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Variable response by aquatic invertebrates to experimental manipulations of leaf litter input into seasonal woodland ponds

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Abstract: Aquatic invertebrates are crucial components of foodwebs in seasonal woodland ponds, and leaf litter is probably the most important food resource for those organisms. We quantified the influence of leaf litter inputs on aquatic invertebrates in two seasonal woodland ponds using an interception experiment. Ponds were hydrologically split using a sandbag-plastic barrier, and a mesh canopy was suspended over one-half of each pond to intercept autumn leaf fall for four years. Subsequently the mesh canopies were removed so recovery could be assessed. In one wetland pond, overall invertebrate biomass and the biomass of certain functional groups declined in the interception half-pond and then rapidly recovered after litter inputs were restored. In this pond, leaf litter was a crucial resource to invertebrates, which is consistent with findings in other detritus-dominated ecosystems. However, in the second wetland pond the relationship between litter and invertebrates was very different, and interception appeared to benefit rather than harm invertebrates. Invertebrates were sensitive to changes in leaf litter input in both ponds, but interactions were not consistent. Highly variable wetland conditions in ponds (seasonal drying, stagnant water) may complicate litter-invertebrate interaction in these habitats.

Key words: community ecology, detritus, litter exclusion, seasonal ponds, wetlands

Introduction

Leaf litter and wood from peripheral forests is the primary energy base for food webs in many headwater streams (VANNOTE et al. 1980). By experimentally breaking the leaf litter connection between a small headwater stream and the adjacent upland forest, WALLACE et al. (1997) induced a dramatic decline in the resident aquatic invertebrate community, which in turn limited salamanders that fed on invertebrates (JOHNSON & WALLACE 2005). Small woodland ponds embedded in forest are in many ways analogous to headwater streams, and detrital inputs from the surrounding forest are probably an important influence on pond ecology (OERTLI 1993, PALIK et al. 2005). However, the relationship between leaf litter and ecosystem processes in small woodland ponds has received scant attention (but see MAGNUSSON & WILLIAMS 2006), particularly how this relationship influences the important invertebrate fauna (BATZER &WISSINGER 1996). We hypothesized that invertebrate populations and communities in small woodland ponds were controlled by leaf litter flux, as they are in headwater streams, and assessed pond invertebrate interaction with leaf litter using an interception experiment in two seasonal woodland ponds of northern Minnesota, USA.

Methods

Study habitats

Because of logistic difficulties, litter manipulation experiments in streams have typically used a single habitat with a paired reference stream (e.g., WALLACE et al. 1997). The small size of wetland ponds permitted us to manipulate two habitats simultaneously. However, seasonal woodland ponds in northern Minnesota presented their own logistic

difficulties. We had previously sampled 66 regional ponds (BATZER et al. 2004) and found that resident invertebrate communities were highly variable, both among and within ponds. In fact, it was common for a taxon to be very abundant one year and rare the next, or vice versa. Because natural variation was so extreme, we could not find ponds that responded similarly, and thus could not justifiably assign replicate pond pairs. Thus, analyses typically used in paired whole-system manipulations (e.g., randomized intervention analyses as used by WALLACE et al. 1997) were not appropriate for these ponds.

We instead opted to use a split-habitat approach (LIKENS 1985) to minimize extraneous variation (details below). We restricted the study to two ponds because of logistic constraints. Specifically, because of copious snowfall, we were required to erect the canopies in late summer and remove them in winter of each year, a time consuming and logistically difficult process. A lack of true replication required us to use a case study approach to evaluate results.

Both study ponds were located in the Sucker Lakes watershed of Chippewa National Forest, Cass County, Minnesota. Of the 66 ponds that we had previously described in that area, the two study ponds were within the normal range of hydrology, water chemistry, and invertebrate community composition. They were chosen primarily because each was small enough to enable us to build canopies. Pond 568 covered 331 m^2, and the hydrology was seasonal, typically drying in late summer of each year and reflooding in autumn or spring. Pond waters were slightly acidic and eutrophic (Table 1). The tree canopy cover over Pond 568 was 90%, and leaf litter input consisted of 42.6% wetland trees (black ash and red maple) and 57.4% upland trees. Pond 288 covered 448

m^2 and had a semi-permanent hydrology, only drying completely during the latter part of dry summers. Pond waters were slightly acidic and eutrophic (Table 1). The canopy cover over Pond 288 was 81%, and leaf litter input consisted of 73.9% wetland trees (almost exclusively black ash) and 26.1% upland trees. The total biomass of leaf litter deposited into both ponds was similar, approximately 200 gm dry mass•m^{-2}.

Litter interception

In August of 1999, the two ponds were divided roughly into equal halves by a sand bag and plastic sheet barrier (Fig. 1) that hydrologically isolated the two halves when ponds were flooded. We then randomly selected one half of each pond for litter interception. A 24-mm mesh-size nylon canopy (Nylon Net Company, Memphis, TN) was suspended over each half-pond to collect autumn leaf fall (Fig. 1). Leaves accumulating on the mesh were blown off to the sides of the pond weekly using a gas-powered leaf blower. This canopy dramatically reduced inputs of upland litter, but many of the small leaflets of black ash penetrated it. To correct this, the mesh canopies installed in autumn 2001 and 2002 were of a finer 6-mm square mesh that reduced inputs of all kinds of litter. By removing and reinstalling canopies yearly we eliminated possible artifacts of canopy presence during the important spring and summer periods when insect colonization and plant growth occurred. Past sampling indicated that litter input during non-autumn periods was minimal (PALIK, unpublished data). In autumn 2003, canopies were not reinstalled and ambient amounts of leaf litter were allowed to enter both halves of each pond, permitting us to collect post-interception recovery data.

Sampling

After litter interception began, we continued to sample the ponds in much the same manner as we had while collecting baseline descriptive data in 1998 and 1999 (BATZER et al. 2004). We measured water depths in each half-pond using a staff gauge (monitored bi-weekly to monthly). Water samples were collected from each half-pond and brought back for laboratory analyses of pH, alkalinity, total N, total P, and dissolved organic C. Herbaceous plant cover was monitored in permanent plots (50 X 50 cm; n = 4 per half pond). Neither water level, water chemistry, nor herbaceous plant cover differed significantly between halves of either pond. We had anticipated that litter interception would decrease levels of dissolved organic C, but apparently ponds received large inputs of dissolved organic C (and other chemicals) from their entire watershed, not only from local leaf flux. Dissolved organic C in each pond occurred at very similar concentrations (Table 1).

Overhead leaf litter inputs into half-ponds were monitored using conical traps (30 cm diameter, 3 per half pond). Box traps measured lateral inputs, but they were negligible compared to overhead inputs (even after the leaf blower was used). Collected leaves were identified and categorized as 1) black ash, 2) other wetland species, or 3) upland species. Dry mass of leaf samples was assessed by oven-drying at 60^{o}C for one night and then weighing.

In mid-May and again in late-June of each year, invertebrates were sampled with four 1-m sweeps of a D-frame net (1-mm mesh, 30 cm wide opening) collected at randomly selected locations in each of the four half-ponds. During periods with extremely low water levels, the number of sweeps was reduced to limit possible impacts

on the confined residual fauna. The ponds contained an abundance of fine sediment, which precluded using a finer mesh size because of clogging problems. We acknowledge that the smallest invertebrates could have washed through the 1-mm mesh, so we use biomass rather than abundance for most analyses. Samples were preserved in 95% ethanol, and then processed in the lab. Invertebrates were identified to family or genus using keys in PENNAK (1989), THORP & COVICH (1991), and MERRITT & CUMMINS (1996), and then enumerated. Invertebrate biomass was assessed by oven drying specimens at 60^{o}C for at least 24 hrs followed by desiccation to determine dry mass. Those specimens were then burned at 500^{o}C, redesiccated, and then reweighed to determine ash-free-dry-mass (AFDM). Alcohol preservation affects mass (fats can be dissolved), and correction factors do not exist for most taxa in the study ponds. Thus, caution should be used when comparing our biomass estimates to other studies.

Analyses

While we had pre-interception data collected in 1998 and 1999 as a baseline for each pond, annual variation in invertebrate communities was extreme, and precluded gradient analyses (e.g., regression) using 1998 and 1999 data as starting points. We present pre-interception data for each pond, but do not analyze it.

Although typical habitats for the region, the two study ponds still differed in many ways, and post-interception invertebrate communities in each varied dramatically from year to year. Thus we analyzed each pond and year separately. Each year, invertebrate biomass in pond halves was contrasted using two-way ANOVA, which accounted for treatment and seasonality (mid-May vs. late-June). We used total biomass, and the mass of individual functional feeding groups (shredders, collectors, scrapers, predators; see

MERRITT & CUMMINS 1996) because we anticipated that different groups might respond differently.

While the above analyses could establish that pond halves were different after the start of interception, we could not determine if differences reflected the influence of litter interception itself or were caused by pre-existing conditions. Lacking pre-interception data stratified by half-ponds, we used post-interception data collected in 2004 to account for variation unrelated to litter manipulation. If differences observed during interception disappeared in 2004, after litter input was restored to the entire pond, we then could infer that earlier treatment differences were caused by interception.

Results

Leaf litter interception

The 24-mm mesh canopies used to intercept autumn leaf fall in 1999 and 2000 mainly influenced inputs of upland litter (Table 2). In Pond 568 (Fig. 1), an average of 49.2% of the upland litter was intercepted, but only 17.2% of the wetland litter; the overall interception rate was 35.2%. In Pond 288, an average of 59% of the upland litter was intercepted, but only 18% of the wetland litter; the overall interception rate was 30.1%. Because upland litter had a greater bulk density than wetland litter, overall rates of leaf interception in autumn 1999 and 2000 were up to 7% more efficient in terms of volume or leaf surface area (data not presented).

. After 6-mm mesh canopies were installed in 2001 and 2002, the majority of the mass input of both upland litter (84.6 – 93.4%) and wetland litter (56.6-80.5%) was intercepted in both ponds (Table 2). Changing net-mesh sizes from 1999-2000 to 2001-

2002 made the canopies function much like stacked sieves. In 1999-2000 the coarse mesh intercepted upland litter, while in 2001-2002 the degree of interception was increased to include both wetland and upland leaf litter. This partially isolated litter inputs of allochthonous (upland) trees from autochthonous (wetland) trees.

Response of invertebrates to litter interception

Invertebrates in both study ponds were influenced by litter exclusion. However, the nature of response differed between Pond 568 and Pond 288.

Patterns in Pond 568: The macroinvertebrate fauna of this pond was numerically dominated by Chironomidae midges (Chironominae), Pisididae (*Sphaerium*) fingernail clams, and Lumbriculidae aquatic worms. Large-bodied Physidae snails (*Aplexa*) and Limnephilidae caddisfly larvae (*Limnephilus*) contributed significant biomass. Annual natural variation was extreme, and individual groups typically varied by an order of magnitude from year to year in the reference half-pond (Fig. 2). Amphibians were rarely encountered in this pond.

In 2000, the first year after interception was initiated, total invertebrate biomass was lower in the interception half-pond than the half-pond with ambient litter input (Fig. 2A; $F_{1, 12} = 11.0$, $P = 0.0062$). This overall pattern was largely due to a significant decrease by collectors (Fig. 2C; $F_{1, 12} = 7.5$, $P = 0.0181$; primarily midges and fingernail clams). The next year (2001), total biomass was again lower in the interception half-pond than in the reference half-pond (Fig. 2A, $F_{1, 12} = 7.6$, $P = 0.0177$), but this time the response was driven largely by a decrease in scraper biomass (Fig. 2D; $F_{1, 12} = 8.7$, $P = 0.0122$; primarily physid snails). In 2002, after the interception level had been increased to include wetland litter (Table 2), total biomass was only marginally lower in the

interception half-pond (Fig. 2A; $F_{1, 12} = 4.5$, $P = 0.0563$). That year, patterns were driven by large increases of limnephilid shredders (Fig. 2B, $F_{1, 12} = 6.6$, $P = 0.0248$) and predators (Fig. 2E; $F_{1, 12} = 5.1$, $P = 0.0439$; primarily Dysticidae beetles and Glossophoniidae leeches). In 2003, Pond 568 was flooded only partially for the May collection and it was dry by June, so few samples were collected. We did not statistically analyze data from that year, but patterns in total biomass between pond halves mirrored those in previous years (Fig. 2A). After litter inputs were restored to natural levels over the whole pond in autumn 2003, invertebrate communities developing in the former interception half-pond in 2004 became almost identical to those in the reference area (Fig. 2A-E; total biomass, $P = 0.5612$; shredder biomass, $P = 0.3511$; collector biomass, $P = 0.7231$; scraper biomass, $P = 0.3968$; predator biomass, $P = 0.9078$). Although the organisms dominating the biomass changed almost yearly, overall biomass was greatest in the reference half-pond for all seven samples collected over the four-year interception period. Only after litter inputs were restored did that pattern reverse, with total biomass in the former interception area being modestly (8%) greater than the reference area.

Patterns in Pond 288: Many of the same taxa that dominated Pond 568 also dominated Pond 288. However, the only macroinvertebrates consistently common in Pond 288 were fingernail clams. Otherwise the community varied greatly from year to year. Chironominae midges were conspicuously abundant in 2000 and Culicidae (*Ochlerotatus*) mosquitoes in 2003. Large Erpodbellidae leeches contributed a considerable amount to total biomass in 2001, while limnephilid caddisflies dominated community biomass in 2002 and *Aplexa* physid snails dominated it in 2003. Amphibians

were typically rare in this pond, but numerous wood frog larvae (*Rana sylvatica*) were encountered in June 2002 (data not presented).

In the first year post-interception (2000), total invertebrate biomass (Fig. 3A; $F_{1, 12}$ = 9.69, P = 0.0090) and collector biomass (Fig. 3C; $F_{1, 12}$ = 11.68, P = 0.0051) differed significantly between halves of Pond 288. However, opposite of Pond 568, total biomass and collector biomass was greatest in the interception half. In 2001, the same trend for higher total biomass in the interception half-pond occurred again ($F_{1, 12}$ = 3.88, P = 0.0725), but this year the response was driven by predators (Fig. 3E; $F_{1, 12}$ = 5.00, P = 0.0451). This predator response was countered by shredder (limnephilid) biomass, which, although not large, was higher in the reference portion of the pond (Fig. 3B; $F_{1, 12}$ = 6.26, P = 0.0278). In 2002, total biomass no longer differed between half-ponds ($F_{1, 12}$ = 3.12, P = 0.1029). However, that year shredder biomass was much greater in the interception half (Fig. 3B; $F_{1, 12}$ = 10.40, P = 0.0073), a reversal of the pattern for limnephilids the previous year. In 2003, scraper biomass increased substantially, and was highest in the reference area ($F_{1, 12}$ = 9.41, P = 0.0098). Limnephilid biomass that year, as in 2002, remained higher in the interception treatment ($F_{1, 12}$ = 15.00, P = 0.0022). In 2004, after natural inputs of leaf litter had been restored to the entire pond, biomass of most groups were very similar in both pond halves (Figs. 3A, B, C, E), with the exception of snail scrapers, which had greater biomass in the former interception half of the pond ($F_{1, 12}$ = 30.34, P = 0.0001) (a reversal of the spatial pattern seen the previous year). Responses by invertebrates to litter interception in Pond 288 were highly variable and somewhat inconsistent. However, patterns in this pond were clearly dissimilar to Pond 568.

Discussion

For forested headwater streams, a consensus has emerged that leaf litter input dominates ecosystem processes (VANNOTE et al. 1980, RICHARDSON 1991, WALLACE et al. 1997, JOHNSON & WALLACE 2005). Leaf litter is the primary food for headwater stream invertebrates, and experimental removal can cause invertebrate communities to collapse (WALLACE et al. 1997). Our hypothesis was that a similar relationship existed in small seasonal ponds embedded in forest. However, our whole-pond studies and recent smaller-scale enclosure studies by MAGNUSSON & WILLIAMS (2006) suggest that the relationship between leaf litter and invertebrates in woodland ponds is less straight-forward than it is in headwater streams.

At first glance, the relationship between leaf litter and invertebrates in Pond 568 (Fig. 2) appeared to mirror patterns observed in forested headwater streams. Consistently lower invertebrate biomass in the interception half-pond relative to the reference half-pond, and the recovery of invertebrates in the interception half-pond after litter was restored, each indicated that leaf litter was a crucial resource for invertebrates in this pond, as it is in forested headwater streams (WALLACE et al. 1997, JOHNSON & WALLACE 2005). However, in some ways responses in this pond differed from those in streams. In streams, there is typically a lag in response to litter interception until the material retained in the channel is exhausted, and the first invertebrates to respond are shredders that are reliant on coarse material for food (WALLACE et al. 1997, EGGERT &WALLACE 2003). In Pond 568, however, a trophic link between leaf litter and invertebrates was less obvious. The initial response was driven by collectors, and a shredder response was not detected until the third year of interception (albeit that was the only year *Limnephilus* was

common in that pond). Overall response was surprisingly rapid given that wetlands naturally retain organic matter and that the first year of interception was only partial. Large amounts of nitrogen-rich black ash litter (see PALIK et al. 2005) penetrated the canopy in the first two years of interception, and only lower quality (relative to black ash) upland litter was effectively intercepted. However, intensifying interception rates during autumn 2001 and 2002 did not elicit a stronger response in Pond 568 than with the previous partial interception. In streams, invertebrates continue to decline as interception efforts are maintained. Rapid post-interception recovery of invertebrates was also not consistent with a trophic response. If the invertebrates in the interception half-pond were responding to food levels, we would have expected a lag in recovery by passive dispersers (mollusks, crustaceans) while they converted increased food to progeny. However, even non-insects recovered within the first year.

Response in Pond 288 defied generalization, but it was clearly different from Pond 568. While many of the same organisms responded simultaneously in both Ponds 568 and 288, the direction of response was often opposite, with biomass being higher in the interception half of Pond 288 (e.g., collector and total biomass in 2000, shredder biomass in 2002). However, in Pond 288, the same organisms could also respond differently from one year to the next (shredders in 2001 vs. 2002, scrapers in 2003 vs. 2004). Like Pond 568, responses were elicited almost immediately, and continued and intensified interception did not accentuate response. After leaf litter inputs were restored to all of Pond 288, most invertebrate groups became remarkably similar between half-ponds, with the exception of snail scrapers. Because some differences occurred between half-ponds even after interception was discontinued, we cannot rule out that the drastic

differences between the two halves of Pond 288 were inherent, and not related to litter input.

It is quite plausible that leaf litter could elicit a variety of responses by aquatic invertebrates in woodland ponds (see also MAGNUSSON & WILLIAMS 2006), and perhaps the variable responses in Ponds 568 and 288 are not unexpected. Studies in streams focus on the value of leaf litter as food. In seasonal woodland ponds, besides food, leaf litter may provide many additional values. Leaf litter can benefit invertebrates by serving as habitat, and, when ponds are dry, protection from desiccation and temperature extremes. However, leaf litter could also stress invertebrates. Decomposition reduces oxygen in already stagnant water (MAGNUSSON & WILLIAMS 2006). In lentic habitats like woodland ponds, it is also possible that soluble toxins in leaf litter could reach sufficient concentrations to stress intolerant organisms. This would not be an issue in streams where water flow flushes toxins away, although even stream invertebrates avoid certain tannin or alkaloid rich leaves (CANHOTO & GRAÇA 1999).

The relative importance of positive or negative influences of leaves to invertebrates might change temporally. In dry years, the importance of litter in protecting aestivating invertebrates or propagules might be important. In wet years, ponds will remain flooded during the heat of the summer and problems with low oxygen concentrations might develop. Invertebrates probably integrate the various costs and benefits provided by litter, and depending on the conditions in a particular pond or year, respond accordingly. In Pond 568, the benefits of litter consistently appeared to out weigh costs, and interception elicited a negative response most years. In Pond 288, the

costs were probably more important, and litter interception frequently increased the biomass of certain invertebrates.

Many physical factors could have influenced our results. The only obvious differences between study ponds were 1) hydroperiod, with Pond 288 typically remaining flooded longer each year, and 2) the quality of the litter, with Pond 288 receiving more black ash litter and Pond 568 receiving more upland litter. However, hydroperiods in both ponds varied greatly from year to year, yet response in Pond 568 was consistent. Further, the hydroperiod of Pond 568 in a wetter year could be similar to the hydroperiod of Pond 288 in a drier one, yet invertebrate responses were not similar in such cases. Any direct link between litter-invertebrate response and hydroperiod was not obvious. It also seemed unlikely that variation in litter quality (i.e., species composition) elicited the differential responses between ponds. In 1999 and 2000, we were only successful at excluding upland litter yet intercepting this material caused completely different responses in each pond. Once wetland litter was also intercepted for the final two years of manipulation, patterns between ponds were somewhat more consistent, with litter exclusion eliciting some negative impacts on invertebrates in both ponds. Perhaps with continued interception at this level, invertebrate responses in both ponds might have become similar.

Because we found pronounced differences between study ponds in the responses of invertebrates to leaf litter manipulation, we cannot predict how invertebrates will interact with leaf litter in the population of ponds in the study region. However, we can conclude that the relationships between leaf litter and invertebrates are probably not consistent across all seasonal woodland ponds (MAGNUSSON & WILLIAMS 2006). Even if

it had been logistically possible to include a much greater number of ponds in this study, it seems unlikely that a clear consensus on response would emerge. We do not advocate such an effort. Our previous work in seasonal woodland ponds has indicated that these habitats are very difficult to categorize, making it hard to find replicate habitats (we could not even find suitable pairs for our two study ponds). For now, it seems prudent to simply assume that litter-invertebrate interactions in seasonal woodland ponds of northern Minnesota are important, yet quite variable and complex.

One reason for initiating our study was to assess mechanistically how forest management might influence imbedded wetland habitats through alteration of litter quantity and quality. Variation in litter flux would be a major short-term change associated with logging near or in woodland ponds. While our results cannot be used to predict specifically how ponds might respond ecologically to forest structural change, they do suggest that a significant change in invertebrate communities is likely with a shift in the quantity of litter flux. Our previous work in this same class of wetlands suggests that a change in species composition of litter, due to successional change or forest management, also will result in changes in invertebrate communities and pond carbon processes (PALIK et al. 2005). Together they suggest strong ecological connectivity between upland and woodland pond ecosystems in many ways similar to the relationships found in other ecotonal systems.

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Table 1. Characteristics of Pond 568 and Pond 288.

	Pond 568	**Pond 288**
Basin size (m^2)	331	448
Water pH	6.6	6.8
Alkalinity ($\mu eq \cdot L^{-1}$)	476	1255
Total N ($mg \cdot L^{-1}$)	1.15	1.48
Total P ($mg \cdot L^{-1}$)	0.77	0.32
Total dissolved organic C ($mg \cdot L^{-1}$)	45.2	45.3
Canopy cover	90%	81%
Litter input ($g \cdot m^{-2} \cdot yr^{-1}$)	198	220

Table 2. Leaf litter fall into reference and interception halves of Pond 568 and Pond 288 in the autumns of 1999 through 2002.

		Pond 568			**Pond 288**		
Autumn	Treatment	Wetland leaves $g \cdot m^2$	Upland leaves $g \cdot m^2$	Total leaves $g \cdot m^2$	Wetland leaves $g \cdot m^2$	Upland leaves $g \cdot m^2$	Total leaves $g \cdot m^2$
1999	Reference half-pond	41.0	135.7	176.8	98.3	65.6	163.8
	Interception half-pond	27.2	76.2	103.4	105.7	26.9	132.5
	Reduction rate	33.6%	43.8%	41.5%	0%	59%	19.1%
2000	Reference half-pond	91.3	106.4	191.7	204.2	52.9	257.1
	Interception half-pond	90.6	48.3	138.9	130.1	21.4	151.5
	Reduction rate	0.8%	54.6%	29.7%	36.3%	59.5%	41.1%
2001	Reference half-pond	97.9	103.4	201.3	151.2	51.8	203.0
	Interception half-pond	19.1	9.7	28.8	34.4	8.0	42.4
	Reduction rate	80.5%	90.6%	85.7%	77.2%	84.6%	79.1%
2002	Reference half-pond	116.7	105.9	226.6	206.0	46.2	252.2
	Interception half-pond	23.8	7.0	30.8	89.5	3.3	92.8
	Reduction rate	79.6%	93.4%	86.2%	56.6%	92.9%	63.2%

Figure legends

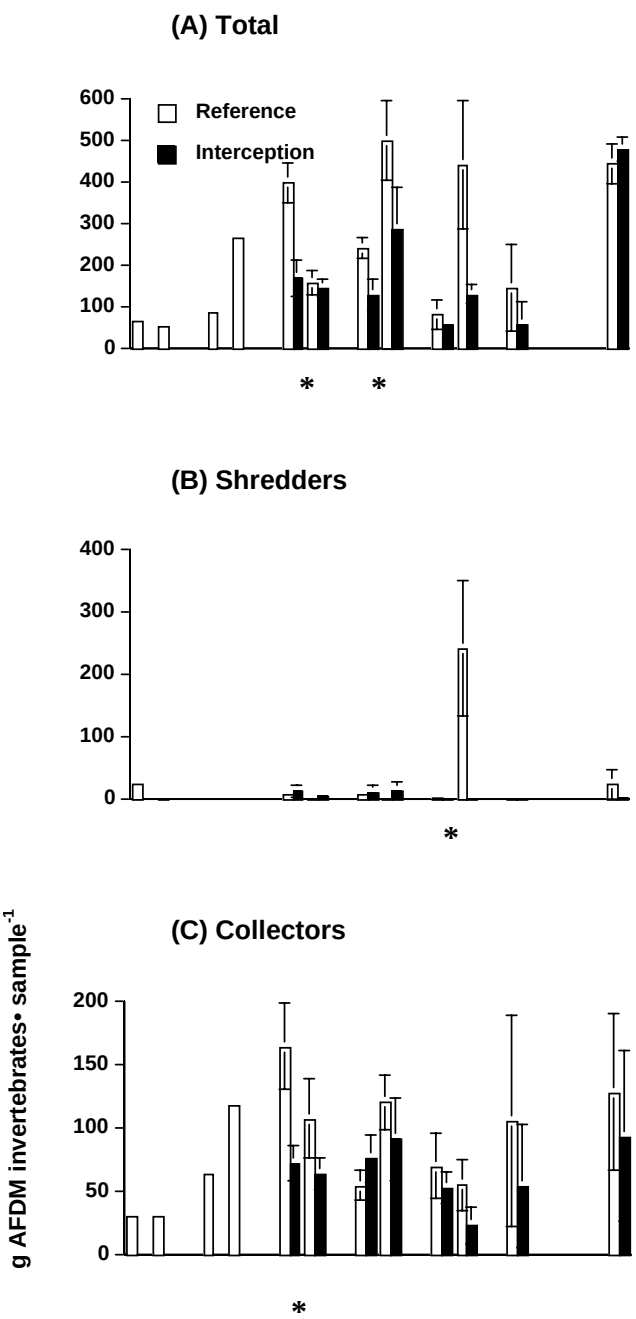
Fig. 1. Mesh canopy over the interception half of Pond 568 after autumn leaf fall. In the foreground is the half of the pond that received ambient leaf input. A plastic and sandbag barrier divided the two halves.

Fig. 2. Relative biomass (per 1-m sweep sample, ± 1 SE) of (A) Total invertebrates, (B) Shredder invertebrates, (C) Collector invertebrates, (D) Scraper invertebrates, and (E) Predator invertebrates in the litter interception and ambient reference halves of Pond 568. * indicates that invertebrates differed significantly ($P < 0.05$) between half-ponds that year. M = May, J = June.

Fig. 3. Relative biomass (per 1-m sweep sample, ± 1 SE) of (A) Total invertebrates, (B) Shredder invertebrates, (C) Collector invertebrates, (D) Scraper invertebrates, and (E) Predator invertebrates in the litter interception and ambient reference halves of Pond 288. * indicates that invertebrates differed significantly ($P < 0.05$) between half-ponds that year. M = May, J = June.

Fig. 1.

Fig. 2.


(A) Total
Reference
Interception
600
500
400
300
200
100
0
*
*
(B) Shredders
400
300
200
100
0
*
(C) Collectors
g AFDM invertebrates• sample-1
200
150
100
50
0
*

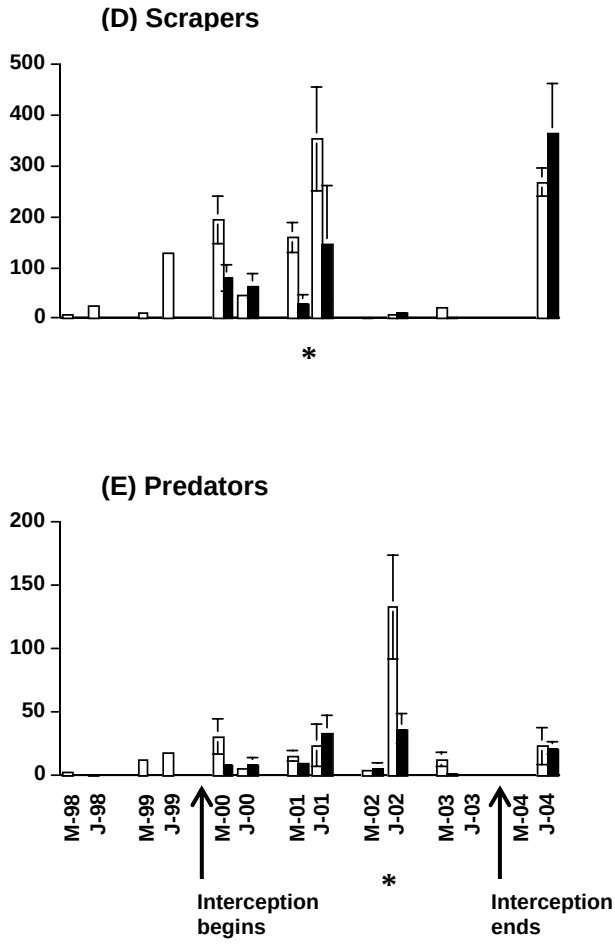
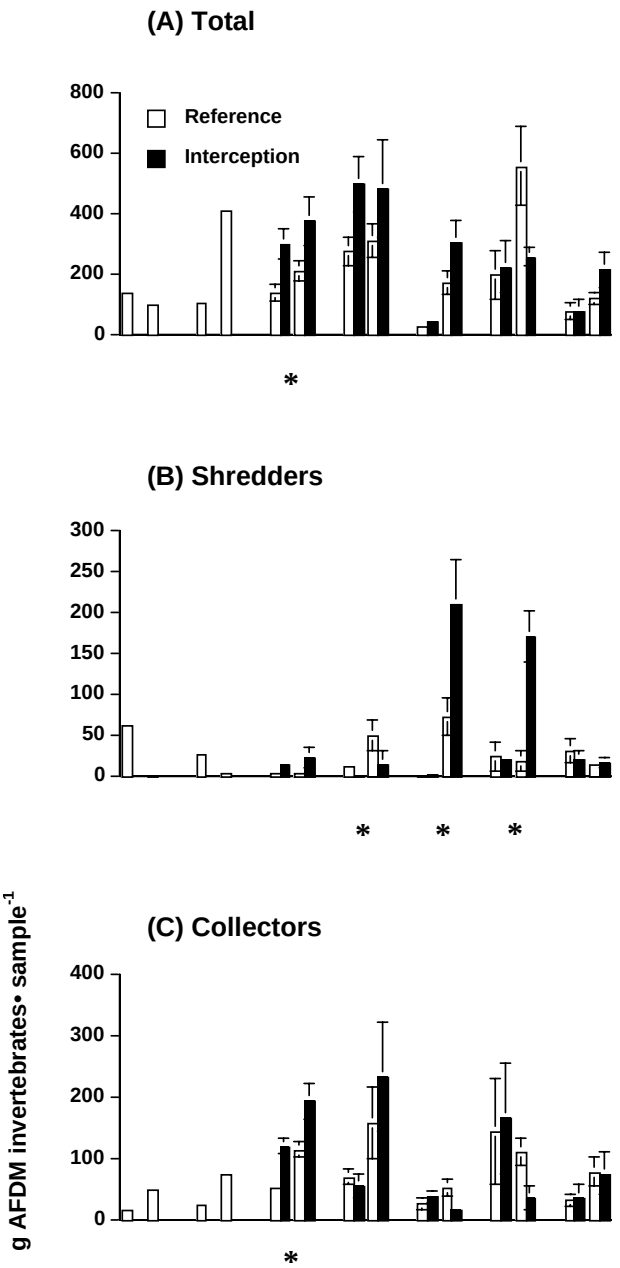
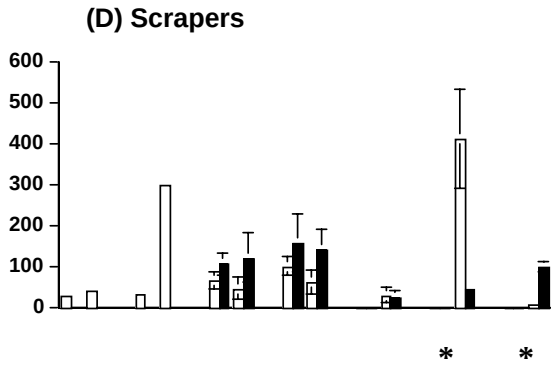
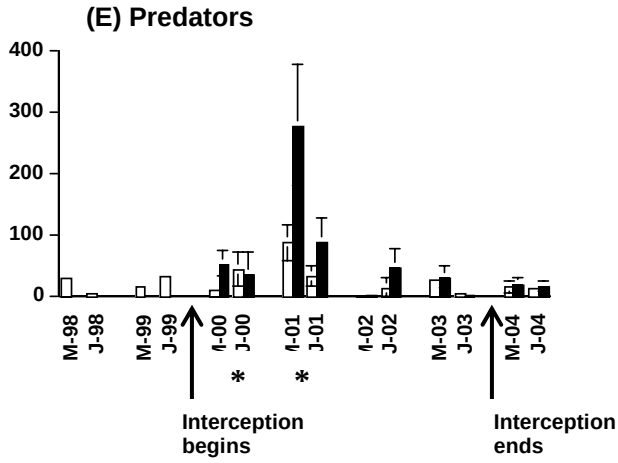

(D) Scrapers
500
400
300
200
100
0
*
(E) Predators
200
150
100
50
0
M-98
J-98
M-99
J-99
M-00
J-00
M-01
J-01
M-02
J-02
M-03
J-03
M-04
J-04
*
Interception begins
Interception ends

Fig. 3.


(A) Total
800
600
400
200
0
Reference
Interception
*
(B) Shredders
300
250
200
150
100
50
0
* * *
(C) Collectors
400
300
200
100
0
*
g AFDM invertebrates• sample-1


(D) Scrapers
600
500
400
300
200
100
0
*
*


(E) Predators
400
300
200
100
0
M-98
J-98
M-99
J-99
M-00
J-00
M-01
J-01
M-02
J-02
M-03
J-03
M-04
J-04
*
*
Interception begins
Interception ends