factors were: 1. presence or absence of 10 dragonfly nymphs (5 Aeschnidae and 5 Libellulidae, representing the ambient assemblage), and 2. presence or absence of 2 young-of-year (YOY) mudminnows (representing a very high density relative to ambient conditions). The experiment was primarily designed to test: 1) whether ambient densities of dragonfly larvae could significantly alter invertebrate abundance and/or relative abundances of individual taxa; and 2) whether the presence of fish would affect predation effects of dragonfly larvae. I did not expect that these small fish could significantly affect macroinvertebrate community composition, because preliminary gut content analysis revealed that their diets mostly consisted of microcrustaceans. I "loaded" the fish-addition treatments with high fish densities to test the hypothesis that even a high density of these fish could not strongly affect macroinvertebrates.

Mesocosms consisted of circular enclosures (0.48 m diameter, 0.185 m^2 basal area) made of fiberglass window screen (approximately 1mm x 1.5mm mesh size) attached to plastic hoops at the top and bottom. Screen bottoms were attached to the lower hoops so experimental units were enclosed by screen on all sides except the top. I installed the enclosures in ~30 cm deep water, but they were >1m in height to ensure that they could not be over-topped by waves if a storm surge occurred during the experiment. I installed 10 blocks of 4 closely-spaced enclosures, with each of the 4 treatment combinations randomly assigned to enclosures in each block (Figure 3.2). I worked one block at a time, installing enclosures as follows. I first decided on the position of the first enclosure, and dropped a separate weighted plastic hoop (same size as enclosure bottoms but without attached mesh) to the substrate. I used a D-frame dipnet to collect detritus and invertebrates until I had cleared the area within the hoop down to the underlying dense root-mat/soil matrix. I quickly transferred collected material to a large plastic water-filled tub for temporary keeping. I then removed the hoop and installed the enclosure in its place. The resulting enclosure was a vertical mesh cylinder with its mesh bottom lying flush on the substrate and its top extending well above the water surface and held in place by three wooden stakes around its perimeter. The top hoop of the enclosure was stapled to the stakes, which were firmly planted in the substrate.

I repeated the installation procedure for the remaining three units in the block, collecting all detritus and animals in the same plastic tub. I carefully examined all collected detritus, removing dragonfly nymphs and retaining them for use in dragonfly-addition treatments. As an attempt to homogenize initial conditions in enclosures within the block, I carefully mixed and stirred the material in the tub by hand, poured it into a 250 μm mesh sieve-bottomed bucket, and distributed it among the four units in the block, using a standard brass sieve as a measuring device to ensure that approximately equal portions of material were added to each unit in the block. In all I installed ten blocks of four units each, in three rows of 4, 4, and 2 blocks. The four treatment combinations were randomly assigned to experimental units in each block, and predators were added to the appropriate units. For dragonfly-addition treatments, I determined density, and Aeschnidae/Libellulidae ratio, by counting all the collected larvae (removed from detritus, as described above) and dividing by the number of enclosures. This resulted in 5 Aeschnidae and 5 Libellulidae larvae collected per enclosure, so I used these densities for treatments. For fish additions, I collected mudminnows with activity traps during the previous two nights.

Experiment 2 design and setup

The second experiment was designed to test whether ambient densities of post-YOY mudminnows could alter invertebrate abundances and/or relative abundances of individual taxa. The experiment was a 2-treatment completely randomized design with 5 replicate enclosures per treatment (Figure 3.3). The fish-addition treatment consisted of the addition of two intermediate size-class mudminnows (~55 mm standard length) collected from the lower wet meadow. This resulted in a 1.57 fish/m^2 mudminnow density, which was a bit higher than estimates of ambient density, but not unrealistically so. Previous sampling over three years indicated that mudminnow densities could be more than double, and total fish densities more than triple, the estimates at the beginning of this study (based on comparisons of catches-per-unit-effort from activity traps). The circular mesh enclosures were similar to those used in the first experiment, but they were larger (1.27 m diameter, 1.27 m^2 basal area). Enclosure placement followed the same method used for the first experiment, except that detritus was not mixed before it was added to enclosures because the experiment was not set up in blocks.

Data collection and analysis

At the close of each experiment, I collected all detritus from each enclosure and transported it from the field in plastic bags. The same day, I removed all very coarse material by hand under running water and preserved the remaining detritus/invertebrates in jars in 95% ethanol for transport to the lab and subsequent sampling. For sampling I used the same radial sample divider described in Chapter 2. To sample Experiment 1 enclosure contents, I thoroughly mixed the detritus/invertebrate mixture in water, divided the material in half using the sample splitter, and randomly selected 3 one-twelfth samples (one-sixth samples from each half, randomly selected), for a total of one-fourth of all material sampled. I washed each sample in a 500 µm sieve and picked all invertebrates from the sample under 10X magnification. I examined distributions of individual taxon abundances, relative abundances (as proportions of sample total), total invertebrate abundance, and taxa richness among treatments and decided to use a log(x+1) transformation. I analyzed data from the more common taxa using fully-factorial 2-way ANOVAs with blocks. The rarer taxa required Kruskal-Wallis non-parametric tests for differences among treatments.

For Experiment 2, I collected 2 one-twelfth samples, for a total of one-sixth of all material sampled. I pooled the two samples and washed the combined sample through a graded series of sieves. I picked invertebrates under 10X magnification from two size fractions: material retained in a 2 mm mesh sieve (the largest size used), and material retained in a 1 mm mesh sieve. Data analyses were performed on individual taxon abundances and relative abundances (calculated as proportion of all invertebrates represented by each taxon) from each size fraction and from the two combined. I examined data distributions for each dependent variable and decided to use log(x+1) transformations. I analyzed the data using t-tests for the more common taxa and non-parametric tests for the more rare taxa.

RESULTS

The ambient community at the experiment site was dominated by Caenidae (*Caenis*) mayfly larvae, isopods of two genera (*Caecidotea* and *Lirceus*), Chironomidae larvae, and amphipods which were almost exclusively *Hyallela azteca* (Table 3.1). Leptoceridae caddisfly larvae (*Oecetis*, *Trianodes*, and many small unidentifiable specimens) and several gastropod genera were also common. Various other taxa occurred at lower abundances, including dragonfly larvae of different sizes, Sphaeriidae clams, Dytiscidae beetle larvae, and Ceratopogonidae fly larvae. Most of the abundant taxa were typical of deeper-marsh communities observed during previous years, while most of the less abundant groups were previously more associated with higher elevations. This community mixture was a result of dramatic water level changes over the previous years.

Experiment 1

Table 3.2 lists individual ANOVA results by indicating main effects (% abundance change with predator addition) and significance levels for all model terms. I considered test results weakly significant if p-values were between 0.1 and 0.05 and strongly significant if they were less than 0.05. I did not hold strictly to a 0.05 α level because previous experience indicated fairly high within-group variability in these invertebrate taxa. Block terms were significant in most tests, indicating that either my attempts to homogenize initial conditions within blocks was successful or that spatial variation in environmental factors caused differences among blocks. Because blocks were spatially segregated, blocks differed in water depth and wave exposure, although these differences were very subtle within the ~10m by ~10m experiment area. Nonetheless, adding dragonflies resulted in only a few significant differences in taxon abundances (summarized in Table 3.3), largely because of highly variable dragonfly effects among blocks. For example, dragonfly larvae effects on isopods were strongly negative in some blocks, and strongly positive or very small in others. However, I found a few negative effects of dragonfly addition over all blocks, including weakly significant reductions in relative abundances (proportions of all invertebrates) of *Lirceus* isopods (-30.8%; p=0.079), damselfly larvae (-20%; p=0.079), and Lymnaidae snails (-50%; p=0.093). Also, caddisfly larvae (Trichoptera) in dragonfly-addition treatments were 27.3% (p=0.004) less abundant than in dragonfly exclusions. This was mainly because the most abundant family, Leptoceridae (*Trianodes* and *Oecetis*), was strongly reduced by dragonfly larvae (p=0.004). The other notable dragonfly effects occurred among two less common taxa (requiring non-parametric tests): Dytiscidae beetle larvae, and Turbellaria (p=0.049 and p=0.024, respectively; Wilcoxon rank sum test) were significantly reduced by dragonfly addition.

Small mudminnows had no negative effects on macroinvertebrates, but did have positive effects on two macroinvertebrate groups. Leeches (Hirudinea) and limpets (Ancylidae) were 100% and 47.7% (p=0.052 and p=0.047, respectively; Wilcoxon rank sum test) higher in fish addition treatments than in those without fish. Also, densities of small, unidentiable Leptoceridae caddisfly larvae were 50.0% higher in fish treatments than in no-fish treatments (p=0.018), which was the opposite of the dragonfly effect on this group. Negative effects of fish presence were confined to very small animals (meiofauna): a 30.4% reduction of cyclopoid copepods (p=0.074, though may not be meaningful because of interaction effects, described below), a 41% reduction of Naididae worms (p=0.012) and a 43.8% reduction of Oribatei soil mites (p=0.032). Meiofauna were not the focus of this study so sampling methods did not reflect their absolute densities, though relative abundances among samples probably represent abundances of large-bodied individuals reasonably well.

The more interesting results of fish addition were significant interactions between predator types that affected several taxa. Interactions affected amphipods (p=0.042) and water mites (Hydracarina; p=0.078) in similar ways. For example, either dragonfly larvae or fish alone reduced amphipod abundances by 21.5% and 29.1%, respectively, but together these predators had the opposite effect (Figure 3.4). Both predators in the same enclosures resulted in an average 5.7% increase in amphipod abundance, compared to no-predator controls. When analyzed in a post-hoc contrast, combining dragonfly-alone with fish-alone treatments vs. the other two, amphipod reduction by solo predator types averaged 27.4% ($p=0.033$). The Fish X Dragonfly interaction was also significant in tests on cyclopoid copepod abundances ($p=0.014$), but the effect was the opposite of the effect on amphipods. Either predator type alone resulted in higher cyclopoid abundances than in the no-predator controls (fish alone: +23.1%; dragonflies alone: +94.9%), while both predator types together caused an 17.9% reduction. A weak Fish X Dragonfly interaction affected Sphaeriidae clams similarly ($p=0.081$).

Experiment 2

The effects of larger mudminnows were more substantial than those of dragonflies or small mudminnows, but results varied among size fractions of sample material (Table 3.4). When data from both fractions were combined, mean total invertebrate density was 29.2% lower ($p=0.054$) among fish-added enclosures (677 animals/sample, or 3198/m^2) than among no-fish enclosures (479 animals/sample, or 2263/m^2). This difference was mostly a result of a 42.1% reduction in large-fraction abundance ($p=0.017$), while the small-fraction difference was non-significant. Mean taxa richness was also significantly lower ($p=0.06$) in the fish treatment (19.2 taxa per sample) than in the no-fish treatment (15.4 taxa per sample). Tests on the combined size-fraction data revealed that fish significantly ($p<0.05$) reduced abundances of Diptera, Mollusca, and Trichoptera, though differences within most lower taxonomic groups within these taxa were not significant. Weakly significant differences ($0.1>p\geq0.05$) between treatments occurred in total abundances of Caenidae mayfly larvae and damselfly larvae. Abundances of the numerically-dominant isopods and amphipods were non-significantly lower in fish treatments, but, conversely, relative abundance of all isopods was significantly higher in the fish treatment (p=0.006). Higher relative abundances of both isopod genera occurred in the fish treatment, though only the *Caecidotea* difference was significant (p=0.085).

Individual-taxon data collected from the larger size fraction of samples produced more significant differences among treatments than those from small fractions (Table 3.5). Among the large-fraction variables, fish caused strongly significant ($p<0.05$) reductions of amphipods and *Lirceus* isopods (Table 3.6), though these were not significantly reduced in the small fraction. In fact, mean *Lirceus* density in the small fraction was non-significantly higher in the fish-added treatment, leading to a 50% larger (p=0.013) relative abundance of *Lirceus* in small fractions from this treatment. Large-fraction mayfly and caddisfly larvae were also strongly reduced by fish, but the small-fraction differences were not significant. Isopods, molluscs, damselfly larvae, and limpets (all large fraction) were all less abundant in the fish treatment, though differences were weakly significant. Relative abundances of isopods in general and specifically *Caecidotea* were higher in fish treatments (both size fractions), while mayfly relative abundance was lower (large fraction only).

DISCUSSION

These results suggest that larger mudminnows at ambient densities can affect the structure of wetland invertebrate communities in Mackinac Bay, but that the effects of dragonfly larvae are weaker. Fish effectively reduced overall densities of invertebrates, and significantly lowered densities of the numerically-dominant taxa, except *Caecidotea* isopods. They failed to significantly reduce most of the less abundant taxa. However, almost all taxa occurred at lower abundances (whether statistically significant or not) in fish enclosures than in no-fish enclosures, so relative magnitudes of change and significant changes in relative abundances may be more informative measures of potential mudminnow effects on community composition. Percent reductions suggested that mayfly larvae and amphipods were particularly vulnerable to fish predation, although relative abundance (proportion of all invertebrates) of amphipods was only non-significantly reduced. The substantal effects of these fish raise the question of whether there was an "enclosure effect", or a tendency of fish to eat more invertebrates from a 1.27 m^2 than they normally would if not penned. While this possibility cannot be completely refuted without a separate study, it seems fairly unlikely because mudminnows are known to be relatively sedentary "ambush" predators (Scott and Crossman 1973), so they probably do not patrol a large area in search of food.

Fish exhibit size-selectivity in prey selection (Mittelbach 1981), favoring larger macroinvertebrates (Wellborn 1994), so it is not surprising that the majority of significant reductions occurred among prey collected from larger size fractions of samples. Among the smaller fractions of samples, no invertebrate taxa were significantly reduced by fish, though taxa richness was. However, small-fraction relative abundances of isopods (total and each genus individually) were higher in fish enclosures, so all other taxa in this size fraction must have been reduced collectively. This reflected the general increase in relative abundance of isopods in both size fractions and collectively, despite the fact that, like most other taxa, their absolute abundance was reduced by fish.

The inability of dragonfly larvae to significantly alter abundances of the most common invertebrate taxa was consistent with the fact that previous studies have shown weak predation effects of dragonflies at best (Fauth 1999). Dragonflies have low metabolic demands compared to fish, and because of their sit-and-wait feeding mode they probably have lower metabolic requirements than more mobile invertebrate predators as well. Nonetheless, their high densities in the study site initially suggested that their effects could be substantial. However, dragonfly larvae often exhibit negative density dependence in feeding and development rates (Anholt and Werner 1998, Johnson et al. 1995), which probably results from interference competition and cannibalism (Crowley and Martin 1989, Hopper et al. 1996, Van Buskirk 1989). Also, it has been suggested that dragonfly larvae reduce densities of other invertebrate predators, leading to indirect survival enhancement in other invertebrate "prey" (Blois-Heulin et al. 1990). In this study, dragonfly larvae significantly reduced densities of all other invertebrate predators collectively by 25% (p=0.002), so indirect benefits to prey may have counteracted direct predation losses.

Interactions between small fish and dragonflies affected abundances of some taxa, as seen in some other studies (e.g. Swisher et al. 1998). Such interactions could occur through direct mechanisms, such as dragonfly detection of chemical signals from fish, as Koperski (1997) observed in damselflies, or aggressive behavior by dragonflies toward fish, but indirect mechanisms are also possible. Some animals, such as nematodes and copepods in this study, may be able to find refuge from one type of predator, but the presence of two predator types occupying different microhabitats may increase the risk of being eaten. Amphipods, on the other hand, were apparently safer from predation when both predator types co-occurred. These animals' high mobility and relatively large size may make them especially vulnerable to both types of predators, but the small size of the fish used in the factorial experiment suggests that predation by fish was not a likely risk for amphipods. Perhaps direct interactions between predator types enhanced amphipod survival when both predators were present.

According to the model proposed by Wellborn et al. (1996), taxa from more permanently-flooded habitats are excluded from temporary habitats by abiotic forces, but in coastal wetlands it may be biotic forces that prevent many invertebrate taxa from reaching high densities in wet meadow zones. The experiments in this study consisted of the addition of wet meadow predators to invertebrate communities that were characteristic of lower elevations during a previous "average" water-level year (1996; see Chapter 1), and these predators reduced the abundances of invertebrate taxa that had not co-occurred with them during that year. Figure 3.5 is the correspondance analysis plot of 1996 data from Chapter 1, including the plotted positions of the most common taxa. Those that were affected by predators in these experiments are underlined. The combined effects of larger mudminnows and dragonfly larvae reduced the abundances and relative abundances of most of the deep-marsh-associated taxa (*Lirceus* isopods, amphipods, and damselfly, mayfly, and caddisfly larvae), while those taxa most associated with the temporarily-flooded lower wet meadow (e.g. Chironomidae, snails) were not significantly affected. Taxa that were previously generally confined to the shallowest high-elevation areas (e.g. larvae of Dytiscidae beetles, Sphaeriidae clams, and Ceratopogonidae flies) were also negatively affected by predators. Many smaller taxa that were formerly common in the wet meadow (copepods, nematodes, Oribatei soil mites, Naididae worms) were apparently reduced by small fish, but the high fish densities used in the factorial experiment were unrealistic, so these effects would presumably be much lower in natural conditions. A particularly interesting result was that *Caecidotea* isopods were not significantly reduced by either predator type, and their proportional representation (relative abundance) in the community was enhanced by fish presence. These generalist animals migrated readily into the wet meadow in previous years, despite mudminnow presence, and their abundances grew notably over the entire elevation gradient over the three-year period ending with this study.

Further examination of the changes seen in the previous three-year period (described in previous chapters) lends more evidence to the roles of predators suggested here. During the "average" year, invertebrate densities, especially in the wet meadow, were fairly low. *Caecidotea* isopods were one of the most successful immigrants from low elevations to the mudminnow-occupied wet meadow. In the next year the water level in the site was much higher, causing permanent wet meadow flooding, and almost all invertebrate taxa that had previously dominated only the deeper marsh invaded the wet meadow. Some of these taxa grew in abundance prodigiously, concurrent with a lowered fish density (Figure 3.6) which probably relieved predation pressure and "opened" the wet meadow to previously-excluded taxa. The lower fish densities at higher elevations may have been a result of invasion by piscivorous fishes (as noted in Chapter 2), suggesting temporal shifts in food chain dynamics.

The year after high water (which was when these experiments were performed) saw reduced wet meadow abundances of many previously deep-marsh associated taxa, which shifted back down the gradient with the lower water levels. However, isopods (both genera), amphipods, and mayflies continued to increase in the wet meadow, which may have partially resulted from the fact that wet meadow fish densities were very low. By late that year most fish, including mudminnows, were concentrated in the slightly deeper water just below the wet meadow. Interestingly, however, invertebrate densities also continued to increase in these lower-elevation zones, despite relatively high fish numbers. Some of this increase may have resulted from down-slope migrations as many invertebrates vacated the wet meadow by migrating or ovipositing in the transition and deep marsh zones.

These observations and the results of the experiments in this study suggest a model of community regulation that differs somewhat from the Wellborn et al. (1996) model. This new model, illustrated in Figure 3.7, is an attempt to explain invertebrate community variation along the coastal wetland elevation gradient as seen in an "average" water-level year ("average" must be used cautiously because year-to-year changes in water level are very common in the Great Lakes). This model depends on a hypothesized series of effects beginning with regulation of dissolved oxygen levels along the elevation gradient. As described in Chapter 2, I measured a dissolved oxygen gradient consisting of saturation levels in the deep marsh, where oxygen production was presumably high, and a fairly steep drop through the transition zone to hypoxia in the wet meadow, where oxygen consumption was probably higher than production (Figure 3.8). Incoming waves probably mixed some of the oxygenated water into the wetland, setting up the gradient. This would be similar to the mechanisms driving water chemistry gradients measured by Cardinale et al. (1998) in a Saginaw Bay coastal wetland, resulting from a gradual energy reduction in waves that moved through the dense vegetation of the wetland. Also, dissolved oxygen levels rose and fell with seiche-induced water level oscillations, so it appeared that dissolved oxygen levels were directly related to water levels. Thus dissolved oxygen at any given point on the gradient is largely determined by water level and the cumulative plant density through which waves pass to reach the point in question. Following the chain of mechanisms (Figure 3.9), dissolved oxygen levels determine which species of fish occupy a region of the gradient and predation effects of these fish cascade through the food web.

Interpreting the experimental and previous observational data in light of this new conceptual model leads to the following. Wet meadow communities usually consist of invertebrate taxa that are rapid colonizers of newly-flooded areas, or those that can endure de-watering and can overwinter in un-flooded substrates (Chapter 1). These animals must also be able to tolerate very low dissolved oxygen levels that are common in the wet meadow. Mudminnows dominate the wet meadow fish community because of their ability to "breathe" air at the water surface. The upper edge of the flooded wet meadow is characterized by taxa that can tolerate alternating flooding and draining (caused by constant seiche activity), but are vulnerable to the predators at lower wet meadow elevations (mudminnows and dragonfly larvae). By contrast, the lower wet meadow community consists of animals whose populations can withstand culling by these predators.

Below the wet meadow, dissolved oxygen levels are higher so more fish species can occupy these wetland zones. Also, flood duration is longer, so more invertebrate taxa can occupy the habitat without risk of losing surface water before completing their life cycles. In this middle portion of the gradient, there is a gradual change in the food web with greater depth, as piscivorous fish become more common at lower elevations. Invertebrates in deep marsh areas may be released from heavy predation pressures because smaller fish are reduced in number by piscivores where habitat structure is less complex

(Werner and Hall 1988, and reviewed therein). Dragonfly larva abundance can also be reduced by larger fish (Morin 1984). Deep marsh "prey" invertebrates may be excluded from higher elevations because they are more vulnerable to the predators encountered there, hence their reductions by predators in this study.

This model suggests a spatial shift in trophic cascade effects, from a very shallow primary-consumer community with little top-down control, to a mid-range secondary-consumer-dominated group, and finally to a deeper tertiary-consumer-dominated food web. In this way, it is similar to the Wellborn et al. (1996) model, except that the boundaries between compartments are permeable: there are no distinct boundaries between habitats, so no boundaries between community members. Because the system is open, animals can respond to habitat change by relocating, so community membership at different points on the gradient is fluid and mediated by abiotic factors. It is also mediated by biotic factors, but these are themselves subject to abiotic control.

This temporally-dynamic nature may, on one hand, allow the persistence of some "fugitive" taxa that would be eliminated from the community in more stable conditions; on the other hand, however, it may exclude many taxa that cannot endure or respond to the abiotic changes characteristic of the system. Thus, the spatial stability of animal populations implied in the Wellborn et al. (1996) model is not present in this new model. Not only are communities not spatially stable in this model, but there are no true communities because their compositions vary constantly. Thus, this model suggests a Gleasonian, or individualistic, view of communities in which individual invertebrate populations constantly shift their spatial distributions in response to environmental changes and largely independent of each other.

This model depends on temporal instability, so it may be less applicable to more slowly-changing, but otherwise similar, habitats. Wetlands with richly-developed and expansive wet meadow habitat may be very rare on shores other than the Great Lakes because: 1) water level fluctuation is usually required for such systems to develop, and 2) human desire for lakeshore properties leads to destruction of wetland habitat above the mean water level. However, the model may be at least partly helpful in furthering understanding of littoral wetlands that don't experience regular water-level changes because it depends on depth and dissolved oxygen as much as flooding duration. The added effect of flood duration is to restrict high-elevation invertebrate community membership to only those taxa that can withstand de-watered periods. Thus, Great Lakes coastal wetlands may differ from littoral communities of inland lakes because of the unique suite of hydrologic factors that are characteristic of the Great Lakes.

Table 3.1. Ambient invertebrate community composition at experiment locations (proportions of community comprised by individual taxa).

Experiment 1		Experiment 2	
Caenidae	0.521	Caenidae	0.281
Caecidotea	0.130	*Caecidotea*	0.204
Macrothricidae	0.061	Chironomidae	0.114
Chironomidae	0.060	Macrothricidae	0.078
Cyclopoda	0.055	Amphipoda	0.072
Amphipoda	0.046	Ostracoda	0.040
Lirceus	0.022	*Lirceus*	0.036
Ostracoda	0.014	Cyclopoda	0.031
Ceratopogonidae	0.009	Naididae	0.019
Planorbidae	0.009	Coenagrionidae	0.014
Naididae	0.008	Leptoceridae	0.010
Hydracarina	0.007	Planorbidae	0.009
Chydoridae	0.006	Sphaeriidae	0.008
Corduliidae	0.005	Chydoridae	0.008
Coenagrionidae	0.005	Lumbriculidae	0.007
Daphniidae	0.005	Hydracarina	0.007
Polycentropodidae	0.004	Daphniidae	0.007
Lumbriculidae	0.003	Ancylidae	0.006
Isotomidae	0.002	Corduliidae	0.005
Hirudinea	0.002	Ceratopogonidae	0.005
Sphaeriidae	0.002	Hirudinea	0.003
Aeschnidae	0.001	Polycentropodidae	0.003
Sminthuridae	0.001	Sididae	0.001
Limnephilidae	0.001	Nematoda	0.001
Leptoceridae	0.001	Limnephilidae	0.001
Phryganeidae	0.001	Phryganeidae	0.001
Hydroptilidae	0.001	Hydroptilidae	0.001
Libellulidae	0.001	Libellulidae	0.001
Harpacticoida	0.001	Harpacticoida	0.001
Oribatei	0.001	Oribatei	0.001

Table 3.2. Experiment 1 main effects (% difference between factor levels) and significance levels of model terms from ANOVAs based on log-transformed abundances.

		Dragonfly larvae		**Fish**		**Drag.XFish**	**Block**
		% change	p	% change	p		
Ephemeroptera:	Caenidae	+18.7	0.276	-7.4	0.731	0.478	**<0.001**
Diptera:	Chironomidae	+0.2	0.713	-10.1	0.139	0.802	**<0.001**
	Ceratopogonidae	+7.5	0.579	-5.1	0.982	0.895	**0.081**
Coleoptera:	Dytiscidae*	**-64.0**	**0.049**	-33.0	0.252		
Trichoptera:	Leptoceridae	**-27.3**	**0.009**	+12.5	0.302	0.776	**<0.001**
	Phryganeidae*	-42.0	0.738	+40	0.558		
	Polycentropodidae*	-46.0	0.137	-9.0	0.471		
	Odonata: Coenagrionidae	-17.6	0.103	-0.9	0.931	0.287	**0.006**
Hemiptera:	Corixidae*	-50.0	0.553	-50.0	0.553		
Collembola:	Isotomidae*	+20.0	0.780	+44.0	0.780		
	Sminthuridae*	+50	0.637	-33.0	0.637		
Crustacea							
Isopoda							
	Caecidotea	-7.7	0.613	-0.3	0.708	0.965	**0.046**
	Lirceus	-23.1	0.272	+14.6	0.181	0.423	**0.003**
Amphipoda		+7.8	0.860	-1.1	0.383	**0.042**	**0.002**
Cladocera*		+80	0.661	-9.0	0.431		
Copepoda: Cyclopoida		+24.1	0.400	**-30.4**	**0.074**	**0.019**	**<0.001**
Ostracoda		+11.0	0.385	+8.0	0.516	0.876	**0.022**
Arachnida							
Hydracarina		-8.4	0.455	+1.3	0.999	0.208	0.129
Oribatei		+28.9	0.316	**-43.8**	**0.032**	0.737	0.226
Annelida							
Oligochaeta:	Naididae	+32.7	0.205	**-41.0**	**0.012**	0.848	0.446
	Lumbriculidae	+12.8	0.367	+4.1	0.666	0.714	**0.002**
Hirudinea		+10.0	0.480	**+100.0**	**0.034**	**0.042**	0.226
Mollusca							
Pelycypoda:	Sphaeriidae*	+30.0	0.350	+17.0	0.289		
Gastropoda:	Ancylidae*	-65.0	0.136	**+48.0**	**0.047**		
	Planorbidae	0.0	0.996	+8.0	0.516	0.327	**0.072**
	Physidae*	-45.0	0.248	+22.0	0.773		
	Lymnaidae*	-43.0	0.180	+20	0.771		
	Hydrobiidae*	-69.0	0.427	-40.0	0.460		
Nematoda		-20.6	0.555	-24.6	0.476	**0.078**	0.411
Platyhelminthes-Turbellaria*		**-82.0**	**0.024**	+17	0.929		
Total invertebrate predators		**-25.0**	**0.002**	+12.1	0.135	1.000	**0.000**
Total abundance		+11.3	0.241	-6.0	0.493	0.234	**0.003**
Taxa richness		-3.5	0.178	+0.7	0.784	0.414	**0.034**

*significance levels represent Kruskal-Wallis test results

Table 3.3. Significant effects of dragonfly larvae: percent changes in dependent variables when dragonfly larvae were added to enclosures.

Dependent variable	% difference	p
Trichoptera abundance	-27.6	0.004*
Leptoceridae abundance	-27.3	0.004*
Lirceus relative abundance	-30.8	0.079*
Coenagrionidae relative abundance	-20.0	0.079*
Lymnaidae relative abundance	-50.0	0.093*
Dytiscidae abundance	-64.0	0.049**
Turbellaria abundance	-82.0	0.024**

* ANOVA of log-transformed data

** Wilcoxon rank-sum test

Table 3.4. Effects of fish addition on taxa abundances and significance levels from Experiment 2 t-tests on log-transformed abundances (effects are % differences relative to no-fish controls).

	Size fraction:	Large		Small		Both	
		% change	p	% change	p	% change	p
Insecta							
Ephemeroptera:	Caenidae	**-70.4**	**0.017**	-34.9	0.246	**-47.1**	**0.078**
Diptera:		-67.9	0.159	-31.2	0.171	**-63.6**	**0.043**
	Chironomidae	-51.3	0.271	+0.5	0.898	-35.4	0.320
	Ceratopogonidae	**-100.0**	**<0.001**	-89.7	0.161	**-94.1**	**0.015**
Coleoptera:	Dytiscidae*	-37.5	0.365	+34.3	0.825	-21.1	0.480
Trichoptera:		**-45.5**	**0.025**	-35.5	0.448	**-41.9**	**0.044**
	Leptoceridae	**-70.0**	**0.048**	-49.6	0.242	**-62.2**	**0.014**
	Phryganeidae*	-20.0	0.410	-32.9	0.861	-18.7	0.405
	Polycentropodidae*	-54.4	0.174	+3.8	0.718	-26.0	0.211
Odonata:	Coenagrionidae	**-36.8**	**0.078**	+0.4	0.970	**-30.9**	**0.087**
	Libellulidae	-55.9	0.254	-	-	-55.9	0.254
Crustacea							
Isopoda:		**-31.2**	**0.066**	+11	0.522	-16.4	0.267
	Caecidotea	-29.1	0.163	-3.3	0.887	-19.9	0.315
	Lirceus	**-35.5**	**0.029**	+32.5	0.134	-12.1	0.386
Amphipoda		**-57.8**	**0.037**	-26.8	0.208	-34.6	0.110
Mollusca		-66.3	0.114	-38.7	0.396	**-54.3**	**0.047**
Pelycypoda:	Sphaeriidae*	**-82.3**	**0.074**	+9.3	0.823	-50.5	0.331
	Gastropoda:	-62.8	0.178	-40.8	0.382	-52.6	0.750
	Ancylidae	**-87.6**	**0.081**	+31.22	0.855	-77.8	0.108
	Planorbidae	-60.9	0.153	-43.0	0.435	-51.2	0.104
	Physidae	-38.1	0.380	-	-	-38.1	0.380
	Lymnaidae*	-1.6	0.147	-46.7	0.451	-61.9	0.343
	Hydrobiidae*	+14.1	0.906	+159.7	0.234	+79.6	0.203
Total abundance		**-42.1**	**0.017**	-17.0	0.273	**-29.2**	**0.054**
Taxa richness		**-30.7**	**0.060**	**-19.0**	**0.086**	**-19.8**	**0.060**

*significance levels represent Kruskal-Wallis test results

Table 3.5. Effects of mudminnows: differences in number of significant results between prey of different sizes

Sample size fraction	# of taxa showing significant differences between treatments
Large (>2mm)	4*, 6**
Small (1mm-2mm)	None
Both combined	2*, 5**

* $0.1 > p \geq 0.05$
** $p < 0.05$

Table 3.6. Effects of mudminnows: % changes in some large-fraction dependent variables when intermediate size-class fish were added to enclosures.

Dependent variable	% difference	p
Isopoda abundance	-31.2	**0.066**
Amphipoda abundance	-57.8	**0.037**
Caenidae abundance	-70.4	**0.017**
Chironomidae abundance	-51.3	0.271
Trichoptera abundance	-45.5	**0.025**
Coenagrionidae abundance	-36.8	**0.078**
Sphaeriidae abundance	-82.3	**0.074**
Gastropoda abundance	-62.8	0.178
Total invertebrate abund.	-42.1	**0.017**
Taxa richness	-30.7	**0.060**
Isopod relative abundance	**+25.0**	**0.067**

* from ANOVA of log-transformed data

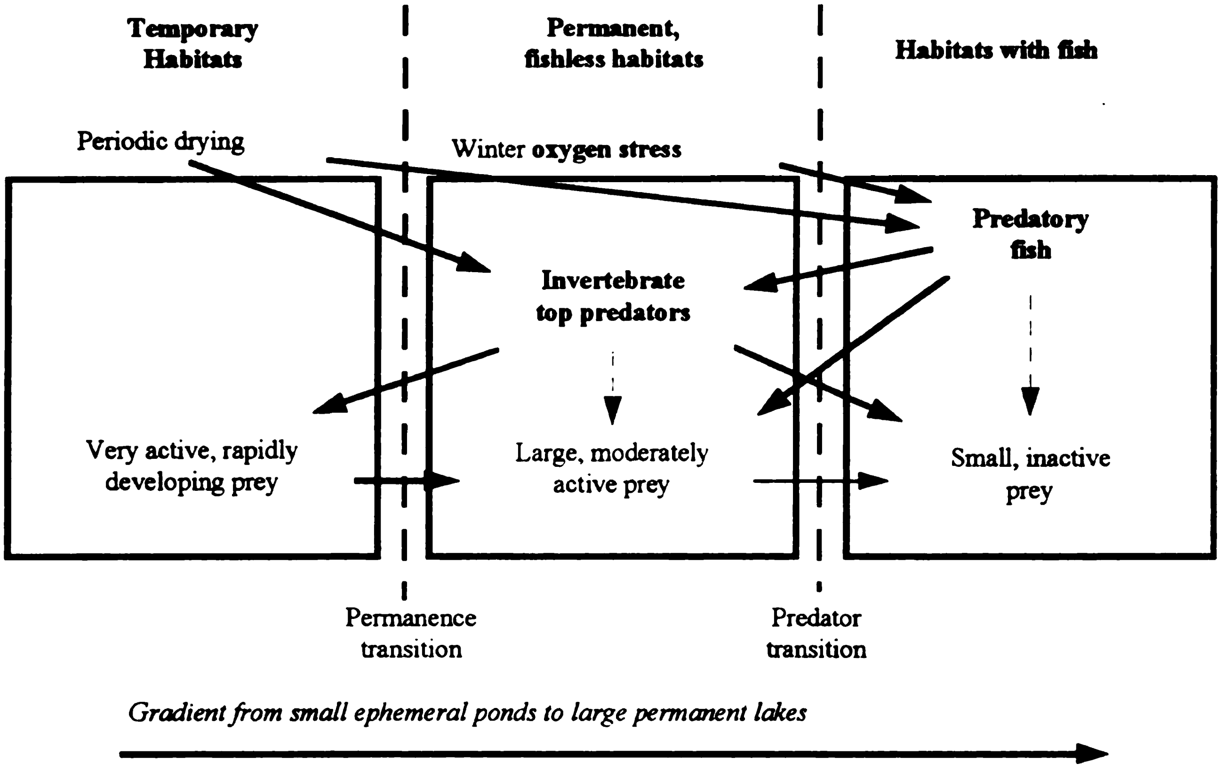


Figure 3.1. Wellborn et al. (1996) conceptual model of community structuring forces in freshwater systems.

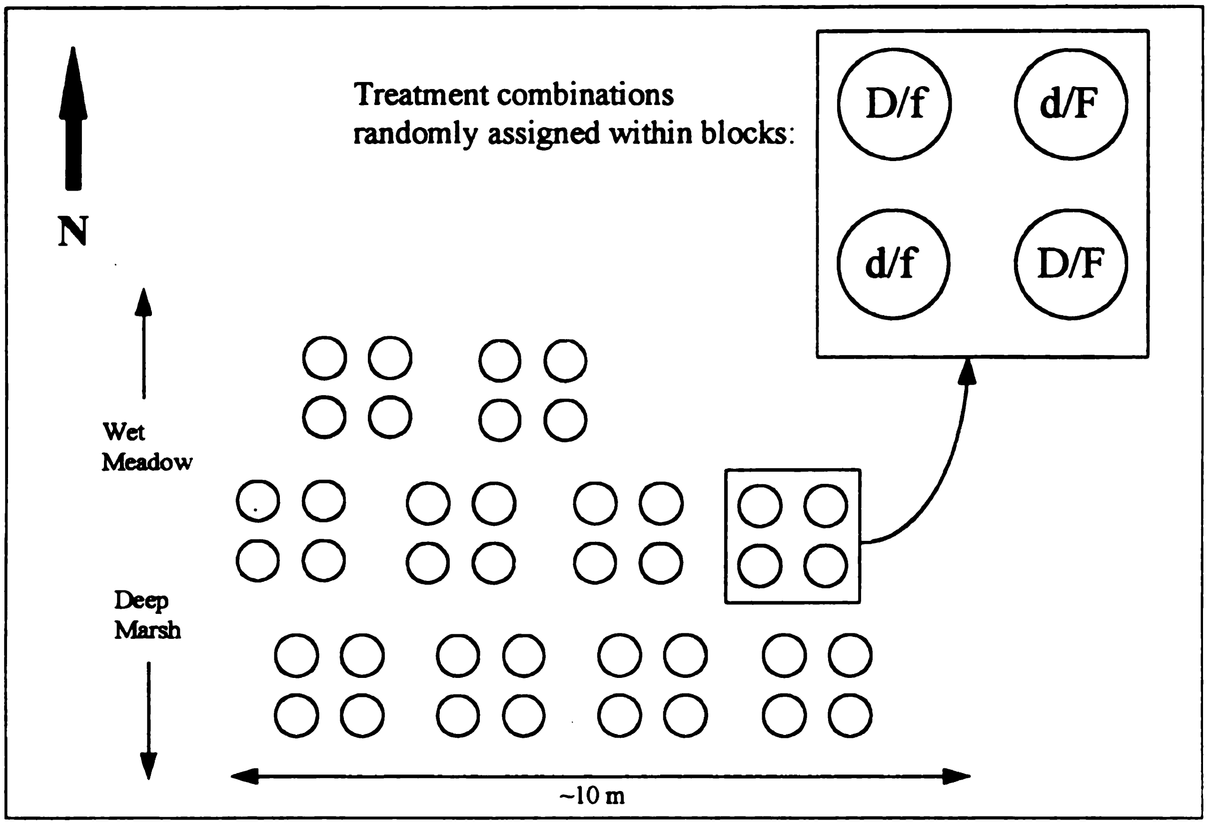


Figure 3.2. Plan view of Experiment 1 in-site block layout (d = no dragonfly larvae; D = dragonfly larvae added; f = no fish; F = fish added).

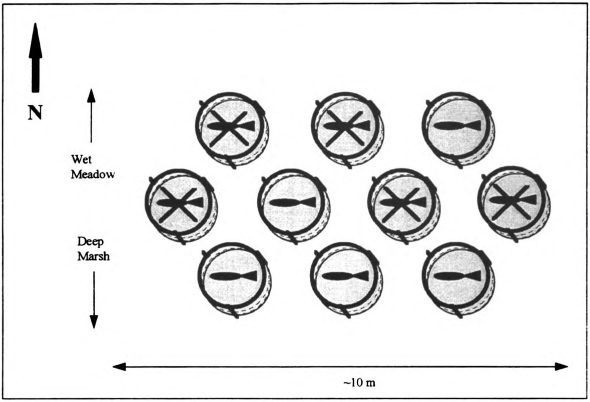


Figure 3.3. Plan view of Experiment 2 in-site enclosure placement, indicating fish addition and exclusion.

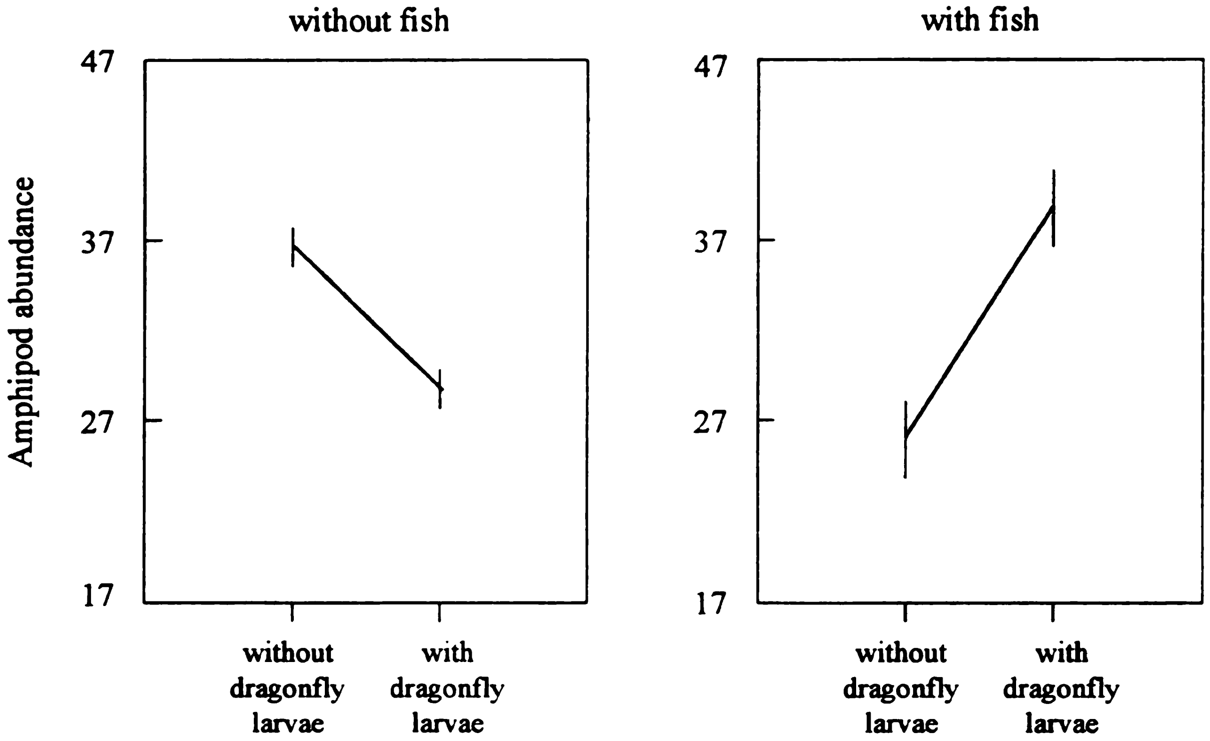


Figure 3.4. Effects of Fish X Dragonfly-larvae interactions on abundances of amphipods in experimental enclosures in Experiment 1 (means with standard errors).

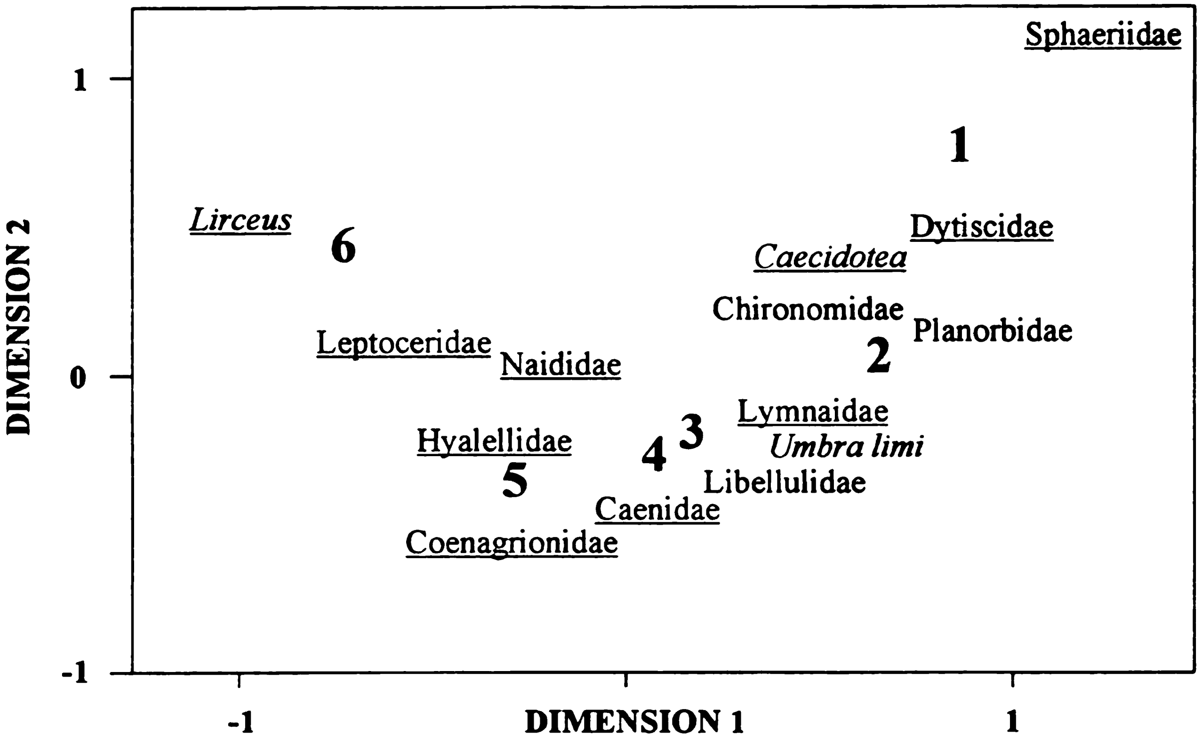


Figure 3.5. Correspondance analysis plot of 1996 data including plotted positions of predators used in experiments and their affected prey. Underlined taxa are those that were significantly affected by predators in enclosures.

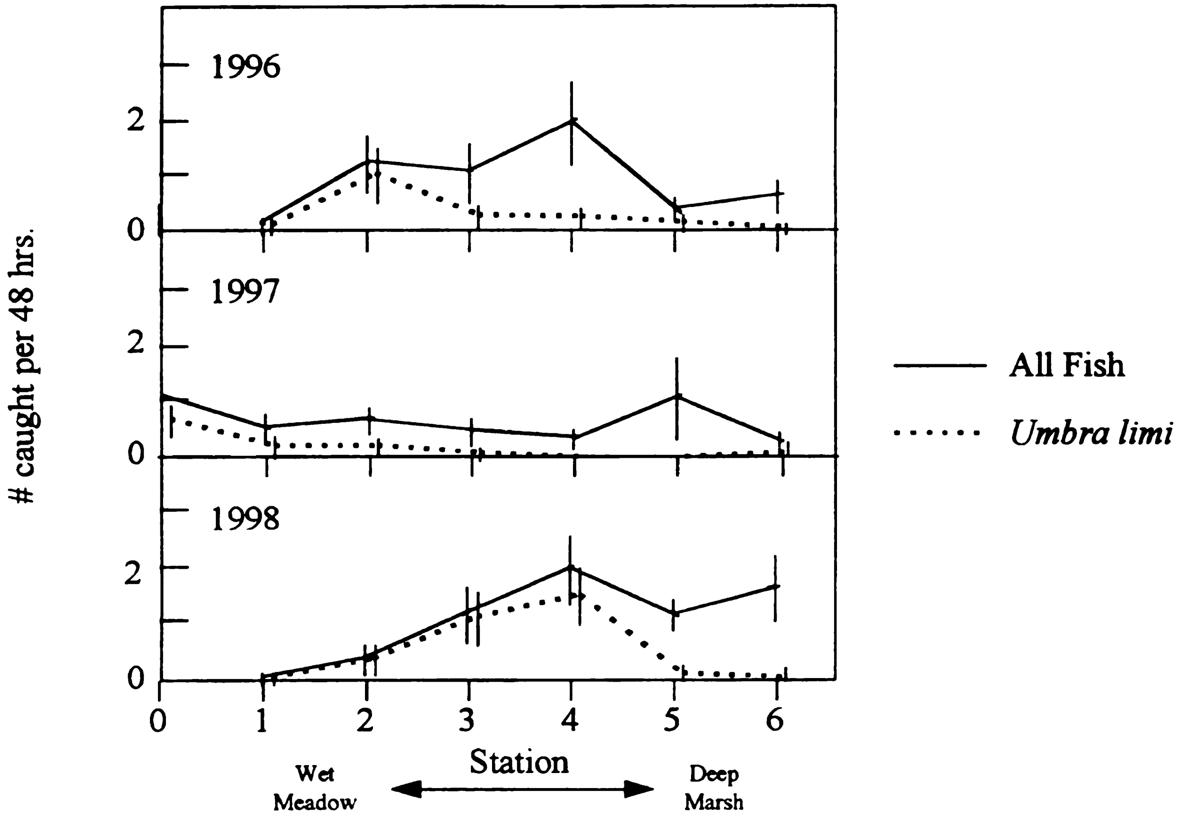


Figure 3.6. Spatial distributions of mudminnows (*Umbra limi*) and all fish species combined during each of 3 years ending with the experiment year (means with standard errors).

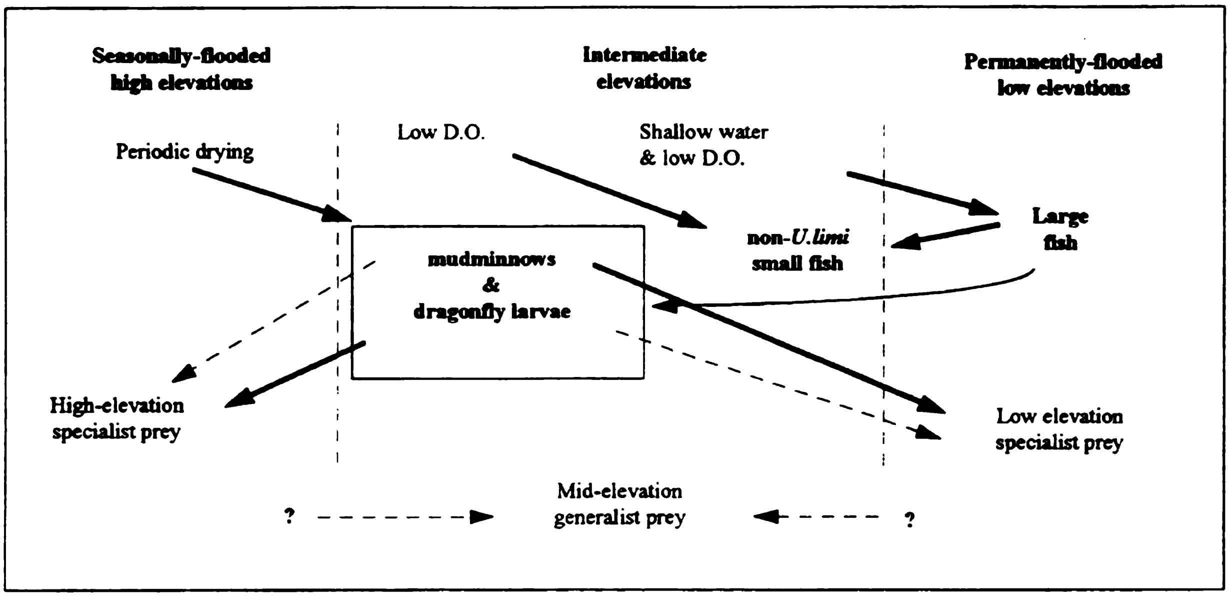


Figure 3.7. Conceptual model of regulation of spatial community variation in Mackinac Bay wetland. Solid arrows represent strong negative effects and dashed arrows represent weaker effects (following diagram format of Wellborn et al. 1996).

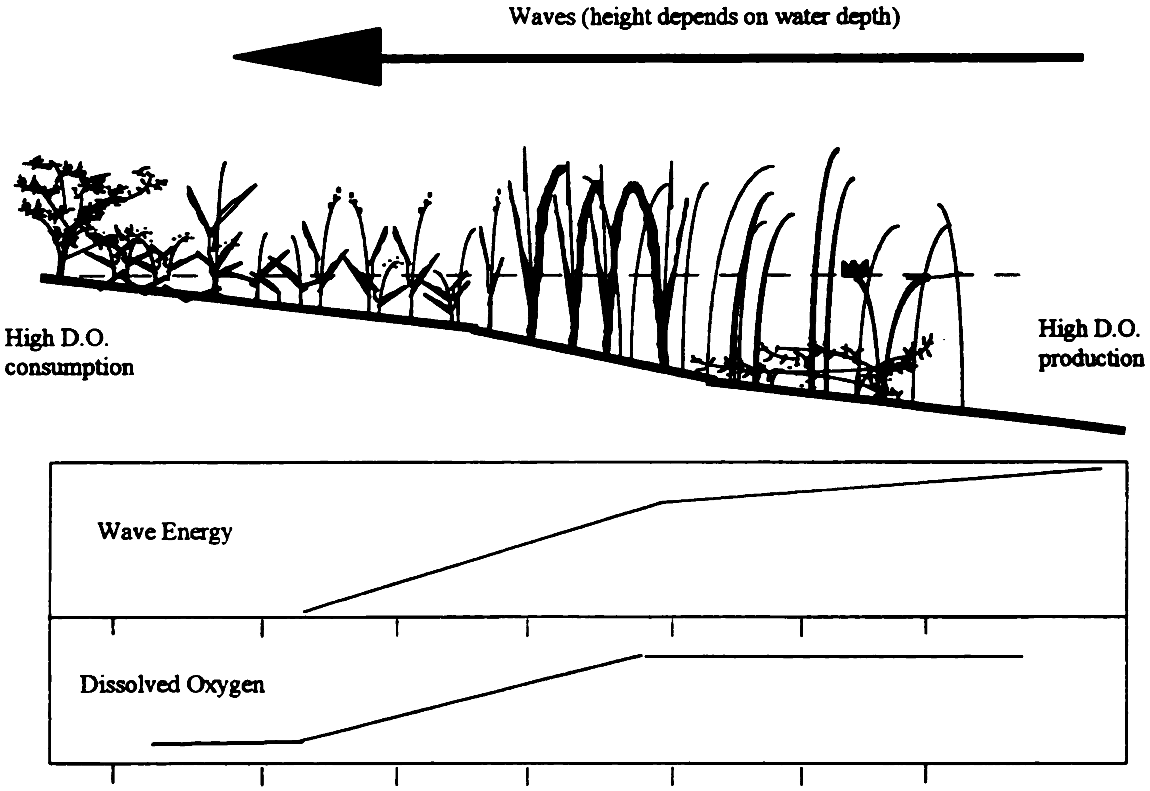


Figure 3.8. Observed spatial patterns in certain abiotic factors in Mackinac Bay wetland.

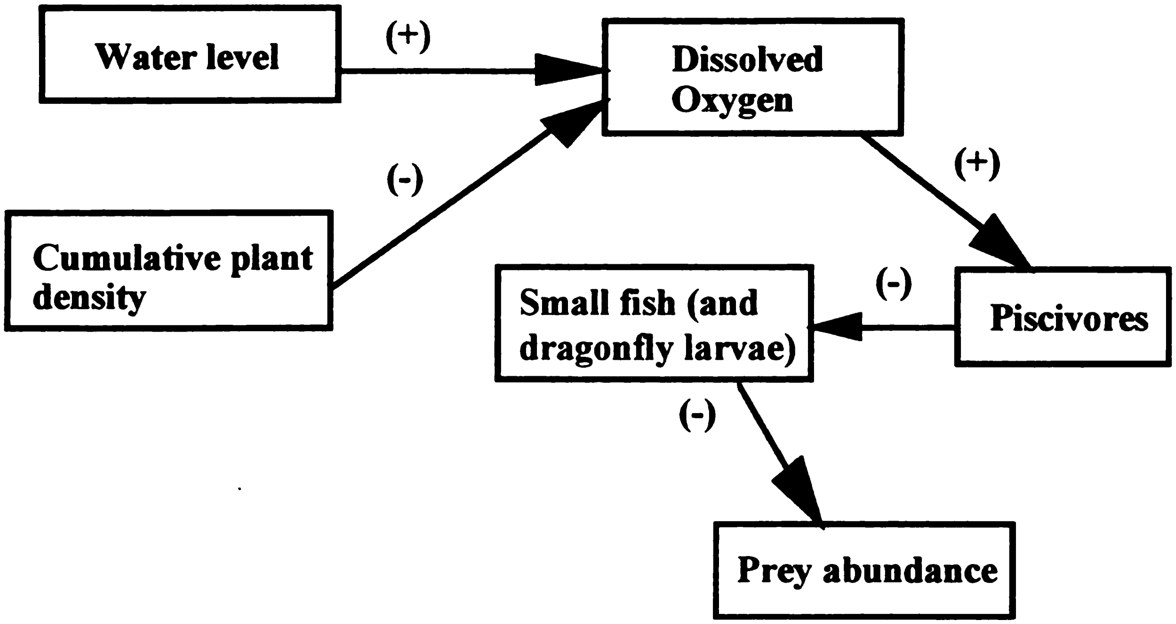


Figure 3.9. Hypothesized chain of mechanisms describing how primary wetland abiotic factors regulate biotic controls on prey invertebrates.

CONCLUSIONS

The results presented in the previous chapters suggest that Great Lakes coastal wetland communities are very dynamic, as are the hydrologic conditions in which they are found. Spatial and temporal complexity in these systems appears to be very high compared to adjacent systems, requiring much further work to fully understand how communities are affected by environmental factors. Chapter 1 provides a substantial data set upon which future studies in the Les Cheneaux Islands region may be based, while Chapters 2 and 3 indicate future research directions for such studies.

Many environmental factors vary along the lake-to-upland coastal wetland ecotone, but flooding characteristics appear to be the most important ultimate driving force behind animal distributions in these complex habitats. Animal communities in wet meadows are affected by periodic draining and, conversely, by the influx of immigrating taxa during high-water periods. Those animals surviving in temporarily-flooded wet meadows have adapted to the flooding regime through drought-tolerance or drought-avoidance mechanisms. A shift from temporary to year-round (or longer) flooding allows many taxa from lower elevations to take advantage of wet meadow habitat, which may negatively affect the temporary-adapted taxa through predation and competition. However, as seen in this study, predation pressures from small fish may actually decrease during high-water periods (probably because piscivorous fish increase in number), allowing many invertebrate taxa to fully exploit the newly-available habitat. Lower-elevation communities appear less affected by water level changes, but extreme lows, not seen in this study, should have effects that are somewhat predictable. If lower-elevation zones are temporarily drained, the invertebrate community there would probably tend to resemble that seen in the 1996 wet meadow, as described in Chapter 1, because the animals usually found at low elevations are not adapted to temporary-flooding conditions.

If high water is sustained for several years, vegetation zones would be expected to shift up-slope, converting wet meadows to transition and deep marsh zones (Burton 1985). Sustained lows should have opposite effects. While vegetation zonation may not have strong direct effects on many animals, it's indirect effects may be very important. As cumulative plant density increases along an imaginary transect from low to high elevations, wave energy and water mixing are reduced, creating water chemistry gradients (Cardinale et al. 1997). These gradients may affect animals in several ways, but the dissolved oxygen gradient in particular is probably largely responsible for fish distributions within coastal wetlands. Chapter 3 suggests that small fish can affect invertebrate communities, so factors affecting fish should also affect their prey. The suggestion of a spatial shift in the wetland trophic web should be studied if we are to develop a complete understanding of community dynamics in coastal wetlands.

This study suggests the importance of different migratory abilities among invertebrate taxa in structuring communities found at different wetland elevations. Because some animals (particularly non-insects) migrate more slowly than others, some invertebrate community changes lag behind water-level changes. Slow migrators follow multi-annual rising water levels, but when levels fall, the receding water line appears to leave many slow-responders stranded in rapidly-draining habitats. Only those taxa that can withstand such draining will survive these conditions, while others must depend on more broad habitat selection for their populations to persist. If global climate changes cause more extreme water-level variation in the Great Lakes, as suggested by Mortsch (1998), wetland invertebrate diversity may decrease as only generalist species will be able to survive.

Other threats to coastal wetland communities, particularly in the Les Cheneaux region, include the effects of shoreline development at the upland end of the wetland continuum, and increased boating activity and channel dredging at the lower end (Gathman and Keas 1999). These two factors can create barriers to up-slope and down-slope migrations of plant and animal communities, reducing habitat and community heterogeneity across the gradient by truncating its ends. This study suggests that the full range of habitat conditions may be required to maintain wetland diversity, so regional planning must be based on long-term probabilities of lake-level variations. This study, combined with other recent work, should be a useful starting point for developing such a long-term outlook, and also may be a foundation for the development of a complete model of the mechanisms driving community variation in some types of Great Lakes coastal wetlands.

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