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Impact of Macroconsumers on Leaf Breakdown and Detritivores in Wet and Dry Wetlands on a Southeastern US Coastal Plain Floodplain

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Abstract

Interactions among macroconsumers (predators and large omnivores) and detritus breakdown are poorly understood on river floodplains. I evaluated the impact of macroconsumers on leaf breakdown, macroinvertebrate abundance and biomass, and fungal biomass on the Great Pee Dee River floodplain using exclosures in 6 wetlands. Sweetgum *(Liquidambar styraciflua)* leaves were held in mesh bags and in leaf packs. After 301 days, breakdown rates (k) were low in all treatments ($k < 0.003$ day^{-1}) and did not significantly differ. Fungal biomass also did not significantly differ between treatments nor did overall macroinvertebrate abundance or biomass. Collector-gatherer invertebrates were significantly more abundant in treatments open to macroconsumers in mesh bags ($P<0.001$). Shredders had significantly higher biomass in packs held in exclosures closed to macroconsumers ($P=0.048$). Lack of rain limited stream-floodplain connectivity so a second, shorter study was done in one flooded wetland. After 98 days, pre-conditioned leaves in mesh bags open to macroconsumers had significantly higher breakdown rates ($k = 0.0078$ day^{-1}) than those closed to macroconsumers ($k = 0.0058$ day^{-1}; $P= 0.050$). Fungal biomass did not significantly differ between treatments. Total macroinvertebrate abundance (but not biomass) was higher in mesh bags open to macroconsumers ($P=0.014$). Scrapers and predators were significantly more abundant in mesh bags opens to macroconsumers ($P=0.001$ and $P=0.004$, respectively) than those closed to macroconsumers. These results indicated macroconsumers had a larger impact on litter breakdown in wet floodplain wetlands than in dry ones.

Introduction

Forested wetlands are economically and environmentally valuable ecosystems (Costanza et al. 1989). The majority of wetland value comes from cycling of energy and nutrients through ecosystem processes (Brinson et al. 1981, Costanza et al. 1989) such as litter breakdown (Webster and Benfield 1986). Aquatic ecosystem processes occur in the presence of organisms like fish, macroinvertebrates, and microbes and these resident species are likely to have an impact on those processes. However, interactions among organisms involved in ecosystem processes are more frequently studied in streams (Oberndorfer et al. 1984, Reice 1991, Malmqvist 1993, Wallace and Webster 1996, Ruetz et al. 2002, Greig and McIntosh 2006) than in wetlands (Batzer 1998, Mancinelli et al. 2002). Within wetland ecosystems, interactions among organisms and detritus breakdown are especially poorly understood on the floodplain.

Leaf litter breakdown is one of the most important ecosystem processes that take place in wetlands. Decomposers, like fungi and macroinvertebrates, involved in leaf litter breakdown make organic matter and nutrients available to other organisms (Webster and Benfield 1986). Fungal biomass positively correlates with leaf litter decay rates and acts as a primary driver of litter processing (Gessner and Chauvet 1994, Gessner et al. 2007). Macroinvertebrate shredders increase the conversion rate of coarse particulate organic matter (CPOM, mainly from leaf litter) to fine particulate organic matter (FPOM) and can be responsible for 56% of FPOM export (Wallace and Webster 1996, Wallace and Hutchens 2000), which is especially significant in river floodplains because floodplains are a key source of FPOM for large river channels (Bison and Bilby 1998). Much of the aquatic research on leaf decomposition and its relationship to microbes and macroinvertebrates has been done in streams. However, ecological processes in a Michigan stream and floodplain are similar (Merritt and Lawson 1992). Yet streams and floodplain wetlands have differing geophysical characteristics and hydroperiods. Streams rarely become completely dry whereas floodplains typically have a seasonal wetting-drying

regimen. Litter breakdown rates can be higher in freshwater wetlands that have periods of flooding and drying compared to those that are permanently flooded (Battle and Golladay 2001). These differences in rates suggest that while processes may be similar between streams and floodplains, differences in underlying mechanisms may be important.

Periodic inundation of floodplains as a result of over-bank flow from rivers creates areas of increased exchange of energy, nutrients, and biota between aquatic and terrestrial ecosystems, which results in a unique physiochemical environment (Junk et al. 1989, Naiman and Decamps 1997, Junk and Wantzen 2004). This exchange between the river channel and floodplain is described by the flood pulse concept (Junk et al. 1989). While the flood pulse concept originated from studies of the Amazon, it also has been successfully applied to rivers in North America (Gutreuter et al. 1999, Benke et al. 2000). Although floodplains offer ecosystem functions similar to other wetland types, floodplains are much more productive (Brinson et al. 1981, Naiman and Decamps 1997) and have higher nutrient content than isolated wetlands (Brinson et al. 1981, Ozalp et al. 2007).

Predator-prey interactions have the potential to create a trophic cascade, which can impact shredder macroinvertebrates, microbes, and leaf litter breakdown rates. While effects on aquatic macroconsumers (i.e., large predators and omnivores) resulting from access to floodplain wetlands have been studied (Junk et al. 1989, Gutreuter et al. 1999), effects of this access on resident communities and ecosystem processes in floodplains are uncertain. Studies examining macroconsumer impact on ecosystem processes and resident biota in ponds, lakes, and streams (Thorp and Bergey 1981, Morin 1984, Butler 1989, Rosemond et al. 1998, Mancinelli et al. 2002) have yielded sometimes conflicting results and are lacking in floodplains. Predatory macroinvertebrates feeding on shredders has led to either no change in leaf litter breakdown (Reice 1991) or a significant decrease in breakdown rates (Oberndorfer et al. 1984). In a laboratory experiment, invertebrate predators decreased shredder density, which also decreased litter breakdown rates (Malmqvist 1993). Yet, when the same experiment was done

in the field there was no decrease in shredder densities, but an overall decrease in leaf litter breakdown rates (Malmqvist 1993). Studies with larger vertebrate aquatic predators are complicated by prey including both predatory and shredder invertebrates. A field experiment found no fish predator effect, which was likely because shredders took refuge in leaf packs and continued to feed (Reice 1991). Yet, a significant vertebrate predator effect on shredder densities and leaf breakdown rates was found in a mesocosm experiment (Greig and McIntosh 2006). More research is needed in a variety of habitats to tease out this complex set of relationships.

Floodplain wetlands naturally undergo wet and dry periods and the impact of macroconsumers on leaf breakdown may vary between periods. For example, as floodplains dry, the floodplain community may be dominated by terrestrial macroconsumers taking advantage of organic carbon and nutrients that originated in water (Junk and Wantzen 2004). No research is available on the impact of macroconsumers on ecosystem processes and benthic communities that exist during the dry phase of the flood pulse. However, some studies have examined the impact of terrestrial macroconsumers in forests, but these studies' findings are inconsistent. For example, in a Northeastern US upland forest, enclosure of salamanders (*Plethodon cinereus*) decreased invertebrate numbers and decreased leaf litter decomposition rates (Wyman 1998). In another enclosure study using the same species of salamander in a Virginia upland forest, there was no impact of salamanders on invertebrate densities or leaf decomposition rates (Homyack et al. 2010). This difference could be the result of differing locations, experimental design, or statistical methods (Homyack et al. 2010), but a six-year unrestricted study of *P. cinereus* effects on invertebrate community structure found that while salamanders did have a top down influence, it could be positive, negative, or neutral depending on season and microclimate (Walton 2013).

The objective of this study was to examine the effect of macroconsumers on leaf litter breakdown and leaf-associated microbial and invertebrate assemblages in floodplain wetlands of a southeastern U.S. river. To address this issue, large omnivores and predators were excluded using cages and the resulting

changes in leaf litter breakdown rates, invertebrate assemblages, and fungal biomass were assessed. I also examined these dependent variables in leaf packs that were open and closed to large invertebrate consumers and shredders like crayfish, which could potentially burrow under experimental cages.

I hypothesized that when compared to open cages, exclusion of macroconsumers from the floodplain community would (1) increase the abundance and biomass of macroinvertebrates, which should (2) result in increased litter breakdown rates. I further hypothesized that macroconsumer exclusion should (3) reduce fungal biomass as a result of increased feeding by macroinvertebrates. Also, when large crayfish were excluded using leaf bags, I expected that (4) leaf breakdown rates would be lower and fungal biomass would be greater in bags than in packs.

Study sites

All study wetlands (= sites) were on Bull Island (N33° 37’55”, W79° 8’35”) on the Great Pee Dee River in Georgetown County in northeastern South Carolina. The Great Pee Dee River is an alluvial river, carrying high sediment loads originating in the North Carolina piedmont (USFWS 1997). The South Carolina portion of the river is meandering and unimpeded by man-made dams or levees. Bull Island is 1880 ha, of which 1860 ha is protected by the Waccamaw National Wildlife Refuge (WNWR, personal communication, M. Craig Sasser); all study sites were within refuge boundaries. The island is bound on the western side by the Great Pee Dee River and on the eastern side by Bull Creek. Bull Island was chosen because it has historically flooded in all but drought years (personal communication, M. Craig Sasser; Ozalp et al. 2007). Sites were on the western side of Bull Island, which has a natural alluvial berm. As a result, any flooding of study sites could be attributed to seasonal flooding rather than daily tidal fluctuation. In addition, Ozalp et al. (2007) found that from 2002-2003 the western side of the island was significantly wetter than the eastern side. Nevertheless, conditions were especially dry for the duration of the initial study (Study A) and no flooding occurred at the study sites, which led to selection of an additional wetter site for a second, shorter (ca. 12 week) study (study B). All sites were classified

at PFO1R (palustrine, forested – broad leaved deciduous, seasonal-tidal water regime) wetlands (Cowardin et al. 1979). Six sites were selected for study A (Figure 1) based on advice of the WNWR manager (M. Craig Sasser) and similarity among sites in wetland type, elevation and slope, which were estimated through topographic and global positioning system (GPS) data. All study A sites were separated by a minimum distance of 280 m. Treatments at all study A sites were 3 m in-land of the riverbank. The one site selected for study B (Figure 1) was connected to the river, but had minimal daily tidal fluctuations.

Experimental design

Study A

Each of the six sites had one open cage and one closed cage. Closed cages excluded macroconsumers, especially vertebrates, while the open cages allowed access. Closed cages without tops enclosed 1 m^2. No tops were used because fish and herpetofauna were assumed to be the dominant macroconsumers during wetland inundation. Closed cages were built with a polyvinyl chloride (PVC) pipe frame, 0.64-cm^2 wire mesh, and were 0.9-m high. Open cages only had the PVC frame to account for cage artifacts (Thorp and Bergey 1981). Six leaf bags and 6 leaf packs were added to each cage. Leaf packs were used to help distinguish effects of burrowing macroconsumers like crayfish as chimneys were observed during site selection. Bags had leaves in 5-mm plastic mesh, whereas leaf packs held leaves loosely bound with twine to a 15 X 20 cm ceramic tile. All bags and packs had approximately 8 g air-dried sweet gum (*Liquidambar styraciflua*) leaves, which had been collected during autumn. Sweet gum leaves were chosen because of availability and presence at the study sites. Sweetgum is classified as a "medium" decomposition-rate species in streams (Reice 1978) and is in the family Hamamelidaceae, which has an average stream breakdown rate between 0.01 and 0.02 d^{-1} (Webster et al. 1995). Four additional bags and packs were brought into the field, returned to the laboratory and processed to measure

handling loss (Benfield 2007). StowAway temperature data loggers recorded temperature every two hours in each cage (24 total).

Samples were placed *in situ* on December 19, 2010. Initial sampling was done 4 weeks after field placement. Subsequent samples were collected every 6-9 weeks depending on hydrologic conditions with the total time *in situ* lasting 301 days (43 weeks).

Study B

Open and closed cages also were used in study B. Six replicates of each cage type were used to assess whether aquatic macroconsumers influence leaf litter breakdown in one inundated wetland. Closed cages were troughs made with an untreated wood frame (*sensu* Zhang et al. (2004); dimensions: 0.45 x 0.45 x 0.9 m) covered in 0.64-cm^2 wire mesh on all sides. Open cages were the wood frame only with mesh removed on all but the bottom panel to account for cage artifacts. The bottom panel was left intact to secure leaf bags. Each cage included 6 bags with 8 g air-dried sweet gum leaves in 5-mm plastic mesh. While cages were being constructed bags were held in a larger 3-mm mesh bags and submerged at the site for 4.5 weeks (beginning 10 December 2011) to allow for fungal colonization and leaching due to the shorter duration of study B. Four additional leaf bags were brought into the field, submerged with experimental bags and then returned to the laboratory and processed to measure handling loss, and baseline fungal and macroinvertebrate colonization. Cages were placed haphazardly and were weighted to stay submerged. StowAway temperature data loggers recorded temperature every two hours in all cages. Water quality measurements were taken at each sampling date (pH, dissolved oxygen, conductivity, and temperature) using YSI Incorporated Model 85 and Thermo Scientific Orion 3 Star portable meters. Cages were in place for 12 weeks and sampled every 4 weeks. Leaves were placed in cages on 15 January 2012.

Methods

On each collection date for study A one bag and one pack were selected haphazardly from each cage at each site and placed individually in Ziploc bags on ice for transport to the laboratory. On each collection date for study B one bag was selected haphazardly from each cage and similarly returned to the laboratory.

Leaf breakdown

Leaf litter was processed according to Benfield (2007). Leaves were washed over two sieves (1-mm and 250-µm mesh), oven dried at 50ºC for 24-48 hours to a constant weight, and weighed. A subsample was ashed in a muffle furnace at 500ºC, placed in a desiccator, weighed, and ash-free dry mass (AFDM) calculated.

Fungal biomass

Fungal biomass was estimated from ergosterol concentrations after lipid extraction and quantification as described in (Gulis and Suberkropp 2007). Two sets of five, 8.6-mm diameter leaf discs per bag or pack were taken within 24 hours of sample collection. One set of discs was used to calculate AFDM, while the other set was preserved in 5 mL of methanol at -20ºC in 20 mL glass scintillation vials until ergosterol extraction.

Macroinvertebrate colonization

Macroinvertebrates were retained on sieves used in rinsing leaves and preserved in 70% ethanol. Macroinvertebrates were sorted using a dissecting microscope, identified to the lowest practical taxonomic level, counted, and body lengths measured (Hauer and Resh 2007). Body lengths were used to estimate biomass using taxon-specific length-mass equations (Benke et al. 1999). Individual taxa also were classified by functional feeding group (Merritt et al. 2008).

Data analysis

Leaf breakdown

The breakdown coefficient (*k*) for AFDM loss was estimated by linear regression of ln-transformed data (exponential model) regressing days of exposure vs. the natural log of percent AFDM. Breakdown coefficients were statistically compared between treatments using analysis of covariance (ANCOVA, *a priori* significance $P \leq 0.05$) with days of exposure being the covariate (Benfield 2007). Comparison of breakdown rates of bags within cages between treatments and packs within cages between treatments were compared similarly.

Fungal biomass

Fungal biomass (B_f) was calculated as mg/g AFDM of leaf discs. B_f is equal to the concentration of ergosterol of the sample extract (C_e) multiplied by the volume of the extract (V_e) and then divided by the product of AFDM from 5 leaf discs and 5.5 (ergosterol to biomass conversion factor in mg ergosterol to g fungal dry mass; Gulis and Suberkropp (2007). Fungal biomass was compared among treatments using one-way analysis of variance (ANOVA, *a priori* significance $P \leq 0.05$) blocked by time, with experimental treatment (open or caged) as the factor. Comparison of fungal biomass in bags within cages between treatments and packs within cages between treatments were compared similarly.

Macroinvertebrate colonization

Total macroinvertebrate abundance and biomass was statistically compared between open and closed cages using one-way ANOVA (a *priori* significance $P \leq 0.05$) blocked by time. Where necessary, data were Log10 (x+1) transformed to meet statistical assumptions. Selected individual taxa and functional feeding groups (FFGs) were compared similarly. Unidentifiable taxa were excluded from statistical comparison of FFGs. Statistical comparison of macroinvertebrates between packs and bags was compared similarly.

Results

Environmental factors

All cages remained intact throughout both studies. No evidence of vertebrates or crayfish were seen or collected in any cages in study A. However, one unidentified larval fish, measuring 16 mm X 5 mm X 1.5 mm, was found on 22 April 2012 in cage one during study B.

Accumulated degree days in study A were 5,374 in open cages and 4,652 in closed cages and were not significantly different from one another ($F_{1,5} = 5.266$, $P = 0.070$). Similarly, degree days in study B did not significantly differ between open and closed treatments ($F_{1,2} = 0.077$, $P = 0.807$) and were 1,392 and 1,405, respectively. Water quality measurements (Table 1) taken during study B were within the range of those found by the USFWS (1997) for the tidally-influenced region of the Great Pee Dee River.

South Carolina experienced drought throughout the study and no overbank flooding occurred. The National Oceanic and Atmospheric Administration's (NOAA) National Climate Data Center reported Palmer Hydrological Drought Index (PHDI) values ranging from severe (PHDI values of -3.0 to -4.0) to extreme drought (PHDI values of -4.0 and higher) for the duration of both studies.

Leaf breakdown

Leaf breakdown (*k*) was slower in study A than in study B (Table 2) likely due to dry conditions. In study A, breakdown rates were not significantly different in cages open or closed to macroconsumers in leaf bags or packs by day ($F_{1,76} = 3.223$, $P = 0.077$; $F_{1,76} = 1.181$, $P = 0.281$) or by degree day ($F_{1,76}=1.756$, $P=0.189$; $F_{1,76}= 0.0002$, $P=0.988$). However, in study B, the leaf breakdown rate by day was higher in cages open to macroconsumers ($P = 0.050$, $F_{1,36} = 4.095$), but there was no difference between open and closed treatments by degree day ($P=0.224$, $F_{1,36}=1.530$).

Fungal biomass

There were no differences in fungal biomass in cages open or closed to macroconsumers in bags ($F_{1,56}$ = 0.909, P = 0.345) or packs ($F_{1,56}$ = 0.043, P = 0.837) in study A (Figure 2) or in study B ($F_{1,32}$ = 0.015, P = 0.905; Figure 3). Fungal biomass generally increased over time in study A and decreased over time in study B. Samples in study B were conditioned for 4.5 weeks before being assigned to treatments so they began with a higher baseline fungal biomass than the leaves in study A. Also, it was possible that study B fungal biomass reached maximum levels during the conditioning period and subsequently decreased during the study period.

Macroinvertebrate colonization

Macroinvertebrate abundance was not different in study A (Figure 4) in cages open or closed to macroconsumers in leaf bags ($F_{1,65}$ = 1.017, P = 0.317) or in leaf packs ($F_{1,65}$ = 0.860, P = 0.940). Study A macroinvertebrates were dominated by collector-gatherers (46-82% of total invertebrates) and predators (Table 3; 12-48% of total invertebrates). Collector-gatherers were significantly more abundant in cages open to macroconsumers in leaf bags (Table 3; $F_{1,65}$ = 47.678, P<0.001) but not in packs and were dominated by Collembola and Oribatidae detritivores (Table 5). Predator abundance was not different between treatments and was dominated by Formicidae and Acarina (Table 5). There were no other significant differences in other FFG abundance between open or closed cages and all other FFGs comprised < 10% of total invertebrates collected by treatment level.

Study A macroinvertebrate biomass (Figure 5) was not statistically different in cages open or closed to macroconsumers in leaf bags ($F_{1,65}$ = 0.023, P = 0.880) or in leaf packs ($F_{1,65}$ = 0.026, P = 0.874). Predator macroinvertebrates had the highest biomass in study A (Table 3; ranging from 56-86% of total invertebrate biomass) and was comprised of mainly Formicidae adults, Araneae, and Carabidae adults (Table 5). Shredders had significantly higher biomass in cages closed to macroconsumers in packs (Table 3; $F_{1,65}$ = 4.067, P = 0.048), but no differences in shredder biomass were seen in bags. Shredder

biomass was low (< 3% of total invertebrates) in all treatments. No other significant differences in biomass were found in other FFGs in study A.

In study B, macroinvertebrate abundance was significantly higher in cages open to macroconsumers (Figure 6; $F_{1,32} = 6.697$, $P = 0.014$). Collectors (gatherers and filterers) and scrapers were dominant in study B (Table 4), together composing 84-87% of total invertebrate abundances. The most abundant collector taxa was Chironomidae (gatherers) and the most abundant scraper taxa was Gastropoda. Dominant collector-filterer taxa were Ostracoda, Daphniidae, and Copepoda (Table 6). Scrapers were more abundant in cages open to macroconsumers ($F_{1,32} = 13.246$, $P = 0.001$). In addition, predators were more abundant in open cages (Table 4; $F_{1,32} = 9.550$, $P = 0.004$) and composed 11-13% of invertebrates. Shredder abundance was low ($\leq$ 3% of total invertebrates by treatment).

Macroinvertebrate biomass in study B was not different in open or closed cages (Figure 7; $F_{1,32} = 1.296$, $P = 0.263$) and there were no significant differences by FFG biomass. Shredder and predator macroinvertebrates made up the majority of invertebrate biomass (35-39% and 34% of total biomass by treatment, respectively) despite their low abundance (Table 4). Shredder taxa with the highest biomass consisted of aquatic crustaceans (Table 6). Predator taxa with the highest biomass were mainly Odonates and Dytiscidae beetles (Table 6).

Discussion

Effects of macroconsumer exclusion varied depending on water availability. In study A, no overbank flooding occurred and all wetlands remained dry, whereas in study B, the floodplain analogue wetland remained completely inundated. When the floodplain was dry leaf decomposition was slow and there was no difference in breakdown rates between cages that did or did not allow access of macroconsumers. In addition, macroinvertebrates (dominated by soil invertebrates) were not more abundant and did not have higher biomass in the exclusion treatment. Fungal biomass accrual was slow

and did not differ when macroconsumer access was restricted. In contrast, when the floodplain was inundated, leaf breakdown rates were higher in cages that allowed access by macroconsumers. Typical wetland macroinvertebrate taxa (Batzer and Ruhí 2013) were more abundant in leaf bags open to macroconsumers. Fungal biomass accumulated more quickly, but was still unaffected by macroconsumer access.

Drought changed the focus of this study. Originally the aim was to investigate the effects of macroconsumers during a natural flooding cycle at many wetlands. However, the focus shifted to looking at effects of macroconsumers during drought (when natural flooding was absent) at many dry wetlands and at one floodplain-analog wetland established after drought affected Study A. Initially, I thought that wetlands would be wet enough to foster many crayfish burrows, which necessitated the use of leaf bags and packs. However, crayfish burrows were largely absent and crayfish were not seen or collected at any wetland during study A. Packs were left in place in case any flooding occurred and to account for any effects of any large terrestrial invertebrates that could not fit through the mesh of the leaf bags.

Leaf breakdown rates were not significantly different when macroconsumer access was restricted to dry wetlands in study A. This is consistent with Homyack et al. (2010) who did not find an impact of salamander predators on leaf litter breakdown. Using stomach lavage, Homyack et al. found that salamanders were generally indiscriminant in invertebrate prey choice and did not influence detritivorous invertebrates. However, study A showed significantly higher collector-gatherer abundance, which was overwhelmingly dominated by detritivorous Collembolans and Oribatids in bags open to macroconsumers with no change in litter breakdown rates. There was also no difference in breakdown rates in packs closed to macroconsumers, despite these packs having significantly higher biomass of terrestrial shredders. Similar weak effects of detritivorous soil invertebrates were seen by Vasconcelos and Laurence (2005), who found that experimental removal of soil invertebrates decreased litter breakdown rates, but that differences in soil invertebrate abundance, richness, and species composition did not. It is more likely that

any vertebrate predator effects on leaf breakdown (i.e., Wyman 1998) found in dry floodplain forests are actually a function of different microclimates in exclusion treatments (Walton 2013).

Leaf breakdown rates were faster in cages open to macroconsumers in the flooded wetland used in study B. This is in contrast to Reice (1991) who did not find a vertebrate predator effect on litter breakdown in a stream and others who found slower decomposition in the presence of a macroconsumer in streams (Rosemond et al. 1998, Greig and McIntosh 2006) or in a lake (Mancinelli et al. 2002). All hypotheses for the outcomes of the above-mentioned studies focus on the relationship between litter breakdown rates and shredder macroinvertebrates. However, shredder abundance and biomass in this study were not different in cages open and closed to macroconsumers. While shredders are responsible for an important portion of litter breakdown in streams (Wallace and Webster 1996, Wallace and Hutchens 2000), this is not the case in wetlands (Batzer and Wissinger 1996, Wissinger 1999). Many leaf decomposition studies on floodplains report a low incidence (and sometimes absence) of shredders (Cuffney and Wallace 1987, McArthur et al. 1994, Langhans and Tockner 2006, Langhans et al. 2008), and as a result linkages between leaf decomposition and shredders are limited in wetlands. Instead, litter decomposition in wetlands is more likely driven by leaching, mechanical and microbial pathways (McArthur et al. 1994, Batzer and Wissinger 1996, Wissinger 1999). At this time the mechanism behind faster decomposition rates in open cages is unclear. It is possible that in study B, despite all possible efforts, leaf bags had more free movement during daily tide fluctuations in open cages than in closed cages, which increased mechanical decomposition. It is also possible that any top-down influence on fungal activity was missed due to the conditioning period.

Breakdown rates were within the range of other floodplain studies using sweetgum leaves in both dry (0.0010-0.0091 day $^{-1}$) and wet (0.0050-0.0124 day $^{-1}$) conditions (Shure et al. 1986, Cuffney and Wallace 1987, McArthur et al. 1994). These rates are much lower than other "medium" speed species in headwater streams and often are more similar to "slow" species (Cuffney and Wallace 1987). In

floodplains, the main driver of leaf decomposition rates was associated with moisture and amount of inundation more than any other factor (Shure et al. 1986, McArthur et al. 1994, Langhans and Tockner 2006), which helps explain the differences in decomposition rates between the dry study A and the wet study B.

Contrary to my hypothesis there were no differences between treatments in either total macroinvertebrate abundance or biomass in study A. Similarly, Homyack et al. (2010) found no difference in macroinvertebrate abundance in leaf packs in the presence of salamander predators. The apparent lack of vertebrate predation pressure may have been exacerbated by drought. Some predatory amphibians forage and consume less when conditions are hotter and drier to avoid desiccation (Walton 2013). Collector-gatherers were more abundant in leaf bags in open cages than in closed ones. Typically, invertebrates emigrate in the presence of invertebrate predators (Wooster and Sih 1995). It was possible small collector-gatherers emigrated from more open areas immediately adjacent to the mesh leaf bags and used mesh bags as protection from nearby invertebrate predators. Also, shredder biomass was higher in packs closed to macroconsumers, but this was a result of a few large terrestrial isopods that were likely too large to enter leaf bags.

Total macroinvertebrate abundance was higher in open cages in study B rather than lower as hypothesized. Predator and scraper abundances were also higher in open cages. In these cases, it was likely that invertebrates were seeking refuge in leaf bags from vertebrate predators as is typically the case when invertebrates are under vertebrate predation pressure (Wooster and Sih 1995). This was particularly likely for the taxa that are large, such as Odonate nymphs, Dytiscidae beetle larvae, and gastropods. Vertebrate predators in wetlands typically select for larger prey (Batzer and Wissinger 1996), and these large taxa would be under increased vertebrate predation pressure.

Fungal biomass was hypothesized to decrease when macroconsumers were excluded. Instead, fungal biomass was similar in cages open and closed to macroconsumer in both studies. I

hypothesize that in study A there was no difference between treatments because environmental conditions were similar between treatments and that soil invertebrates may not have the same impact on fungal biomass that better studied stream invertebrates do. Results for study B contrast with results reported by Rosemond et al. (2001) and Mancinelli et al. (2002), which found significantly higher fungal biomass in the presence of macroconsumers in a tropical stream and in a lake littoral zone. These different outcomes may be because aquatic hyphomycetes are less affected by detritivorous invertebrates in wetlands since there are relatively few shredders in wetlands, and shredders are known to directly graze on and remove fungal biomass (e.g. Suberkropp et al. 1983). Fungal biomass levels were similar to a floodplain in Italy (Langhans and Tockner 2006), but to my knowledge this is the first study measuring fungal biomass in Southeastern US floodplains.

Results from this study point to areas of research needed to better understand detritivore interactions in these wetlands. While it is generally thought that organic matter is largely decomposed in wetlands by leaching, mechanical fragmentation and microbial pathways, the relative importance of each of these processes have not been fully evaluated. Baldy et al. (2002) estimated the relative contributions of fungi and bacteria to leaf decomposition in a European floodplain, but such data are absent from the Southeastern US floodplains. Also, invertebrate population dynamics in wetlands are highly variable and this is especially true when trying to tease out predation relationships, which frequently do not follow expected food chains (Batzer 2013). It is unclear whether Southeastern US floodplain invertebrate food webs vary along river continua and within floodplains (Batzer 2013).

My study shows that the impact of macroconsumers depends on hydrologic conditions. When the floodplain is dry, there is little to no impact of macroconsumers on litter breakdown, macroinvertebrates, and fungi. However, flooded wetlands display complex interactions and appear to act differently than other freshwater systems. More research will be necessary to better understand the long-term patterns associated with floodplain trophic interactions.

References

Battle, J. M., and S. W. Golladay. 2001. Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. American Midland Naturalist **146**:128-145.

Batzer, D. P. 1998. Trophic interactions among detritus, benthic midges, and predatory fish in a freshwater marsh. Ecology **79**:1688-1698.

Batzer, D. P., and A. Ruhí. 2013. Is there a core set of organisms that structure macroinvertebrate assemblages in freshwater wetlands? Freshwater Biology **58**:1647-1659.

Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Review of Entomology **41**:75-100.

Benfield, E. F. 2007. Decomposition of leaf material. Pages 711-720 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology (Second Edition). Academic Press, San Diego.

Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. Ecology **81**:2730-2741.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society **18**:308-343.

Bison, P. A., and R. E. Bilby. 1998. Organic matter and trophic dynamics. Pages 373-398 *in* R. J. Naiman and R. E. Bilby, editors. River Ecology and Management: Lessons from the Pacific Coastal Ecoregion (First Edition). Springer, New York.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics **12**:123-161.

Butler, M. J. 1989. Community responses to variable predation: field studies with sunfish and freshwater macroinvertebrates. Ecological Monographs **59**:311-328.

Costanza, R., S. C. Farber, and J. Maxwell. 1989. Valuation and management of wetland ecosystems. Ecological Economics **1**:335-361.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS/-79/31, Washington, D.C.

Cuffney, T. F., and J. B. Wallace. 1987. Leaf litter processing in Coastal Plain streams and foodplains of southeastern Georgia, USA. Archiv für Hydrobiologie. Supplementband. Monographische Beiträge **76:** 1-24.

Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology **75**:1807-1817.

Gessner, M. O., V. Gulis, K. A. Kuehn, E. Chauvet, and K. Suberkropp. 2007. Fungal decomposers of plant litter in aquatic ecosystems. Pages 301-324 *in* C. P. Kubicek and I. S. Druzhinina, editors. Environmental and Microbial Relationships. Springer Berlin Heidelberg.

Greig, H. S., and A. R. McIntosh. 2006. Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs. Oikos **112**:31-40.

Gulis, V., and K. F. Suberkropp. 2007. Fungi: biomass, production, and sporulation of aquatic hyphomycetes. Pages 311-325 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology (Second Edition). Academic Press, San Diego.

Gutreuter, S., A. D. Bartels, K. Irons, and M. B. Sandheinrich. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences **56**:2282–2291.

Hauer, F. R., and V. H. Resh. 2007. Macroinvertebrates. Pages 435-454 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology (Second Edition). Academic Press, San Diego.

Homyack, J. A., E. B. Sucre, C. A. Haas, and T. R. Fox. 2010. Does Plethodon cinereus affect leaf litter decomposition and invertebrate abundances in mixed oak forest? Journal of Herpetology **44**:447-456.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110-127 *in* D.P. Dodge, editor International Large River Symposium Canadian Special

Publications Fisheries Aquatic Sciences. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Junk, W. J., and K. M. Wantzen. 2004. The flood pulse concept: new aspects, approaches and applications - an update. Pages 117-140 *in* R. Welcomme and T. Petr, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume I. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand.

Langhans, S. D., S. D. Tiegs, M. O. Gessner, and K. Tockner. 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. Aquatic Sciences **70**:337-346.

Langhans, S. D., and K. Tockner. 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, Northeastern Italy). Oecologia **147**:501-509.

Malmqvist, B. 1993. Interactions in stream leaf packs: effects of a stonefly predator on detritivores and organic matter processing. Oikos **66**:454-462.

Mancinelli, G., M. Costantini, and L. Rossi. 2002. Cascading effects of predatory fish exclusion on the detritus-based food web of a lake littoral zone (Lake Vico, central Italy). Oecologia **133**:402-411.

McArthur, J. V., J. M. Aho, R. B. Rader, and G. L. Mills. 1994. Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. Journal of the North American Benthological Society **13**:57-67.

Merritt, R., and D. Lawson. 1992. The role of leaf litter macroinvertebrates in stream-floodplain dynamics. Hydrobiologia **248**:65-77.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An introduction to the aquatic insects of North America. 4 edition. Kendall Hunt Publishing Company.

Morin, P. J. 1984. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. Ecology **65**:53-60.

Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics **28**:621-658.

Oberndorfer, R. Y., J. V. McArthur, J. R. Barnes, and J. Dixon. 1984. The effect of invertebrate predators on leaf litter processing in an Alpine stream. Ecology **65**:1325-1331.

Ozalp, M., W. H. Conner, and B. G. Lockaby. 2007. Above-ground productivity and litter decomposition in a tidal freshwater forested wetland on Bull Island, SC, USA. Forest Ecology and Management **245**:31-43.

Reice, S. R. 1978. Role of detritivore selectivity in species-specific litter decomposition in a woodland stream. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie **20**:1396-1400.

Reice, S. R. 1991. Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. Journal of the North American Benthological Society **10**:42-56.

Rosemond, A. D., C. M. Pringle, and A. Ramírez. 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. Freshwater Biology **39**:515-523.

Rosemond, A. D., C. M. Pringle, A. Ramírez, and M. J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. Ecology **82**:2279-2293.

Ruetz, C. R., R. M. Newman, and B. Vondracek. 2002. Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. Oecologia **132**:307-315.

Shure, D. J., M. R. Gottschalk, and K. A. Parsons. 1986. Litter decomposition processes in a floodplain forest. American Midland Naturalist **115**:314-327.

Thorp, J. H., and E. A. Bergey. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology **62**:365-375.

USFWS. 1997. Proposed establishment of Waccamaw National Wildlife Refuge: Final environmental impact statement. Department of the Interior, Fish and Wildlife Service **1**:1-308.

Wallace, J. B., and J. J. Hutchens. 2000. Effects of invertebrates in lotic ecosystem processes. Pages 73-96 *in* D. C. Coleman and P. F. Hendrix, editors. Invertebrates as webmasters in ecosystems. CABI Publishing, New York, NY.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology **41**:115-139.

Walton, B. M. 2013. Top-down regulation of litter invertebrates by a terrestrial salamander. Herpetologica **69**:127-146.

Webster, J., J. Wallace, and E. Benfield. 1995. Organic processes in streams of the Eastern United States. Pages 117-187 *in* C. Cushing, K. Cummins, and G. Minshall, editors. Ecosystems of the World 22: River and stream ecosystems. Elsevier, New York, NY.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics **17**:567-594.

Wissinger, S. A. 1999. Ecology of wetland invertebrates: sythesis and applications of conservation and management. Pages 1043-1086 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley & Sons, Inc.

Wooster, D., and A. Sih. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos **73**:3-8.

Wyman, R. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity & Conservation **7**:641-650.

Zhang, Y., J. S. Richardson, and J. N. Negishi. 2004. Detritus processing, ecosystem engineering and benthic diversity: a test of predator-omnivore interference. Journal of Animal Ecology **73**:756-766.

Table 1. Mean water quality parameters (± 1 SE) for the study B wetland by collection date.

Date	DO (mg/L)	Conductivity (µs/cm)	pH
11 Feb 2012	4.3 ± 0.2	76.5 ± 3.2	6.8 ± 0.0
25 Mar 2012	2.2 ± 0.1	105.9 ± 0.0	6.5 ± 0.1
22 Apr 2012	2.1 ± 0.1	116.0 ± 0.5	6.7 ± 0.1

Table 2. Leaf breakdown rates (k) expressed per day and degree day (± 1 SE) for bags or packs in cages open or closed to macroconsumers. Similar superscript letters denote treatments that were not statistically different within each study.

Experimental Level	***k* (day^{-1})**	**R^2**	***k*(degree day^{-1})**	**R^2**
Study A				
Bag Open	0.0019 ± <0.001[a]	0.840	0.0003 ± <0.001[a]	0.734
Bag Closed	0.0023 ± <0.001[a]	0.832	0.0004 ± <0.001[a]	0.702
Pack Open	0.0023 ± <0.001[a]	0.607	0.0003 ± <0.001[a]	0.586
Pack Closed	0.0020 ± <0.001[a]	0.780	0.0003 ± <0.001[a]	0.682
Study B				
Bag Open	0.0078 ± 0.001[a]	0.830	0.0012 ± <0.001[a]	0.808
Bag Closed	0.0058 ± 0.001[b]	0.834	0.0009 ± <0.001[a]	0.821

Table 3. Mean macroinvertebrate abundance (individuals per sample) and biomass (mg AFDM per sample; ± 1 SE) by functional feeding group for study A. Superscripts denote statistical differences by leaf bags or leaf packs.

Functional Feeding Group	Bag Open	Bag Closed	Pack Open	Pack Closed
Abundance				
Predator	13.6 ± 2.1[a]	62.2 ± 39.8[a]	11.6 ± 1.7[a]	38.0 ± 23.3[a]
Shredder	0.3 ± 0.1[a]	0.2 ± 0.1[a]	0.1 ± 0.07[a]	0.3 ± 0.1[a]
Collector-gatherer	97.3 ± 13.9[a]	24.6 ± 5.2[b]	56.8 ± 8.7[a]	47.8 ± 7.0[a]
Collector-filterer	--	--	--	--
Scraper	5.0 ± 1.0[a]	4.2 ± 1.4[a]	6.3 ± 2.2[a]	5.7 ± 1.7[a]
Piercer-herbivore	0.1 ± 0.1[a]	0.1 ± 0.1[a]	0.2 ± 0.1[a]	0.1 ± 0.1[a]
Biomass				
Predator	5.17 ± 0.89[a]	18.74 ± 9.56[a]	3.69 ± 1.66[a]	8.63 ± 4.01[a]
Shredder	0.39 ± 0.16[a]	0.16 ± 0.08[a]	0.02 ± 0.01[a]	0.21 ± 0.10[b]
Collector-gatherer	0.40 ± 0.06[a]	0.30 ± 0.05[a]	0.27 ± 0.04[a]	0.22 ± 0.04[a]
Collector-filterer	--	--	--	--
Scraper	0.45 ± 0.18[a]	0.26 ± 0.11[a]	0.56 ± 0.20[a]	0.41 ± 0.14[a]
Piercer-herbivore	<0.01 ± 0.00[a]	<0.01 ± 0.00[a]	<0.01 ± 0.00[a]	<0.01 ± 0.00[a]

Table 4. Mean macroinvertebrate abundance (individuals per sample) and biomass (mg AFDM per sample; ± 1 SE) by functional feeding group for study B. Superscripts denote statistical differences by treatment.

Functional Feeding Group	Bag Open	Bag Closed
Abundance		
Predator	18.2 ± 2.4[a]	10.4 ± 1.3[b]
Shredder	4.1 ± 1.4[a]	1.7 ± 0.4[a]
Collector-gatherer	39.4 ± 2.8[a]	34.6 ± 6.1[a]
Collector-filterer	41.9 ± 11.5[a]	34.3 ± 10.3[a]
Scraper	33.9 ± 13.5[a]	11.3 ± 2.2[b]
Piercer-herbivore	--	--
Biomass		
Predator	5.82 ± 1.81	4.53 ± 1.97
Shredder	6.44 ± 0.43	4.66 ± 0.46
Collector-gatherer	3.13 ± 0.33	3.13 ± 0.58
Collector-filterer	0.23 ± 0.07	0.36 ± 0.13
Scraper	1.06 ± 0.17	0.68 ± 0.17
Piercer-herbivore	--	--

Table 5. Proportion (%) of total abundance and biomass for study A by treatment level of the top 10 most dominant taxa.

Taxa	Bag Open	Bag Closed	Pack Open	Pack Closed
Abundance				
Oribatidae	60.4	26.8	52.2	28.9
Collembola	21.3	19	24.3	24
Formicidae adult	0.2	33.1	0.8	18.5
Acarina	8.3	5.7	9.6	7.1
Formicidae immature	0	7	0	11.3
Psocoptera immature	1.6	1.9	4.2	3.8
Araneae	2.2	2.4	1.6	1.5
Thysanoptera immature	1.7	1	1	1.3
Gastropoda	0.8	0.8	1.2	0.4
Psocoptera adult	0.2	0.3	0.8	0.5
Total abundance (ind.)	4282	4620	3279	3529
Biomass				
Formicidae adult	0.91	54.2	3.7	45.3
Araneae	52.2	30.3	22.7	16.5
Carabidae adult	8.4	0.3	19.2	11.8
Hymenoptera	3.2	2.2	14.1	5.3
Orthoptera adult	1.9	1.6	1.7	7.6
Gastropoda	4.9	1.5	8.2	0.4
Heteroptera adult	4.2	3.1	1.5	0.3
Chilopoda	1.7	1.1	8.4	1.8
Psocoptera immature	1.4	0.7	4.1	2.4
Collembola	2.3	0.9	2.1	1.3
Total biomass (mg AFDM)	291.29	782.07	237.21	406.51

Table 6. Proportion (%) of total abundance and biomass for study B by treatment of the top 10 most dominant taxa.

Taxa	Open	Closed
Abundance		
Chironomidae	24.4	34.3
Gastropoda	24.5	12.3
Ostracoda	12.8	14.5
Daphniidae	11	12
Copepoda	6.2	10.2
Tanypodine	7.6	5.9
Hydracarina	4.1	4
Oligochete	2	0.9
Gammarus	1.7	0.5
Oribatidae	0.9	0.7
Total abundance	2478	1661
Biomass		
Gammarus	32.3	13.7
Chironomidae	14.3	19.2
Cambaridae	4.8	18.3
Enallagma	10	9.56
Argia	10.2	7.8
Gastropoda	6.3	5.1
Hyrdovatus immature	0	11
Neurocordulila	7	0
Hydroporus immature	3.6	1.7
Caecidotea	1.4	2.7
Total biomass (mg AFDM)	303.94	242.28

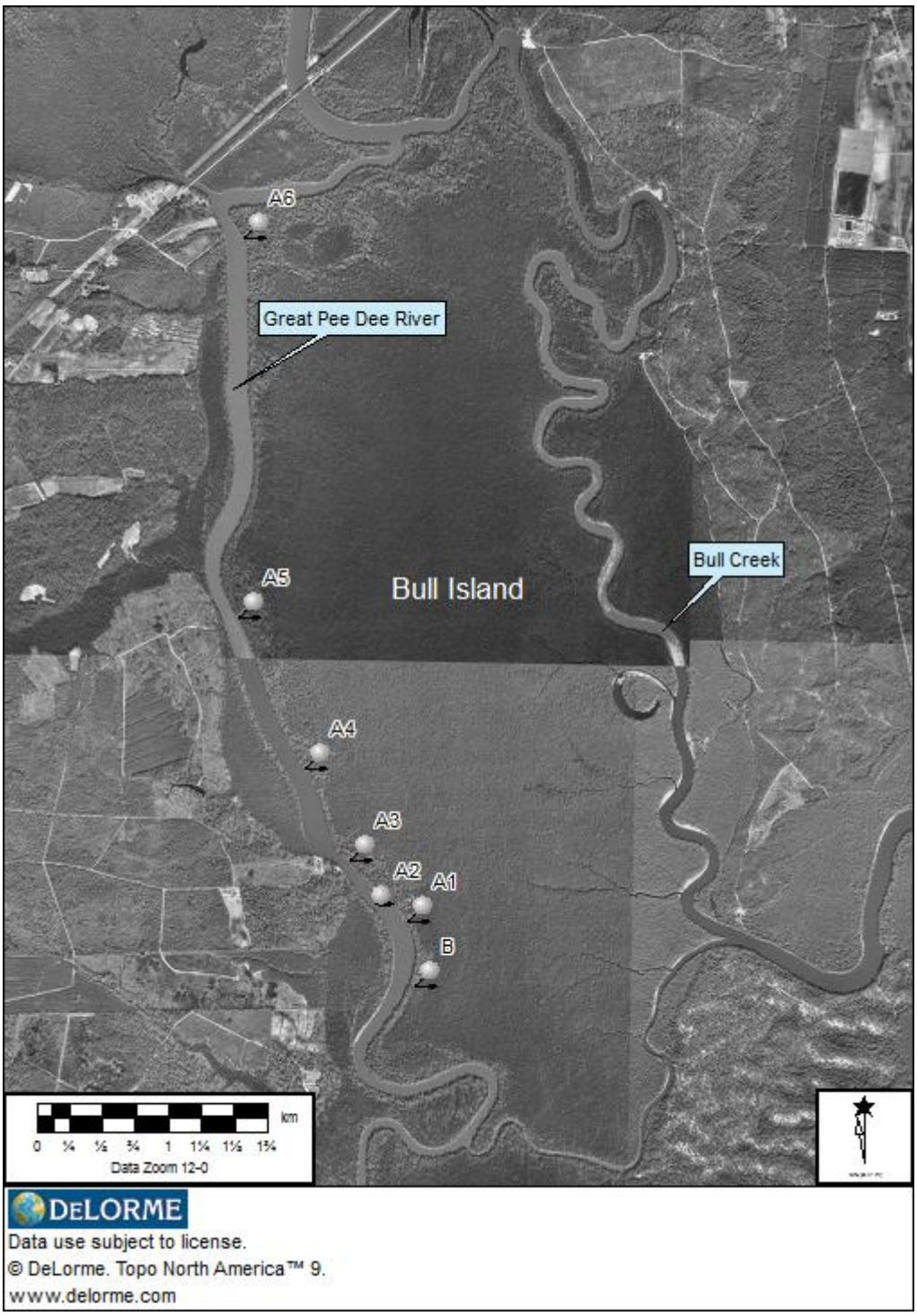

Figure 1. Aerial imagery of Bull Island, SC with marked sites for study A and B.

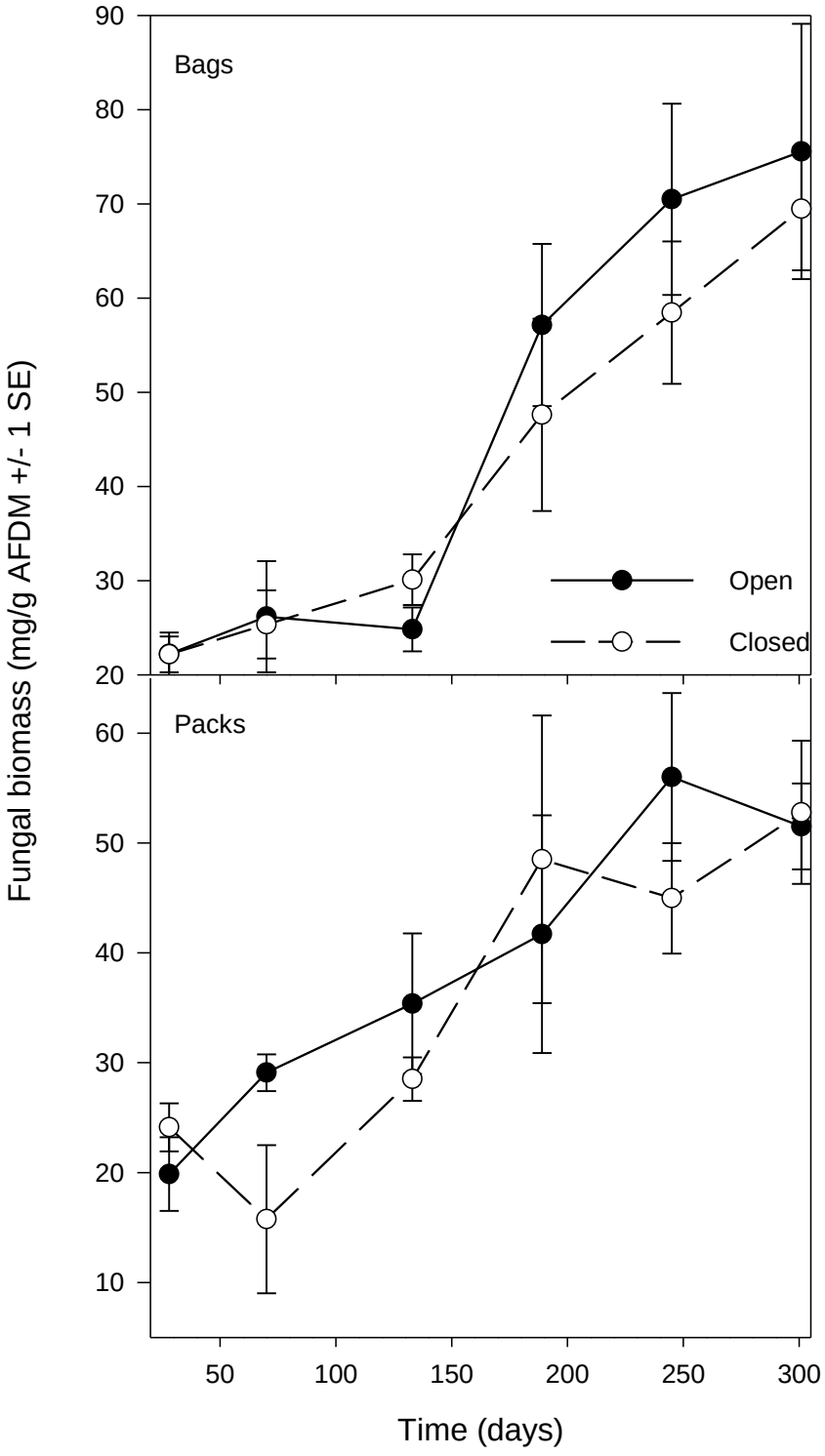

Figure 2. Mean fungal biomass (mg/g AFDM ± 1 SE) over time in leaf bags (top) and packs (bottom) open and closed to macroconsumers in study A.

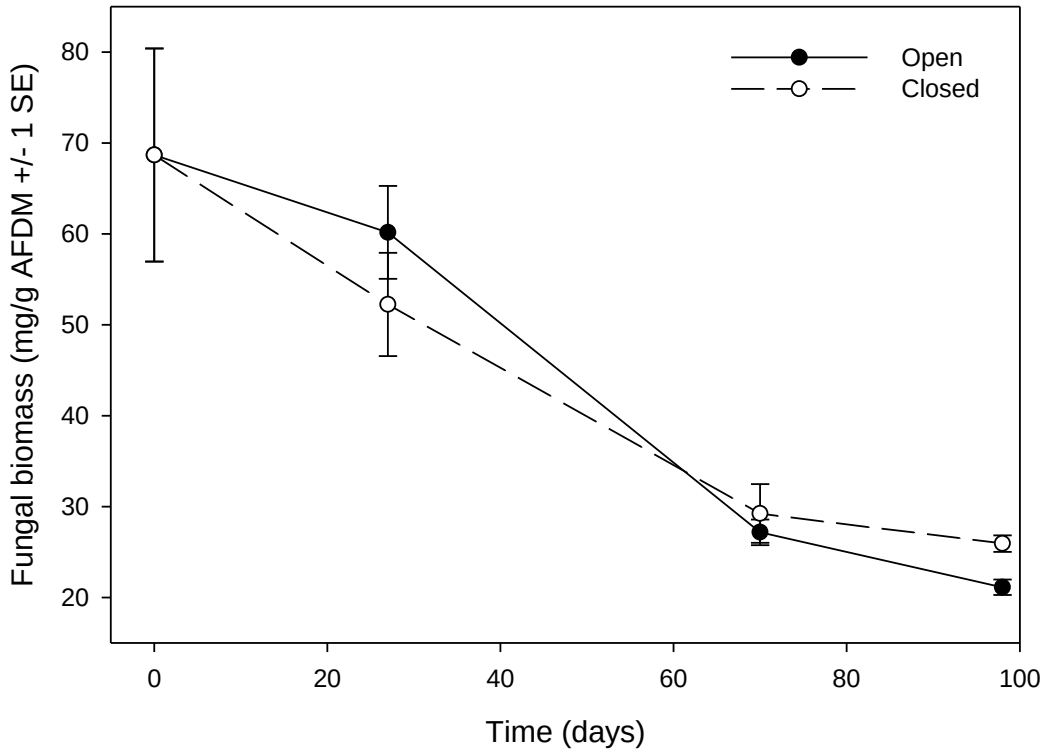

Figure 3. Mean fungal biomass (mg/g AFDM ± SE) over time in leaf bags open and closed to macroconsumers in study B.

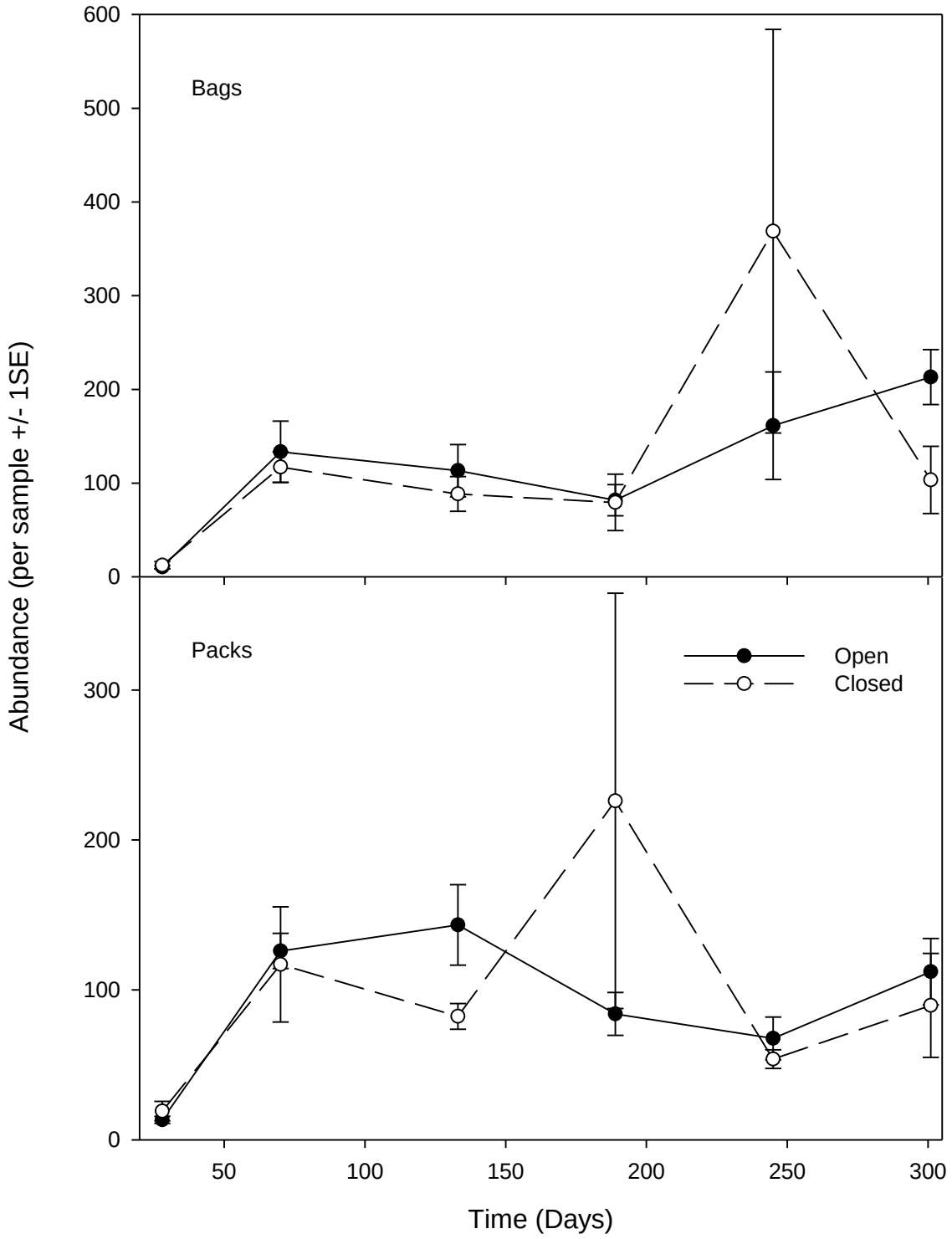

Figure 4. Mean macroinvertebrate abundance (per sample ± 1 SE) of leaf bags (top) and leaf packs (bottom) open and closed to macroconsumers in study A.

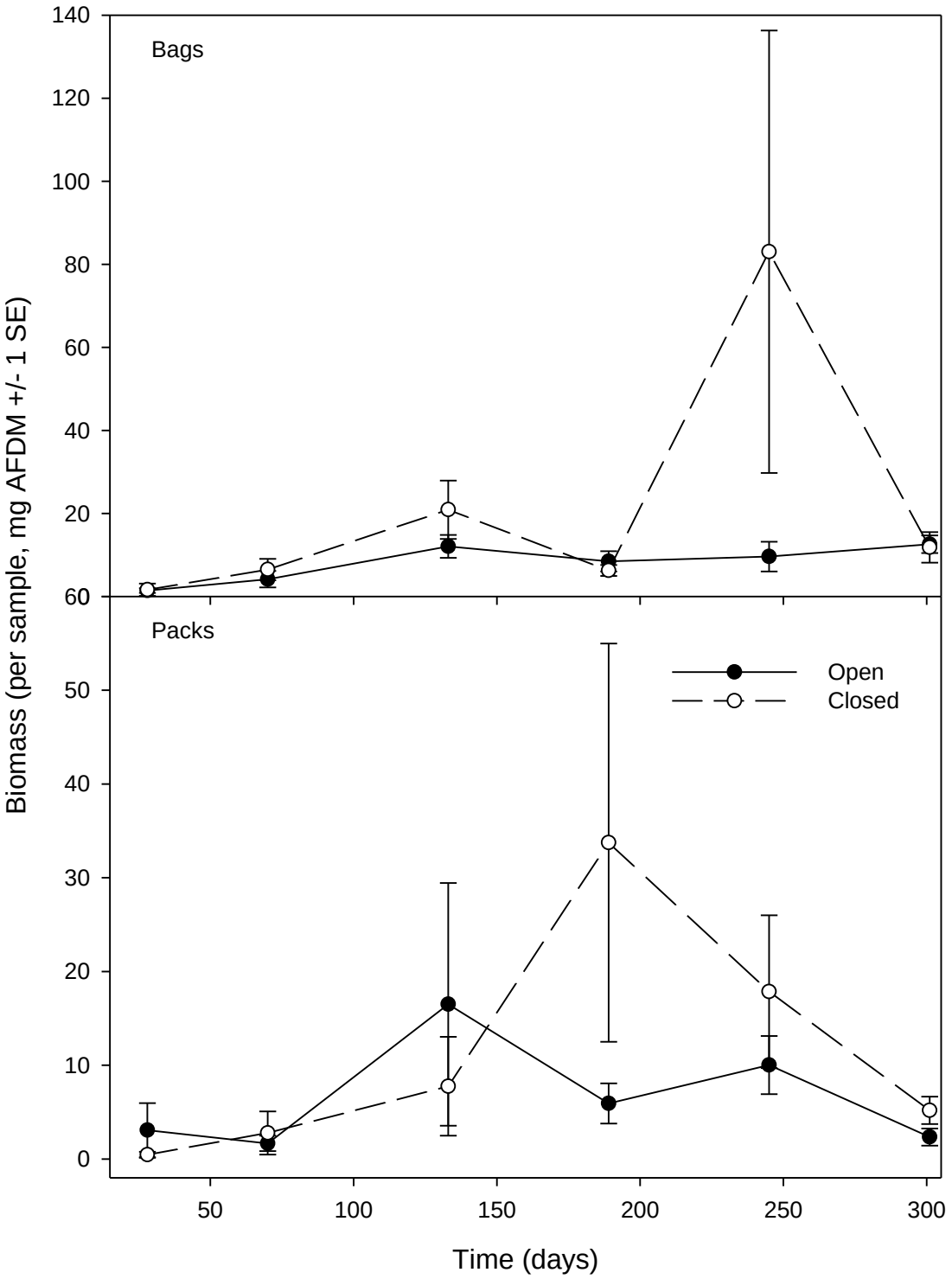

Figure 5. Mean macroinvertebrate biomass (per sample, mg AFDM ± 1 SE) of leaf bags (top) and leaf packs (bottom) open and closed to macroconsumers in study A.

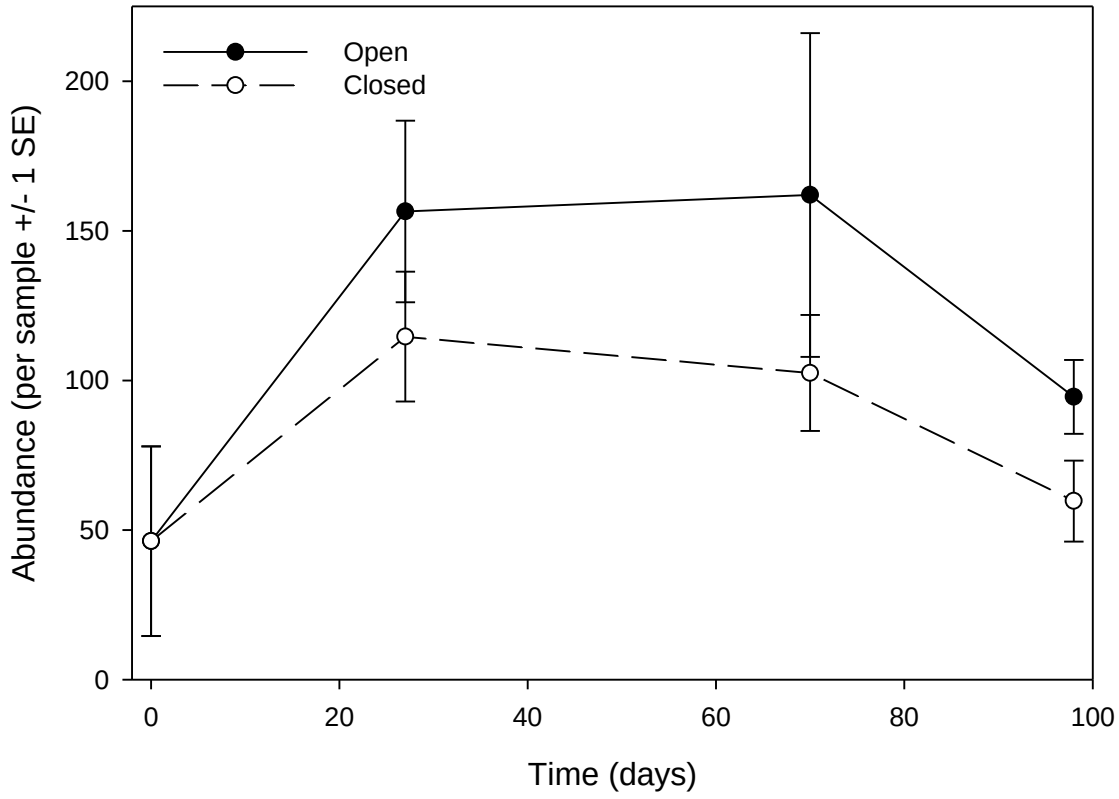

Figure 6. Mean macroinvertebrate abundance (per leaf bag sample ± 1 SE) in litter bags in cages open or closed to macroconsumers for study B. Day zero represents the baseline mean abundance after 4.5 weeks conditioning.

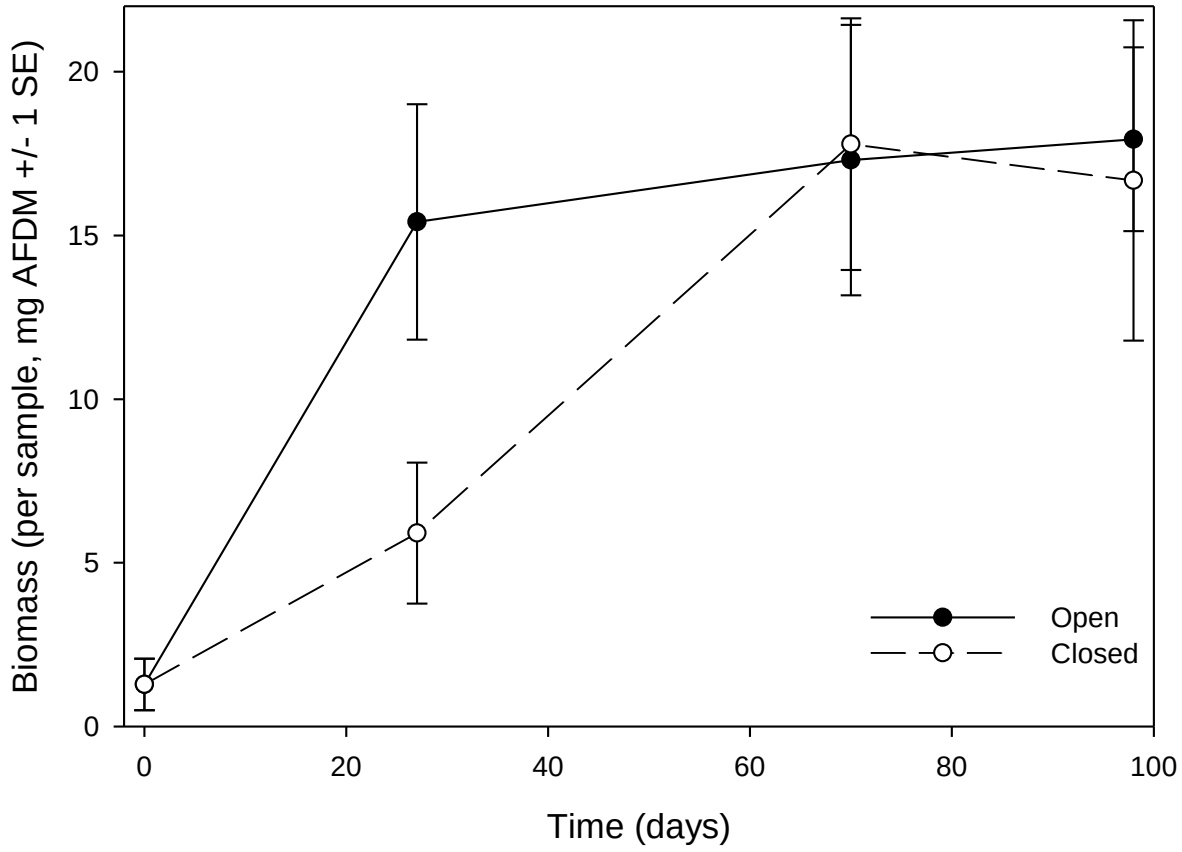

Figure 7. Mean macroinvertebrate biomass (per sample, mg AFDM) in litter bags in cages open or closed to macroconsumers for study B. Day zero represents the baseline mean biomass after 4.5 weeks conditioning.