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Litter accumulation in emergent marshes: investigating the effects of litter on wetland invertebrates and the processes controlling litter distribution and accumulation

by

Jay Richard Christensen

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

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Iowa State University
Ames, Iowa
2007

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Dedicated to my wife Amy Cahoon Christensen
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CHAPTER 1. GENERAL INTRODUCTION

INTRODUCTION

Effects of Litter

The influence of litter on abiotic conditions and plant community structure has long been recognized in terrestrial systems (Grime 1979, Knapp and Seastedt 1986, Vogt et al. 1986, Carson and Palmer 1990, Facelli and Pickett 1991, Xiong and Nilsson 1999, Sayer 2006). The results of many forest studies indicate that forest leaf litter is vital to biogeochemical cycles as well as being a driver of microclimate conditions and plant/microbe interactions at the soil surface (see Sayer 2006). Likewise, researchers in grassland and old field systems have documented that litter influences light (Knapp 1984, Foster and Gross 1998), temperature (Knapp 1984), soil moisture (Knapp and Seastedt 1986), and nitrogen availability (Knapp and Seastedt 1986, Knapp et al. 1998, Johnson and Matchett 2001). Changes to abiotic conditions influence grassland invertebrate communities (Seastedt 1984), primary production (Knapp and Seastedt 1986, Carson and Palmer 1990), seedling recruitment (Hoffman 1996, Wilsey and Polley 2003), and grassland diversity (Foster and Gross 1998, Fynn et al. 2004). Research in grasslands has also emphasized the importance of disturbance by grazing (Wilsey and Polley 2003) and fire (Knapp and Seastedt 1986, Johnson and Matchett 2001, Knops 2006) in reducing accumulated litter stocks. Horticulture and gardening have also long benefited from the properties of litter (mulch) to suppress unwanted germination and production.

Despite the attention in terrestrial systems, fewer studies have considered the influence of persistent litter in wetland systems. Emergent marshes are among the world’s most productive ecosystems and many emergent macrophyte tissues, such as Typha spp. leaves and stems or Phragmites stems, break down slowly due to their refractory nature (Polunin 1982, Polunin 1984). High annual production coupled with slow litter breakdown rates can lead to large accumulations of litter. The large amount of litter is important in the cycling of carbon and nutrients (Brinson et al. 1981, Polunin 1984, Webster and Benfield 1986, Wetzel 2001) and can also have large direct and indirect effects on the local environment. Litter has been shown to influence abiotic conditions in wetlands by decreasing

These environmental changes can influence the biota of the wetland. Litter from emergent species has been shown to inhibit seed germination (McNaughton 1968, van der Valk 1986, van der Putten et al. 1997), decrease plant diversity (Bohlen 1990, Jordan et al. 1990, Weltzin 2005), and decrease the production of the parent species (Haslam 1971, Graneli 1989, Jordan et al. 1990, van der Putten et al. 1997). The influence of litter on local abiotic conditions and plant communities may have a large influence on wetland invertebrate communities.

**Influence on Invertebrate Community**

Previous researchers have documented invertebrate distributions across open water to emergent interior gradients which often include a litter gradient (Dvorak 1970, Voigts 1976, McLaughlin and Harris 1990, Murkin et al. 1992), but there has been little experimental work done on the influence of emergent litter on wetland invertebrates. In the first two papers, natural and manipulative studies were conducted from the edge to the emergent interior (2003-2005) to determine what influence litter structure has on invertebrate distributions. The first paper examines the changes in the wetland invertebrate community under a naturally increasing gradient of litter from the edge to the emergent stand interior, as well as the community response to manipulated levels of litter in the emergent interior. Accumulated litter may heavily influence spatial distributions and composition of wetland invertebrates. The second paper more specifically investigates the horizontal and vertical distribution of an abundant wetland invertebrate, *Hyalella azteca* (Saussure), across the edge to interior gradient and under manipulated levels of litter, examining the possibility of vertical compression in relation to changes in litter density.
Litter Processes in Plant Communities

Despite the potential influence of litter on wetland systems and their biota, little attention has been given to the process of litter accumulation. The process of litter accumulation depends on the following factors: 1) an emergent species’ spatial extent which is highly influenced by water level fluctuations (van der Valk and Davis 1978, van der Valk 2000), 2) annual primary production which can vary depending on climate (Morris and Haskin 1990), and 3) the breakdown rate of the emergent species litter (Polunin 1984) which can be influenced by many factors including water depth (van der Valk et al. 1991, Hietz 1992, Neckles and Neill 1994, Bedford 2005). Those species that have a large spatial extent, high production, and low breakdown rates would be expected to accumulate litter and potentially influence the local abiotic conditions and associated biota.

The third paper focuses on estimating breakdown rates that are appropriate for the study of litter accumulation. Live biomass and litter data from a 10 year, replicated, large scale experiment at Delta Marsh, Manitoba were provided by Dr. A.G. van der Valk and major findings from the overall study are summarized in Murkin et al. (2000). The difference between accumulated litter and aboveground live biomass for three species was used to investigate litter breakdown rates. The three species, *Phragmites australis* (Cav.) Trin., *Typha x glauca* Godr., and *Scolochloa festuacea* (Willd.) Link, differ in their rate of breakdown (Murkin et al. 1989, van der Valk et al. 1991). The study compared the observed values of accumulated litter with a mass-balance model that linked annual production estimates with an exponential decay function of litter breakdown. Breakdown rates were first estimated using breakdown values derived from litter bag studies conducted at Delta Marsh. A mass-balance derived breakdown rate was also fit from the model to accurately predict litter mass when compared to observed litter accumulations.

The process of litter accumulation can be highly influenced by disturbance (Knapp and Seastedt 1986). Within wetlands, water level fluctuations are a disturbance which can influence the spatial extent of emergent wetland plants (Weller and Spatcher 1965, van der Valk and Davis 1978), production (van der Valk and Davis 1980, Squires and van der Valk 1992), and breakdown rates of litter (van der Valk et al. 1991, Hietz 1992, Neckles and Neill 1994, Battle and Golladay 2001, Bedford 2005). In the absence of other disturbances, stable
water levels may lead to static distributions of emergent species and continual growth at optimum water depths which could potentially lead to large accumulations of litter.

The final paper models the different components of litter accumulation and investigates litter accumulation patterns of a widespread emergent, the hybrid cattail, *Typha glauca*. Using the 10 year Delta Marsh data set, a spatial distribution model for four emergent macrophytes was developed. The distribution model is driven by species specific water depth tolerances and is modified from Seabloom et al. (2001) to track dominant and subdominant emergent plant distributions under stable water levels following a drawdown disturbance. The inclusion of subdominants should allow for greater accuracy in heavily mixed stands that are present after drawdowns (van der Valk 2000). The spatially dynamic plant distribution model is then combined with a production model and a litter breakdown model to estimate the accumulation of *Typha* litter for 10 years following the original disturbance. The paper examines the response of plant distributions and potential expansion and analyzes the pattern of litter accumulation in the absence of disturbance. The study also allowed comparison between emergent distributions and litter after the drawdown disturbance with emergent distributions and litter conditions prior to the disturbance.

The investigation of plant distributions and litter accumulation under stable water levels is especially relevant when considering the altered hydrology of many wetland systems (Galatowitsch and van der Valk 1998) and the potential spatial extent and high production of many emergent species (Zedler and Kercher 2004). Dynamic spatial models such as those developed in this study may provide useful tools to better understand underlying assumptions and mechanisms related to the expansion of litter producing species and the potential influence of their litter in wetlands.

**DISSERTATION ORGANIZATION**

This dissertation is made up of six chapters. Chapter 1 is a general introduction to the research addressed in the subsequent chapters and outlines the general structure of the dissertation. Chapters 2 through 5 are the four manuscripts that are being submitted to refereed journals. Chapter 2, entitled “Wetland invertebrate community responses to varying densities of emergent litter in a prairie pothole emergent marsh”, investigates the direct and
indirect influences of litter on invertebrate communities and provides general invertebrate assemblages for various emergent habitats that differ in litter densities. Chapter 3, entitled “The horizontal and vertical distribution of Hyalella azteca (Amphipoda) in an emergent freshwater wetland: effects of increased litter” investigates how an abundant invertebrate responds both horizontally from the edge to interior and vertically within the water column to changes in litter, dissolved oxygen, and vegetation. Chapter 4, entitled “Estimating litter accumulation of emergent macrophytes: litter bag versus mass balance approaches”, models litter accumulation using two different measures of litter breakdown to obtain accurate estimates of litter accumulation to match observed quantities of accumulated litter. Chapter 5, entitled “Modeling emergent macrophyte spread and the accumulation of Typha litter following a drawdown”, investigates the response of species distributions to stable water levels when subdominants and dominant distributions are included and examines where and how Typha litter accumulates after 10 years of stable water levels. Chapter 6 states general conclusions from the findings of the included manuscripts.

LITERATURE CITED


CHAPTER 2. WETLAND INVERTEBRATE COMMUNITY RESPONSES TO VARYING EMERGENT LITTER IN A PRAIRIE POTHOLE EMERGENT MARSH

a paper to be submitted to the journal Wetlands

Jay R. Christensen, William G. Crumpton

ABSTRACT

Abundant emergent plant litter produced in the interior of dense emergent stands may directly or indirectly influence invertebrate communities. Low litter may provide beneficial structure and refuge while high litter may shade out vegetation and algae and decrease oxygen concentrations. Within an emergent stand, a transect study from the edge to interior and an interior litter manipulation study were performed to investigate the impact of increasing litter on the invertebrate community. Under lower litter conditions in the interior, total invertebrate abundance was similar to the edge but the emergent interior was dominated by hypoxic-tolerant nektonic species. Under high litter conditions in the interior, invertebrate abundance decreased and the invertebrate community was different from lower litter levels, supporting semi-aquatic species and very hypoxic-tolerant taxa. Anoxia was present at high litter treatments, while moderate and low litter treatments showed prolonged hypoxia. Lemnid densities were much lower in the high litter treatment. Lower invertebrate abundance may be related to losses in lemnids that were displaced by high litter. When considering litter and spatial position, a gradient of three habitats emerge that differ in their invertebrate community, 1) the interior with high litter, anoxia, and few lemnids, 2) the interior with low litter, hypoxia, and abundant lemnids and 3) the edge with low litter, higher dissolved oxygen, and high submersed or lemnid vegetation.

INTRODUCTION

Invertebrate community composition can be influenced by numerous factors in wetland systems including predation (Hanson and Butler 1994, Hanson and Riggs 1995, Zimmer et al. 2001), vegetation (Voigts 1976; Brown et al. 1988, Olson et al. 1995, Murkin
and Ross 1999, McCormick et al. 2004), and litter. Dense, emergent vegetation and persistent plant litter are conspicuously present in many freshwater wetlands. When compared to open water edges, the emergent interior typically experiences decreased water mixing (Leonard and Luther 1995) and lower dissolved oxygen (DO) (Rose and Crumpton 1996, Murkin et al. 1992, Suthers and Gee 1986) which would favor hypoxic-tolerant taxa. Light availability is decreased (Radar 1999, Rose and Crumpton 1996), important epiphytic food is reduced (Grimshaw et al. 1997) and submersed vegetation habitat is reduced (Voigts 1976). Litter provides additional substrate for epiphyton (Campeau et al. 1994), or may be a food source for detritivores (Campeau et al. 1994, Batzer 1998). Litter increases structure and heterogeneity in the water column which could influence predation searching efficiency (Crowder and Cooper 1982, Gilinsky 1984, Zimmer et al. 2001). Despite the conspicuous presence of litter and its potential importance in emergent wetlands, the dynamics of litter and its influence on invertebrate dynamics are seldom studied (Moore et al. 2004, Murkin and Ross 2000, Levin et al. 2006).

Total invertebrate abundance decreases with increasing emergent vegetation coverage (Voigts 1976, Nelson et al. 2000, Neira et al. 2005) and with distance into the interior from the edge of open water (McLaughlin and Harris 1990, Cardinale et al. 1997, MacKenzie and Kaster 2004). Increasing emergent vegetation is correlated with decreases in community richness (Radar 1994) or diversity (Cardinale et al. 1997, MacKenzie et al. 2004). As plant composition shifts toward persistent vegetation, the invertebrate community shifts from algal-associated and DO-sensitive invertebrates to detrital and hypoxic-tolerant invertebrate communities (Houston and Duivenvoorden 2002, McCormick et al. 2004). Litter may contribute to these patterns but litter abundance has rarely been quantified. With changes in litter, shifts in community composition may occur even if overall invertebrate densities remain the same.

Litter abundance within the interior of the emergent stand may be variable due to water-level induced shifts in dominant vegetation (van der Valk and Davis 1978), variation in production (Shay and Shay 1986) or decomposition, variation due to wind events (Bolhen 1990) or variation created by muskrats (de Szalay and Cassidy 2001). If litter levels are relatively low in the interior, invertebrates in the emergent interior may benefit from the
positive influence of litter as structural habitat or food. If litter levels are high in the interior, the invertebrate community could be negatively influenced by decreased oxygen and increased shading. The influence of differing litter levels on the abundance, distribution, and structure of invertebrate communities has not been addressed.

The main objective of this research was to examine the effects of different litter levels on invertebrate abundance and community composition in emergent stands. We examined invertebrate and litter distributions along a gradient of increasing litter from the emergent stand edge into the interior. We then examined the response of invertebrates to an experimental manipulation of litter densities within the emergent interior.

**METHODS**

**Study Site**

This research was conducted at Anderson Lake Marsh, a 65 Ha semi-permanent natural prairie pothole located in Hamilton Co., IA, USA (42° 18’50” N, 93° 37’32” W). Multiple aspects of Anderson Lake have been investigated over the years, contributing significantly to the study of muskrats, waterfowl, and wetland vegetation dynamics (Pammel 1898, Errington 1963, Weller and Spatcher 1965, Davis and van der Valk 1978, Roosa 1981, Rose and Crumpton 1996). During the present study, the dominant emergent vegetation was *Typha spp* (mostly of the hybrid *T. glauca* Godr., hereafter referred to as *Typha*) with lemnids (primarily *Spirodela polyrhiza* (L.) Scheid and *Lemna trisulca* (L.)) interspersed among the cattails. Some submersed aquatic species, *Ceratophyllum demersum* (L.) and *Utricularia macrorhiza* Le Conte were found at the emergent edge, while the more open regions included water lilies (*Nuphar lutea* (L.) and *Nymphaea odorata* Ait.), with *Potamogeton pectinata* (L.) Boerner in the deepest areas. The areas of study are indicated in figure 1.

**Transect Study**

Following a drawdown in 2000, the east side of the large island where the study was performed (figure 1) was in regeneration and slight expansion during the summer of 2004. From July to September of 2004, continuous water quality data loggers (AQUA 2000,
Biodevices Inc. Ames, IA, USA) recorded dissolved oxygen concentrations and water temperature at a depth of 10-15 cm and 30-35 cm in 20 min intervals at two transects at the emergent edge and ten meters into the interior.

During the same time period, three transects were randomly selected each month and vegetation, litter, and invertebrate samples were taken at the edge and 10 meters into the interior. Edge samples were collected from a 10 ft pontoon boat. A portable 5 m x 1.5 m floating dock was assembled 10 m into the interior at each sampling point 2 weeks prior to sampling. Two sub-samples were taken at 2.5 m and 5 m along the dock at each sampling location. Samples were collected using a 90 cm long .11 m² PVC cylinder that was quickly forced through the vegetation (a spade cut through rhizomes when necessary) until a seal was formed. All vegetation (emergent and floating) and litter at or below the water surface were removed, washed, and bagged. Invertebrates within vegetation were rinsed in a large sorting pan and put through a 250 micron sieve. Invertebrates still within the sampling PVC cylinder were pumped out by a nested-sieve (1 mm and 250 um sieves) chamber and pump (modified from Major et al. 1998) and preserved in 70% ethanol. At the lab, all collected vegetation and litter were sorted by species or family (as with the lemnids). Samples were separated into live and dead tissue, preliminarily table dried for 1 week, oven dried at 65 °C for 48 hours, and weighed. Invertebrates were sorted in bottom-light translucent pans, identified to the lowest possible taxon (typically genus) and enumerated.

**Interior Litter Study**

Distance from the edge is correlated to numerous parameters (i.e. predation risk, light, DO, submersed aquatic vegetation) that potentially affect invertebrate distributions. Due to these confounding effects, an experiment was undertaken to investigate the effects of different litter densities at a constant distance from the edge. *Typha* litter densities in 2003-04 had been much lower than densities reported in a previous study at Anderson Lake Marsh in 1994-95 (Rose 1996). To understand how varying levels of litter would influence the invertebrate community, a large range of *Typha* litter densities, from .5 kg/m² to 2 kg/m² were used. The 2 kg/m² value equaled emergent interior litter densities reported by Rose (1996) and Rose and Crumpton (1996). In the late spring of 2005, three replicate plots were
selected where three 4 X 10m treatment plots could be established. All plots were on the northeast side of the island and main wetland shore (figure 1), 8-12m to the interior from the open-water-emergent edge. The replicate plots were similar in depth (40-60cm) and in large areas (35m long) that did not have visible disturbances within the plot, such as muskrat lodge formation. The three treatments were a high litter (HL) density with approximately 2 kg litter/m², a moderate litter (ML) density with approximately 1 kg litter/m², and a litter removal or low litter (LL) density where remaining stems constituted .25-.5 kg litter/m². At each replicate plot, the three 4 X 10 treatment plots were randomly assigned. A 2m access path to the open water was created between each treatment plot.

Litter was manipulated by clearing the 4 X 10m area of litter with pitchforks, clearing 4 X 1m columns at a time. Standing litter stems and live plants were not removed. As columns of litter were being removed, already removed litter was placed in a wooden box with a screen bottom, shaken three times, and weighed. A wet weight to dry weight relationship had been established with 30 preliminary samples ($r^2=0.93$) and wet litter was weighed and placed back into the HL and ML plots to achieve the desired densities. Litter from the LL plots was transported to the HL plots and used to supplement the HL plots. Litter plots were left alone for 3-4 weeks, prior to the onset of sampling.

At two of the three replicate plots, 2 data loggers were placed in the center of each treatment to measure dissolved oxygen and temperature at 5 cm and at 30 cm.

Monthly vegetation and invertebrate samples were taken from July through September 2005 in the same manner as in the 2004 transects. One day prior to sampling a treatment plot, the portable dock was placed in the plot so that one quarter of the plot could be sampled. The quarter to be sampled each month was randomly chosen prior to the start of the sampling. Vegetation samples and invertebrate samples were then taken back to the lab and processed as described above.

Dry weights of living *Typha*, *Typha* litter, and lemnids, as well as total invertebrate abundance, taxa richness, Shannon-Weiner index ($H'$), and community similarity were determined.
Statistical analysis

*Transect Study.*

To compare the edge to the interior in 2004, split-plot ANOVAs were run for *Typha* live dry weight, *Typha* litter dry weight, lemnid biomass, total invertebrate abundance, and Shannon-Weiner diversity index (H’). Month was used as the split as new transects were chosen each month. Total invertebrate numbers were ln(x+1) transformed to meet conditions of normality in all ANOVA and t-tests. Invertebrate community similarity was determined by Multi-response permutation procedures (MRPP) (Mielke and Berry 2001) for the edge and interior for each of the three months as run by PC-ORD. The distance measure used in the analysis was Euclidean distance. Sorenson distances yielded similar results and are not reported here. Indicator species analysis tests (Dufrene and Legendre 1997) were run through PC-ORD for each month to determine how well the taxa separated between the edge and interior. The indicator species analysis test produces an indicator value for each taxon at the edge and in the interior (defined groups). The indicator value is obtained by first calculating the proportional abundance of the species in a group compared to the total abundance across all groups. This percentage represents the degree of fidelity a taxa shows to a group. Next, a relative frequency of the taxa is calculated by summing up presence/absence data of the taxa in each group and dividing by the total number of samples in each group. The relative frequency proportion is a measure of constancy in a group. The proportion of abundance and frequency are then multiplied to calculate the Indicator Value (IV). Therefore, if a taxon is found predominantly in one group (for example the interior) and is found consistently in the samples of that group, it would have a high IV. PC-ORD then evaluates the significance of the IV for each taxa by means of Monte Carlo randomization with 1000 randomizations to determine how likely the IV is due to chance, and a p value is generated. To better estimate the potential constraints of dissolved oxygen on invertebrates, the percentage of each 24 hour period under 1 ppm was calculated. The 1ppm constraint was chosen because higher mortality and reduced fitness for many wetland invertebrates occurs around 1 ppm (Nebeker et al. 1992, Irving et al. 2004).
**Interior Litter Study.**

Dry weights of living *Typha*, *Typha* litter, lemnids, log transformed total invertebrate abundance, and the Shannon-Weiner index (H’) were compared across treatments using split-plot ANOVAs, with the split between plots. All ANOVAs were performed using SAS. Community similarity was again analyzed using MRPP each month with the three treatments. When MRPP indicated a difference in similarity, contrasts between manipulations were performed. A MRPP analysis including the 2004 interior and the three litter treatments was performed to indicate the level of similarity between manipulated and unmanipulated interior since no control plot was included in 2005. Species indicator analysis tests within the interior were also performed to determine indicative taxa in the different treatments.

**RESULTS**

**Transect Study**

Consistent patterns were seen in cattail distribution from the edge to interior (figure 2). Total cattail weight within the water column was similar between the edge and the interior, but the amount of live and dead cattail was significantly different between the edge and interior (live $F_{1,6}=19.48 \ p<.005$, dead $F_{1,6}=13.17 \ p=.01$). Live vegetation predominated at the edge while more dead vegetation was collected in the interior. There was a significant increase ($t=3.93, \ p=.008$) in live material between July and August while no seasonal change occurred in the dead material. No statistical differences were observed with lemnids or with submerged aquatic vegetation between the edge and interior due to high variability.

Dissolved oxygen in the interior showed greater hypoxia at 10-15 cm depth and continual hypoxia at 30 cm below the surface (figure 3).

Total invertebrate abundance did not differ between the edge and the interior and a list of the most abundant taxa is provided in table 1. The Shannon-Weiner index, which accounts for relative composition, found significantly lower diversity in August in the interior (month*zone $F_{2,6}=36.02, \ p<0.001$) due to the increased dominance of amphipods. MRPP also found community differences between the edge and interior in August ($p=0.02$). Indicator Species analysis from all three months, especially in August, indicated that
detritivores, collector – gathers, and predators were present in the interior while the edge was indicated by algal filter feeders, collector-gatherers, and predators (as classified by Merritt and Cummins (1996) and Smith (2001)) (table 2).

**Interior Litter Study**

Significant differences existed among the litter treatments in 2005. Total cattail biomass and dead cattail litter biomass was predictably highest in the high litter treatment and that difference was maintained throughout the study period ($F_{2,4}=104.2$, $p<0.001$) (figure 4). Live cattail biomass did not differ between treatments (figure 4). Lemnids (primarily *Spirodella polyrhiza* and *Lemna trisulca*) were significantly lower in high litter plots ($F_{2,4}=15.51$, $p=0.01$), while equally present in low and moderate plots. Dissolved oxygen was lowest in the high litter treatment though all treatments exhibited extended periods of hypoxia (figure 5).

The natural log of total invertebrate abundance was significantly lower in the high litter treatment ($F_{2,4}=45.0$, $p=0.002$). There was no significant difference between the moderate and low litter treatments. There was a significant negative relationship between the natural log of total invertebrate abundance and litter biomass ($r^2=.50$, $p<0.001$) (figure 6). The Shannon-Weiner index indicated that the high litter treatment had significantly higher diversity ($F_{2,4}=17.76$, $p=0.01$) with lower abundance of the dominant species and more rare species (Table 3). MRPP showed community dissimilarity in July ($p=0.01$) and August ($p=0.008$). Contrasts within MRPP in July and August showed the high litter treatment was significantly different from the low and moderate plots (all $p$-values $<0.036$). MRPP tests showed no difference in September which was highly variable with proportions. The indicator species analysis was consistent with the monthly community similarity analysis. In July and August, detritivores and semi-aquatic species were indicative of the high litter treatment, while collector – gatherers, microcrustaceans, and their predators were present in the low treatment (as classified by Merritt and Cummins (1996) and Smith (2001)). These indicator species showed a consistent gradient from low treatments to high treatments with the moderate treatments showing intermediate values, with the one exception being leeches (table 4).
MRPP indicated that there was no significant difference between the 2004 interior samples and the low treatment. The moderate plot was slightly dissimilar in July (p=0.07), and significantly dissimilar in August (p=0.03) from the 2004 interior. The high litter treatment community was significantly different than the 2004 interior community in July (p=0.028), and August (p=0.02). There were no differences between treatments in September.

**DISCUSSION**

At high litter levels, litter did have a strong influence on the invertebrate community, producing a significant negative relationship between total invertebrate abundance and litter amounts. The interior litter study demonstrated that high litter could induce shifts in the community. The numbers of abundant nektonic taxa such as amphipods and copepods were reduced in the high litter treatments and other more anoxic-tolerant taxa like *Mansonia* (a plant breathing culicid), oligocheates, Scirtidae (marsh-loving beetles) and semi-aquatic species increased, contributing to higher diversity. Voigts (1976) found that under conditions of low water and accumulated litter that amphipod numbers were reduced and isopod numbers increased. In a six-year study of a seasonally inundated *Phragmites* bed where litter was quantified, isopods and leeches were positively associated with increasing litter and the authors stated that the community shifted from aquatic species toward semi-aquatic species to terrestrial species as water levels decreased (Bedford and Powell 2005). Others have also reported community shifts towards detrital and/or hypoxic-tolerant invertebrate communities as plant composition or densities shifted toward more dense, litter producing vegetation (Houston and Duivenvoorden 2002, King and Brazner 1999, McCormick et al. 2004, Neira et al. 2005). For example, emergent traps in dense vegetation in Great Lakes Marshes were dominated by anoxic tolerant and semi-aquatic dipteran species while more sparse vegetation was dominated by aquatic midges (King and Brazner 1999).

When litter was lower as in the transect study or in the low and moderate treatments, litter did not have the pronounced effect on the invertebrate community that was seen in the high litter treatment. In the few studies of similar scale to our study, patterns of total invertebrate abundance from the edge to stand interior have been ambiguous. In some studies
edges harbored more invertebrates (Marklund et al. 2001, Bailey and Litterick 1993) which were correlated to food availability and dissolved oxygen. Some members of the invertebrate community in the transect study had high indicator values for the edge. Nektonic collector-filterers of algae and fine particulate detritus and their predators were present mainly at the emergent edge as has been seen in other studies (Dvorak 1970, Olson et al. 1995). Their limited distributions may be due to algal resources at the edge (Blindow 1987, Marklund et al. 2001) or responses to dissolved oxygen. Those found exclusively at the edge breathe by abdominal or caudal tracheal gills or temporary air stores (Eriksen et al. 1996) and may be unable to endure prolonged periods of hypoxia (Apodaca and Chapman, 2004).

At this fine scale of tens of meters it is probable that multiple mechanisms influence total invertebrate abundance in the interior. Litter was not quantified in the above-mentioned studies, but in the current transect study, the emergent interior and edge were relatively low in litter. The high litter manipulation suggests that litter strongly influences invertebrate communities at higher levels but that under lower litter conditions other mechanisms more strongly control the resulting invertebrate abundance and composition in the emergent interior.

If litter directly influenced the invertebrate community only through increased food, substrate, or refuge then an increase invertebrate abundance would be predicted. Litter has been shown to be limiting to invertebrate abundance in some terrestrial and stream systems (David et al. 1991, Wallace et al. 1999). Within wetlands, studies conducted in open water showed increased invertebrate production with added litter (Campeau et al. 1994, Batzer 1998) but litter base-levels were likely low. Within dense emergent stands, litter removal did not decrease abundance but instead resulted in increases in invertebrate abundance (Murkin et al. 1982, Neckles et al. 1990). Similarly, the current study found more invertebrates under lower litter levels than at high litter levels. Even for some strict detritivores like isopods, abundances were similar across treatments in the interior. Neckles et al. (1990) suggested that litter resources do not limit most interior invertebrates. Some detritivorous species like oligochaetes, Scirtidae (marsh beetles), and Tipulidae (crane flies) did increase in abundance in the high litter treatment potentially because of increases in their preferred habitat of organic material in close proximity to the water surface.
Litter can also influence dissolved oxygen which can influence invertebrate community structure. The pattern of decreasing dissolved oxygen into the interior has been observed in many studies (Dvorak 1970, Suthers and Gee 1986, Murkin et al. 1992, Rose and Crumpton 1996, McCormick and Laing 2003). In the interior litter study, high litter plots exhibited almost continually anoxic conditions as in 1994-95 (Rose and Crumpton 1996). Hypoxia was less severe at lower litter levels in the interior but they also experienced periods of hypoxia, implying that the amount of litter in the immediate vicinity only partially influences the observed oxygen concentrations. Larger changes in DO may be more related to the connection to open water mixing (Leonard and Luther 1995, Losee and Wetzel 1993, Cardinale et al. 1997). The manipulated plots were created 8-10 meters into the interior so the level of connectedness to open water was equal between treatments. Gradual addition of litter structure from the edge into the emergent interior led to more depressed oxygen concentrations in a preliminary study at Anderson Lake (see appendix). Dissolved oxygen was relatively low in all litter treatments in the current study but many taxa were still abundant in the lower treatments. Amphipods and copepods are known to be tolerant of hypoxia (Sprague 1963, Nebeker et al. 1992, Smith 2001, Irving et al. 2004) and amphipods can undergo surface breathing (Irving et al. 2004). Their reductions in the high litter either indicate a fine threshold response to hypoxia that may be linked to the duration of hypoxia or other factors influenced their disappearance from the high litter treatment.

Litter can indirectly influence invertebrate communities by influencing existing vegetation. Strong effects of litter on lemnids were only observed in the high litter interior of the transect study. Litter was often present at the water surface in the high litter treatment and presumably displaced the lemnids. Bohlen (1990) found that litter additions caused a decrease in *Lemna minor* and Rose (1996) also found in the majority of his transects that lemnid biomass decreased in the interior under high litter levels. Submersed vegetation was lost in another area of Anderson Lake Marsh when litter was added to the emergent interior (see appendix). Lemnids (Sklar 1985, Harper and Bolen 1996) and submersed vegetation (Krull 1970, Downing and Cyr 1985, Olson et al. 1995) can harbor high numbers of invertebrates and increases in submersed vegetation are correlated with simultaneous increases in invertebrate abundance (Voigts 1976, Murkin et al. 1991). Due to the vegetative
losses, the more dominant invertebrate taxa may have lost the habitat or food resources that were supplied by the lemnids and total invertebrate abundance declined.

If litter densities and spatial position are considered together, the samples that were taken from the current studies indicate conditions that can be broken up into three main categories: 1) an interior habitat with high levels of hypoxia, little floating vegetation, and high levels of accumulated litter, 2) an interior habitat with intermediate to high levels of hypoxia, abundant floating vegetation, and low to moderate levels of accumulated litter, and 3) an edge habitat with low levels of hypoxia, the presence of submersed and floating vegetation, and low levels of accumulated litter. The high litter interior is indicated by much lower numbers of nektonic taxa and increases in the plant-breathing mosquitoes, detritivorous beetles, oligocheates, and crane flies. All either breathe atmospheric-derived oxygen, or are highly tolerant of hypoxia and can take advantage of organic carbon near the water surface. The second habitat is dominated by nektonic species that are tolerant of hypoxia in the interior and have ample floating vegetation. The final habitat located at the edge includes the hypoxic-tolerant nektonic species as well as less tolerant nektonic collector-filterers of algae and fine particulate detritus and their predators.

Wet-dry cycles within marshes are well documented (Weller and Spatcher 1965, van der Valk and Davis 1978, Roosa 1981) and can have strong effects on invertebrates (Murkin and Ross 2000). As marshes experience increased litter production or are drawn down at different stages in the wet-dry cycle (Nelson and Kadlec 1984), litter levels in the water column may increase. Less tolerant taxa may be compressed into smaller areas of habitat, and more tolerant or semi-aquatic taxa may expand (Bedford and Powell 2005). The compression and expansion of different taxa could influence different ecosystem processes. Shifts in the invertebrate community may influence higher trophic levels like waterfowl and fish as invertebrate prey either decrease in the interior or are compressed towards the emergent edge. It is important to understand how litter and invertebrates may interact with changes in the wet-dry cycle. Managers and designers in restoration and creation wetlands need to be aware of how hydrological changes may influence production and litter dynamics that may influence invertebrates. The actual dynamics of emergent litter in marshes are poorly
documented and more study needs to be done to better understand litter accumulation (Moore et al. 2004) and its potential effect on the surrounding trophic community (Levin et al. 2006).

ACKNOWLEDGEMENTS

Support of J. Christensen’s dissertation was provided by the Graduate College, the Environmental Science Program, the Ecology and Evolutionary Biology Interdisciplinary Program and the Department of Ecology, Evolution, and Organismal Biology of Iowa State University. We thank Philip Dixon for statistical consultation and the Brian Wilsey lab for access to PC-ORD software and materials. We thank the many undergraduate students for their hard work at Anderson Lake and “bug-picking” in the lab, and the owners of Anderson Lake for their support and access to Anderson Lake. J. Christensen would like to additionally thank Jana and Greg Stenback, Bradley Miller, and Amy Christensen for their constant encouragement and advice.

LITERATURE CITED


Table 1. The average relative percent of the most abundant invertebrates sampled from the edge (0T) and ten meters into the interior (10E) during July-September 2004. All taxa that had an average relative percent of >5% at the edge or interior during one month are shown. Standard deviation for monthly average (n=3) shown in parenthesis.

<table>
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<th></th>
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<th>September</th>
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<td>Edge</td>
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Table 2. Indicator species for July-September of 2004 at the emergent edge and ten meters into the interior. Indicator values (100=100% fidelity to zone and 100% occurrence in samples at that zone) calculated according to Indicator Species Analysis (see methods). All taxa included here had a Monte Carlo derived p value <.10. MRPP analysis indicated that the community was significantly different in August. Legend for feeding habit (Merritt and Cummins 1996, Smith 2001): CG-collector-gatherer, D-detritivore, F-filterer, H-herbivore, P-predator, SC-scraper. Legend for respiration (Merritt and Cummins 1996, Smith 2001): AT- atmospheric breather, C-cutaneous, CoxG-coxal gills, G-gills, PB-plant breather, PL-plastron, TAS-temporary air store, TG- tracheal gills

<table>
<thead>
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<th>Sep-04</th>
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<td>Feeding Habit</td>
<td>Respiration</td>
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<td>91</td>
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Table 3. The average relative percent of the most abundant invertebrates at the three litter treatments the interior in July-September 2005. All taxa that had an average relative percent of >5% at one of the treatments during one month are shown. Standard deviation for monthly average (n=3) shown in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
<th>September</th>
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<td>Low Litter Mod Litter High Litter</td>
<td>Low Litter Mod Litter High Litter</td>
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<td>0.01 (.00) 0.02 (.02) 0.03 (.02)</td>
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<td>0.80 (.03) 0.74 (.08) 0.42 (.08)</td>
<td>0.59 (.20) 0.75 (.14) 0.46 (.18)</td>
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<tr>
<td>Brachiopoda</td>
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<td>0.01 (.01) &lt;.01 - &lt;.01</td>
<td>0.07 (.13) &lt;.01 - -</td>
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<td>Cladocera</td>
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<tr>
<td>Copepoda</td>
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<td>0.02 (.02) 0.01 (.02) 0.01 (.01)</td>
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<tr>
<td>Isopoda</td>
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<td>&lt;.01 - 0.02 (.02) 0.06 (.02)</td>
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Table 4. Indicator species for interior litter study across the three treatments. Indicator values (100=100% fidelity to zone and 100% occurrence in samples at that zone) calculated according to Indicator Species Analysis (see text). All taxa included here had a Monte Carlo derived p value <.10. MRPP analysis indicated that the high litter invertebrate community was significantly different in July and August. Legend for treatment with max indicator values: LL-low litter, ML-moderate litter, HL-high litter. See table 2 for feeding habit legend

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<td>ML</td>
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</table>

Legend: CG=Consumers, D=Detritivores, P=Predators, F=Filter Feeders
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CHAPTER 3. THE HORIZONTAL AND VERTICAL DISTRIBUTION OF
HYALELLA AZTECA (AMPHIPODA) IN AN EMERGENT FRESHWATER
WETLAND: EFFECTS OF INCREASED LITTER

A paper to be submitted to the journal of Hydrobiologia

Jay R. Christensen and William G. Crumpton

ABSTRACT

The edge and interior of emergent vegetation stands often display distinct differences in the abundance of oxygen, light, and litter. These differences may significantly affect the horizontal and vertical distributions of Hyalella azteca (Saussure), an abundant and trophically important invertebrate. Relative horizontal and vertical distributions of Hyalella azteca were sampled in transect studies from the edge and interior of a dense cattail (Typha spp.) stand and under manipulated levels of litter within the interior. Litter and lemnid densities increased from the edge to interior, while dissolved oxygen decreased from the edge to interior. In transect studies, activity traps showed the emergent interior experiences increased Hyalella azteca abundance with most individuals inhabiting the top portion of the water column. Compared with low litter treatments in the emergent interior, Hyalella azteca abundance under high litter was significantly reduced. Results suggest that litter accumulation dynamics influence the horizontal and vertical distribution of Hyalella azteca, which may influence competition and susceptibility to predation. Litter dynamics need to be considered when investigating the influence of emergent stands on invertebrate spatial distributions.

INTRODUCTION

Semi-permanent freshwater marshes often develop marked zonation of deeper open water areas surrounded by dense stands of emergent vegetation that vary with water level changes. The interior of these emergent stands experiences lower dissolved oxygen (DO) (Dvorak, 1970; Rose & Crumpton, 1996; Murkin et al., 1992), decreased light availability (Rose & Crumpton, 1996) and increased litter densities (Rose & Crumpton, 1996). Litter
may play a major role in creating and exacerbating the observed conditions of interior emergent stands by shading the water column (Grimshaw et al., 1997) and increasing structure which decreases water mixing (Leonard & Luther, 1995; Cardinale et al., 1997).

Despite the potential effect of litter on light, oxygen availability, food resources, and refugia, few studies have considered the effect of litter on wetland invertebrate distributions. At the scale of hundreds of meters, the horizontal distribution of invertebrates shows significantly lower invertebrate densities in the interior of emergent stands. Decreases within emergent stands are correlated to decreases in epiphyton (Cardinale et al., 1997) and DO (MacKenzie & Kaster, 2004; MacKenzie et al., 2004). Reductions in light and DO also occur on smaller spatial scales (Rose & Crumpton, 1996) but invertebrate studies on the scale of tens of meters have had mixed results, with some reporting higher abundance in the interior (Dvorak, 1970; Murkin et al., 1992), at the edge (Voigt, 1976; McLaughlin & Harris, 1990) or no discernable pattern (King & Brazner, 1999). Litter accumulation in the interior of emergent stands may also vary. Variation in emergent production and decomposition may result in low or high levels of litter that could then differentially influence the invertebrate community. The effects of litter could shed additional light on the variability in small scale invertebrate horizontal distributions in dense vegetation.

Differences in the vertical distribution of invertebrates may also be influenced by litter. DO concentrations and available light have shown a vertical profile as well as a horizontal pattern in emergent stands (Rose & Crumpton, 1996). Densities of invertebrates may be similar across the edge-to-interior gradient but hospitable conditions for invertebrates may decline with increasing depth in the interior. The resulting vertical compression into the upper water column could influence competition and predation risk. Vertical compression and trophic consequences have been observed experimentally (Kolar & Rahel, 1993) and in vertically stratified lakes and estuarine systems where fish and invertebrates undergo compression due to hypoxia (Wright & Shapiro, 1990; Rabalais & Turner, 2001). Despite the potential presence of hypoxia, vertical distributions of invertebrates have not been investigated within wetland systems. In shallow wetlands where litter inputs are high, vertical compression could become so severe that intolerant invertebrates are pushed out of interior stands.
*Hyalella azteca* (Saussure) is a common amphipod in submersed and emergent stands and amphipods are important prey items of fish (Zimmer et al., 2001), amphibians (Olenick & Gee, 1981), and waterfowl (Krapu & Reinecke, 1992). *Hyalella azteca* is a nektonic species that feeds on both epiphyton and detritus (Hargrave, 1970; Smith, 2001) and is moderately tolerant of hypoxic conditions but experiences reduced growth, fecundity and survival under hypoxia (Irving et al., 2004; Nebeker et al, 1992). Due to its high abundance, mobility, and potential response to hypoxia, *Hyalella azteca* may respond both horizontally and vertically to changes in litter. The objective of this study was to explore the influence of different amounts of litter on the horizontal and vertical distributions of *Hyalella azteca* through transect studies and an experimental study in the interior.

**METHODS**

**Study Site**

This research was conducted at Anderson Lake Marsh, a 65 Ha semi-permanent natural prairie pothole located in Hamilton Co., IA, USA (42° 18’50” N, 93° 37’32” W). Advances in the study of muskrats, waterfowl, and wetland vegetation dynamics have included Anderson Lake as a study site (Pammel, 1898; Errington, 1963; Weller & Spatcher, 1965; Davis & van der Valk, 1978; Rose & Crumpton, 1996). In this study, *Typha* spp (almost exclusively the hybrid *T. glauca* Godr.) dominated the emergent zone. Lemnids (primarily *Spirodela polyrhiza* (L.) Scheid and *Lemna trisulca* (L.)) were found interspersed among the cattails with *Ceratophyllum demersum* (L.) and *Utricularia macrorhiza* Le Conte present at the emergent edge.

**Transect Studies**

In mid July and mid August of 2003, *Hyalella azteca’*s relative horizontal and vertical distribution was estimated along randomly selected transects each month on the east side of the island adjacent to open water (figure 1). From July to September 2005, transects were selected each month within two areas on the west end of the wetland (figure 1). The 2005 transect had low litter densities (150-300g dry weight) and were sheltered from open water mixing. At each transect, multi-level activity traps were deployed at the edge of the emergent
stand and 10-11 meters into the interior. In 2005, activity traps were also deployed at 4m and 8m to estimate intermediate relative densities. The activity trap design follows that of Murkin et al. (1983). Activity traps have been shown to give accurate estimates of relative abundance for selected taxa, including amphipods (Murkin et al., 1983; Turner & Trexler, 1997). So that traps at three levels could be easily used, traps were positioned on a slotted angle post with clamping conduit hangers instead of by wire suspension. Due to lower water levels in August 2003, traps could be deployed at only 2 levels in the interior. At each sampling point, water depth was measured, and traps were bolted to the pole so that they would sample the top 15 cm, the midpoint (15-30 cm) and the bottom (10 cm above the sediment surface) of the water column. Glass 0.95 L jars were filled with filtered lake water and a funnel (15 cm outside diameter and 1.8 cm inside diameter) was secured by S-hooks and rubber bands. To deploy the traps, the pole was carefully lowered into the water with the traps facing upward, pushing the base of the pole 40 cm into the sediment. Once fully underwater, the traps were rotated to a perpendicular position, taking care that the funnels were not dislodged by surrounding litter. Activity traps were left for 24 hours and then removed. The contents of the jar were passed through a 250 µm sieve and preserved in 70% ethanol. In the lab, *Hyalella azteca* were sorted in bottom-light translucent pans and enumerated.

From June to August of 2003, continuous water quality data loggers (AQUA 2000, Biodevices Inc. Ames, IA, USA) were deployed at the emergent edge and ten meters into the interior along two transects to measure dissolved oxygen concentrations and water temperature. Loggers were deployed at a depth of 10-15 cm and 30-35 cm. In 2005, data loggers were not available and dissolved oxygen and temperature were taken from 12:00-14:00 at depths of 2 cm, 5 cm, 10 cm, 20 cm, and 30 cm at each sampling point along the transects. In 2003 five vegetation/litter transects were randomly selected each month, with three adjacent to the activity traps samples. Vegetation sampling was done at the edge and at 10m into the interior with a 90 cm long, 0.11 m² PVC cylinder. The cylinder was forced through the vegetation, vegetation was clipped off at the water surface and all vegetation and litter were removed, washed, and bagged. Percent cover was estimated for submersed and floating vegetation. In 2005, transects within each section were in close proximity and the 2003 method was too destructive so vegetation samples of the top 20 cm of the water column
were taken at each sample point. A 15 cm diameter Plexiglas tube with a filed edge at the bottom was inserted into the water column to 20 cm depth. A flat board was slid along the bottom to enclose the area and any vegetation outside the tube was clipped and discarded. The tube and board were lifted out of the water and all vegetation in the cylinder was bagged. At the lab, all vegetation was sorted, preliminarily table dried for 1 week, oven dried at 65 °C for 48 hours, and weighed.

**Interior Litter Study**

Litter densities in the interior of the 2003 and 2005 transects, (0.3-0.6 kg/m²) were much lower than amounts found in Anderson Lake Marsh in a 1994 study conducted prior to recent drawdowns (2.0 kg/m²)(Rose & Crumpton, 1996; Rose & Crumpton, 2006). In the late spring of 2005, three replicate plots located at a constant distance from the edge were selected where three 4 by 10m treatment plots could be established. All replicate plots were on the northeast side of the island and main wetland shore (figure 1), 8-12 m to the interior from the open-water-emergent edge. The three treatments were a high litter (HL) density with approximately 2.0 kg litter/m², a moderate litter (ML) density with approximately 1.0 kg litter/ m², and a low litter (LL) density where remaining stems constituted 0.25-0.5 kg litter/m². At each plot, the three 4 by 10 m treatments were randomly assigned. A 2 m access path to the open water was created between each treatment.

Litter was manipulated by clearing the 4 by 10m area of litter with pitchforks by clearing 4 by 1m columns at a time. Standing litter stems and live plants were not removed. As columns of litter were being removed, already removed litter was placed in a wooden box with a screen bottom, shaken three times, and weighed. A wet weight to dry weight relationship had been established with 30 preliminary samples (r²=0.93) and wet litter was weighed and placed back into the HL and ML treatments to achieve the desired densities. Litter from the LL treatments was transported to the HL and used to supplement the HL treatment. Plots were left alone for 3-4 weeks, prior to the onset of sampling.

Relative *Hyalella azteca* densities and vegetation were sampled monthly from July to September 2005. Multi-level activity traps, as described above, were used in the study. One day prior to sampling a treatment, a portable dock was placed in the treatment so that one
quarter of the treatment could be sampled with minimal disturbance. The quarter to be sampled each month was randomly chosen prior to the start of the sampling. With the dock in place, the multi-level activity traps were randomly deployed along the dock. After 24 hours, the activity traps were removed. At two of the three plots (limited by the number of loggers available) 2 data loggers were placed in the center of each treatment to measure dissolved oxygen and temperature at 5 cm and at 30 cm. Monthly vegetation samples were collected in the same manner as in 2003 to obtain whole water column litter weights. Vegetation samples and invertebrate samples were taken back to the lab and processed as described above.

**Statistical Analysis**

*Transect Studies*

To examine horizontal differences, the relative abundance of *Hyalella azteca* of the three multi-level traps were summed together to provide a whole water column estimate. Those numbers were then ln(x+1) transformed to meet conditions of normality in all ANOVA and t-tests. To compare the edge to the interior in 2003, split-plot ANOVAs were run for *Typha spp.* litter dry weight, submersed aquatic vegetation (SAV) coverage, lemnid coverage and *Hyalella azteca* horizontal relative abundance. Month was used as the split as new transects were chosen each month. Vertical distributions compared the top trap with the combined middle and bottom traps. Data were ln(x+1) transformed and a split-split-plot ANOVA was used to split months and multi-level sampler location. In the 2005 transects, split-plot ANOVAs with the split between plots compared *Typha* live dry weight, *Typha* litter dry weight, SAV coverage, lemnid coverage and *Hyalella azteca* horizontal relative abundance across distances. An additional split was used to consider the top and middle-bottom traps. Contrasts between the top and combined middle and bottom traps were run for each distance to determine if vertical compression was significant.

Dissolved oxygen data from 2003 were analyzed to estimate the potential constraints of dissolved oxygen on *Hyalella azteca*. The percentage of each 24 hour period above 1 ppm at 10cm depth was calculated and an average over the study period is reported. The 1 ppm constraint was chosen because higher mortality and reduced fitness for *Hyalella azteca* occurs at 1.2 ppm (Nebeker et al., 1992; Irving et al., 2004). Recorded DO measurements
from the 2005 transect were placed in Surfer (Golden Software Inc. version 8), mapped using triangulation with linear interpolation, and the depth at 1 ppm was recorded. Dissolved oxygen in the 2005 transects was analyzed as the percent of the water column above 1 ppm at the time of sampling. All three months showed similar patterns and an average of the three months is reported.

**Interior Litter Study**

Cattail biomass, relative horizontal *Hyalella azteca* abundance from the litter manipulations were compared across treatments using split-plot ANOVAs, with the split between litter treatment plots. The vertical relative abundance was compared by ANOVA using a split-split plot with a split between plots and at each multi-level sampler. Contrasts between the top trap and combined middle and bottom traps were run for each treatment to determine if vertical compression was significant. Tests of cattail biomass, lemnid biomass, and DO in the manipulated plots are reported elsewhere (Christensen and Crumpton, chapter 2). All ANOVAs were performed using SAS.

**RESULTS**

**Transect Studies**

*Hyalella azteca* showed higher relative abundance in the interior in the 2003 transects ($F_{1,10}=4.77$, $p=.05$) and a similar trend was observed in the 2005 transects. Vertical compression was significantly greater in the interior in 2003 ($F_{1,15}=9.38$, $p<.01$) (figure 2a) while significant compression was present at all points in 2005 ($F_{1,4}=68.8$, $p=.001$)(figure 2b). Litter densities in 2003 were significantly higher ten meters in the interior with 754.7 g/m$^2$ than at the edge with 168.0 g/m$^2$ ($F_{1,12}=128.9$, $p<.001$). Lemnids were greater in the interior in 2003 (% coverage)($F_{1,12}=58.1$ $p<.001$). Dissolved oxygen decreased from the edge to the interior in both transect studies. The average daily proportion of severe hypoxia in the interior was 37.6% compared with 28.3% at the open water edge in 2003. In 2005 the percentage of the water column above 1 ppm decreased from 24% at the edge to 14% at 11m.
**Interior Litter Study**

Higher relative *Hyalella azteca* densities were found in low and moderate litter treatments than in the high treatment ($F_{2,4}=10.1, p=.03$). Vertical compression increased as litter increased from low to moderate amounts, with the largest compression found in the moderate litter treatment (figure 3). Very low abundance was observed in both the upper and lower traps in the high litter treatment (figure 3). Overall, litter biomass (g/m²) showed a negative relationship with transformed *Hyalella azteca* relative abundance ($r^2=.30$) (figure 4).

**DISCUSSION**

**Horizontal Distribution**

Despite lower dissolved oxygen levels, the interior of the transect studies consistently had higher relative abundance of *Hyalella azteca*. Murkin et al. (1992) found higher relative abundance of Cladocera nine meters into a hypoxic stand and suggested that this distribution was in response to predation risk. Researchers have found that fish searching efficiency decreases with increasing plant density (Crowder & Cooper, 1982; Gilinsky, 1984). Fathead minnows are the only fish predator in Anderson Lake, and they are known to feed on amphipods (Zimmer et al., 2001). Studies have shown that in the presence of fish, invertebrates, including amphipods, will remain in hypoxic vegetated areas but will readily abandon vegetated areas when fish are absent (Rahel & Kolar, 1990; Kolar & Rahel, 1993). Fathead minnows are tolerant of lower dissolved oxygen (Davis, 1975) but at Anderson Lake 93 % to 100% of fathead minnows were caught in 2003 and 2005 were in the open water or at the edge (appendix B) and *Hyalella azteca* may have experienced reduced predation-risk in the interior. Alternate sampling artifacts of diel horizontal migration (Timms & Moss, 1984; Lauridsen et al., 1999; Burks et al., 2002) or differential behavioral responses to activity traps at the edge and interior (Turner & Trexler, 1997) were considered but preliminary day-night sampling failed to show diel migration of *Hyalella azteca* and quantitative samples taken in the interior litter manipulation study showed similar abundance patterns to activity traps (Christensen and Crumpton, chapter 2).

*Hyalella azteca* abundance was higher in the emergent interior than at the edge in the transect studies but the abundance of litter in the interior was relatively low. Under
manipulated high litter amounts, *H. azteca* abundance was reduced, indicating the potential for horizontal compression. Preliminary tests of incremental litter additions from the edge to the interior conducted at Anderson Lake also suggest horizontal compression (appendix A). Increases of litter can lead to the loss of other vegetation (Bohlen, 1990). Christensen and Crumpton (chapter 2) found that lemnid biomass was similar between the low and moderate plots while lemnids were lost in the high litter treatment, and in another preliminary litter addition study at Anderson Lake Marsh, submersed vegetation was lost with increasing litter (appendix A). *Hyalella azteca* has been shown to have a positive relationship to submersed vegetation (Voigts, 1976; Murkin et al., 1991; Murkin & Ross, 1999). The loss of such vegetation in the interior due to increased litter may constrict inward invertebrate distributions. This negative response at high litter conditions may indicate a threshold response to litter, where the positive refuge/food benefits of litter are outweighed by losses to vegetation and/or low dissolved oxygen. Nelson & Kadlec (1984) hypothesized that seasonal temporal changes including DO and water levels within emergent vegetation would force invertebrates towards the edge, speculating that interior conditions may be suitable in spring but could decline under higher summer temperatures. Bedford & Powell (2005) found decreases in aquatic invertebrate abundance as water levels decreased in *Phragmites* stands. Predation pressures and hypoxia have resulted in intermediate distributions in many aquatic organisms, including African cichlids (Chapman et al., 1996; Randle & Chapman, 2004), sunfish (Miranda & Hodges, 2000), several zooplankton (Wright & Shapiro, 1990; Tessier & Welser, 1991), and mysids (Horpilda et al., 2003).

**Vertical Compression**

While horizontal distributions of *Hyalella azteca* may be influenced by predation and interior conditions related to high litter, vertical compression occurred throughout the edge and interior, adding an additional dimension to *Hyalella azteca*’s response to its surroundings. The compression was often greater in the interior than at the edge, indicating that individuals in the interior not only experience higher abundance but do so in a smaller vertical space. Interior compression may be due to lower oxygen concentrations or a shift from a combination of submersed vegetation and lemnids at the edge to a more restricted two
dimensional habitat of lemnids in the interior. Within the interior, the degree of compression increased from the low to moderate litter amounts until very few individuals were collected under high litter. Christensen and Crumpton (chapter 2) found DO was highest in the low litter plot, slightly lower in the moderate plot and anoxic in the high litter plot. *Hyalella azteca* can tolerate hypoxia, and even severe hypoxia for short periods of time, though *Hyalella azteca* often utilize surface breathing under hypoxia in laboratory settings (Sprague, 1963; Nebeker et al., 1992; Irving et al., 2004). The higher compression in the moderate plot could be related to oxygen stress. In the high litter treatment, litter occluded the water surface, excluding lemnids and their potential refuge (Christensen and Crumpton, chapter 2). The combination of extended anoxia and lemnid exclusion may have led to very low relative abundance in the high litter treatment. Vertical compression due to hypoxia has been observed in many aquatic organisms, including marine benthos (Pihl et al., 1991; Taylor & Eggleston, 2000), blue crabs and shrimp (Eggleston et al., 2005; Bell & Eggleston, 2005; Craig & Crowder, 2005), estuarine fish (Breitburg, 1994; Breitburg et al, 1999), zooplankton (Horppila et al., 2003; Wright & Shaprio, 1990; Tessier & Welser, 1991), freshwater fish (Miranda et al., 2000) and invertebrates (Kolar & Rahel, 1993).

**Implications**

Horizontal and vertical compression may influence the population and community dynamics of wetland invertebrates like *Hyalella azteca*. Compression may influence within-population interactions, as competitive differences based on size have been documented in *Hyalella azteca* (Wellborn, 2002) and cannibalism occurs within amphipods (Dick et al., 1993; MacNeil et al., 1997). Hypoxic compression reduced fitness and increased cannibalism for juvenile blue crabs (Eggleston et al., 2005). Compression may also influence trophic relationships for *Hyalella azteca* and result in increased overlap with invertebrate predators which influence *Hyalella azteca* population dynamics (Wellborn, 1994). Increased overlap with predators has been seen in Gulf of Mexico and Chesapeake Bay invertebrate communities (Breitburg et al., 1999; Breitburg et al., 2003; Eby & Crowder, 2002; Eby & Crowder, 2004). Increased predation due to vertical compression has been observed for invertebrates (Kolar & Rahel, 1993; Horppila et al., 2003), polychaetes (Pihl et al., 1991;
Nestlerode & Diaz, 1998), prey of hypoxic-tolerant jellyfish (Decker et al., 2004), and tadpoles (Moore & Townsend, 1998). Parasites may also influence *Hyalessa azteca* populations (Kokkotis & McLaughlin, 2006) and could increase transmission in compressed populations. The compression and habitat shifts due to hypoxia not only influence specific predator-prey dynamics but potentially impact the entire community and ecosystem function (Lenihan et al., 2001; Jewett et al., 2005; Levin et al., 2006).

The difference discovered between low natural litter levels measured in the current transect studies and much higher levels of a previous transect study (Rose & Crumpton, 1996) raise interesting questions of the annual dynamics of litter in the emergent interior. Though considered highly variable both spatially and temporally, long-term changes in litter are poorly documented (Day et al., 1998). The current study combined with past studies of Anderson Lake Marsh (Rose & Crumpton, 1996) suggests that large changes in litter may occur over annual scales and under conditions of high litter levels, the horizontal and vertical compression of invertebrates may be profoundly influenced. Given the cyclical nature of wetland vegetation (van der Valk & Davis, 1978) and its litter, it is important to better understand how these potentially expanding and contracting habitats (both horizontally and vertically) affect invertebrates in the wetland trophic structure. More study needs to be done to better understand litter dynamics (Moore et al., 2004) and its potential effect on the surrounding trophic community (Levin et al., 2006). As we better understand litter and its association with invertebrates, we can better develop management practices in wetlands that consider litter and its interaction with biota.

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**LITERATURE CITED**


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Figure 1 – Anderson Lake with predominant vegetation and location of study sites: A-2003 transect study, B-2005 transect study, C- Interior litter study
Figure 2. Vertical distribution of transformed relative densities of *Hyalella azteca* in the top activity trap and in the combination of the middle and bottom activity traps from the edge into the emergent interior in A) the 2003 transects. $F_{1,15}=9.38, p<.01$ and in B) the 2005 transects. $F_{1,4}=68.8, p=.001$. * - indicates significant vertical compression ($p<.05$) using ANOVA contrasts. Standard error bars are shown.
Figure 3. Comparison of the vertical distribution of *Hyalella azteca* at the litter means for the high, moderate and low litter treatments. The solid line is the relative densities in the top activity trap, the dashed line is the relative densities in the combined bottom and middle activity traps. * denotes vertical compression based on ANOVA contrasts where p<.05. Standard error bars shown.
Figure 4. Correlation of natural log transformed Hyalella azteca and litter dry weight in the interior litter study. Three vertical traps were summed to produce relative Hyalella azteca numbers. $r^2=.30$
CHAPTER 4. ESTIMATING LITTER ACCUMULATION OF EMERGENT MACROPHYTES: LITTER BAG VERSUS MASS BALANCE APPROACHES

A paper to be submitted to Wetlands

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ABSTRACT

Litter accumulation within emergent macrophyte marshes may significantly influence abiotic conditions and biota but litter is rarely considered in emergent macrophyte studies. Litter is defined here as the standing and fallen litter that can be collected using harvest methods in the field. Litter accumulation can be estimated using annual production and breakdown rates from litter bag studies. It can also be measured by using a mass balance approach to estimate breakdown rates of litter produced. A five year study conducted in Delta Marsh, Manitoba measured annual standing crop and harvested accumulated litter of Phragmites australis (Cav.) Trin., Typha glauca Godr., and Scolochloa festuacea (Willd.) Link. These species differ in their level of refractory material and hence amount of litter that is expected accumulate. Litter bag breakdown rates consistently overestimated litter accumulation for all species. Mass balance derived rates for Phragmites and Typha tracked observed values and the breakdown rates of the two species were significantly different ($F_{1,14}=5.07$, $p=.03$). Breakdown rates differed across depths as well ($F_{2,14}=4.35$, $p=.04$). The mass balance approach was not suitable for Scolochloa which breaks down quickly. Litter bag studies may not be suitable to predict harvested litter accumulation. The mass balance approach can provide more reliable estimates of litter accumulation for emergent species with recalcitrant litter.

INTRODUCTION

In wetlands dominated by emergent species, at the end of the growing season much of the emergent production remains as standing and fallen litter that begins to breakdown. Emergent macrophyte standing litter begins to breakdown through leaching of soluble
compounds (Polunin 1984) and through fragmentation of culms due to wind storms, ice scour, and other forces (Davis and van der Valk 1978a). Culms that topple over and fragments of culms are described as fallen litter. Fallen litter is often in the water column and becomes more available to biological breakdown by microbes and fungi. Litter particle-size decreases with time and dissolved and fine particulate organic matter becomes susceptible to further decomposition, transport within the wetland, or incorporation into the sediment. For some emergent macrophytes, the process of breakdown occurs slowly due to the refractory chemical composition of its tissues (Polunin 1982) and standing or fallen litter can persist for years (Davis and van der Valk 1978a).

In this paper, litter refers to the standing and fallen litter that can be collected using harvest techniques (i.e. harvested or harvestable litter). It is this litter that can be seen in the field and that greatly influences light, temperatures, and water movement in the lower levels of emergent stands. Litter has been shown to decrease soil and water temperatures (Haslam 1971, Weltzin et al. 2005) and reduce light availability due to shading (Graneli 1989, Bohlen 1990, Rose and Crumpton 1996, Weltzin et al. 2005). Structure decreases water velocities and mixing (Leonard and Luther 1995) and litter increases have been correlated to decreased oxygen concentrations (Rose and Crumpton 1996), lower redox potentials (Weisner and Graneli 1989, Armstrong et al. 1996, van der Putten 1997), and increased sediment accretion rates (Rooth and Stevenson 2000, Rooth et al. 2003). Litter has also been shown to directly or indirectly influence the plant community by inhibiting seed germination (van der Putten et al. 1997, van der Valk 1986) and primary production (Haslam 1971, Graneli 1989, Jordan et al. 1990, van der Putten et al. 1997). Removal of litter increased plant diversity (Bohlen 1990, Jordan et al. 1990, Meyerson et al. 2000, Weltzin et al. 2005) and stimulated production of the parent species (Haslam 1971, van der Valk and Davis 1978a, Graneli 1989).

Given the effects that accumulated litter can have on abiotic conditions and biota, it is surprising that very few freshwater emergent macrophyte studies consider the process of litter accumulation. Emergent litter accumulation is a function of emergent production and breakdown rates of emergent litter. Considerable attention has been given to the processes of emergent production (see Brinson et al. 1981, Westlake et al. 1998) and breakdown rates (see
Brinson et al. 1981, Webster and Benfield 1986), but few freshwater wetland studies have combined production and breakdown rates to investigate the process of litter accumulation.

Breakdown rates are typically estimated using the litter bag method and can vary as a function of moisture (van der Valk 1991, Bedford 2005) and oxygen availability (Godshalk and Wetzel 1978, Brinson et al. 1981, Hietz 1992). Although litter bags studies have helped understand many of the factors influencing the breakdown of emergent litter (Webster and Benfield 1986), it is unclear how well breakdown rates derived from litter bag studies relate to actual litter breakdown in the field and to litter accumulation rates. When litter breakdown rates from litter bag studies have been combined with production to estimate litter accumulation, rates of litter accumulation are overestimated in old fields (Wiegert and Evans 1964, Wiegert and McGinnis 1975) and in tidal wetlands (Findlay et al. 1990, Windham 2001 but see Valiela et al. 1985). An alternative approach would be to calculate breakdown rates based on a mass balance analysis of measured annual production inputs and litter accumulation. This approach, however, seems never to have been used to estimate litter accumulation rates.

The objective of this research was to estimate litter breakdown rates that accurately reflect the in-situ processes controlling litter accumulation. We investigated litter breakdown for multiple emergent species across different water depths using a novel mass balance model to estimate breakdown rates. We also estimate long-term litter accumulation using breakdown rates obtained from litter bag studies. Estimates of litter accumulation using both approaches are compared to measured values of harvested litter. Data for both approaches was derived from studies of litter decomposition, primary production, and litter standing crops in a series of experimental marshes in the Delta Marsh, Manitoba, Canada (Murkin et al. 2000).

**METHODS**

**Study Site**

The Marsh Ecology Research Program (MERP) was conducted at Delta Marsh, Manitoba and was designed as a long-term, replicated, large scale experiment to investigate the influence of water level fluctuations on the production and distribution of wetland plants,
animals, and nutrient cycling. The analyses conducted in this research are based on production and litter data which were previously collected as part of the MERP study. A complete review of the MERP study methodologies and conclusions can be found in Murkin et al. (2000). In 1979, ten diked marshes, all approximately 5 Ha, were created within Delta Marsh along the southern shore of Lake Manitoba. Water levels of Lake Manitoba and Delta Marsh were stabilized with the construction of the Fairford River Dam in 1961 which reduced water fluctuations within the marsh from +/- 2.1m to +/- 0.3 meters from the 30 yr mean of 347.5 m above mean sea level (AMSL) (Batt 2000).

**Water Level Manipulations**

In 1980 all ten marshes were maintained at mean water levels (347.5 m AMSL) and the monitoring of species distributions and production began. Eight of the marshes were flooded 1 meter above 347.5 m in 1981 and the other two were similarly flooded in 1982. All the marshes were flooded for two years and then drawn down to 0.5 m below the normal levels for two years (in the eight marshes flooded in 1981) or one year (in the two marshes flooded in 1982). This drawdown allowed for the germination of annuals and emergents as predicted by van der Valk and Davis (1978b). The flood-drawdown water regime essentially “reset” the accumulated emergent litter to zero as most emergent production was killed with high water (van der Valk 2000) and remaining litter was subject to multiple years of breakdown. In 1985 the ten cells were flooded to varying levels. Four marshes were returned to the 30 yr average water level of 347.5 m AMSL while six marshes were flooded to 0.3 or 0.6 m above normal for the duration of the study. The current study does not address the effect of flooding above the historic mean water level, so the six non-normal water level marshes are not included. With the return of water levels to the 30 year average in the four normal water level marshes, annual vegetation died and emergent vegetation responded to water levels according to their different water depth tolerances (van der Valk et al. 1994, van der Valk 2000, Seabloom et al. 2001).
Emergent Species of Interest

Sufficient data are available to track three emergent species that differ in their general breakdown rates and their level of water depth tolerance. All emergent species studied were perennial, rhizomatous plants that are active in the growing season from late May-early June until late August with similar annual production values. *Phragmites australis* (Cav.) Trin. litter (stems) typically has the lowest breakdown rate (van der Valk et al. 1991, Murkin et al. 1989) and is most common 30 to 70 cm above the water table but can extend to 50 cm deep in these marshes (de Swart et al. 1994). *Typha glauca* Godr. litter is more easily broken down than *Phragmites* (van der Valk et al. 1991, Webster and Benfield 1986) and is tolerant of deeper water, with the highest probability of occurrence at a water depth of 15 cm (de Swart et al. 1994). *Scolochloa festucacea* (Willd.) Link is more easily broken down then *Phragmites* or *Typha* (van der Valk et al. 1991, Neckles and Neill 1994) and occupies areas slightly above the water table to just below the water table (de Swart et al. 1994).

Quadrat Clippings

Each of the diked marshes were evenly divided into ten zones and a transect was randomly selected within each zone for each year. Four samples were taken from each transect so that 40 samples were taken in each marsh, each year. At each sampling point all live and dead material was clipped at the substrate within a 1m x 1m quadrat, separated into live and dead material, sorted by species, and placed in burlap bags. Water depths were recorded at the time of sampling. All samples were dried at 80 °C and weighed. Live standing and litter crop samples were taken primarily in the month of August but in some years sampling extended well into September. During each season, the sampling schedule was randomized so that seasonal bias within a given marsh was avoided. Two reference areas located on either side of the ten diked marshes were also sampled each year. One reference was predominately covered by *Phragmites* while the other was mostly *Typha*.

Turnover Study

Standing crop estimates often underestimate total production because they do not take into account mortality during the same season (Dickerman et al. 1986). A one-year turnover
study was conducted at Delta Marsh in 1981 to correct for possible underestimation of live standing crop values. The procedure was done for *Phragmites* and *Typha*. Permanent plots were established in the Delta Marsh in healthy stands of both species. Beginning in June, live shoots and dead shoots were tagged and enumerated every two weeks. Tagging ensured the identity of pre-existing shoots, old dead stems, flowering shoots, new shoots, and new dead stems that occurred during each time period. During each sampling period, 25-50 live stems (and flowering stems when available) were harvested from an adjacent area to the permanent plot, dried at 80 °C, and weighed. A turnover value was calculated by accounting for stems that were lost during the two week time period and multiplying those lost stems by the average of stem weights during the same time period. Loss values were summed until the sampling of the maximum standing crop (Aug. 28, 1981). The summed loss value was divided by the maximum standing crop to provide an estimate of % turnover. In 1987, the average sampling date was more than 2 weeks later in the year, so estimates of % turnover for 1987 were based on the September 11, 1981 turnover sampling period which increased the % turnover 1.5 times for *Typha* and 2.5 times for *Phragmites*. The turnover values for August (at peak standing crop) were within the range of values observed in the literature (table 1) and were used to correct production input into litter in the model.

Mass balance model

A mass balance model was created based on measured standing crop and accumulated litter for *Phragmites*, *Typha*, and *Scolochloa* for each marsh, stratified by water depths, for the period from 1985 until 1989. The water depths considered were areas of dry land (above 1 cm water depth) and water depth intervals of 1-20 cm, and 21-40 cm. Very few emergent samples were found in water deeper than 40cm. The model incorporates a single negative exponential function (Wieder and Lang 1982) to estimate litter breakdown rates.

Mathematically, the model is as follows for each species at each water depth interval:

\[
L_{t,s,d} = L_{t,s,d}e^{-k_{s,d} (t-1)} + \sum_{i=1}^{t-1} SC_{i,s,d}e^{-k_{s,d} (t-i)} + \sum_{i=2}^{t} T_{i,s,d}e^{-k_{s,d} (t-i)}
\]

Where \( L_{t,s,d} \) = accumulated litter at year \( t \), \( t= \text{year} \), \( s= \text{species} \), \( d= \text{water depth interval} \), \( k = \text{species specific breakdown rate at that water level} \), \( SC = \text{live standing crop of the previous} \)
year, and $T$ = turnover of the current year’s production which does not undergo breakdown in the current year but does undergo breakdown in subsequent years.

Accumulated litter and subsequent breakdown rates for *Phragmites* were assumed to be associated primarily with *Phragmites* stems which breakdown at a much slower rate than leaves (Gessner 2000, Bedford 2005). Multiple studies have shown that stems constitute 75-80% of aboveground *Phragmites* biomass (Kvet 1971, Kvet 1973, Kirschner et al. 2001, Asaeda et al. 2002) so *Phragmites* standing crop was multiplied by 80% so that the accumulation, breakdown, and disappearance of stems were investigated. Litter bag breakdown rates for each species at the various water depths were obtained from studies performed within Delta Marsh from the same time period (1985-1987) (Wrubleski et al., unpublished) as the litter accumulation data used in the mass balance estimates. Breakdown rates were within the range of published values for the separate species (table 2). The litter bag breakdown rates were placed in the mass balance model for each species at each water depth and the estimated litter accumulation was compared to observed litter accumulations. Alternatively, breakdown rates were fit to the mass balance model to estimate the difference between production inputs and observed accumulated litter for each species at each water depth for each marsh. The rate was fit to the model using a least squares fitting procedure. An average breakdown rate was calculated for each species at each depth and was plotted against the average litter bag estimates from Delta Marsh to see if the two rates were similar. Average live standing crop and accumulated litter for each species were log-transformed ($\ln+1$) to meet conditions of normality and year and water depth were compared using ANOVA. Non-transformed values are shown in all figures. Mass balance-derived breakdown rates were compared using ANOVA for species and water depth.

**RESULTS**

Live standing crop and accumulated litter differed significantly across years and water depths for *Typha* and *Scolochloa* and the interaction of water depth and year was significant for *Scolochloa* (table 3) (figure 1). Litter accumulation from all three species was poorly predicted by the litter bag breakdown rates at all water depths (figures 2-4). The mass-balance based breakdown rates (table 4) were able to track observed accumulation rates for
*Phragmites* (figure 2) and *Typha* (figure 3). Mass-balance breakdown rates were significantly lower for *Phragmites* than *Typha* ($F_{1,14}=5.07$, $p=0.03$) and significant for water depth ($F_{2,14}=4.35$, $p=0.04$) with litter in non-submersed areas breaking down more quickly than the areas under water (table 4). The mass balance model could not fit a reasonable breakdown rate for *Scolochloa*. The fitted breakdown rates for *Scolochloa* often did not converge within the least squares procedure, consistently predicting the exponential breakdown rate as extremely large. Mass-balance based breakdown rates for *Phragmites* and *Typha* were much greater than litter bag breakdown rates at similar water depths and deviated from the expected 1:1 ratio (figure 5).

**DISCUSSION**

**Litter Bag Breakdown Rates**

The overestimation of litter accumulation using litter bag breakdown rates is consistent with findings from shorter term studies in old fields (Wiegert and Evans 1964, Wiegert and McGinnis 1975) and emergent tidal marshes (Findlay et al. 1990, Lee 1990, Windham 2001). Short comings of litter bag studies have been noted by numerous authors (Boulton and Boon 1991, Heard et al. 1999, Schnitzer and Neely 2000). Much of the physical fragmentation of standing or fallen emergent litter is through wind, rain, and snow storms (Davis and van der Valk 1978a, Bohlen 1990, Welsch and Yavitt 2003), but litter material in mesh bags may be protected from physical fragmentation (Davis and van der Valk 1978a, Heard et al. 1999). The enclosure of the material also limits the transport of fine particulate organic matter (FPOM) to other areas of the marsh or to the sediment, and the enclosure may also influence oxygen diffusion (Webster and Benfield 1986). In addition, litter bags placed on the surface of existing litter may also have different rates of breakdown than litter that is at the middle or bottom of the accumulated pile, especially in areas above the water table that are subject to desiccation (van der Valk et al. 1991). The retention of small particles, the potential influences of enclosure on environmental conditions, and their location on the substrate may contribute to an overestimation of harvestable accumulated litter.
Mass Balance Derived Breakdown Rates

The standing crop and litter estimates used to determine mass balance breakdown rates were collected by clipping standing and fallen litter within quadrats. Most of the emergent litter studies that demonstrated litter effects on plant diversity, production, or the abiotic environment, also removed litter using similar methods (Haslam 1971, Graneli 1989, Bohlen 1990, Meyerson et al. 2000, Weltzin et al. 2005). The mass balance breakdown rates derived from clipped quadrat methods provide an estimate that can be used in conjunction with vegetation production models to predict long-term accumulations of harvestable litter and potential influences of litter on the wetland system.

Species

When considering species specific breakdown rates of *Phragmites* stems and *Typha*, the mass balance breakdown rates showed that *Phragmites* stems disappeared more slowly than *Typha*, which follows findings from litter bag studies in Delta Marsh (Murkin et al. 1989, van der Valk et al. 1991, Wrubleski et al., unpublished). Multiple authors report low breakdown rates in *Phragmites* stems and *Typha* (table 2) and those have been correlated to high levels of refractory material like lignin (Polunin 1984, Gessner 2000). Davis and van der Valk (1978b) found lower toppling rates for more refractory species like *Typha* and *Schoenoplectus fluviatilis (Torr.) M.T. Strong* versus other less refractory species like *Schoenoplectus tabernaemontani (K.C. Gmel.) Palla*. The mass balance model could only fit breakdown rates for more refractory species. *Scolochloa* values seemed to be poorly predicted by past production which may indicate that little of the previous year’s growth is left by the following August when litter was collected. Small amounts of remaining litter from the previous year would be swamped out by turnover litter produced in the current year. Some species may breakdown too quickly to assign annual mass balance breakdown rates based on annual litter crops. A more frequent sampling time period would be needed to estimate breakdown rates for less refractory species (Dickerman et al. 1986) but such material would likely not contribute significantly to long-term litter accumulation.
Water Level

The mass balance breakdown rates of both species suggested a negative relationship between water levels and breakdown rate. These findings run contrary to the litter bag findings of van der Valk et al. (1991) which reported decreased breakdown in litter bags in dry areas of the wetland presumably due to desiccation of the microbial community. Though desiccation may occur, microbial breakdown begins on standing litter even under dry conditions (Barlocher and Biddiscombe 1996, Kuehn et al. 2004) and fungal growth might be reduced in litter bags (Barlocher and Biddiscombe 1996). Litter in dry areas may also be subject to increased physical fragmentation when not enclosed in litter bags. Higher elevations in these marshes are found on the northern side of the marshes which are hit first by NNW winter winds and snow drifts from Lake Manitoba. Within the water column, stalks and litter might be more protected from winds. Differences in toppling might also account for the breakdown differences between elevations. Dead standing stalks are typically weakened at the air-water interface by microbial action (Davis and van der Valk 1978b) so deeper water has more of the standing stalk remaining in the water column. Bicknese (1987) and Murkin et al. (1992) also reported low oxygen in Delta Marsh vegetation and microbial breakdown is lower under low oxygen (Godshalk and Wetzel 1978). More study is needed to look at different aspects of litter breakdown (physical, microbial, invertebrate, etc) across water depths and determine whether the relative importance of such mechanisms changes at different water depths.

Implications

Due to its more refractory chemical composition, Phragmites is often most closely associated with litter accumulation and its litter is often cited as having impacts on the surrounding environment and plant community (Haslam 1971, Graneli 1989, Windham 2001, Meyerson et al. 2000), especially in areas where Phragmites ecotypes (Saltonstall 2002) are considered invasive (Windham 2001, Mal and Narine 2004). It is important to be able to predict litter accumulation to understand its dynamics and impact on ecosystem processes. Aseada et al. (2002) attempted to join modeled production (~1,000g/m²/yr) with litter bag breakdown rates (0.1825 yr⁻¹) to investigate nutrient and sedimentation dynamics in
Phragmites stands. Within five years, Phragmites litter accumulation was predicted to reach 3000-3500 g/m² which is much higher than typically observed (table 5). Likewise, in our mass balance model, if production values were maintained at 1,000 g/m²/yr, based on litter bag study breakdown rates of 0.2145 ± 0.051 (yr⁻¹) (see table 2), Phragmites litter would be predicted to reach 2170-2634 g/m² within 5 years and 2969-4228 g/m² within 10 years (figure 6). If the average breakdown rate for Phragmites stems derived from the mass balance model, 1.41 ± 0.32 (table 4), is combined with constant annual production of 1,000 g/ m², Phragmites litter biomass is nearly an order of magnitude lower and would range from 267-526 g/m² (figure 6). These values are well within the range reported in non-tidal freshwater wetlands (table 5) and seem to provide a more reasonable estimate of litter accumulation than estimates based on litter bag breakdown rates. Relying on such elevated litter accumulations from litter bag studies could lead to erroneous predictions regarding the potential effects of such high litter on abiotic conditions and plant communities.

Limitations

While the mass balance breakdown rates seem to provide adequate predictions of litter accumulation in Delta Marsh, it is unclear how applicable these rates are in other regions. Delta Marsh experiences high winds, large snow accumulation, and lower production than marshes at lower latitudes. Since fragmentation is influenced by storm events and climate (Davis and van der Valk 1978a, Bohlen 1990) the relative importance of physical fragmentation on breakdown rates within the MERP marshes may be higher than rates found at lower latitudes or in areas of less extreme weather. However, higher temperatures at lower latitudes could also increase the relative importance of microbial fragmentation. In addition, breakdown rates in these lower producing stands may not be the same as in higher producing stands since the degree of physical fragmentation due to wind, waves, and snow could differ in denser stands (Clevering 1998). Davis and van der Valk (1978b) suggested that dense live Typha growth from one year protected the standing litter of the previous year which decreased toppling rates but such effects of production on breakdown rates have not been studied. Denser stands also often have reduced oxygen (Rose and Crumpton 1996) which may lead to lower breakdown rates (Hietz 1992). More study of
the influence of physical and microbial fragmentation on unenclosed breakdown rates in low and high production sites is required and provides an interesting and exciting direction in the study of litter accumulation processes.

Conclusion

The current study has shown that in order to estimate in-situ accumulations of harvestable litter, breakdown rates other than those derived from litter bag studies need to be considered. A mass balance derived breakdown rate has been generated that can more accurately track litter accumulations in Delta Marsh and can reasonably predict litter accumulations when coupled with production models. Harvested litter accumulation and production values should be measured over multiple years at differing climates and under higher production levels to compare those rates with the mass balance breakdown rates found in this study. Detailed studies should also look more specifically at the influence of factors such as litter age, water depths, and seasonality on unenclosed breakdown rates. This study has demonstrated that a mass balance approach may be useful in investigating factors of litter accumulation in emergent macrophytes and may lead to more accurate estimations of accumulated litter and its potential effects on wetland systems.

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LITERATURE CITED


Windham, L. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21:179-188.
Table 1. Turnover results for the 1981 turnover study at Delta Marsh and supporting literature for turnover estimates applied to standing crop values in the model.

<table>
<thead>
<tr>
<th></th>
<th>Typha spp.</th>
<th>Phragmites</th>
<th>Scolochloa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standing</td>
<td>% in-season loss</td>
<td>Standing</td>
</tr>
<tr>
<td>1981 study at 8-28</td>
<td>1096</td>
<td>0.10</td>
<td>733</td>
</tr>
<tr>
<td>1981 study at 9-11</td>
<td>1253</td>
<td>0.15</td>
<td>596</td>
</tr>
<tr>
<td>van der Valk and Davis 1978a</td>
<td>2106</td>
<td>0.09</td>
<td>-</td>
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<td>Mason and Bryant 1975</td>
<td>1127.7</td>
<td>0.29</td>
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<td>-</td>
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Table 2. Litter bag derived breakdown rates for Phragmites stems, Typha spp, and Scolochloa from multiple experiments with similar mesh bag size. Dry – above water column, Int-sub – intermittently submerged, Sub – entirely submerged for length of experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>species</th>
<th>k rate</th>
<th>SE</th>
<th>mesh</th>
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<tbody>
<tr>
<td>van der Valk et al. 1991</td>
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<td>0.04</td>
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<td>0.792</td>
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<td>Typha latifolia</td>
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<td></td>
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Table 3. ANOVA results for annual live and litter crops (ln+1) for three species across years (1985-1989) and three water depths >=0cm, 1-20cm, 21-40cm.

<table>
<thead>
<tr>
<th>Species</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>F Ratio</th>
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</tr>
<tr>
<td>depth</td>
<td>2</td>
<td>30.09</td>
<td>15.40</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>depth*yr</td>
<td>8</td>
<td>26.22</td>
<td>3.36</td>
<td>0.001</td>
</tr>
<tr>
<td>Typha</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>4</td>
<td>38.16</td>
<td>9.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>depth</td>
<td>2</td>
<td>7.093</td>
<td>3.54</td>
<td>0.04</td>
</tr>
<tr>
<td>depth*yr</td>
<td>8</td>
<td>5.54</td>
<td>0.69</td>
<td>ns</td>
</tr>
</tbody>
</table>

Table 4. Mass balance breakdown rates (Kmb) for the three species, at three water depths, fit to observed litter values using a simple exponential model based on past annual production.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Species</th>
<th>Kmb</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>0cm</td>
<td>Phragmites</td>
<td>2.01</td>
<td>.53</td>
</tr>
<tr>
<td>1-20cm</td>
<td>Phragmites</td>
<td>1.29</td>
<td>.46</td>
</tr>
<tr>
<td>21-40cm</td>
<td>Phragmites</td>
<td>.93</td>
<td>.65</td>
</tr>
<tr>
<td>Overall mean</td>
<td>Phragmites</td>
<td>1.41</td>
<td>.32</td>
</tr>
<tr>
<td>0cm</td>
<td>Typha</td>
<td>3.54</td>
<td>.53</td>
</tr>
<tr>
<td>1-20cm</td>
<td>Typha</td>
<td>1.94</td>
<td>.46</td>
</tr>
<tr>
<td>21-40cm</td>
<td>Typha</td>
<td>1.61</td>
<td>.46</td>
</tr>
<tr>
<td>Overall mean</td>
<td>Typha</td>
<td>2.36</td>
<td>.28</td>
</tr>
<tr>
<td>0cm</td>
<td>Scolochloa</td>
<td>&gt;5</td>
<td>-</td>
</tr>
<tr>
<td>1-20cm</td>
<td>Scolochloa</td>
<td>&gt;5</td>
<td>-</td>
</tr>
<tr>
<td>21-40cm</td>
<td>Scolochloa</td>
<td>&gt;5</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 5. Summary of ranges of live production and litter mass for *Phragmites* and *Typha* spp. in a variety of different systems.

<table>
<thead>
<tr>
<th>Production range</th>
<th>Litter mass</th>
<th>species</th>
<th>system</th>
<th>source</th>
</tr>
</thead>
<tbody>
<tr>
<td>774-850</td>
<td>800-1600</td>
<td><em>Phragmites</em></td>
<td>FW wetland</td>
<td>a</td>
</tr>
<tr>
<td>153-399</td>
<td>225-496</td>
<td><em>Phragmites</em></td>
<td>FW wetland</td>
<td>b</td>
</tr>
<tr>
<td>1080</td>
<td>271-395</td>
<td><em>Phragmites</em></td>
<td>FW lake</td>
<td>c</td>
</tr>
<tr>
<td>na</td>
<td>~200-400</td>
<td><em>Phragmites</em></td>
<td>FW lake</td>
<td>d</td>
</tr>
<tr>
<td>~320-720</td>
<td>~300-850</td>
<td><em>Phragmites</em></td>
<td>FW lake</td>
<td>e</td>
</tr>
<tr>
<td>6410</td>
<td>5037</td>
<td><em>Phragmites</em> 20 yr</td>
<td>FW tidal</td>
<td>f</td>
</tr>
<tr>
<td>~1800</td>
<td>2435</td>
<td><em>Phragmites</em> 5 yr</td>
<td>FW tidal</td>
<td>f</td>
</tr>
<tr>
<td>1785-1925</td>
<td>1224-2380</td>
<td><em>Phragmites</em></td>
<td>Brackish tidal</td>
<td>g</td>
</tr>
<tr>
<td>814-1786</td>
<td>980</td>
<td><em>Phragmites</em></td>
<td>Brackish tidal</td>
<td>h</td>
</tr>
<tr>
<td>500</td>
<td>250</td>
<td><em>Phragmites</em></td>
<td>Brackish tidal</td>
<td>i</td>
</tr>
<tr>
<td>na</td>
<td>~1000-2000</td>
<td><em>Phragmites</em> - interior</td>
<td>Salt marsh</td>
<td>j</td>
</tr>
<tr>
<td>781-1754</td>
<td>1457-1580</td>
<td><em>Typha</em> spp</td>
<td>FW wetland</td>
<td>a</td>
</tr>
<tr>
<td>408-896</td>
<td>183-619</td>
<td><em>Typha</em> spp</td>
<td>FW wetland</td>
<td>k</td>
</tr>
<tr>
<td>298-704</td>
<td>83-485</td>
<td><em>Typha</em> spp</td>
<td>FW wetland</td>
<td>b</td>
</tr>
<tr>
<td>Na</td>
<td>200-1200</td>
<td><em>Typha latifolia</em></td>
<td>Created wetlands</td>
<td>l</td>
</tr>
<tr>
<td>425-638</td>
<td>248-422</td>
<td><em>Typha latifolia</em></td>
<td>Riverine marsh</td>
<td>m</td>
</tr>
<tr>
<td>~1500-1900</td>
<td>~700-800</td>
<td><em>Typha</em> spp</td>
<td>FW tidal</td>
<td>n</td>
</tr>
<tr>
<td>~1700</td>
<td>~500</td>
<td><em>Typha</em> spp</td>
<td>FW tidal</td>
<td>f</td>
</tr>
<tr>
<td>1750</td>
<td>500</td>
<td><em>Typha angustifolia</em></td>
<td>Brackish tidal</td>
<td>i</td>
</tr>
</tbody>
</table>

Figure 1. Average live standing crop from 1985 to 1989 across three water depth intervals for three species, *Phragmites*, *Typha*, and *Scolochloa*. Averaged from the four experimental marshes. Note different y-axis for each species. Standard error bars are shown.
Figure 2. Observed and modeled litter standing crops for *Phragmites australis* in the MERP marshes, stratified by water depth. Kmb - mass balance fit breakdown rates (see table 4), Klb - litter bag rates (see table 2 Wrubleksi data). See methods for model explanation. Shaded areas are +/- 1 SE for k estimate and standard error bars shown for observed litter averages.
Figure 3. Observed and modeled litter standing crops for *Typha glauca* in the MERP marshes, stratified by water depth. Kmb - mass balance fit breakdown rates (see table 4), Klb - litter bag rates (see table 2 Wrubleksi data). See methods for model explanation. Shaded areas are +/- 1 SE for k estimate and standard error bars shown for observed litter averages.
Figure 4. Observed and modeled litter standing crops for *Scolochloa festucacea* in the MERP marshes, stratified by water depth. Klb - litter bag rates (see table 2 Wrubleksi data). See methods for model explanation. Note the change in y-axis for 0cm. Shaded areas are +/- 1 SE and standard error bars shown for observed litter averages.
Figure 5. Comparison of fitted breakdown rates (k-mb) against litter bag breakdown rates (k-lb) for *Phragmites* (diamond) and *Typha* (triangle) across 3 water depths – 0cm, 1-20cm, 21-40cm. (litter breakdown rates used with permission from Wrubleski et al., unpublished). Standard error bars shown.
Figure 6. Hypothetical litter accumulation of *Phragmites* with a constant annual production of 1000 g/m². Klb- litter bag derived breakdown rate for *Phragmites* of 0.2154 +/- 0.051. Kmb-Mass-balance derived breakdown rate for *Phragmites* of 1.41 +/- 0.32. Shaded area is +/- 1 SE.
CHAPTER 5. MODELING EMERGENT MACROPHYTE SPREAD AND THE ACCUMULATION OF *TYPHA* LITTER FOLLOWING A DRAWDOWN

a paper to be submitted to the journal Aquatic Botany

Jay R. Christensen, Arnold G. van der Valk, William G. Crumpton

ABSTRACT

Emergent species, such as the cattail hybrid (*Typha glauca* Godr.), can often accumulate litter within wetlands due to their large spatial extent, high annual production, and slow breakdown rates. High litter accumulation may influence local abiotic conditions, other biota, and ecosystem processes. A spatial model of litter accumulation was developed for *Typha* that included a spatial distribution model, a production model, and a litter breakdown model. The spatial distribution model included dominant and subdominant species and was developed to predict changes in the spatial distributions for each of the most common emergent species (*Typha glauca*, *Phragmites australis* (Cav.) Trin., *Scolochloa festucacea* (Willd.) Link, and *Schoenoplectus tabernaemontani* Palla) after a drawdown in an experimental marsh complex. Emergent stands are often heavily mixed following a drawdown and the inclusion of species as subdominants should better predict emergent distributions and expansion. The *Typha* distribution model was then combined with a *Typha* production model and a litter breakdown model to predict patterns of *Typha* litter accumulation. In areas where *Typha* was classified as subdominant at the start of the model, *Typha* often became dominant as less flood-tolerant dominant emergent species died out. Predicted *Typha* and *Scolochloa* distributions had greater spatial extents than observed distributions prior to the drawdown. *Phragmites* distributions, however, were underestimated by the model and neither the observed nor the predicted distributions reached pre-drawdown coverage. Predicted *Typha* litter accumulation reached pre-disturbance levels 5-6 years after the drawdown. Litter mass increased quickly in areas of *Typha* expansion with moderate increases in areas of the wetland where stands were >2 years old. According to the model, litter also persisted for several years in areas where *Typha* was extirpated. The plant distribution model illustrates the importance of including subdominants and understanding
persistence when studying emergent expansion. The implications of *Typha* litter accumulation and its potential effects on wetlands are also discussed.

**INTRODUCTION**


Litter accumulation in a wetland is a function of: 1) the emergent species’ spatial distribution, 2) its annual production, and 3) its litter breakdown rate. The process of litter accumulation is spatially and temporally complex in marshes because plant distributions and litter breakdown rates vary with different water depths and the process occurs over multiple years (van der Valk et al. 1991, Squires and van der Valk 1992, Battle and Golladay 2001, Bedford 2005, Christensen et al., Chapter 4). Spatial distributions and litter accumulation of emergents, and their interactions with water levels can be examined through modeling which is well suited for studying complex spatial interactions that occur over longer time scales.

In this paper, we investigate the accumulation of litter in a series of marshes in an experimental wetland complex in the Delta Marsh (Murkin et al. 2000a). Data were collected as part of this study on the mass of both live and dead emergent vegetation for five years after a drawdown. In the Delta Marsh, the cattail hybrid (*Typha glauca* Godr.) has been expanding as it has throughout much of the eastern US and into Canada (Galatowitsch et al. 1999). It is highly productive (Shay and Shay 1986, van der Valk and Davis 1978a), and is an aggressive species that responds quickly to disturbance when it can displace native
vegetation (Galatowitsch et al. 1999, Zedler and Kercher 2004). *Typha glauca* also produces persistent litter which can accumulate in mature stands (Shay and Shay 1986, Rose and Crumpton 1996, Rose and Crumpton 2006). The implications of the spread of *Typha glauca*, especially its litter accumulation patterns, are our major foci.

In order to model *Typha* litter accumulation, we need to know its distribution, primary production, and litter breakdown rate. Adult *Typha* distributions depend on multiple factors including water depths (Squires and van der Valk 1992, van der Valk 1994) and the preemptive presence of other emergent species that either temporarily or permanently exclude *Typha* from a location (Grace 1987, van der Valk 2000, van der Valk 2005). Multiple spatial distribution models have been developed to track changes in distributions of wetland vegetation with changes in water depth, focusing on functional groups (Poiani and Johnson 1993, Ellison and Bedford 1994, Poiani et al. 1996) or species (Seabloom et al. 2001). These spatial models have only allowed for one group or species to inhabit a location at one time. During a drawdown the germination of multiple emergent species creates heavily mixed emergent stands when the area is re-flooded (van der Valk 2000). Models that only allow for one species to exist in one location must simplify stand composition to include just the dominant species (van der Valk 2000). The presence of subdominant species is lost and could limit the model’s ability to predict future distributions and potential expansion. Current models of the vegetation dynamics of the Delta Marsh (de Swart et al. 1994, Seabloom et al. 2001) do not take subdominants into account.

In this study, a plant distribution model (Seabloom et al. 2001) driven by species specific water depth responses was modified to allow for more than one species to occupy the same location simultaneously. The inclusion of both dominant and subdominant species should better predict emergent distributions after a drawdown. The distribution of *Typha* predicted by this expanded model is then combined with a production model for *Typha* and a litter breakdown model (Christensen et al. Chapter 4) to predict *Typha* litter accumulation patterns for ten years after the drawdown ended. We are restricting our consideration of emergent litter accumulation to only *Typha* litter because there is not enough data to develop production and litter breakdown models for the other dominant emergent species in the Delta Marsh. To test the reliability of our expanded model, predicted distributions of emergent
species are compared to known distributions based on low-level aerial photographs. Predicted *Typha* litter accumulation patterns across depths are also compared to measured litter accumulation patterns.

Our main goals in this paper are to determine: (1) if an expanded vegetation dynamics model that includes subdominant species improves our ability to predict the post-drawdown distribution of emergent species; and (2) if we can predict the litter accumulation patterns of *Typha glauca*. Being able to predict litter accumulation patterns will enable us to refine models of various processes in the Delta Marsh and other wetlands, including rates of the nutrient cycling, rates of methane release, the distribution of anoxic zones, and the distribution of invertebrates.

**METHODS**

**Study Site**

The Marsh Ecology Research Program (MERP) at Delta Marsh, Manitoba was a long-term, replicated, large scale experiment that investigated the influence of water level fluctuations on the production and distribution of wetland plants. The current study utilizes data that were previously collected as part of the MERP study. A complete review of the MERP study methodologies can be found in Murkin et al. (2000a). In 1979, ten diked marshes, each approximately 5 ha, were created within Delta Marsh along the southern shore of Lake Manitoba. Water levels of Lake Manitoba and Delta Marsh were stabilized in 1961, reducing water fluctuations within the marsh from +/- 2.1 m to +/- .3 meters around the 30 yr mean of 347.5 m above mean sea level (AMSL) (Batt 2000).

In 1980 the marshes were maintained at 347.5 m AMSL and baseline data on species distributions and production were collected. Two additional reference areas of similar size were also included in the study and were located on either side of the ten diked marshes. The reference marshes were subject to the water level fluctuations of Delta Marsh but were not subject to water manipulations carried out in the ten experimental marshes. All ten marshes were flooded 1 m above the 30 yr average for two years and then drawn down to 0.5 m below the normal levels for one to two years. The drawdown allowed for the germination of annuals and emergents as predicted by van der Valk and Davis (1978b). In 1985 four marshes were
returned to the 30 yr average water level of 347.5 m AMSL (normal) and the current study examines litter accumulation in the normal marshes after the flooding-drawdown event and compares it to baseline conditions (1980). With the return of water levels to the 30 year average in the four normal water level marshes, annual vegetation died and emergent vegetation began the regenerating phase of the wet-dry cycle (van der Valk et al. 1994, van der Valk 2000).

**Model Development and Validation**

*Plant Distribution Model*

*Typha glauca* is tolerant of shallow to deeper water, with the highest probability of occurrence at a water depth of 15 cm (de Swart et al. 1994). Pre-emption and the overlap of potential distributions of other emergent species may influence the realized distribution of *Typha glauca* (van der Valk 2000, van der Valk 2005). Therefore, three other rhizomatous emergent species common in Delta Marsh were also included in the distribution model. *Phragmites australis* (Cav.) Trin. is most common 30 to 70 cm above the water table but can extend to 50 cm deep in these marshes (de Swart et al. 1994) and can be found concurrent with *Typha glauca* (Shay and Shay 1986). *Scolochloa festucacea* (Willd.) Link occupies areas slightly above the water table to just below the water table (de Swart et al. 1994). *Schoenoplectus tabernaemontani* Palla (formerly *Scirpus validus*) is only intermittently present in the experimental marshes and is intolerant of flooding. *Schoenoplectus acutus* var. *acutus* was dominant in many of the deeper areas in 1980 and is often found with *Typha* (Shay and Shay 1986) but no stands were reported in 1985 and very few dominant stands developed afterward (van der Valk 1994, van der Valk 2000, Seabloom et al. 2001) Since no stands, dominant or subdominant, were reported in 1985, *S. acutus* responses were not included in the distribution model. *Typha glauca, Phragmites australis, Scolochloa festucacea* will be referred to by their generic epithets from this point forward.

The MERP study included elevation surveys and vegetation maps that were digitized by previous researchers (de Swart et al. 1994, Seabloom et al. 2001). Digital vegetation maps were delineated by identifying dominant plant species from low level (610 m) infrared aerial photographs and verifying dominant species at the sites during each fall from 1980-1989 (de
Swart et al. 1994). On site verification also allowed the inclusion of subdominant species on coverage maps for many areas that were not homogeneous. For the current study, digital elevation and vegetation coverage maps were placed within ArcMap (ESRI) and georeferenced. The elevation maps were converted into 3x3 m grid cells for the spatial model and then normalized to the constant 30 year water depth elevation of 347.5 to provide water depths. From the vegetation maps for 1980 and 1985-1989, separate 3x3m grids were created for each major species, *Phragmites*, *Typha*, *Scolochloa*, and *S. tabernaemontani*, that indicated areas of dominance, subdominance, and areas where the species was not present. Areas within 5 meters of dikes and the original borrow pits were also excluded from the grids. The 1985 maps indicated high dominance by *S. tabernaemontani* in many areas which died out after 1985. Limited areas were reported as dominant by *S. tabernaemontani* in 1985 with no subdominants, but the same areas were dominated by *Typha* and *Phragmites* in 1986. Since neither species can germinate under water (Galinato and van der Valk 1986, Seabloom et al. 1998, Baldwin et al. 2001) and spread at rates of 3m/yr (Yeo 1964), it is presumed that they were present as subdominant species in 1985 but were not accounted for in *S. tabernaemontani* stands.

This distribution model did not attempt to predict distributions during the flooding-drawdown event (1981-1984) but used species distribution grids in 1985 during the first year of re-flooding as the starting point for the model. The 3x3m species grid cells are discrete units that are subject to a set of rules that dictate the response to flooding, the potential for rhizomatous growth, and the interaction with neighboring cells during each time step. The model generally follows the rules developed for perennial adults with rhizomatous dispersal and flooding damage in Seabloom et al. (2001) but with the addition of subdominants. For each species, each cell in the grid is designated as one of five states: 1) dominant and actively growing, 2) dominant and inactive, 3) subdominant and active, 4) subdominant and inactive, or 5) empty (figure 1).

The state of the species’ dominance and activity is determined by its response to flooding. Flooding tolerance was estimated by probability curves modified by Seabloom et al. (2001) that were originally determined by de Swart et al. (1994). De Swart et al. (1994) fit logistic regression models to the probability of occurrence for the main emergent species at
varying water depths using distribution data from 1980 in the experimental cells. Since *S. tabernaemontani* was not abundant in 1980, regressions were not possible. Seabloom et al. (2001) assumed *S. tabernaemontani* had distributions similar to *Scolochloa* and a similar lack of tolerance to deeper water. Seabloom et al. (2001) normalized the distribution to water depth and converted each species to a 0 to 1 probability scale (figure 2). In this distribution model, the water depth in a given cell is compared to the water depth response curves of the species that occupy that cell. If the water depth is deeper than the species’ optimum water depth (where probability = 1) then a random value from 0 to 1 is compared with the probability of water tolerance for that cell. If the random number is greater, the plant experiences flooding damage. All dominant species were assumed to be in the reproductively active stage in 1985. If water depth exceeds a species water depth tolerance, the emergent stand becomes dominant, inactive. Emergent species have been shown to cease expansion and growth when stressed in deeper water (McKee et al. 1989, Squires and van der Valk 1992, Weisner and Strand 1996). A species could return to the active state if water levels receded or could drop to the subdominant, inactive state in the next time step if water levels continue to exceed its tolerance. Rhizomatous emergents can often withstand up to two years of high flooding until reserves are exhausted and the plant dies (Squires and van der Valk 1992, van der Valk 1994). If water levels exceed flood tolerance in a subdominant, inactive stand, the stand dies and the cell is designated as empty. A subdominant, active stand can rise to the state of dominant when the previous dominant species has been reduced to subdominant or lost. If more than one subdominant is present in a cell, the species with the higher probability based on water depth responses is selected to become dominant.

Only dominant, active stands can spread to neighboring cells. Only cells directly adjacent to the dominant stand are selected and the neighboring cells must be empty of other species. A random draw is compared with the water depth tolerance of the species to determine if the neighboring cell is suitable. Using a 3x3m grid ensures that rhizomatous growth does not exceed 3m-4m expansion/yr which is the rate suggested by Yeo (1964) for *Typha* and *Phragmites* (Clevering and van der Toorn 2000).

The model was begun in 1985 with the first year of reflooding and was run for ten years until 1994. The output of the distribution model was separate 3x3m grid distribution
predictions for each of the four species from 1986-1994. The proportion of the marshes dominated by each species was created from estimates of each grid. Analysis of the accuracy of modeled distributions was done by comparing the predicted designation of each cell with the observed designation from 1986-1989. The proportion of each marsh predicted correctly was obtained along with the model error including all different combinations of failed predictions (ie. predicted dominant vs. observed empty, predicted subdominant vs. observed dominant, etc). The model was also compared to pre-disturbance 1980 distributions to indicate the similarity and difference for *Typha*, *Phragmites*, and *Scolochloa* during its recovery from disturbance.

**Production Model**

Live production estimates used in investigating *Typha* litter accumulation came from two sources. *Typha* production began slowly during the drawdown and began to noticeably increase 3-4 years after flooding returned, presumably allocating much more photosynthates to below ground storage during the initial re-flooding years (van der Valk 2000). During the first five years, production estimates used in the model were from observed production estimates obtained from clipped quadrats in the fall. Once production had increased toward maturity by the end of the observed period, a production model calibrated from one of the mature reference marshes was implemented to give general production estimates for the final five years of the simulation.

Each of the diked and reference marshes was evenly divided into ten zones and a transect was randomly selected within each zone, each year. Four samples were taken from each transect so that 40 samples were taken in each marsh, each year. At each sampling point all live and dead material was clipped at the substrate within a 1m x 1m quadrat, separated into live and dead material, sorted by species, and placed in burlap bags. Water depths were recorded at the time of sampling. All samples were dried at 80 °C and weighed. Live standing and litter crop samples were taken primarily in the month of August. During each season, the sampling schedule was randomized so that seasonal bias within a given marsh was avoided.
One of the reference marshes in Delta Marsh was predominately *Typha glauca* and was used to calibrate the production model used in the later five years of the simulation. Above ground clipped quadrats were taken from 1980-1989 for the reference marsh. Below ground material was also collected from 20 samples, two in each of the 10 zones, in the reference marsh every late spring and fall (see Murkin et al. 2000a for more detail) but due to inconsistencies in sampling only 1984-1989 values are used here. Below ground material was not separated by species but since the reference marsh was dominated by *Typha*, belowground estimates were assumed to be predominantly from *Typha*. Unlike the experimental marshes that had a constant water level, the reference marshes were subject to the 30cm variations typical of the larger Delta Marsh and Lake Manitoba. Production was estimated by combining: 1) rhizome stocks with translocation estimates, 2) a temperature component that influenced growth and rhizome loss, and 3) a rainfall component that negatively influenced production when rainfall from June and July amounts dropped below 50% of the 30 year average.

Rhizomes stocks are essential to initial emergent growth in the spring (Gustafson 1976, Fiala, 1976, Grace and Wetzel 1981, Aseada et al. 2006). Non-structural carbohydrates are translocated upwards during growth initiation and then photosynthates are translocated back into belowground biomass for maintenance, growth, and future reserves throughout the summer and fall. Rhizome components have been used in multiple models for rhizomatous emergents including *Typha* (Tanaka et al. 2004, Aseada et al. 2005, Hai et al. 2006) and *Phragmites* (Aseada and Karunaratne 2000, Soetaert et al. 2004, Aseada et al 2002, Aseada et al. 2006). Studies of emergents have estimated that between 10 and 25% of the initial rhizome biomass is translocated up to aboveground growth in the spring (Westlake 1982, Aseada and Karunaratne 2000, Aseada et al. 2005). Downward translocation of carbohydrates varies across latitude (McNaughton 1966, Aseada et al. 2005) with estimates of 45-79% of current aboveground production for *Typha latifolia* and *Typha angustifolia* (Aseada et al. 2005). Downward translocation occurs once aboveground production is established beginning in mid-summer until senescence (Fiala 1976, Gustafson 1976, Aseada et al. 2006), which in the Delta marsh would be from July through mid-September. In the simulation, during the month of June when growth was initiated, an estimate of 18% of
belowground biomass for upward translocation and a value of 74% for downward translocation fit well with observed measurements of belowground biomass and fall within the ranges given above. Rhizome loss (a combination of respiration and mortality) per month was temperature dependent and an estimate of 12.8% of biomass per month fit observed data well and is similar to estimates of 15.0% in Asaeda et al. (2005).

A growth parameter for aboveground production, which incorporated production and respiratory losses during the growing season, was calibrated at 1.056 g/g/mo. to the reference data and was temperature dependent using the Arrhenius constant of 1.07 at 20 °C. Monthly averages of daily mean temperature were used. The rate of production in the reference marsh was also influenced by rainfall in years where June rainfall dropped below 50% of the 30 year June average. When June rainfall was above 50% of the 30 year average, the rainfall parameter remained 1. The rainfall parameter value was calculated as the percentage below 50% of the 30 year June average. The summer of 1988 was a hot, dry year at Delta Marsh with only 38% of the average rainfall in June and production decreased during that year. Van der Valk and Davis (1980) showed that dry conditions can negatively impact emergent plants and Morris and Haskin (1990) showed a strong correlation from precipitation patterns from June-August during 5 years within a *Spartina alterniflora* marsh. The rainfall parameter helped explain the decrease in production for 1988 in the reference cells, but since the litter accumulation model used actual production values from 1985-1989, and no years from 1990-1994 had rainfalls far below the 30 year average, the rainfall parameter does not influence the litter accumulation model, only the initial calibration of the production model. The calibrated model tracked aboveground and below ground production within the *Typha* dominated reference cell (Figure 3).

When the production model was initially applied to the experimental marshes and run for the entire length of the simulation, 1985-1994, it resulted in very low biomass due to an extremely low initial belowground biomass. It is possible that the low production during the first years of *Typha* growth results from very high translocation rates of aboveground photosynthates to below ground reserves (van der Valk 2000) that are different from our model calibrated in a mature stand. Few studies have investigated the allocation of reserves in newly generated stands and thus it was decided to use actual data during maturation and
simulated values once the stands were more mature. In addition, belowground biomass was not separated by species, so in the early mixed stands it was impossible to determine the proportion of belowground biomass allocated to *Typha*. Once the stand were more mature, the assumption was made that the majority of below ground biomass was *Typha* as it had begun to dominate and other emergents had declined (van der Valk 2000, van der Valk 2005). Estimates of 490 g/m² of belowground biomass were reported in the fall of 1989 (van der Valk 2000). Using 490 g as the initial below ground estimate, the model was run with a monthly time step and the output of annual aboveground and below ground biomass was reported. The model produced reasonable aboveground production numbers ranging from 274 – 351 g/m² (table 1) which is similar to the lower range of values produced in the reference cells (298-704 g/m²). Below ground production ranged from 604-897 g/m² which are in the lower range of values found in the reference cells (650-1400 g/m²) and similar to belowground biomass found in 1980 (870 g/m²). Belowground to aboveground ratios for the simulated experimental marshes averaged 2.4. This ratio is below the observed ratios in the reference cells (3.3) but above other ratios, 1.4-1.8, from similar latitudes (Dykyjova 1971, Graver et al. 1988, Aseada et al. 2005). The observed (1985-1989) and simulated (1990-1994) annual production values (table 1) were placed within the litter breakdown model to arrive at litter accumulation estimates.

*Litter Breakdown Model*

Litter breakdown rates were calculated from a mass balance model as described by Christensen et al. (Chapter 4). Briefly, the breakdown rates were estimated by fitting a breakdown rate to a mass balance model that incorporated measured annual standing crops, an exponential breakdown function (Wieder and Lang 1982) and observed accumulated litter over five years. Breakdown rates for *Typha* were fit for each marsh, stratified by water depth, over the period from 1985 until 1989. Water depth layers were elevations above the water level (>0cm), 1-20cm, and 21-40cm. Mathematically, the model is as follows for each water depth interval:

\[
L_{t,d} = L_{t,d}e^{-k_d(t-1)} + \sum_{i=1}^{t-1} S_{t,i}d e^{-k_d(t-i)} + \sum_{i=2}^{t} T_{t,i}d e^{-k_d(t-i)}
\]
Where \( L_{t,d} \) = accumulated litter at year \( t \), \( t=\text{year}, d=\text{water depth interval}, k=\text{breakdown rate at that water level}, \ SC=\text{live standing crop of the previous year}, \) and \( T=\text{turnover of the current year’s production which does not undergo breakdown in the current year but does undergo breakdown in subsequent years}. \) The turnover rate was estimated from a turnover study conducted in 1981 which estimated within season turnover as 10% of standing crop (Christensen et al. Chapter 4).

**Combined Models and Output**

The litter accumulation was simulated for each cell within the grid for *Typha* during each year from 1985 to 1994. The water depth at each cell determined which breakdown rate was used +/- normalized variation around the mean breakdown rate. Based on the output of the distribution model, if a cell was determined to be dominated by *Typha*, the full production value +/- normal variation from the annual production model was assigned to the cell. If a cell was designated as *Typha*-subdominant, a quarter of the production value was used, which followed the approximate ratio of biomass in dominant stands versus subdominant stands in the observed 1985-1989 data (see appendix B, table 2). A production value of 0 was given to cells that were designated as empty. The output from the combined models included grid values of accumulated litter (g/m\(^2\)) for each year from 1985-1994 for the four marshes and based on marsh averages, an average accumulated litter was obtained for each year across the three water depths and across stand ages for 1994. Production and breakdown rates used in the model are provided in table 1.

**RESULTS**

**Modeled and observed distributions 1985-1989**

Areas dominated by *Typha* in 1985 were estimated at only 2.4% of the total area but quickly increased in 1987 as subdominant areas became dominant (figure 4). Modeled predictions of the proportion of modeled wetland area dominated by *Typha* and *Scolochloa* tracked the observed proportion but the model failed to track the area of *Phragmites* dominant stands (figure 4). By 1989, modeled and observed estimates of the areal extent of
dominant *Typha* and *Scolochloa* converged to within 2.8 % and 0.5 % respectively (figure 4). The modeled designation of individual grid cells of *Typha* matched observed designations in 62-69% of grid cells over the four years (table 2). *Typha* had some underestimation of subdominant and dominant stands in areas of deeper water (figure 5) such as marsh 3 but also had an overestimation of 9% due to subdominant stands achieving dominance over *Phragmites* and *S. tabernaemontani* and subsequently expanding in marsh 4 (figure 6, 7a). *Scolochloa* distributions based on each grid cell were well predicted by the model (table 2) with the majority of the bias being attributed to an underestimation of subdominant stands in marsh 4 and greater dominance in marsh 7 than predicted (figure 8,9a). Some areas of *Scolochloa* also expanded more than the observed distributions, resulting in an 8% overestimation by 1989 (Figure 9a). *Phragmites* existed as subdominant or in small refugial stands in 1985 which died out in the model but still persisted in reality (Figure 10). Most model error for *Phragmites*, 12-27%, was attributed to an underestimation of species present as the dominant or subdominant in a stand (figure 11a). The model correctly predicted 61-74% of the *Phragmites* grid cells which consisted primarily of empty cells and the established stands at the highest elevations (figure 5 and 10). For *S. tabernaemontani*, by the end of the observed period the model accurately predicted 87% of the distribution with most of the remaining bias attributed to an underestimation in the persistence of *S. tabernaemontani* as a subdominant species (figure 12).

**Comparison to Baseline Year**

*Typha* began with few areas of dominance in 1985 compared to 1980 but after two years of lag time, subdominant areas of *Typha* became dominant and began to expand until it surpassed the 27 % total wetland area dominated by *Typha* in 1980 (figure 4). Dominant *Scolochloa* in 1985 was much higher than in 1980 and declined through the observed period as dominance in deeper water was lost (figure 4). Despite the initial decline, the model predicted a stabilization of *Scolochloa* distributions at 22% of total wetland area (figure 4) compared to the 10% coverage of wetland area observed in 1980. *Phragmites* area before the flooding-drawdown event was 25.2% but observed estimates of area fluctuated after the drawdown and only reached 17% in 1986 before declining in subsequent years (figure 4).
Comparing individual grid cells between predicted designations and 1980 designations, modeled *Typha* returned to areas previously dominated by *Typha* in 1980 (Figure 7b) but also expanded into areas not dominated by *Typha* in 1980, as seen in the divergence of predicted dominant cells vs. empty 1980 cells (Dom vs Empty in figure 7b). Modeled *Scolochloa* occupied all areas previously occupied in 1980 and also experienced expansion of dominants and subdominants (figure 9b). For *Phragmites*, the predictive model extirpated subdominant stands that were considered suboptimal in the first years of flooding, resulting in a consistent difference of 22% of areas that were previously dominated by *Phragmites* in 1980 (figure 11b).

**Litter accumulation**

*Typha* litter accumulation increased at all depths through the 10 year simulation (figure 13). Accumulation was greatest at the 1-20 cm water levels due to increasing expansion and dominance by *Typha* at optimal shallow water depths, increasing production through maturation, and intermediate breakdown rates. After 5-6 years, litter accumulation at the 1-20cm and 21cm+ water levels surpassed the average litter accumulation seen in 1980. Litter above the water level failed to reach levels seen in 1980. Litter accumulation increased with stand age when dominant stands of *Typha* had reached mature levels of production, quickly accumulating during the first 2-3 years and increasing more slowly in later years (figure 14). Litter decreased in stands where *Typha* was no longer dominant though substantial amounts of litter were present for several years after *Typha* was extirpated from an area (figure 14).

**DISCUSSION**

**Distributions**

Including subdominants improved predictions of *Typha* distributions in areas where flood intolerant species like *S. tabernaemontani* dominated in 1985 but were quickly replaced by species like *Typha*. Without the presence of *Typha* as a subdominant, colonization of empty areas would have been severely limited and dependent on vegetative expansion from the isolated dominant stands that only covered 2.4% of the wetland in 1985.
The inclusion of subdominant species distributions adds to the Seabloom model (Seabloom et al. 2001) in that more than one species can exist in a cell, but the necessary resolution for subdominants was lacking in the 1985 vegetation coverages. Maps sometimes did not include subdominant species even if present or more often coverages were mapped to highlight the dominant distribution, ignoring the necessary spatial detail of the understory species. The inclusion of subdominants within the Seabloom model that predicted seedlings from the seedbank could potentially allow for greater detail regarding subdominants and combining the two models could better predict the distribution of subdominant species instead of solely relying on the more generalized maps provided by aerial photos in 1985.

The distribution model also reiterated the importance of stochastic events on the distribution and composition of emergent species in wetlands. Welling et al. (1988) found differing levels of emergent germination and survival between the two drawdown years, possibly based on differences in soil moisture between years. Due to the stochastic event of the drawdown, though many regions returned to distributions seen prior to the disturbance, the composition of some marshes according to model predictions appeared to change when compared to 1980. This is the case when considering the observed loss of *Phragmites* compared to 1980 (figure 10) and the predicted shifts of *Typha* and *Scolochloa* (figures 6 and 8). Such changes may not persist if other factors such as exploitative competition (not modeled) could reverse some of the changes indicated in the model (Bertness and Ellison 1987, Grace 1987). For instance, *Schoenoplectus acutus* was dominant in 12.9% of the marshes in 1980 but based on dominant and subdominant vegetation coverages in 1985, *S. acutus* was absent. In 1988-1989, small pockets of *S. acutus* were present as subdominants and dominants (van der Valk, 2000) and *S. acutus* may through time build up again and dominate areas of deeper water.

The distribution model also demonstrated the need to better understand water depth tolerances and the relative importance of other factors that may be influencing the persistence of species. Much of the error for the modeled distributions of *Typha, Scolochloa* and *Phragmites* was due to premature predicted loss of stands to inundation. *Phragmites* stands observed as dominants or subdominants in 1989 (figure 10) were below elevations (figure 5) considered the optimum elevations (30-70 cm above the water table) after 20 years of stable
water levels (de Swart et al. 1994). The current distribution model added two years to the flooding damage lag times used in Seabloom et al. (2001) but actual stands of *Phragmites* continued to persist well after the model predicted extirpation. Experimental studies of emergent responses to water levels are at most two years (Squires and van der Valk 1992, Coops et al. 1996, Vretare et al. 2001, White and Ganf 2002). Squires and van der Valk (1992) showed similar growth in treatments of *Phragmites* and *Typha* in 70 cm or less. Data from the high flooding years in the MERP study suggest that very high water levels can extirpate emergents after 2-3 years (van der Valk 1994) but under less extreme water depths, it appears that lower levels of stabilized flooding must have a slower effect on emergent declines. Much longer persistence times or factors other than water depth tolerance may have created the 1980 distributions used by de Swart et al. (1994). After 20 years of stable water levels, exploitative competition may have also influenced the 1980 distributions (Grace and Wetzel 1981, Weisner 1993). Conditions related to the flooding response of emergents to stable and fluctuating water levels at moderate depths require further long-term study.

**Litter Accumulation**

Patterns of *Typha* litter accumulation from shallow water to deeper water are similar to patterns seen in other natural emergent stands. Clevering (1998) suggested that deeper more lakeward stands of *Phragmites* had smaller amounts of litter accumulation than shallower more interior stands. Christensen and Crumpton (Chapter 2) also found lower litter at the edge of a cattail stand than in the interior. Clevering (1998) attributed the pattern to stronger wave action which would increase aeration and physical breakdown of litter. Increased breakdown in deeper areas may be seen in other more wave-driven systems (Hietz 1992), but the modeled breakdown rates used here in the Delta Marsh had lower breakdown rates in deeper water (table 2, Christensen et al. Chapter 4). The lower amounts of litter in deeper water could be driven by the decreasing spatial extent of *Typha* in deeper water which would reduce the average litter accumulation within the depth interval.

Alternatively, expansion at the edge into deeper water would also result in the same pattern of lower litter with increasing depth. Recent expansion of 1-2 years would not allow for sufficient litter build up. This study demonstrated that litter accumulation increases with
stand age and it took at least 2-3 years to reach relatively steady levels of litter mass. Stands of *Typha* in an Iowa marsh that were low in litter (Christensen and Crumpton Chapter 2, appendix) had only been dominated by *Typha* for 1-2 years (Rose et al. in prep). Data from productive mesocosms planted with *Typha* found steady increases in *Typha* litter over a 4 year time period with little indication of reaching equilibrium at the end of the study (Crumpton, unpublished). Rooth et al. (2003) found much higher litter accumulation in 20 yr *Phragmites* stands when compared with 5 yr *Phragmites* stands but there are few other studies relating stand age and litter. Within old field systems that experienced minimal disturbance, researchers suggested that litter accumulates in the early stages of development and quickly reaches a stage of equilibrium (Odum 1960, Facelli and Carson 1991, Facelli and Picket 1991). The rate of accumulation and subsequent stage of equilibrium depends highly on breakdown rates, with lower breakdown rates increasing the time until equilibrium. Breakdown rates may vary with local and regional changes in climate (Brinson et al. 1981), and may also be dependent on the production of the existing stand which may provide protection from physical breakdown (Davis and van der Valk 1978, Christensen et al. Chapter 4). The study of litter accumulation with differing levels of production and at different latitudes and climates is an important avenue of research when considering the potential effects of litter on abiotic and biotic processes.

The simulation also suggests that there is a lag time of several years in litter breakdown as it persists in areas that have lost production. *Typha* litter has persisted in emergent wetland for several years in areas with little production (Rose and Crumpton 1996, Rose and Crumpton 2006). Other studies have observed the persistence of *Phragmites* litter even as living stands have been killed (Kvet 1973). This lag time may prove important as abiotic conditions typical of an emergent stand may persist even in the absence of live material. In addition, residual litter may influence the colonization of the area by other species that may continue to be excluded by preemption (van der Valk 2005).
Implications

Species Shifts

Distributional shifts in species from the wetland plant community may be important to ecosystem processes within wetlands, especially when the species differ in an attribute such as litter persistence (Windham 2001, Levin et al. 2006, Zedler and Kercher 2004). The lack of *Schoenoplectus acutus* and *Phragmites* in shallow to deeper water after the drawdown allowed for the expansion of *Typha* into areas previously dominated by *S. acutus*. *S. acutus* litter has been found to breakdown more rapidly than *Typha* (Murkin et al. 1989). Under the prediction from the model, areas of the wetland now dominated by *Typha* would experience higher levels of litter accumulation. Aerial photos over a 50 year period suggest that *Typha* is expanding in the Delta Marsh at the expense of other emergents (Shay et al. 1999). *Typha glauca* is considered an aggressive species throughout North America (Galatowitsch et al. 1999, Zedler and Kercher 2004), and similar expansions of *Typha* and the aggressive ecotype of *Phragmites* (Saltonstall 2002) have been documented in the Great Lakes, prairie potholes, and Canada (Wilcox et al. 2003, Mulhouse and Galatowitsch 2003, Mal and Narine 2004, Zedler and Kercher 2004). Decomposing litter can hold large amounts of nutrients (Facelli and Pickett 1991, Kadlec et al. 2000) and shifts in species dominance and litter accumulations could potentially influence nutrient cycling (Meyerson et al. 2000, Farnsworth and Meyerson 2003, Fickbohm and Zhu 2006). Shifts in species and litter might also influence abiotic conditions (McCormick and Laing 2003, Levin et al. 2006, Neira et al. 2006) which could influence biogeochemical cycles (Rose and Crumpton 2006), invertebrates (McCormick et al. 2004, Christensen and Crumpton Chapter 2,3) and trophic food webs (Neira et al. 2005, Levin et al. 2006).

Disturbance

Disturbance through fire (though rare, Thompson 1981) and water level fluctuations (Davis and van der Valk 1978) can be important in the process of litter accumulation, influencing both emergent distributions and breakdown rates. The flooding-drawdown event that occurred over three years in the MERP study eliminated production (van der Valk 1994) and virtually eliminated all litter mass. The lack of disturbance (i.e. stabilization of water
levels) may allow monodominant stands to develop (Shay et al. 1999, Zedler and Kercher 2004) and this model predicted that litter would accumulate as stands age. After the disturbance event, simulated litter mass rose to exceed levels found in 1980 within 5-6 years after the drawdown event. If water levels remain stable and don’t allow for resetting events of the system (flooding or drawdown or both), litter can accumulate within the monodominant stands and potentially effect abiotic conditions (Haslam 1971, Rose and Crumpton 1996, Rose and Crumpton 2006) and biota (Christensen and Crumpton, Chapter 2,3).

Wetland management often uses water level fluctuations to influence the wetland plant community, primarily focusing on managed drawdowns to encourage the regeneration of emergent species (Kaminski and Prince 1981, Kadlec and Smith 1992, Murkin et al. 2000b). The effect of drawdowns on litter is unknown. Moist litter exposed to the air can breakdown more rapidly (Bedford 2005) but if litter desiccates sufficiently during a drawdown, breakdown rates may decrease (van der Valk et al. 1991). In addition to drawdowns, high flooding may also influence litter accumulations. Many water control structures present in managed wetlands may not permit extended high water events (Galatowitsch and van der Valk 1998) that would reset plant distributions, production, and litter levels in moderate and shallow depths. Flooding events could influence litter accumulation by depressing production (van der Valk 1994) and increasing breakdown rates of previously dry material (van der Valk et al. 1991). Further study of the process of litter accumulation during drawdown and flooding events is needed. When considering the combined stages of the wet-dry cycle, the sequence of stages, i.e. regenerating vegetation → flooding → drawdown vs. regenerating vegetation → drawdown → regenerating vegetation, may have a strong influence on litter accumulation and requires further study.

Potential Feedback Loops

The model presented in this study assumes that primary production and accumulated litter are independent. Some studies suggest that under increasing litter accumulation, decreased temperatures (Haslam 1971), reduced light (Graneli 1989), or built up toxins (Armstrong et al. 1996) decrease production of the stand itself (Jordan et al. 1990, Clevering
1998, van der Putten 1997). This negative feedback could create a cyclic oscillation of production and litter as has been observed in old field systems (Tilman and Wedin 1991). Inspection of the Delta Marsh data set for such patterns with *Typha* proved inconclusive and thus a negative feedback on production was not included in the model. Preliminary evidence of negative feedback was present for *Phragmites* in the Delta Marsh data though there were too few points of high litter to reach a definitive conclusion. Positive feedback might also occur between breakdown rates and accumulated litter. As litter becomes more dense, it may provide protection against further physical fragmentation (Davis and van der Valk 1978) and lead to slower decomposition rates and increases in accumulation. Preliminary evidence and anecdotal evidence warrant further research of feedbacks loops within the process of litter accumulation in emergent stands of *Typha* and *Phragmites*.

**Conclusion**

Litter accumulation is a dynamic process that depends on the spatial distribution of macrophytes, their annual production, and breakdown rates of their litter. Each of these components interacts with disturbance, i.e. changing or stable water levels. This study found a modeled expansion of *Typha* and a reduction of *Phragmites* in a wetland experiencing a flooding-drawdown event followed by stable water levels. The expansion of *Typha* was possible through the inclusion of subdominants in the model. Once *Typha* expanded into optimum water depths, monodominant stands developed and rapidly accumulated litter. More study needs to be undertaken in wetlands to address the persistence of species under stable and fluctuating water levels. Likewise, more experimental study and modeling is needed to explore the interaction of litter dynamics and water levels. Further research is needed to better understand the potential effects of litter accumulation from expanding species like cattail hybrids on abiotic conditions, biota, and ecosystem processes.

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Table 2. Average percent similarity of predicted distributions for four species compared to observed distributions from 1986-1989

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Figure 1. Schematic of model state of species within the spatial distribution model. Grey arrows indicated flooding damage which is determined from water depth response curves (figure 2) and cell water depth. Black arrows indicate reactivation (no longer dormant) or an increase from subdominant to dominant which is determined from water depth response curves (figure 2), cell water depth, and the state of other species in the same cell. The cycling black arrow represents vegetative expansion into adjacent cells which depends on water depth response curves (figure 2), adjacent cell water depth, and the state of other species in the adjacent cell.
Figure 2. Water depth response curves for four main emergent plants as determined by logistic regressions by de Swart et al. (1994) as normalized by Seabloom et al. (2001). The curves dictate the probability of flooding damage and the probability of vegetative expansion within the spatial distribution model.
Figure 3. Calibrated result of modeled aboveground (AG) and belowground (BG) biomass (g/m²) from a reference cell dominated by *Typha glauca* at Delta Marsh, Manitoba as compared to observed aboveground and belowground biomass from 1980-1989. Observed belowground biomass is only available from 1984-1989.
Figure 4. Observed and modeled proportions of wetland area designated as dominant for three main emergent species, *Phragmites australis*, *Typha glauca*, and *Scolochloa festucaea*, from 1985-1989 for observed values and 1985-1994 for predicted values. Both the observed and predicted proportions are an average proportion from four experimental marshes at Delta Marsh, Manitoba.

Figure 5. Water depth categories for the four normal marshes. Green – areas above the water level (dry land), Light blue – 1-20 cm of water, Blue – 20-40 cm of water, Dark Blue – 40+ cm of water.
Figure 6. *Phragmites australis* species distributions for observed distribution in 1980 (at top), observed distributions in 1989 (middle) and predicted distributions for 1989 (at bottom) for four experimental marshes in Delta Marsh, Manitoba. Water levels were kept at 347.5 meters above sea level. Green – dominant stands, Red – subdominant stands, Grey – empty (but potentially occupied by another species).
Figure 7. The average percentage of modeled area that was in error for *Phragmites australis* calculated from A) predicted distributions - observed distributions from 1986-1989 and B) Predicted – observed 1980 distributions from 1986-1994. Average based on error from four marshes kept under stable water levels. Dom – dominant classification in the grid cell, Sub – subdominant classification in the grid cell.
Figure 8. *Scolochloa festucacea* species distributions for observed distribution in 1980 (at top), observed distributions in 1989 (middle) and predicted distributions for 1989 (at bottom) for four experimental marshes in Delta Marsh, Manitoba. Water levels were kept at 347.5 meters above sea level. Green – dominant stands, Red – subdominant stands, Grey – empty (but potentially occupied by another species).
Figure 9. The average percentage of modeled area that was in error for *Scolochloa festucacea* calculated from A) predicted distributions - observed distributions from 1986-1989 and B) Predicted – observed 1980 distributions from 1986-1994. Average based on error from four marshes kept under stable water levels. Dom – dominant classification in the grid cell, Sub – subdominant classification in the grid cell.
Figure 10. *Typha glauca* species distributions observed distribution in 1980 (top), observed distributions in 1989 (middle-top), predicted distributions for 1989 (middle-bottom), predicted distributions for 1994 (bottom) for four experimental marshes in Delta Marsh, Manitoba. Water levels were kept at 347.5 meters above sea level. Green – dominant stands, Red – subdominant stands, Grey – empty (but potentially occupied by another species).
Figure 11. The average percentage of modeled area that was in error for *Typha glauca* calculated from A) predicted distributions - observed distributions from 1986-1989 and B) Predicted – observed 1980 distributions from 1986-1994. Average based on error from four marshes kept under stable water levels. Dom – dominant classification in the grid cell, Sub – subdominant classification in the grid cell.
Figure 12. The average percentage of modeled area that was in error for *Schoenoplectus tabernaemontani* calculated from predicted distributions - observed distributions from 1986-1989. Average based on error from four marshes kept under stable water levels. Dom – dominant classification in the grid cell, Sub – subdominant classification in the grid cell.
Figure 13. Mean predicted litter accumulation for *Typha glauca* at three different water depth intervals. Standard deviation of four marshes shown. Diamonds are average litter accumulations from the four marshes in 1980 at the three water depth intervals.
Figure 14. Simulated mean Typha litter accumulation (g/m²) in 1994 separated by stand age, averaged from four experimental marshes. Stand age refers to the number of consecutive years a grid cell was designated as dominant Typha including 1994 (ie. 1yr - Typha dominant in 1994, 2yr – Typha dominant in 1993-1994, etc). “Minus” years displayed on the right side of the graph indicated that Typha was not dominant in the grid cell in 1994 but had been dominant Typha the previous year (minus 1yr) or 2 years previous or 3+years previous. Standard error bars are shown.
CHAPTER 6. GENERAL CONCLUSIONS

Invertebrate Findings

Despite the conspicuous presence of accumulated litter and its potentially important influence in wetland systems, litter accumulation has largely gone unstudied in invertebrate studies. The manipulative litter studies included in Chapters 2 and 3 found that high litter accumulation does influence abiotic conditions and associated biota. Decreases in dissolved oxygen, lemnids, and submersed vegetation were all observed in response to increases in litter as suggested in other studies (Voigts 1976, Suthers and Gee 1986, Bohlen 1990, Rose and Crumpton 1996). Either directly and/or indirectly, high litter influenced the invertebrate community by shifting the community toward hypoxic tolerant or semi-aquatic taxa. Vertical shifts in *Hyalella azteca* (amphipoda) distributions were also documented as *Hyalella azteca* was pushed upwards in the water column under moderate amounts of litter and virtually eliminated from high litter areas. The population, community, and trophic consequences of plant litter induced shifts are an interesting avenue of research, especially when considering potential changes to litter dynamics due to aggressive/exotic species (McCormick et al. 2005, Neira et al. 2005, Levin et al. 2006, Neira et al. 2006).

Spatial Distribution and Litter Models

Given that high litter can influence abiotic and biotic components of wetlands, the second portion of this research begins to investigate how and where litter accumulates within wetlands. Since the process of litter accumulation is complex, occurs over extended periods of time, and requires difficult and labor intensive data collection, the ability to model emergent stands and the process of accumulation is important in building a framework of understanding. The evaluation of litter breakdown through mass-balance modeling by using production inputs and observed accumulation is an exciting direction of research. The work presented here points toward a better understanding of litter breakdown rates and potentially what drives litter breakdown rates that are relevant to harvested litter accumulation. Litter accumulation in the Delta Marsh system was more realistically estimated using a mass balance approach to litter breakdown than using litter bag breakdown estimates. The derived
breakdown rates varied between species and across water depths. The use of the mass balance models in estimating litter breakdown appears to be a promising approach but further work in more productive systems and under different climatic conditions is encouraged to better evaluate the validity of the mass balance approach and to determine the range of breakdown values that might exist under different conditions.

Combining the modeled breakdown rates with modeled emergent species distributions allowed for an investigation into the process of litter accumulation in the Delta Marsh. The wetland plant distribution model illustrated the importance of including subdominants in distribution modeling. Though more work needs to be done to better understand emergent macrophyte persistence under stable water levels, *Typha* coverage increased through time in the experimental marshes. Under stable water levels, litter accumulation occurred at water depths where *Typha glauca* depth tolerances permitted the development of mature stands. With its persistent litter, the average marsh litter levels surpassed pre-disturbance accumulation levels only 5-6 years after the disturbance event. Under manipulated water levels, mature emergent stands may quickly reach higher levels of litter after only 2-3 years and remain under high litter for extended periods of time. The question remains as to what effect litter at high levels has on plant production and if that effect may vary through time. Productive stands may begin to experience degenerative conditions under high litter (Graneli 1989, Jordan et al. 1990, Armstrong et al. 1996), creating local oscillations between production and litter accumulation (Tilman and Wedin 1991). This study also predicted that litter may persist for several years after plant stands have been killed, potentially influencing the colonization by other species. When considering the impacts of aggressive species on wetland systems, the impacts of litter accumulation on ecosystem processes need to be explored.

Though this study focused on distributions and breakdown under stable water levels, the effect of water level fluctuations on litter needs to be explored in wetlands. Experimental water levels changes included in the Delta Marsh study showed the potential importance of water level disturbance on litter levels, as a combination of high water and drawdown virtually eliminated litter from the experimental marshes. Both flooding and drawdown may similarly reduce litter accumulation but each could potentially reduce litter though different
components of the litter accumulation process. Flooding could decrease production and litter breakdown may increase in previously dry areas (van der Valk et al. 1991). Drawdown may not reduce production greatly (van der Valk and Davis 1980) but could greatly increase litter breakdown (Bedford 2005).

**Combination of Invertebrates and Spatial Litter Dynamics**

Combining the two portions of this research together, it is important to consider that the response of invertebrates to litter may vary depending on the spatial context of a wetland. Litter accumulation may be heterogeneous within the interior, which may dampen the effect of litter on invertebrate distributions. Invertebrates under high litter could remain in the interior and simply move to an adjacent interior area of low litter. But if litter accumulation is homogeneous or becomes more homogeneous through time under stable conditions, distributional shifts from the interior may be more dramatic.

It is interesting to also consider how these invertebrate responses and potential trophic consequences would occur and vary in a temporal context in a wetland. Within a year, invertebrate responses to identical levels of litter may be different in the spring, summer and fall, as invertebrate densities change, temperature and DO change, and floating vegetation changes (Nelson and Kadlec 1984). As wetlands go through the wet-dry cycle across multiple years, researchers have documented shifts in the invertebrate community (Voigts 1976, Murkin and Ross 1999, Murkin and Ross 2000, Wrubleski 2005), which have primarily been related to shifts in dominant vegetation and few have considered the influence of litter. Multiple years of stable water levels may induce higher litter levels which could create conditions similar to the moderate and high litter level treatments, while fluctuations within the wet-dry cycle may not allow litter to develop and could create conditions similar to the low litter treatments. The further investigation of litter accumulation throughout the natural wet-dry cycle and the potential influence of litter on primary production, biogeochemical cycles, and trophic relationships is needed.

These studies have shown that litter manipulations can be used to address questions of litter influences on abiotic and biotic wetland components and this work encourages more manipulation studies, especially of aggressive species that potentially could influence
ecosystem processes. Mass balance breakdown rates that use standing crop and litter biomass can be used to estimate litter breakdown and should be applied to more regions and during flooding and drawdown events. To support litter manipulation studies and increase our general understanding of the litter process, simulation and spatial modeling should also play an important role in understanding how litter accumulation changes with emergent species, type of disturbance, and frequency of disturbance.

**LITERATURE CITED**


APPENDIX A: LITTER MANIPULATIONS FROM THE MARSH EDGE INTO THE EMERGENT INTERIOR

INTRODUCTION

Semi-permanent freshwater marshes often develop marked zonation of deeper open water areas surrounded by dense stands of emergent vegetation. The interior of the stand typically experiences greater emergent litter densities than at the edge (Rose and Crumpton 1996, Christensen and Crumpton Chapter 2), as well as lower dissolved oxygen (DO) (Dvorak 1970, Rose and Crumpton 1996, Murkin et al 1992, Suthers and Gee 1986), decreased light availability (Rader 1999, Rose and Crumpton 1996) and decreased vegetation (Bohlen 1990, Rose and Crumpton 1996, Christensen and Crumpton Chapter 2). Litter, through its possible effects on DO and vegetation, may also influence invertebrates, but few studies have considered the effect of litter on horizontal and vertical invertebrate distributions. Chapter 3 considered natural increases in litter from the edge to the interior and found either increases in the interior or no difference between the edge and interior for the amphipod, *Hyalella azteca* (Saussure). Vertical compression was greater at moderate litter levels in the interior and when litter was increased up to high levels *Hyalella azteca* was found in low abundance. It is possible that in shallow wetlands were litter inputs are high, vertical compression could become so severe that intolerant invertebrates like *Hyalella azteca* could be pushed out of interior stands towards the edge. By physically adding litter from the edge to the interior, the effects of litter on abiotic conditions, vegetation, and the horizontal and vertical distribution of *Hyalella azteca* across the edge to interior gradient can be better understood. Our objective was to determine if *Hyalella azteca* would experience a horizontal as well as vertical shift toward the edge in areas where high litter persisted in the interior. We investigated the potential shift of *Hyalella azteca* through a comparative experiment where an area supplemented with litter in the interior was compared with areas that had naturally low levels of litter in the interior.
METHODS

Study Site

This research was also conducted at Anderson Lake (formerly Goose Lake), and a full description of this semi-permanent natural prairie pothole can be found in chapters 2 and 3. The area of the present study was located on the southwest side of the Lake in an area that had recently become dominated by *Typha spp* (mostly of the hybrid *T. glauca* Godr.) (Rose et al, in prep) with members of the Lemnaceae (primarily *Spirodela polyrhiza* (L.) Scheid and *Lemna trisulca* (L.)) and *Ceratophyllum demersum* (L.) and *Utricularia macrorhiza* Le Conte interspersed among the cattails.

Transect Study

In 2005, two plots, 5 meters in width and stretching from the edge to 12 meters inward, were studied from July to September. The area had naturally low litter densities based on preliminary sampling and were adjacent to the 2005 natural transect plots described in Chapter 3. The 5m by 12m plots were delineated and litter from outside the area was added incrementally to simulate the pattern of increased litter in the interior. No litter was added from the edge (0m) to 4m in the plot. From 4m to 8m, approximately 450g dry weight of cattail litter were added to each square meter. From 8m to 9m, 900g dry weight were added to each square meter. From 9m to 12m, 1350g dry weight were added to each square meter.

Methods and timing for activity traps, dissolved oxygen and vegetation in the increased litter transects were identical to the methods used for the 2005 transects in Chapter 3 and were collected on the same days. In brief, dissolved oxygen and temperature were taken from 12:00-14:00 at depths of 2cm, 5cm, 10cm, 20cm, and 30cm at each sampling point along the transects. Vegetation samples of the top 20cm of the water column were taken at each sample point with a 15cm diameter Plexiglas tube. At the lab, all vegetation was sorted, preliminarily table dried for 1 week, oven dried at 65 degrees C for 48 hours, and weighed.

To sample invertebrates, a transect was selected in each plot each month that extended from the edge to 12 meters inward. At each transect, multi-level activity traps were
deployed at the edge of the emergent stand, 4m, 8m and 11 meters into the interior. The multi-level activity trap is modified from the design of Murkin et al (1983) and was described in detail in Chapter 3. The traps sampled the top 15 cm, the midpoint (15-30 cm) and the bottom (10 cm above the sediment surface) of the water column. Activity traps were left for 24 hours and then removed. The contents of the jar were passed through a 250 micron sieve and preserved in 70% ethanol. In the lab, *Hyalella azteca* were sorted in bottom-light translucent pans and enumerated.

**Statistical Analysis**

To examine horizontal differences from the edge to the interior, the relative abundance of *Hyalella azteca* of the three multi-level traps were summed together to provide a whole water column estimate. Those numbers were then ln(x+1) transformed to meet conditions of normality in all ANOVA and t-tests.

Results from the litter addition transects were compared with the natural areas that were originally reported in Chapter 3 and those results are also be included these figures for easy comparison. To test comparisons of the 2005 transects with the increased litter transects, a different approach was required as distance into the interior was related to litter density treatments. Therefore, a strip plot ANOVA (Milliken and Johnson 1984) was used to compare litter treatment, distance, and the interaction of litter treatment and distance, which is the experimental unit of interest. These strip plot ANOVAs were run for *Typha* dry weight, lemnid dry weight, *Ceratophyllum* dry weight and *Hyalella azteca* relative horizontal abundance. For vertical distributions of transformed *Hyalella azteca*, an additional strip was added into the ANOVA model to incorporate position at each of the multi-level sampling locations.

Recorded DO measurements were placed in Surfer (Golden Software Inc. version 8), mapped using triangulation with linear interpolation, and the depth at 1 ppm was recorded. Dissolved oxygen in the 2005 transects and the litter addition transect were analyzed as the percent of the water column above 1 ppm at the time of sampling. All three months showed similar patterns and an average of the three months is reported.
RESULTS

The highest relative densities of *Hyalella azteca* were not at the farthest interior position. A non significant trend showed the greatest relative abundance at 4m into the interior (figure 1a). Vertical compression was significant across litter additions ($F_{1,4}=20.8$, $p=.01$). Contrasts revealed that no vertical compression was seen at the edge and at 4m but was significantly present at 8 ($p=.01$) and marginally different at 11m ($p=.07$) (figure 1c). With litter added to mimic conditions of increasing litter into the interior, litter increased predictably from the edge to the interior due to the incremental additions ($F_{3,3}=7.8$, $p=.06$)(figure 2). Submersed vegetation was lost from the interior and was significantly greater at the edge ($F_{3,3}=812.3$, $p<.001$)(figure 2). The percentage of the water column above 1 ppm decreased from 29% at the edge to 2% at 11m.

DISCUSSION

Litter addition can lead to the loss of submersed vegetation (this study, Voigts 1976), floating vegetation (Rose and Crumpton 1996, Christensen and Crumpton Chapter 2), and other annuals and emergent vegetation (Bohlen, 1990). *Hyalella azteca* has been shown to have a positive relationship to submersed vegetation (Voigts 1976, Murkin et al 1991). The loss of such vegetation habitat in the interior due to increased litter may constrict interior invertebrate distributions.

Dissolved oxygen was more depressed within the interior when litter was added than at equal distances into the interior without litter. The amount of structure influences mixing (Leonard and Luther 1995) and so the greater litter structure may reduce mixing and DO concentrations. Litter also reduces light availability (Rose and Crumpton 1996, Grimshaw et al 1997) and shading to submersed vegetation and algae (Grimshaw et al 1997) could reduce diel DO concentrations resulting from photosynthesis. Low DO might also influence inward invertebrate distributions.

Though not statistically significant, an intermediate distance (4 meters) yielded the greatest relative abundance when litter was added to the interior and submersed vegetation and DO declined. Adjacent to those areas were no litter was added and submersed vegetation
remained, the greatest abundance was found in 11 meters into the interior. These findings of a possible intermediate distribution indicate a possible distribution shift that could relate predation pressures at the edge (primarily fish predators) with the combined conditions of litter increases, reduced DO, and/or submersed vegetation decreases. Intermediate distributions based on predation and hypoxia constraints have been documented in many aquatic organisms, including, African cichlids (Chapman et al 1996, Randle and Chapman 2004), sunfish (Miranda and Hodges 2000), several zooplankton (Wright and Shapiro 1990, Tessier and Welser 1991), and mysids (Horppila et al 2003). If large areas of the interior experience higher litter accumulations, it is possible that less tolerant organisms may be forced towards the edge and could ultimately suffer higher predation from fish. With a greater sample size, more litter manipulations could be undertaken to determine if the intermediate distributions truly occur.

LITERATURE CITED


Figure 1. Natural log transformed relative densities of *Hyalella azteca* in Litter Added (A&C) and No Litter Added (B&D) transects. Horizontal total relative abundance of transformed *Hyalella azteca* (ind/summed vertical traps) (A&B) from 0m to 11m (0m=open water edge). Relative vertical abundance in activity traps (C&D) located at the top versus combined middle-bottom traps from 0m to 11m. Note: due to transformations the vertical means (right) will not sum to match total combined means (left) Standard error bars shown.
Figure 2. Comparisons of Litter Added (LA) and No Litter (NL) plots. Top panel - DO isopleths from LA (left) and NL (right) with distance into the interior (0m=open water edge). Depth is in cm and all isopleth increments are .5 ppm. Bottom panel - *Typha spp.* biomass and *Ceratophyllum demersum* biomass in the top 20 cm of the water column measured at 0m, 4m, 8m, and 11m into the stand. Error bars are standard error.
APPENDIX B: ADDITIONAL SUPPORTING DATA

Table 1. The total numbers and % of total for Fathead minnows (*Pimephales promelas* Rafinesque) found in the open water, at the edge, interior during the combined years of 2003 and 2005, using activity traps and a quantitative stovepipe sampler. The open water was only sampled in 2003 (n=6) and the edge and interior were sampled in 2003 (n=6) and in 2005 (n=18).

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Table 2. The average biomass of live material present in experimental marshes of MERP study from quadrat samples taken in areas designated as dominant or subdominant by *Typha glauca* for each year of the study following drawdown. The ratio of biomass in subdominant areas to biomass in dominant areas is given with the overall average of .239. A value of .25 was used in the litter accumulation model for production estimates of Typha in subdominant areas (see chapter 5 – methods).

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0.239 mean ratio