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

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Abstract: Plant litter produced in the interior of dense emergent stands may directly or indirectly influence invertebrate communities. Low litter may provide structure and refuge to invertebrates while high litter may displace vegetation and decrease oxygen concentration. Within an emergent stand, an edge-to-interior transect study and an interior litter treatment study were performed to investigate the impact of increasing litter densities on the invertebrate community. The interior had more litter, lemnid biomass, and hypoxia than the edge but did not differ in total invertebrate abundance. Low and moderate litter plots in the interior treatment study experienced higher lemnid biomass and greater total invertebrate abundance than the high litter plots, but the high litter plots were characterized by higher invertebrate diversity. There was a significant negative relationship between litter and invertebrate abundance in July and August. Invertebrate patterns were driven primarily by amphipod abundance and may be related to the use of lemnids as habitat. Hypoxic-tolerant and semi-aquatic taxa were associated with high litter, while several algal-feeding taxa were associated with the edge. High litter can reduce abundant invertebrates that support higher trophic levels and shift invertebrate communities. These findings underscore the importance of understanding long-term litter accumulation dynamics in wetland systems.

Keywords: amphipods, cattail hybrid, detritus, litter accumulation, lemnids.

INTRODUCTION

Semi-permanent freshwater marshes often develop open water areas surrounded by dense stands of emergent vegetation (Weller and Spatcher 1965; Cowardin et al. 1979). Spatial distributions of invertebrates can be heavily influenced by vegetation zones (Voigts 1976; Brown et al. 1988; Olson et al. 1995; Murkin and Ross 1999; McCormick et al. 2004). Invertebrate abundance and diversity are often negatively correlated with emergent vegetation coverage (Voigts 1976; Nelson et al. 2000; Neira et al. 2005) and with distance into the interior from the open water edge (McLaughlin and Harris 1990; Cardinale et al. 1997; MacKenzie and Kaster 2004; MacKenzie et al. 2004;).

Within the interior of emergent vegetation stands, litter can accumulate and potentially exert a strong influence on invertebrate patterns. At low densities, litter can provide a food source for detritivores (Campeau et al. 1994; Batzer 1998), substrate for epiphyton (Campeau et al. 1994), and refuge from fish predation (Crowder and Cooper 1982; Gilinsky 1984; Zimmer et al. 2001). As emergent litter accumulates, litter can shade out or displace epiphyton, submersed vegetation, and floating vegetation (Voigts 1976; Grimshaw et al. 1997). High litter can also contribute to hypoxia (Suthers and Gee 1986; Murkin et al. 1992; Rose and Crumpton 1996) by increasing carbon supplies for decomposition and decreasing water mixing (Leonard and Luther 1995).

Although the accumulation of litter in emergent stands could significantly alter conditions for invertebrate communities, the influence of litter on invertebrates within freshwater emergent stands is seldom studied (Murkin and Ross 2000; Levin et al. 2006). The main objective of this research was to examine the effects of litter 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 wetland interior. We then examined the response of invertebrates to an experimental manipulation of litter densities within the emergent stand.

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; Figure 1) at the southern end of the Prairie Pothole Region (PPR). *Typha* spp. dominate the emergent zone (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, and water lilies (*Nuphar lutea* (L.) and *Nymphaea odorata* Ait.) were found at the emergent edge. Water depth at the study sites was > 40 cm and remained relatively constant throughout the study.

Edge-Interior Study

From July to September of 2004, we compared invertebrate communities and associated vegetation and litter densities at the *Typha*-open water edge and 10 m into the interior of a *Typha* stand. Each month, three paired edge and interior sites were randomly selected from a *Typha* stand on the marsh's island (Figure 1). Two weeks prior to each sampling date, portable floating docks (5 m long) were placed at interior sites, running parallel to the open water edge. The docks minimized disturbance to the water column during sampling. Samples were collected using a 90 cm long, 0.11 m^2 PVC cylinder (37 cm diameter) that was quickly forced through the vegetation (a spade cut through rhizomes when necessary) until a seal was formed in the wetland sediments. Two sub-samples, spaced 3 m apart, were collected from a boat at edge sites and from the docks at interior sites. Within the cylinder, all live vegetation and standing and fallen litter at or below the water surface were removed, washed, and bagged. Invertebrates within vegetation were rinsed in a large sorting pan and collected on a 250 μm sieve. Invertebrates within the cylinder were pumped out by a nested-sieve (1 mm and 250 μm sieves) chamber and pump (modified from Major et al. 1998) and preserved in 70% ethanol. In the laboratory, all vegetation and litter samples were separated into live and dead tissue, allowed to air dry for 1 week, then oven dried at 65°C for 48 hours, and weighed to the nearest 0.01 g. Invertebrates were sorted in back-lit translucent pans, identified to the lowest practical taxon using Merritt and Cummins (1996) and Smith (2001), and enumerated. The average of the two sub-samples for each edge and interior site was used in all analyses. Water quality data loggers (AQUA 2000, Biodevices Inc. Ames, IA, USA) were also deployed at two permanent edge and interior sites. The loggers recorded dissolved oxygen (DO) concentration at 20 min intervals from two depths: shallow (water depth = 10–15 cm) and moderate (water depth = 30–35 cm).

Interior Litter Study

In 2005, a litter experiment in the emergent interior investigated the effects of different litter densities at a constant distance from the edge. This was done to reduce confounding parameters associated with proximity to open water that potentially affect invertebrate distributions (i.e., predation risk, water mixing). Three large emergent stands were selected where treatment plots could be established 8–12 m into the interior from the open-water-emergent edge (Figure 1). The stands were similar in depth (40–60 cm) and in large areas (40 m long) that did not have visible disturbances, such as muskrat lodge formation. At each stand, three 4 X 10 m plots were cleared of fallen litter with pitchforks. Litter within the interior was coarse and the pitchfork removed most litter in the water column. Standing litter stems and live plants were not 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 (linear regression analysis, r^2=0.93, $p < 0.01$). Wet litter was weighed and placed into randomly assigned plots to create three litter treatments: a high litter (HL) density treatment with the equivalent of 2 kg dry litter/m^2, a moderate litter (ML) density treatment with the equivalent of 1 kg dry litter/m^2, and a low litter (LL) density treatment where remaining stems constituted 0.25–0.5 kg dry litter/m^2. Litter plots were left alone for 3–4 weeks, prior to the onset of sampling.

Monthly vegetation and invertebrate samples were taken from a randomly assigned quarter of each 4 X 10 m plot from July through September 2005 using the 0.11 m^2 tube sampler and portable docks. Vegetation samples and invertebrate samples were processed, identified, and enumerated as described for the 2004 sampling. At two of the three replicate stands, a data logger was placed at 5 cm below the water surface in the center of each plot to measure dissolved oxygen every 20 min.

Statistical analysis

Edge-Interior Study. We used analysis of variance (ANOVA) to compare *Typha* dry weight, *Typha* litter dry weight, lemnid dry weight, total invertebrate abundance, taxon-richness, and the Shannon-Wiener index (H') between the edge and interior locations of emergent vegetation stands. The ANOVAs included zone (edge or interior), month, and zone x month interactions. Monthly samples were considered independent since new transects were selected each month. When significant, least squares means were compared using the Bonferroni correction. Total invertebrate numbers were ln (x+1) transformed to meet conditions of normality. A multivariate community analysis, multi-response permutation procedures (MRPP) (Mielke and Berry 2001), was used to check for differences between edge and interior communities for each of the three months. The distance measure used in the analysis was Euclidean distance. Sorenson distances yielded similar results and are not reported here. Indicator species analysis (ISA) tests (Dufrene and Legendre 1997) were also conducted for each month to identify taxa predominantly found at the edge or interior. ISA provided an indicator value (IV) for each taxon; if a taxon was found primarily in the interior and was found consistently in the interior samples, it would have a high IV for the interior. A Monte Carlo randomization procedure with 1000 randomizations was used and those taxa with an alpha value less than 0.10 are reported to show dominant distribution patterns of taxa despite the small monthly sample size. ANOVAs were run using PROC GLM (Statistical Analysis Software, Version 9.2, SAS Institute Inc., Cary, NC) and all MRPP and ISA tests were performed using PC-ORD (MjM Software, version 5, Glendedon Beach, OR). Dissolved oxygen (DO) data were summarized by calculating the percentage of each 24 hour period under severe hypoxia (DO < 1 ppm) and an average daily percentage was reported.

Interior Litter Study. *Typha* dry weight, *Typha* litter dry weight, lemnid dry weight, log transformed total invertebrate abundance, taxon richness, and H' were compared across stands and litter treatment plots using a repeated measures analysis of variance (Statistical Analysis Software, Version 9.2, SAS Institute Inc., Cary, NC). Repeated measures were used to account for possible dependency in plots across time. When significant, least squares means were compared within each month using the Bonferroni correction. Differences between invertebrate communities in the three litter densities were analyzed by MRPP each month. When significant, pair-wise comparisons using MRPP between treatments were performed. ISA tests of the three treatments were also performed for each month. No control plot was included in 2005 but MRPP comparisons may be made to the 2004 interior transect community. The litter densities of the 2004 interior were similar to the manipulated densities of the low and moderate plots, however the comparison must be treated with caution since year-to-year variability in the invertebrate communities may exist. Step-wise multiple regression analysis that included *Typha* litter, live *Typha*, and lemnid dry weight was used to determine what model would best explain invertebrate abundance within each month (PROC REG within SAS; Statistical Analysis

Software, Version 9.2, SAS Institute Inc., Cary, NC). All MRPP and ISA tests were conducted using PC-ORD (MjM Software, Glendedon Beach, OR).

RESULTS

Edge-Interior Study

Typha dry litter mass was 2.5 times greater in the interior than at the edge ($F_{1,12} = 22.1$, $p < 0.001$), averaging 578.8 and 225.8 g/m^2, respectively (Table 1). Live *Typha* showed a significant interaction between zone and month ($F_{2,12} = 5.8$, $p = 0.018$) as live *Typha* at the edge increased after July (Table 1). Lemnids were greater in the interior ($F_{1,12} = 5.0$, $p = 0.046$) with a average dry weight of 19.4 g/m^2 in the interior compared to 8.9 g/m^2 at the edge (Table 1). Submersed aquatic vegetation had higher abundance at the edge than in the interior ($F_{1,12} = 15.1$, $p = 0.002$) and declined through the summer ($F_{2,12} = 6.0$, $p = 0.015$). The interior also experienced a greater percentage of each day under severe hypoxia; 52.9% and 99.5% at shallow and moderate depths compared to 9.1 % and 21.6% at similar depths at the edge.

Total invertebrate abundance (natural log) and taxon richness did not differ between edge and interior communities (Table 1). H’ diversity was lower in the interior in August (month x zone $F_{2,12}$=11.9, $p = 0.001$; Table 1). MRPP also found community differences between the edge and interior in August ($p = 0.020$).

Overall, a total of 55 taxa were identified from the 2004 samples; 37 taxa were found at both the edge and interior while 8 taxa were exclusive to the edge and 10 taxa were only found in the interior (Table 2). Amphipods were the most abundant invertebrate taxon at both the edge and interior (Table 3) and were associated with the interior in August (Table 4). Cladocerans and chironomids were also abundant and associated with the edge (Table 3 & 4). ISA identified several other edge taxa including: two mayflies (*Callibaetis* sp. and *Caenis* sp.), a water boatman (*Trichocorixa* sp.), a backswimmer (*Notonecta* sp.), a damselfly larvae (*Enallagma* sp.), water mites, and planorbid snails (Table 4). Pigmy back swimmers (*Neoplea* sp.) and pyralid moths were abundant in the interior (Table 3 & 4) and ISA identified copepods, isopods, and a hydrophilid beetle larvae (*Enochrus* sp.) as primarily in the interior during one month or more (Table 4).

Interior Litter Study

Typha litter mass varied significantly with month x litter interactions ($F_{4,8} = 10.4$, p = .003); high litter mass was greater in July than in later months (Table 5). Live *Typha* biomass did not differ among treatments. Lemnids differed among treatments ($F_{2,4} = 13.1$, p = 0.018) and months ($F_{2,8} = 6.8$, p = 0.019), with an average biomass of 11.6 g/m^2 in HL plots, compared with 38.6 and 38.3 g/m^2 in the LL and ML plots, respectively (Table 5). Severe hypoxia occurred 99.9% (SD ± 0.7%) of each day in HL plots, 96.5% (SD ± 6.7%) in ML plots, and 87.5% (SD ± 15.7%) in LL plots.

Total invertebrate abundance differed across treatments ($F_{2,4} = 45.0$, p = 0.002) and months ($F_{2,8} = 6.2$, p = 0.024) with the lowest abundance in the HL plots (Table 5). LL and ML plots did not differ in total invertebrate abundance. Taxon richness did not differ among litter treatments but H' values were greater for HL plots than LL and ML plots ($F_{2,4} = 17.8$, p = 0.010) (Table 5). Step wise regression indicated that in July, *Typha* litter dry weight explained 90.9% of total invertebrate abundance (Figure 2) while lemnid dry weight explained an additional 5.8%. In August, 82.1% of the variation for total invertebrate abundance was explained by *Typha* litter dry weight and it was the only significant variable (Figure 2). No vegetative parameters were significant in explaining the invertebrate abundance in September, although lemnids explained 41.2% of the variation in invertebrate abundance while *Typha* litter dry weight explained 24.4% of the variance. MRPP showed community dissimilarity in July (p = 0.014) and August (p = 0.008), with the HL community differing from the LL and ML communities (all p-values < 0.036). MRPP tests showed no differences in September. MRPP also indicated that there was no significant difference between the 2004 interior samples and LL and ML plots in July. The 2004 plots were significantly dissimilar from ML plots in August (p = 0.029). The high litter treatment community was significantly different than the 2004 interior community in July (p = 0.028), and August (p = 0.022).

A total of 50 taxa were identified across the three treatments with 27 taxa found at all three treatments and 9 found in only one treatment (Table 6). As in the 2004 transects, amphipods were the most abundant invertebrate taxa in the 2005 litter treatments with higher abundance in the LL and ML plots than in the HL plots (Table 7). ISA determined that amphipods, cladocerans, pyralid moth larvae, a dragonfly (*Pachydiplax* sp.), and Tanytarsini midges were associated with LL plots for at least one month (Table 8). In July and August, ISA tests showed leeches were associated with the ML treatment, while oligocheates and *Coquillettidia* mosquitoes were abundant and associated with HL treatments (Tables 7 & 8). Two coleopterans (*Enochrus* sp. and Scirtidae), tipulids, and spiders were also associated with HL during one month (Table 8).

DISCUSSION

Typha Litter, Lemnids, and Hypoxia

During the 2004 edge-interior study, the interior had more litter, lemnids, and hypoxia than the edge, which is consistent with results from other studies in the PPR (Suthers and Gee 1986; Murkin et al. 1992; Rose and Crumpton 1996). The stand interior has less wave and wind action which slows toppling rates for litter (Davis and van der Valk 1978), shelters lemnids (McLay 1974), and decreases mixing which creates hypoxic conditions (Leonard and Luther 1995). Hypoxia slows litter decomposition (Godshalk and Wetzel 1978), which allows for greater litter accumulation.

Although the 2005 litter treatments showed the anticipated differences in litter, *Typha* litter dry weight in the HL plots decreased after July, while staying relatively constant in the LL and ML plots. It is unclear why this loss of over 600 g/m^2 occurred but it may be due to the location of the litter in the water column. Litter in the HL plots extended throughout the water column up to the surface and may have allowed the shifting of litter outside of the treatments plots during storm events. Lemnids were consistently lower in the HL plots, presumably due to the displacement of lemnids by litter at the water surface (Bohlen 1990). The decrease of lemnids across all litter plots in September is likely a result of decreased solar radiation and cooler temperatures with the onset of fall. Severe hypoxia was pronounced in all the litter plots, regardless of the amount of litter. Rose and Crumpton (1996) also found severe hypoxia in interior stands and suggested that the lack of mixing with open water areas and decreased atmospheric gas exchange due to litter and surface cover by lemnids could exacerbate hypoxic conditions.

Invertebrate Abundance and Communities

Despite differences in litter, lemnid biomass, and DO in the edge-interior study, no differences in total invertebrate abundance were observed. In similar studies, patterns of total invertebrate abundance from the edge to stand interior are varied; from highest abundance at the edge (Voigts 1976; Schalles and Shure 1989; McLaughlin and Harris 1990), to higher abundance in the interior (Dvorak 1970, Murkin et al. 1992), to few differences between zones (King and Brazner 1999). Variable invertebrate patterns likely result from different community interactions (i.e. variations in predators, nutrient conditions, and plant species) and different sampling mechanisms that introduce bias (i.e., collecting only nektonic taxa or only emerging taxa). In addition, invertebrate communities are often dominated by a few taxa that can influence overall distribution patterns depending on their habitat requirements. In this study, amphipods, which are often abundant in lakes and wetlands of the PPR (Voigts 1976; Olson et al. 1995; Murkin and Ross 1999; Zimmer et al 2001), dominated total invertebrate abundance and community measures. High abundance of amphipods in the interior in August 2004 reduced H' diversity while lower amphipod abundance in the 2005 July and August HL plots resulted in greater evenness and community differences. The strong negative relationship between litter and invertebrates was also the result of amphipod abundance.

Litter may influence invertebrate abundance through several mechanisms; lower litter conditions may enhance food resources (Hargrave 1970; Campeau et al. 1994; Batzer 1998), reduce predation from fathead minnows (*Pimephales promelas*) (Crowder and Cooper 1982; Gilinsky 1984; Hanson and Riggs 1995; Zimmer et al 2002), or shelter high lemnid densities that can provide habitat (Sklar 1985; Harper and Bolen 1996). In low litter plots, where lemnids were sheltered but not displaced by litter, amphipods and other abundant taxa may have responded to the higher lemnid densities. Pyralid moth larvae constructed cases exclusively out of lemnids. Amphipods, copepods, and cladocerans were primarily collected amidst the lemnids instead of the underlying litter (personal observation, J. Christensen), which supports the assertion that lemnids provide important habitat (Sklar 1985; Harper and Bolen 1996). *Neoplea* sp. were also more abundant in LL and ML plots and are important microcrustacean predators.

Higher litter can also directly or indirectly influence members of the invertebrate community. High litter can increase detrital food resources (Dvorak 1970) and hypoxia (Magnusson and Williams 2006; Batzer and Palik 2007), and can shift invertebrate communities towards hypoxic-tolerant and semi-aquatic species in shallow ponds (Bedford and Powell 2005; Magnusson and Williams 2006) or seasonal woodland ponds (Batzer and Palik 2007). Others have reported community shifts towards hypoxic-tolerant or detrital invertebrate communities as plant composition shifted to more litter-producing vegetation (Houston and Duivenvoorden 2002, McCormick et al. 2004, Neira et al. 2005). Several taxa in this study were associated with high litter, including hypoxic-tolerant taxa like *Coquillettidia* mosquitoes, oligocheates, tipulids, Scirtidae, and semi-aquatic spiders. While benefiting some tolerant taxa, high litter, associated with the loss of lemnids, may result in the overall reduction of invertebrate abundance, as was suggested by the regression analysis in this study. The reduction of amphipods under high litter conditions may have trophic implications as abundant amphipods are important prey for fish and waterfowl (Krull 1970; Hanson and Riggs 1995). Similar negative responses to high litter have been suggested for other important prey taxa, including chironomids (Murkin et al. 1982). The effects of high litter on amphipods and other invertebrates needs to be further researched in the PPR as this study was limited to one wetland during 1–2 years and invertebrate communities can be highly variable between wetlands (Zimmer at al. 2002; Batzer and Palik 2007; Poi de Neiff et al. 2009;) and between years (Voigts 1976; Murkin and Ross 1999; Bedford and Powell 2005; Batzer and Palik 2007).

Unlike the interior, taxa associated with the edge may not be as influenced by litter. Several taxa were indicative of the edge including filter-feeders and collector-gatherers (cladocerans, chironomids, and mayflies) as well as their predators (*Trichocorixa* sp. and *Enallagma* sp.) (Merritt and Cummins 1996; Smith 2001). The emergent edge has long been considered distinct from the open water and interior (Batzer and Wissinger 1996) and high abundance at the edge is often associated with algal resources (Cardinale et al. 1997; Marklund et al. 2001). Wetland systems are often assumed to be detrital based systems but algal resources can often be an important resource within wetland systems (Crumpton 1989; Euliss et al. 1999; Murkin and Ross 2000; Hart and Lovvorn 2003) and deserve further study.

Emergent litter can exert a strong influence on wetland invertebrate communities. The negative influence of high litter density, whether direct or indirect, can reduce abundant invertebrates that are important to higher trophic levels (Krull 1970; Hanson and Riggs 1995). These findings underscore the importance of understanding litter accumulation dynamics in wetland systems and how they interact with hydrology. For example, stabilized water levels might lead to litter accumulation and reductions in invertebrate abundance in interior stands. More long-term study is needed to better understand litter-invertebrate interactions (Murkin and Ross 2000), litter accumulation dynamics (Moore et al. 2004), and potential impacts on wetland trophic function (Levin et al. 2006).

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Table 1. Overall and monthly means for *Typha* litter, live *Typha*, lemnids, Submersed Aquatic Vegetation (SAV), total abundance, taxon richness, and the Shannon-Wiener Index in Anderson Lake Marsh, 2004, and their resulting F values from ANOVAs. ANOVA for total abundance was log transformed but original values are shown. Zone refers to the open water-stand edge and ten meters into the stand interior.

	Overall Average		July		August		September		Zone	Month	ZonexMonth
	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Effect	Effect	Interaction
Typha litter (g dry weight/m^2)	225.8	578.8	183.0	599.5	264.9	618.9	229.5	518.0	$F_{1,12}$ = 22.1***	$F_{2,12}$ = 0.3	$F_{2,12}$ = 0.2
Live *Typha* (g dry weight/m^2)	704.6	371.2	408.9	391.2	896.6	478.3	808.2	244.2	$F_{1,12}$ = 24.0***	$F_{2,12}$ = 6.0*	$F_{2,12}$ = 5.8*
Lemnids (g dry weight/m^2)	8.9	19.4	8.7	21.5	1.6	22.3	16.3	14.4	$F_{1,12}$ = 5.0*	$F_{2,12}$ = 0.2	$F_{2,12}$ = 2.0
SAV (g dry weight/m^2)	6.8	0.6	13.7	1.4	4.7	0.1	2.0	0.2	$F_{1,12}$ = 15.1**	$F_{2,12}$ = 6.0*	$F_{2,12}$ = 3.8
Total abundance (indv./m^2)	9881	10629	12023	9788	9678	15218	7940	6880	$F_{1,12}$ = 0.3	$F_{2,12}$ = 2.0	$F_{2,12}$ = 0.5
Taxon Richness	25.4	24.8	25.6	24.7	26.0	25.7	24.7	24.0	$F_{1,12}$ = 0.1	$F_{2,12}$ = 0.2	$F_{2,12}$ = 0.1
Shannon - Wiener Index	1.5	1.3	1.4	1.4	1.6	1.0	1.5	1.6	$F_{1,12}$ = 9.7**	$F_{2,12}$ = 5.0*	$F_{2,12}$ = 11.9**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. Presence/Absence of taxa and abundance ranks at the open water-stand edge and 10 meters into the stand interior in Anderson Lake Marsh, 2004. Abundance rank includes multiple ties.

Class/Order	Suborder/Family	Tribe/Genus	Edge	Interior	Rank
Hirudinea			x	x	7
Oligocheata			x	x	15
Gastropoda	Planorbidae		x	x	11
	Physidae		x	x	30
	Lymnaeidae		x		35
Bivalvia	Sphaeriidae		x		38
Amhipoda	Hyalellidae	*Hyalella* sp.	x	x	1
Isopoda	Isopoda	*Caecidotea* sp.	x	x	8
Branchiopoda	Anomopoda		x	x	2
Copepoda			x	x	3
Acariformes	Hydrachnidia		x	x	13
Araneae			x	x	20
Entomobryomorpha	Isotomatidae		x	x	31
Poduromorpha	Poduroidae			x	44
Symphypleona	Sminthuridae			x	50
Ephemeroptera	Baetidae	*Callibaetis* sp.	x		14
	Caenidae	*Caenis*	x	x	16
Odonata	Aeshnidae	*Anax* sp.	x	x	19
	Libellulidae	*Pachydiplax* sp.	x	x	37
	Coenagrionidae	*Enallagma* sp.	x	x	12
Hemiptera	Belostomatidae	*Belostoma* sp.	x	x	17
	Nepidae	*Ranata* sp.	x	x	33
	Pleidae	*Neoplea* sp.	x	x	5
	Corixidae	*Trichocorixa* sp.	x	x	9
		Hesperocorixa	x		47
	Notonectidae	*Notonecta*	x	x	18
		Bouena sp.	x	x	44
	Mesoveliidae		x	x	22
	Aphididae		x	x	10
Trichoptera	Polycentropodidae	*Cernotina* sp.	x		50
	Leptoceridae	*Triaenodes* sp.		x	38
Lepidoptera	Pyralidae		x	x	6
Coleoptera	Haliplidae	*Peltodytes*	x	x	40
	Dytiscidae	*Hydroporus* sp.	x	x	25
		Celina sp.		x	50
		unknown sp.	x	x	44
	Hydrophilidae	*Enochrus sp*	x	x	29
		Sphaeridiinae	x		50
	Staphylinidae	*Carpelimus* sp.		x	50
	Curclionidae		x	x	35
	Carabidae			x	47
	Lampridae		x	x	21
Diptera	Ceratopogonidae		x	x	40
	Chaoboridae	*Chaoborus* sp.	x	x	22
	Chiromonidae	Chrionomini	x	x	4
		Tanytarsini	x	x	28
		Tanypodinae	x		50
	Culicidae	*Coquillettidia* sp.	x	x	33
		Culex sp.		x	40
	Psychodidae		x		49
	Tipulidae	*Dicronota* sp.	x	x	25
	Stratiomyiidae	*Odontomyia* sp.		x	40

	Syphridae			x	24
	Muscidae	*Limnophora* sp.		x	31
Cypriniformes	Cyprinidae	*Pimephales promelas*	x	x	25

Table 3. Mean monthly invertebrate abundance (individuals/m^2) at the open water-stand edge and ten meters into the stand interior in Anderson Lake Marsh, 2004. Bold values are significant ($p<0.10$) in the Indicator Species Analysis.

			July		August		September	
rank			Edge	Interior	Edge	Interior	Edge	Interior
1	Amphipoda	*Hyalella* sp.	6589	5598	3759	**11803**	3785	3224
2	Branchiopoda	Anomopoda	2664	570	**2852**	857	2083	129
3	Copepoda		272	**2368**	906	1235	721	319
4	Diptera	Chrionomini	**711**	251	**1173**	72	**385**	69
5	Hemiptera	*Neoplea* sp.	259	243	149	**425**	180	**950**
6	Lepidoptera	Pyralidae	6	7	12	**120**	53	**1395**
7	Hirudinea		420	304	246	212	152	86
8	Isopoda	*Caecidotea* sp.	95	192	28	**190**	38	456
9	Hemiptera	*Trichocorixa* sp.	**627**	56	**101**	1	29	18
10	Hemiptera	Aphididae	0	0	192	86	130	82
11	Gastropoda	Planorbidae	72	67	22	22	**63**	6
12	Odonata	*Enallagma* sp.	82	12	**18**	4	**126**	4
13	Acarina	Hydrachnidia	20	6	**22**	4	56	10
14	Ephemeroptera	*Callibaetis* sp.	**37**	0	**26**	0	**41**	0
15	Oligocheata		3	1	15	47	10	20
16	Ephemeroptera	*Caenis* sp.	**76**	1	6	0	9	0
17	Hemiptera	*Belostoma* sp.	3	7	38	6	3	4
18	Hemiptera	*Notonecta* sp.	20	1	**23**	0	3	0
19	Odonata	*Anax* sp.	12	7	12	0	13	3
20	Araneae		1	4	4	18	7	10
	remaining taxa		56	91	76	115	54	95

Table 4. Monthly indicator species and corresponding indicator values, as determined by Indicator Species Analysis, at the open water-stand edge and ten meters into the stand interior in Anderson Lake Marsh, 2004. Taxa with p value < 0.10 shown.

			Indicator Value	
July 04			Edge	Interior
	Edge affiliation			
	Ephemeroptera	*Callibaetis* sp.	100	0
	Ephemeroptera	*Caenis* sp.	98	1
	Hemiptera	*Trichocorixa* sp.	92	8
	Diptera	Chironomini	74	26
	Fish	*Pimephales promelas*	100	0
	Interior affiliation			
	Copepoda	Copepoda	10	90
Aug 04				
	Edge affiliation			
	Branchiopoda	Anomopoda	77	23
	Arachnida	Hydrachnidia	83	17
	Ephemeroptera	*Callibaetis* sp.	100	0
	Odonata	*Enallagma* sp.	80	13
	Hemiptera	*Notonecta* sp.	100	0
	Hemiptera	*Trichocorixa* sp.	99	0
	Diptera	Chironomini	94	6
	Diptera	Tanytarsini	83	11
	Interior affiliation			
	Amphipoda	*Hyalella* sp.	24	76
	Isopoda	*Caecidotea* sp.	13	87
	Hemiptera	*Neoplea* sp.	26	74
	Lepidoptera	Pryalidae	9	91
	Coleoptera	*Enochrus* sp.	0	100
Sept 04				
	Edge affiliation			
	Gastropoda	Planorbidae	91	9
	Ephemeroptera	*Callibaetis* sp.	100	0
	Odonata	*Enallagma* sp.	97	2
	Diptera	Chironomini	85	15
	Interior affiliation			
	Hemiptera	*Neoplea* sp.	16	84
	Lepidoptera	Pryalidae	4	96

Table 5. Overall and monthly means by litter treatment for *Typha* litter, live *Typha*, lemnids, total abundance, taxon richness, and the Shannon-Wiener Index in Anderson Lake Marsh, 2005, and their resulting F values from repeated measures ANOVAs. ANOVA for total abundance was log transformed but original values are shown. LL – low litter, ML – moderate litter, HL – high litter.

	Overall Average			July			August			September			Litter	Month	Litterx
	LL	ML	HL	LL	ML	HL	LL	ML	HL	LL	ML	HL	Effect	Effect	Intera
Typha litter (g dry weight/m^2)	394.0	824.7	1408.8	327.2	901.3	1858.2	399.5	754.7	1161.8	455.4	818.0	1206.3	$F_{2,4}$ = 100.1***	$F_{2,8}$ = 10.7**	$F_{4,8}$ = 1
Typha live (g dry weight/m^2)	159.1	130.2	126.2	0.0	0.0	129.4	184.9	213.9	132.4	292.3	176.6	116.7	$F_{2,4}$ = 0.2	$F_{2,8}$ = 1.6	$F_{4,8}$ = 0
Lemnids (g dry weight/m^2)	38.6	38.3	11.6	81.6	46.1	16.0	31.3	48.4	18.1	3.0	20.4	0.8	$F_{2,4}$ = 13.1*	$F_{2,8}$ = 6.8*	$F_{4,8}$ = 2
Total abundance (indv./m^2)	8628	6932	2988	7880	4874	2447	11626	8424	3623	6377	7497	2895	$F_{2,4}$ = 45.0**	$F_{2,8}$ = 6.2*	$F_{4,8}$ = 0
Taxon Richness	21.0	20.8	22.8	19.3	18.7	22.0	20.7	23.3	24.0	23.0	20.3	22.3	$F_{2,4}$ = 6.2	$F_{2,8}$ = 1.5	$F_{4,8}$ = 0
Shannon - Wiener Index	1.2	1.2	2.0	1.1	1.4	1.9	0.9	1.2	2.1	1.5	1.1	1.9	$F_{2,4}$ = 17.8*	$F_{2,8}$ = 0.3	$F_{4,8}$ = 0

* $p < 0.05$, ** $p <0.01$, *** $p <0.001$

Table 6. Presence/Absence of taxa and abundance ranks by litter treatment in Anderson Lake Marsh, 2005. Abundance rank includes multiple ties. LL – low litter, ML – moderate litter, HL – high litter.

Class/Order	Suborder/Family	*Tribe/Genus*	LL	ML	HL	Rank
Hirudinea			x	x	x	7
Oligocheata			x	x	x	13
Gastropoda	Planorbidae		x	x	x	14
	Lymnaeidae		x	x	x	19
	Physidae		x	x	x	21
Amhipoda	Hyalellidae	*Hyalella* sp.	x	x	x	1
Isopoda	Asellidae	*Caecidotea* sp.	x	x	x	2
Branchiopoda	Anomopoda		x	x	x	10
Copepoda			x	x	x	3
Acariformes	Hydrachnidia		x	x	x	24
Araneae			x	x	x	16
Entomobryomorpha	Isotomatidae		x	x	x	15
Poduromorpha	Poduroidae		x	x	x	22
Ephemeroptera	Baetidae	*Callibaetis* sp.	x	x		36
Odonata	Aeshnidae	*Anax* sp.	x			48
	Libellulidae	*Pachydiplax* sp.		x		29
	Coenagrionidae	*Enallagma* sp.		x		42
Hemiptera	Belostomatidae	*Belostoma* sp.	x	x	x	20
		Lethocerus sp.	x			42
	Pleidae	*Neoplea* sp.	x	x	x	4
	Corixidae	*Trichocorixa* sp.	x	x	x	24
	Notonectidae	*Bouena* sp.		x	x	38
	Mesoveliidae		x	x	x	27
	Saldidae				x	48
	Aphididae		x	x	x	9
Trichoptera	Leptoceridae	*Triaenodes* sp.	x	x		42
Lepidoptera	Pyralidae		x	x	x	5
Coleoptera	Dytiscidae	*Hydroporus* sp.	x	x	x	17
		unknown sp.			x	42
	Hydrophilidae	*Enochrus* sp.	x	x	x	11
	Staphylinidae	*Carpelimus* sp.	x	x	x	34
	Scirtidae		x	x	x	12
	Curclionidae		x	x	x	26
	Lampridae		x	x	x	35
Diptera	Ceratopogonidae				x	42
	Chaoboridae	*Chaoborus* sp.	x	x		38
	Chiromonidae	Chrionomini	x	x	x	8
		Tanytarsini	x	x		32
		Tanypodinae	x	x	x	27
	Culicidae	*Coquillettidia* sp.	x	x	x	6
		Uranotania sp.		x		30
		Culex sp.		x	x	32
	Psychodidae		x		x	38
	Tipulidae		x	x	x	18
	Stratiomyiidae	*Odontomyia* sp.	x	x	x	23
	Ephydridae	*Octhera* sp.	x		x	38
		unknown sp.	x			42
	Sciomyzidae			x		48
	Syphridae		x	x	x	31
	Muscidae	*Limnophora* sp.	x		x	37

Table 7. Mean monthly invertebrate abundance (individuals/m^2) of most abundant taxa by litter treatment in Anderson Lake Marsh, 2005. Litter treatments are designated as LL – low litter, ML – moderate litter, HL – high litter. Bold values are significant ($p<0.10$) in the Indicator Species Analysis.

			July			August			September		
rank			LL	ML	HL	LL	ML	HL	LL	ML	HL
1	Amphipoda	*Hyalella* sp.	**5830**	3070	1029	**9330**	6310	1547	3947	6091	1556
2	Isopoda	*Caecidotea* sp.	348	547	477	173	222	459	266	222	167
3	Copepoda		716	278	99	699	509	79	99	88	20
4	Hemiptera	*Neoplea* sp.	351	360	108	392	260	196	228	287	129
5	Lepidoptera	Pyralidae	12	32	26	117	149	64	**754**	146	211
6	Diptera	*Coquillettidia* sp.	50	23	**208**	50	70	**266**	137	85	155
7	Hirudinea		94	**272**	108	88	**193**	53	50	85	56
8	Diptera	Chrionomini	29	41	58	123	205	53	85	123	135
9	Hemiptera	Aphididae	26	0	0	322	161	73	102	35	44
10	Branchiopoda	Anomopoda	99	9	3	**96**	6	3	444	6	0
11	Coleoptera	*Enochrus sp*	18	29	**73**	18	120	205	26	96	70
12	Coleoptera	Scirtidae	0	0	9	47	67	190	20	15	**47**
13	Oligocheata		9	18	**58**	18	23	**149**	12	47	41
14	Gastropoda	Planorbidae	82	61	18	18	6	9	0	3	3
15	Collembolla	Isotomatidae	6	12	6	9	18	26	18	58	38
16	Araneae		3	6	9	3	9	**58**	18	15	50
17	Coleoptera	*Hydroporus* sp.	20	26	41	9	12	18	12	9	12
18	Diptera	Tipulidae	0	0	6	0	18	32	15	3	**44**
19	Gastropoda	Lymnaeidae	53	18	6	6	12	0	6	9	3
20	Hemiptera	*Belostoma* sp.	23	15	15	9	6	12	6	9	0
	remainder		111	58	91	102	50	132	132	67	117

Table 8. Monthly indicator species and corresponding indicator values, as determined by Indicator Species Analysis, by litter treatment for Anderson Lake Marsh, 2005. LL – low litter, ML – moderate litter, HL – high litter. Taxa with p value < 0.10 shown.

			Indicator Value		
July 05			LL	ML	HL
	Amphipoda	*Hyalella* sp.	59	31	10
	Annelida	Hirudinea	20	57	23
	Annelida	Oligocheata	7	21	69
	Coleoptera	*Enochrus* sp.	5	24	61
	Diptera	*Coquillettidia* sp.	12	3	74
Aug 05			LL	ML	HL
	Amphipoda	*Hyalella* sp.	54	37	9
	Branchiopoda	Anomopoda	92	4	1
	Odonata	*Pachydiplax* sp.	100	0	0
	Annelida	Hirudinea	26	58	16
	Annelida	Oligocheata	9	12	78
	Diptera	*Coquillettidia* sp.	9	18	69
	Arachnida	Arachnida	1	8	83
Sept 05			LL	ML	HL
	Lepidoptera	Pyralidae	68	13	19
	Diptera	Tanytarsini	100	0	0
	Coleoptera	Scirtidae	25	12	57
	Diptera	Tipulidae	16	2	71

List of Figure Captions

Figure 1. Anderson Lake (Hamilton Co., IA) showing the predominant vegetation and location of study sites for the monthly transects studied in 2004 and the three stands and three interior litter treatment plots within each stand studied in 2005.

Figure 2. Relationship between litter dry weight and the natural log of total invertebrates in Anderson Lake Marsh, 2005. July and August relationships were significant in a step-wise regression analysis. July, $r^2 = 0.909$, $p < 0.001$, August, $r^2 = 0.821$, $p < 0.001$.

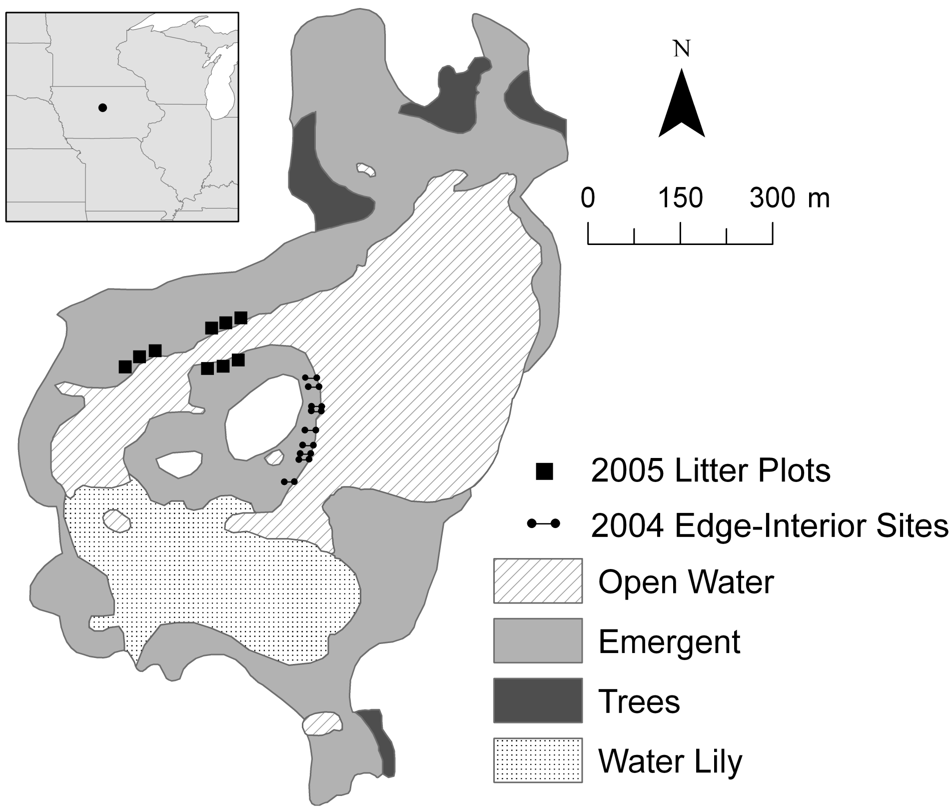
N
0
150
300 m
2005 Litter Plots
2004 Edge-Interior Sites
Open Water
Emergent
Trees
Water Lily

Figure 1.

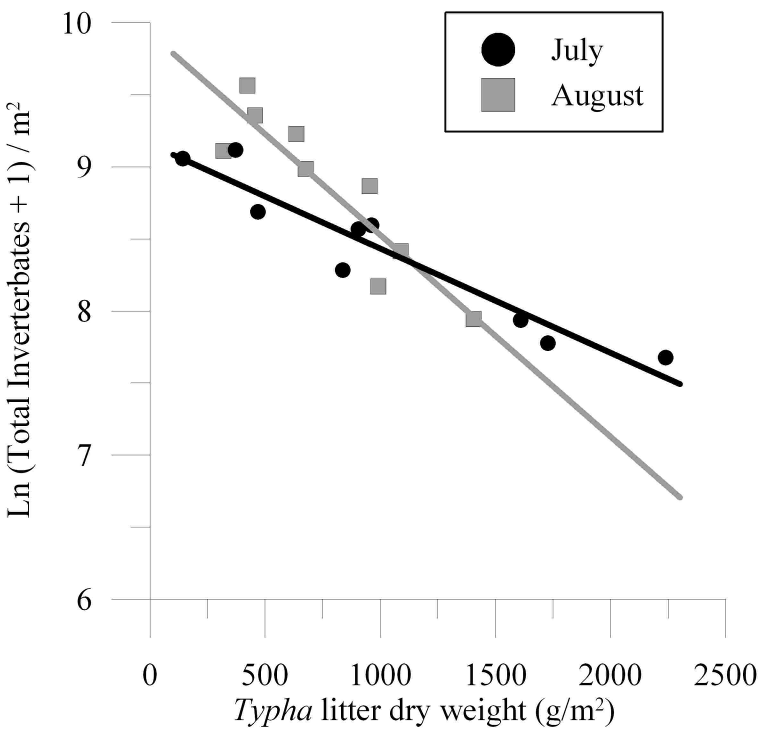
10
9
8
7
6
Ln (Total Inverterbates + 1) / m2
July
August
0
500
1000
1500
2000
2500
Typha litter dry weight (g/m2)

Figure 2.