RESPONSES BY MACROINVERTEBRATES TO CATTAIL LITTER QUALITY AND TIMING OF LITTER SUBMERGENCE IN A NORTHERN PRAIRIE MARSH[1]

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Abstract: An experiment was conducted in the Delta Marsh in south-central Manitoba to assess the effects of initial litter quality, duration of litter submergence, and season of submergence on invertebrate abundance and biomass. Samples of two types of hybrid cattail (*Typha glauca*) litter were added to the marsh throughout the spring and summer and subsequently collected at monthly intervals. Green cattail litter gathered during the preflowering stage contained higher levels of N and P than senesced litter collected from the same stand later in the year. Although the green litter contained higher nutrient levels throughout the season, there was no preference by invertebrates between the two litter types provided. There was a tendency for higher invertebrate densities, especially collector-filterers, to be associated with litter that had been submersed longer. Examination of seasonal patterns of invertebrate functional group abundance showed scrapers with early spring peaks in abundance and biomass. Shredder populations were at peak levels slightly later in the season than scrapers. As the season progressed, shredder and scraper populations declined to relatively low levels. Collector-filterers and predators dominated the invertebrate fauna during August and September.

Key Words: cattail, decomposition, Delta Marsh, functional group, invertebrates, litter.

INTRODUCTION

Peak invertebrate densities and biomass in wetlands are expected to coincide with periods of maximum litter input (Nelson and Kadlec 1984). The underlying premise is that macroinvertebrate abundance in these systems is related to primary production through detrital food chains (Fenchel and Jorgensen 1977, Danell and Sjöberg 1979, Smock and Harlowe 1983). Temperate wetlands receive substantial litter inputs from emergent vegetation stands during the spring as litter fragmented by winter storms enters the water column (Davis and van der Valk 1978). There is also some litter input throughout the ice-free period through stem toppling and animal activities. The invertebrate response to seasonal inputs of litter in wetlands has received little attention.

The nutritional quality of litter also varies over time and may affect invertebrate populations. For example, growing shoots, as might be added by muskrats (*Ondatra zibethicus*) through their feeding and lodge building activities, are considerably richer in N and P than are leaves that fall into the water following natural senescence and fragmentation (Boyd and Hess 1970, Klopatek 1978, Nelson and Kadlec in press). Many aquatic macroinvertebrates are generalists and have the capacity to switch to more nutritive substrates when they become available (Cummins 1973, Motyka *et al.* 1985). Detritivorous invertebrates in streams and salt marshes show a preference for well-conditioned, high quality leaf litter (Barlocher and Kendrick 1975a, Tenore *et al.* 1984, Motyka *et al.* 1985). Food quality has been shown to affect fat contents and growth rates (Ward and Cummins 1979, Valiela *et al.* 1984, Garden and Davies 1988), consumption rates (Iversen 1974), and assimilation efficiencies of detritivorous larvae (Barlocher and Kendrick 1975b).

Our objective in this study was to determine the invertebrate response to hybrid cattail (*Typha glauca*) leaf litter of different nutritional qualities submersed at various times throughout the growing season. *Typha glauca* is a hybrid of *T. angustifolia* and *T. latifolia* (Scoggan 1978-79).

METHODS

Study Area

The study area was located in a narrow channel in the Delta Marsh in south-central Manitoba, Canada (50° 11'N, 98° 19'W). The channel was approximately 15 x 300 m in area, and varied between 40 and 100 cm in depth. The dominant emergent vegetation bordering the channel was cattail, common reed (*Phragmites australis*), and hardstem bulrush (*Scirpus lacustris* spp. *glaucus*). Nomenclature follows Scoggan (1978-79). From early June through mid-August, the channel was dominated by a dense bed of sago pondweed (*Potamogeton pectinatus*) above the 80 cm depth contour.

Experimental Design

Known weight litter samples were added to the marsh during the spring and summer of 1980 and then removed at approximately monthly intervals (Table 1). Ten replicates of 10 date treatments and 2 nutrient levels (green and senesced cattail litter) were arranged in two main blocks (5 replicates per block) in a randomized block design. Included in date treatments were duration of submergence and season of submergence. Two different nutrient levels were obtained by collecting cattail leaves at different times of the year. One set of leaves was collected at the preflowering phenological stage (June 1979) (green litter). A second set was collected from the same stand after fall senescence (February 1980) (senesced litter). All litter was dried at 70°C to constant weight immediately following collection and again just prior to placement in the marsh. Following grinding in a 40-mesh Wiley Mill, total Kjeldahl N and total P were determined before and after submergence according to methods of the American Public Health Association (1980) by the Soils, Water, and Plant Analysis Laboratory at Utah State University. Green litter (2.77 ± 0.05% N, 0.29 ± 0.01% P, n = 3) had higher ($P<0.05$) concentrations of N and P than senesced litter (0.63 ± 0.03% N, 0.05 ± 0.003% P, n = 3).

Table 1. Schedule of sample deployment and collection, Delta Marsh, 1980.

Date removed from marsh	Date added to marsh: May G[a]	May S[b]	June G	June S	July G	July S	August G	August S	Total
June	10	10							20
July	10	10	10	10					40
August	10	10	10	10	10	10			60
September	10	10	10	10	10	10	10	10	80
Total	40	40	30	30	20	20	10	10	200

Series "T"; Series "M"; Series "W"

[a] Green cattail litter
[b] Senesced cattail litter

Dissolved Oxygen and Water Temperature

Dissolved oxygen (DO) concentrations were determined at weekly intervals from 6 randomly selected sampling stations to elucidate seasonal DO trends in the study channel. Diurnal DO fluctuations were measured once each in early and mid summer. Two samples were taken every 4 h at each of 3 randomly selected stations. Resulting diurnal DO curves were then used to correct weekly DO data to predict minimum DO concentrations for those days. All environmental DO samples were taken at the sediment surface with an empty containment tube and the collecting mechanism. Oxygen concentrations were measured with a precalibrated Orion oxygen meter.

Maximum and minimum daily water temperatures at the sediment surface were recorded weekly with submersible min/max thermometers positioned at 3 permanent sampling sites. Water temperatures were also taken whenever water samples for DO analyses were collected to provide DO correction factors.

Sampling Invertebrates

Standard litter bags, although widely used in decomposition studies, do not control sedimentation rates among samples, may exclude large invertebrates, and may lose small invertebrates during sample retrieval. In response to these problems, transparent acrylic litter containment tubes (6.4 cm I.D. x 30 cm long), each containing approximately 5 g of dried litter, were used in this study. Large-mesh polyethylene screen (7.9 mm openings) was fastened over each end of the tube to prevent the litter from escaping, yet allowed most macroinvertebrates free access to and from the litter sample. Each tube was attached to a stake so, when submersed, the bottom of the tube rested on the sediment surface. After the prescribed number of days, the tube, litter, and surrounding water were collected by closing off each end of the tube with rubber stoppers before removal from the marsh.

Invertebrates were separated from the litter and preserved in 70% ethanol. Samples were stained with Rose Bengal (100 mg/l as per Marson and Yevich 1967) to facilitate the enumeration of small individuals. After sieving into 7 size classes (U.S. Standard Sieve Nos. 5 (4 mm mesh size), 7 (2.8 mm), 10 (2 mm), 14 (1.4 mm), 18 (1 mm), 25 (0.71 mm) and 35 (0.5 mm)), the invertebrate samples were sorted and counted. Invertebrate taxa were placed into functional groups (as defined by Cummins 1973) according to several sources (Merritt and Cummins 1978, Pennak 1978, Anderson and Sedell 1979, Sutcliffe *et al.* 1981, among others) (Table 2). Identification to family was usually sufficient to establish functional level based on feeding mechanisms (Cummins 1973).

To obtain biomass estimates, invertebrates were dried at 100°C for at least 24 h and cooled in a dessicator prior to weighing. Mean weights (n = 50) were calculated for all size classes of commonly occuring taxa. Invertebrates stored in

Table 2. Functional group classification of macroinvertebrate taxa collected, Delta Marsh, Manitoba.

SHREDDERS	SCRAPERS
Amphipoda	Gastropoda
Talitridae	Physidae
Gammaridae	Lymnaeidae
	Planorbidae
COLLECTORS-FILTERERS	PREDATORS
Nematoda (Phylum)	Phynchobdellida
Oligochaeta (Class)	Glossophoniidae
Cladocera (Order)	Trombidiformes (Sub-Order)
Ephemeroptera	Hydrachnidae
Caenidae	Odonata
Baetidae	Lestidae
Hemiptera	Coenagrionidae
Corixidae	Aeshnidae
Trichoptera	Coleoptera
Hydroptilidae	Haliplidae
Leptoceridae	Gyrinidae
Phryganeidae	Dytiscidae
Diptera	
Ceratopogonidae	
Chironomidae	
Ephydridae	

70% ethanol lose weight with time, however the weight-loss function is asymptotic, with little loss occurring after 60 days (Howmiller 1972, Wiederholm and Eriksson 1977). All invertebrates were stored in 70% ethanol for at least 4 months prior to drying and weighing. Thus, the biomass estimates derived are best viewed as relative biomass indices.

Statistical Analyses

Split-plot analysis of variance was used to analyze effects of length and season of submergence and nutrient levels of litter on invertebrate abundance and biomass. The effects of litter type and season were considered fixed, while those of block and row within block were random. Prior to analysis, the data transformation required to stabilize the variance of each variable was calculated using Taylor's Power Law, as described by Downing (1979) and Allen (1984). Log(x+1) transformations were required for each variable analyzed. Protected least significant difference tests (LSD) were used for planned mean comparisons (Carmer and Swanson 1973). All analyses were conducted on the B6800 at Utah State University using STATPAC (Hurst 1973).

RESULTS

Physical Environment

Although higher and more variable water temperatures are normal during the mid-summer months in the Delta Marsh (Murkin 1983), water temperatures in the study channel showed little change from May through September 1980, with a mean weekly temperature of 18.3 ± 3.0° C (Nelson 1982).

Estimated daily minimum DO concentrations indicated that aerobic conditions (>3 mg/l as defined in Suthers and Gee (1986)) persisted above the sediment-water interface throughout the study except for a single day in July when a level of 2 mg/l (moderate hypoxia as defined by Suthers and Gee (1986)) was recorded.

Invertebrate Response

Split-plot, 2-factor ANOVA established date (season and length of submergence) as having a significant effect ($P<0.05$) on numbers and biomass of invertebrates for all functional groups other than predator biomass (Table 3). The main effect of substrate quality did not significantly influence numbers or biomass of any functional group. Scraper biomass responded differently to substrate quality at different times of year ($P<0.05$).

Functional group response patterns to four stages of litter decomposition (Series "W", Table 1) were evaluated after controlling for seasonality of invertebrate abundance and biomass (Figure 1). No strong differential preference for decomposition stage was observed, although the total number of individuals per sample increased with time submersed ($P<0.05$). Both abundance and biomass of collector-filterers increased as litter aged ($P<0.05$).

Invertebrate numbers and biomass from substrates conditioned to the same stage (30 days) (Series "M", Table 1) were used to evaluate seasonal shifts for each functional group (Figure 2). Total macroinvertebrate numbers and biomass declined only slightly through the summer, even though strong seasonal shifts ($P<0.05$) in abundance and biomass occurred among shredders and scrapers. Both shredders and scrapers showed highest abundance and biomass early in the season with shredder populations reaching peak levels slightly later than scraper popula-

Table 3. Split-plot, 2-factor ANOVA results on log (x+1) transformed macroinvertebrate abundance and biomass data.

	Totals	Shredders	Scrapers	Collector-Filterers	Predators
A. BIOMASS					
Main Plots:					
Blocks	NS[1]	NS	$P<0.05$	NS	NS
Row within block (R)	NS	NS	NS	NS	NS
Sub Plots:					
Substrate(S)	NS	NS	NS	NS	NS
Date(D)	$P<0.05$	$P<0.05$	$P<0.05$	$P<0.05$	$P<0.05$
SxD	NS	NS	$P<0.05$	NS	NS
RxS	NS	NS	NS	NS	NS
RxD	NS	NS	NS	NS	NS
RxSxD	NS	NS	NS	$P<0.05$	NS
B. NUMBERS					
Main Plots:					
Blocks	$P<0.05$	NS	NS	$P<0.05$	NS
Row within block (R)	NS	NS	NS	NS	NS
Sub Plots:					
Substrate(S)	NS	NS	NS	NS	NS
Date(D)	$P<0.05$	$P<0.05$	$P<0.05$	$P<0.05$	NS
SxD	NS	NS	NS	NS	NS
RxS	NS	NS	NS	NS	NS
RxD	NS	NS	NS	NS	NS
RxSxD	$P<0.05$	NS	NS	$P<0.05$	NS

[1]Not significant ($P>0.05$)

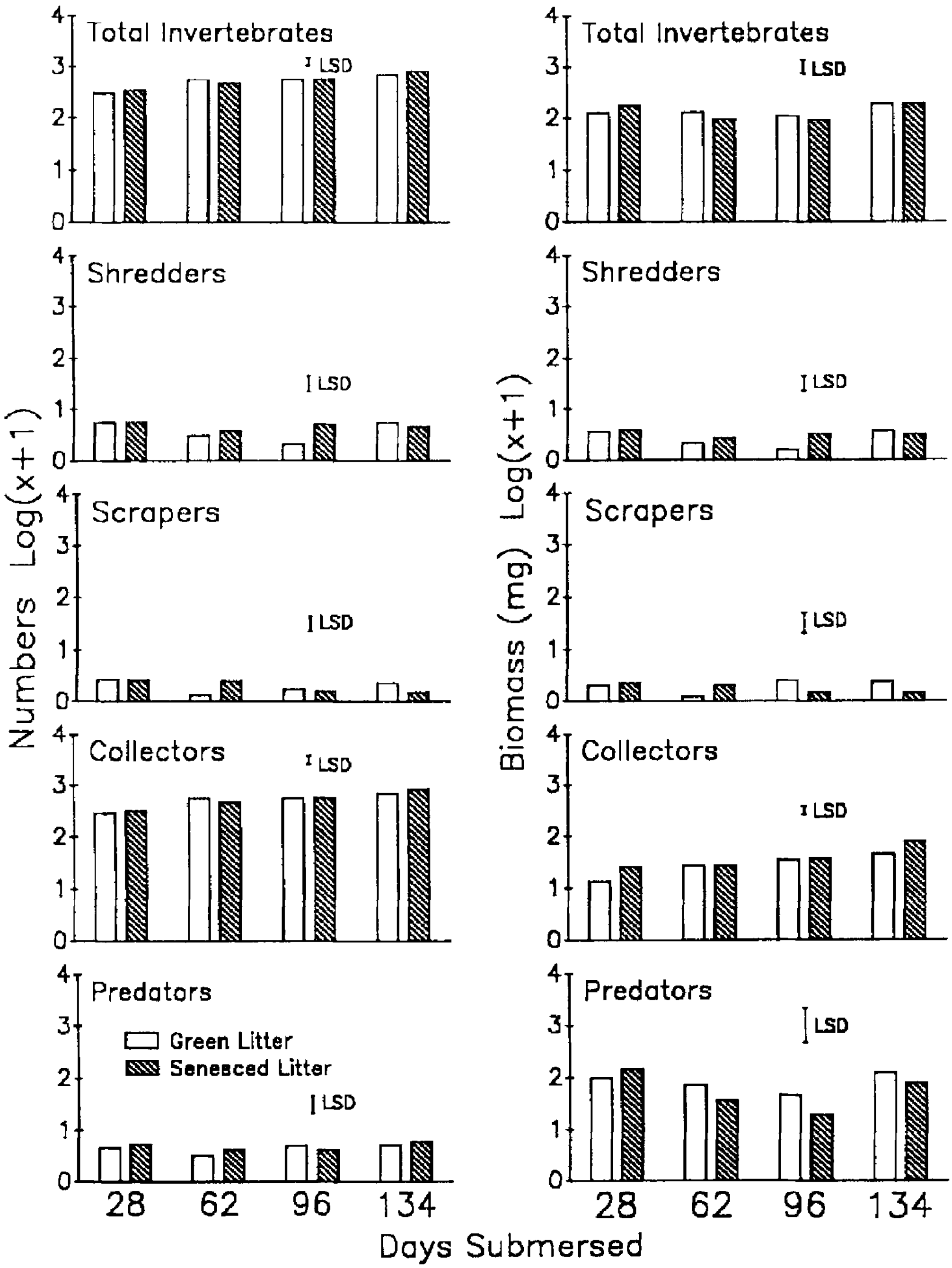

Figure 1. Macroinvertebrate functional group colonization patterns on *Typha* sp. leaf litter during late summer (Series "W", Table 1). LSD - least significant difference range ($P<0.05$) for comparison of days submersed.

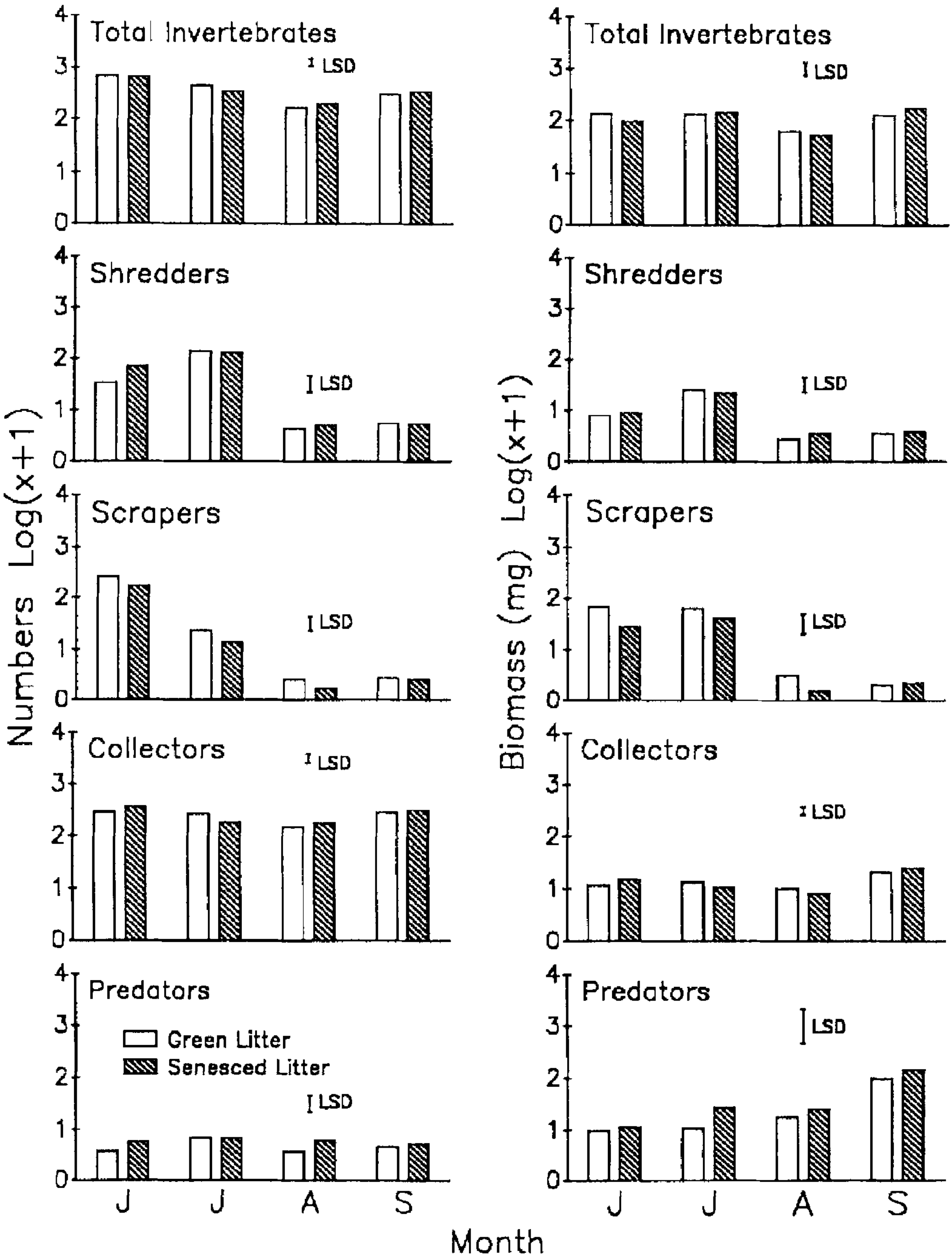

Figure 2. Macroinvertebrate functional group colonization patterns 30 days after submergence of *Typha* sp. leaf litter during each summer month (Series "M", Table 1). LSD - least significant difference range ($P<0.05$) for comparison of months.

tions. Collector-filterers and predators dominated the invertebrate fauna during August and September. Predatory invertebrate biomass increased significantly ($P<0.05$) in late summer, while both numbers and biomass of collector-filterers remained approximately constant throughout the summer.

Group responses to detritus of different ages sampled throughout the summer (Series "T", Table 1) (Figure 3) yielded nearly identical results to functional group response to litter conditioned for 30 days (Series "M", Table 1).

DISCUSSION

Water temperatures were stable throughout the study period and therefore likely had little impact on invertebrate levels within the study area. In addition, oxygen levels did not appear to be a factor affecting invertebrate numbers.

Litter nutrient content (Garden and Davies 1988) and leaf texture (Anderson and Sedell 1979), which influence microbial conditioning rates, are two important factors in determining food quality for macroinvertebrate colonizers. In this study, the percent dry-weight N and P in green litter remained consistently higher than in senesced litter submersed at the same time (Nelson and Kadlec, in press). In spite of these differences in litter quality, there was no differential choice by macroinvertebrates of the 2 types of litter. Others have shown that nutrient content may play a minor role in food selection by detritivores (Smock and Harlowe 1983, Gleason 1986). Lawson *et al.* (1984) suggest that microbial community structure may be more important to detritivores than total nutrient content of the litter. Rietsma *et al.* (1988) suggest that phenolic acid content of the litter may be more important in controlling food choice by detritivores than the actual nutrient content. Unfortunately, phenolic acid content of the two litter types was not measured in our study.

Our experimental design may be responsible in part for the lack of choice between the 2 litter types. Because only small discrete samples of litter were added to the marsh at any time, overall invertebrate densities were not affected. The sampling tubes were open systems and in effect, we sampled invertebrate populations whose densities were already established by natural detrital input patterns. The vast quantities of senesced substrate available in the surrounding environment likely overwhelmed any impact by the small amounts of the higher quality litter. Additionally, when the widest range of experimental substrate choice was available (September, Series "W"), natural invertebrate life history patterns dictated low abundance and biomass of shredders and scrapers. Any preference test was essentially negated, after controlling for season, by the absence of these two functional groups. Collector-filterers (primarily Chironomidae) responded in proportion to their abundance, and predators, as expected, failed to show a specific colonization pattern.

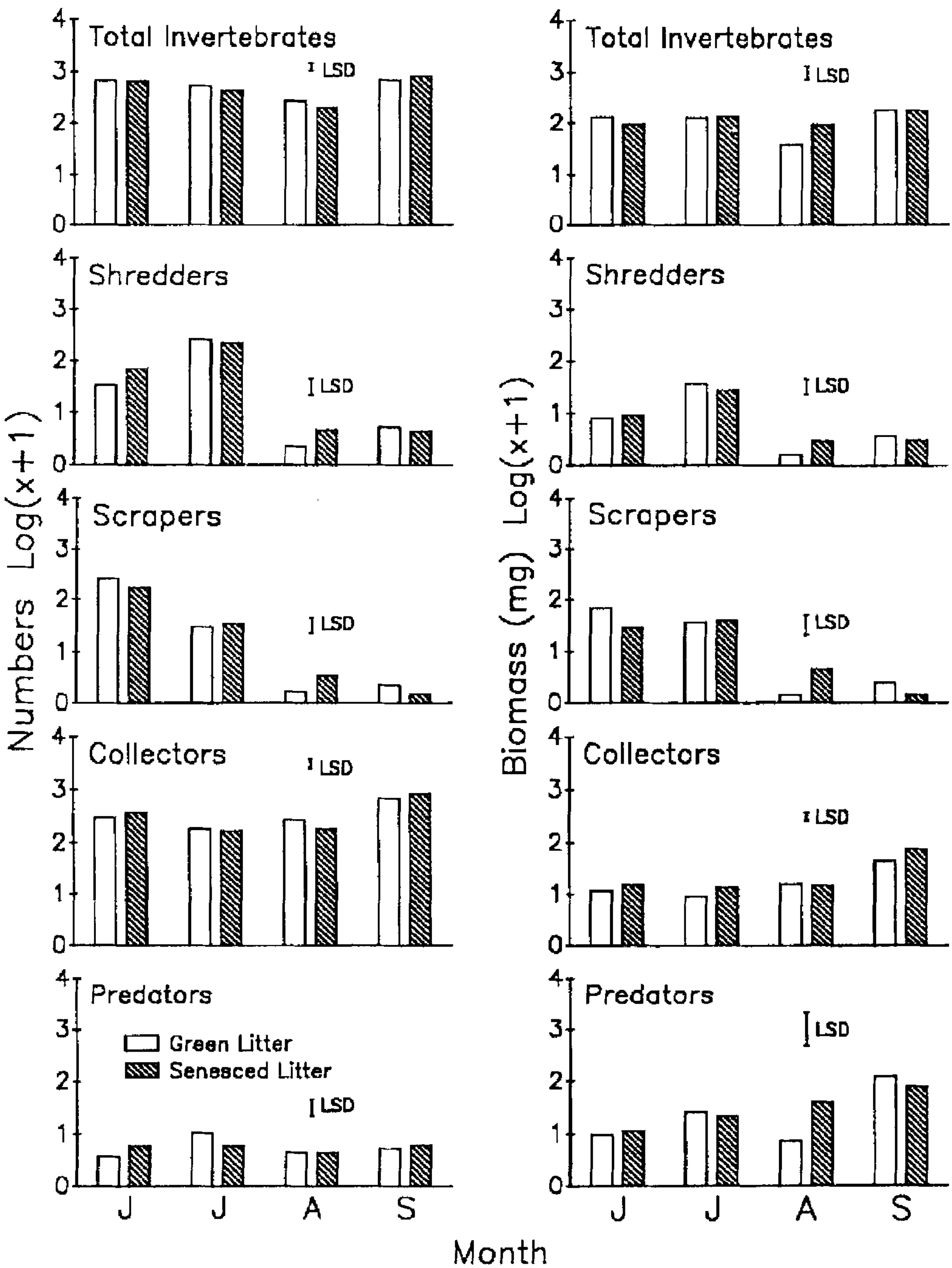

Figure 3. Macroinvertebrate functional group colonization patterns on *Typha* sp. leaf litter through the summer (Series "T", Table 1). LSD - least significant difference range (P<0.05) for comparison of months.

The tendency for more invertebrates to be associated with litter that has been submersed longer has been observed by other workers in salt marshes (Findlay and Tenore 1982, Tenore *et al.* 1984). Detritus derived from vascular plants like cattail with high structural material content require some processing by microbes before the nutrients within the plant tissues are available to consumers. The increase in collector-gatherers on older litter is likely a direct result of the longer processing period and the fragmentation of the litter particles over time.

Seasonal patterns of functional group abundance recorded during this study provide some evidence for the influence of litter on invertebrate distribution and abundance in wetland environments. Scrapers (primarily snails) showed early spring peaks in abundance and biomass that correspond to early spring inputs of fragmented emergent leaf litter. Scrapers likely take advantage of the plentiful surface areas provided by the abundant coarse particulate organic matter (CPOM, >1.0 mm), which are richly colonized by epiphytes (Anderson and Cummins 1979). Pip and Stewart (1976) showed seasonal peaks in abundance and biomass of snails in roadside ditches along the Delta Marsh identical to those observed in this study.

Shredders probably responded, as did scrapers, to microbial and algal conditioning of CPOM litter. Because scrapers feed primarily on the surface of CPOM particles and shredders feed both on the surface and within the litter particle, shredders may prefer litter that has conditioned longer. This may explain why shredder populations peaked later in the season than scraper populations. As the season progressed and the availability of CPOM decreased, shredder and scraper populations declined to relatively low levels.

Collector-filterers should be well-suited to the wetland environment because an abundance of fine particulate organic matter (FPOM, <1.0 mm) exists throughout the season (Nelson and Kadlec 1984). In most aquatic environments, however, FPOM quality likely declines as particles become more refractory through the summer (Ward and Cummins 1979). In our study, this seemed to be the pattern. Collector-filterers numbers and biomass declined slightly until mid-August when rapid senesence and decomposition of the sago pondweed beds occurred and provided an enriched, fine particulate food resource to the collector-filterer community (see Howard-Williams and Davies 1979, Carpenter 1980). In response, collector-filterer biomass increased significantly by the September sampling.

As expected, predator populations did not respond directly to seasonal inputs of detritus. Their distribution and abundance are probably influenced mostly by prey abundance (Anderson and Cummins 1979).

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