Role of animal detritivores in the breakdown of emergent plant detritus in temporary ponds

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Abstract: Few in situ studies have investigated the biological drivers of detritus processing in shallow lentic systems, despite abundant evidence that vascular plant detritus is a primary source of nutrients and energy. In particular, the relative importance of microbial decomposers and animal detritivores to overall detritus breakdown is poorly documented. Caddisfly larvae (Trichoptera: Limnephilidae) are often the biomass-dominant animal detritivores in high-elevation and high-latitude ponds and wetlands in the northern hemisphere. The larvae of many limnephilid caddisfly species are shredders that rely on detritus as their primary food source, and they may therefore play an important role in litter breakdown in lentic systems. Here, we manipulated abundances (present/absent) of caddisfly larvae in shallow montane ponds in Colorado, and compared sedge detritus breakdown rates across treatments. We found that coarse particulate organic matter (CPOM) was converted to fine particulate organic matter (FPOM) 2 to 3× faster when caddisflies were allowed access to the detritus than when not, indicating that caddisflies play a key role in litter breakdown in these temporary habitats. Dietary data from the 6 species of caddisflies in the ponds revealed that all primarily consume CPOM derived from vascular plants, although the ratios of CPOM and FPOM in the diets varied among species. The biomass of caddisflies relative to detrital inputs is particularly high at our study sites compared with other eutrophic, low-elevation wetlands. Thus, we suspect that animal detritivory relative to microbial processing may be especially high in these ponds. Future in situ, whole-community studies in basins that differ in hydroperiod, nutrient status, and ratio of detrital inputs to detritivore biomass will be needed to construct a general model of detritus breakdown in shallow lentic freshwater habitats.
Key words: detritus, litter breakdown, wetlands, temporary ponds, caddisfly larvae, shredders, detritivores, lentic vs lotic ecosystems

Most energy and nutrients from vascular plant production enters aquatic food webs as detritus. Plant detritus is initially colonized by microbes (fungi, bacteria) and then consumed by animal detritivores (Cebrián 1999, Moore et al. 2004, Gessner et al. 2010). The relative contribution of microbial decomposers and animal detritivores to the breakdown (physical degradation) and decomposition (chemical oxidation) of detritus in aquatic systems is best understood in streams (Hieber and Gessner 2002, Taylor and Chauvet 2013). In situ comparisons of breakdown rates in leaf packs with and without shredders and studies that compare microbial and animal detritivore secondary productivity have quantified the role of detritivores in accelerating detritus breakdown in streams (Anderson and Sedell 1979, Webster and Benfield 1986, Wallace et al. 1997, Graça 2001, Hieber and Gessner 2002). In contrast, the relative contribution of animal detritivores and microbial decomposers to the rates of detritus breakdown in shallow standing waters, such as ponds, wetlands, and the littoral zones of lakes, is poorly documented.

Allochthonous and autochthonous detritus and the microbial complexes that form on them are major sources of nutrients and energy that fuel secondary production in wetlands (Oertli 1993, Rubbo et al. 2006, Stoler and Relyea 2011, Earl and Semlitsch 2013, Holgerson et al. 2016; Balik et al. 2018), and microcosm studies demonstrate that several groups of detritus shredders (e.g., limnephilid caddisflies, amphipods, isopods) and biofilm grazers (e.g., snails, tadpoles) rely on detrital resources (e.g. Graça et al. 1993, Inkley et al. 2008, Jannot et al. 2008, Chung and Suber-

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kropp 2009, Brady and Turner 2010). However, the contribution of shredders to the overall breakdown rates of detritus may often be trivial in standing waters compared with streams for 2 reasons. First, in many shallow lentic habitats there are few detritus-consuming animals relative to the annual inputs of detritus (Batzer et al. 2014). Surveys across many types of wetlands have shown that detritus shredding invertebrates are typically rare or absent in many wetland food webs (Batzer and Ruhí 2013, Batzer and Boix 2016). Second, the biofilms that accumulate on and in wetland detritus (fungi, bacteria, algae) are more complex than biofilms in streams; thus, microbial decomposition may play a proportionately larger role in the overall breakdown of detritus in wetlands than in streams (Kuehn et al. 2000, 2014, Buesing and Gessner 2006, Boon et al. 2015, Su et al. 2015). In spite of these studies and the expected contrast with streams, to our knowledge no published studies have directly compared in situ detritus breakdown with and without animal detritivores in wetland habitats.

The purpose of this study was to measure the importance of animals to the breakdown rate of sedge detritus in montane kettle-pond marshes during their wet phase. These high-elevation, shallow wetlands dry in late summer and remain dry until they fill with snowmelt in spring (Wissinger et al. 1999). The limnephilid caddisflies that often dominate invertebrate biomass in north-temperate, high-elevation ponds and wetlands depend on detritus to grow, develop, and reproduce (Wissinger et al. 1996, Jannot et al. 2008, Klemmer et al. 2012). Caddisflies increase the breakdown rates of detritus in microcosm studies (Jannot et al. 2008, Klemmer et al. 2012), but it is not clear whether they significantly influence detritus breakdown rates in situ in the context of the natural volume of detrital inputs in ponds. We therefore manipulated access to detritus in situ to assess the effects of detritivores on sedge detritus breakdown in these ponds. We hypothesized that detritus breakdown rates would be higher with vs without caddisfly foraging. We also quantified the proportional abundance of coarse and fine detritus in the diets of the caddisfly species that we observed in these habitats to provide corroborative evidence for the potential role of each species in detritus breakdown.

METHODS

We performed the experiments in 3 montane (2850 m elevation) kettle-pond wetlands in a mid-valley moraine near the Rocky Mountain Biological Laboratory in the Elk Mountains of Colorado, USA. We chose the 3 ponds (K1: lat 38.942998, long −106.976362; K5: lat 38.946106, long −106.97555; K6: lat 38.944813, long −106.977252) from a cluster of shallow ponds and marshes we have surveyed since 1990 because they are similar in depth (~1-m maximum depth) and have similar emergent vegetation (primarily the sedge *Carex aquatilis*; see Fig. 1). During this study,



Figure 1. Kettle-pond wetland in the East River Valley near the Rocky Mountain Biological Laboratory (photo by Angus McIntosh).

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water-level and temperature data loggers (TruTrack WT-HR series, Intech Instruments, Christchurch, New Zealand) indicated that the 3 basins had similar hydroperiods and remained dry under the snowpack during winter, filled with subniveal melt water during May–June, and then dried again in July. Animal activities that affect detritus breakdown occur primarily during the aquatic phase of the hydroperiod, and annual censuses of the invertebrate communities over the past 28 y indicate that limnephilid caddisflies typically make up 50–70% of all animal biomass, although the relative abundance of species has shifted over time (SAW, unpublished data). Limnephilid caddisflies are the only taxon in the ponds that are explicitly described as vascular plant shredders in the literature (e.g., Williams and Feltmate 1992, Merritt et al. 2008).

We therefore focused on measuring rates of detritus breakdown with and without limnephilid caddisflies. At the start of the experiment, 6 species of caddisflies (*Grammotaulius lorettae* Denning, *Limnephilus externus* Hagen, *L. tarsalis* Banks, *L. secludens* Banks, *L. sublunatus* Provancher, and *L. picturatus* McLachlan) were present in the 3 kettle ponds. Five of the species have been present since 1990, whereas *L. sublunatus* first appeared in the 2000 annual census (Wissinger et al. 2016). Other omnivorous taxa in the ponds whose diets can include detritus were chironomid midges, snails, and tadpoles (Altig et al. 2007; Brady and Turner 2010, Silveira et al. 2013, Stoler et al. 2016a, b). The other common invertebrate taxa were either predators (dragonflies, damselflies, dytiscid beetles, water bugs, chironomids) or FPOM consumers (e.g., culicid fly larvae, chironomid larvae; see food webs in Wissinger et al. 1999).

Quantifying caddisfly abundances and diets

Prior to starting the experiment in early June 2012, we quantified inter-pond variation in the biomass and species composition of the caddisfly assemblage by using a D-frame (1-mm mesh) net to take 4 replicate 0.33 m^2 samples in each pond. We counted all caddisfly larvae in these samples, assigned individuals to instars based on reference-collection head-width categories, and used known biomass values for each instar of each species (Wissinger et al. 2003). We removed 10 larvae of each instar of each species from their cases and measured their ash-free dry mass (AFDM). We dried (55°C for 48 h), weighed, and combusted (500°C for 4 h) individuals of each instar of each species (see Wissinger et al. 2003). We used individual AFDM and sample counts to estimate species-specific and total caddisfly biomass in each pond.

We used a 2nd subset of 10 individuals of each species to quantify interspecific differences in diet (Wissinger et al. 1996; also see Balik et al 2018). Briefly, we removed the entire digestive tract from the body and preserved the contents in 95% ethanol. We added Congo red stain to identify chitin. After 4 d, we pipetted 1 mL aliquots of homogenized gut contents in ethanol onto Sedgewick–Rafter counting chambers (Wildlife Supply Company, Yulee, Florida). We separated the particulate matter and quantified the relative amounts of: 1) coarse plant detritus >1 mm), 2) amorphous fine detritus, 3) algal cells, and 4) invertebrate exoskeletons, which were stained by the dye. We then calculated the % contribution of each diet category as the area covered by each category divided by the total area covered by all diet items.

Field experiment

We used an animal exclusion experiment to assess how much detritus was consumed by macroinvertebrates. Experimental units consisted of small plastic storage containers (0.026-m^2 area) that were filled with glass marbles as ballast and 5 g of air-dried sedge (*C. aquatilis*) litter (~200 g/m^2), which is within the range of annual detritus inputs in these ponds (ranges from <50 g/m^2 along open shorelines to >1500 g/m^2 in dense sedge stands; SAW unpublished data; also see Klemmer et al. 2012). We collected dead sedge leaves from *C. aquatilis* stands on the edge of each kettle pond and air-dried the detritus for 3 days before constructing the detritus trays for each pond. To estimate the initial oven-dried starting mass, we drew 6 additional ~5 g samples from the same dried material and then weighed them after drying each sample at 55°C for 48 h.

We created 2 experimental treatments: a 'caddis' treatment in which containers were covered with 20-mm mesh that allowed macroinvertebrate access to the detritus and a 'no-caddis' treatment in which containers were covered with 2-mm mesh that excluded caddisflies and other large macroinvertebrates (Fig. S1). We used plastic containers instead of mesh bags in the experiment to minimize the loss of detritus from the bottoms of the containers, independent of shredder activity (see reviews in Hieber and Gessner 2002, Tiegs et al. 2008). We filled all containers with water and placed them at pond side for 3 days to waterlog the litter and reduce floating when the containers were deployed into the ponds. We placed 8 containers (4 caddis and 4 no-caddis treatments) at each of 3 sites (north, west, east) in each pond, for a total of 24 containers in each pond. We collected pairs of containers (1 caddis, 1 no-caddis) at each of the 3 sites in each of the 3 ponds at 10-d intervals (10, 20, 30, 40 d) during which time all ponds were still wet.

At each sampling date, we gently removed the detritus containers from the ponds and placed them into separate buckets to retain any spillage. The contents of each container were spread into a large sorting pan and all macroinvertebrates were removed and retained for identification. We then washed the CPOM through a 1-mm net and retained the FPOM that passed through the net. We oven-dried (55°C for 72 h) the CPOM and FPOM fractions to estimate the dry mass remaining on each date.

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We tested for mesh size effects other than the direct effects of allowing/excluding detritivores (i.e., differences in litter loss between the 2 treatments associated with differences in microbial decomposition, meiofaunal invertebrate activity, or spillage associated with mesh size [see Hieber and Gessner 2002, Tiegs et al. 2008]) by placing an additional 6 replicates of each treatment in pond K5 inside a larger invertebrate exclusion cage (1-mm mesh, 0.25 m^2; Klemmer et al. 2012).

Statistical analyses

We conducted all statistical tests with mixed-effects models as implemented in the *nlme* package (Pinheiro et al. 2015) in R (version 3.3.1; R Development Core Team 2016). We considered each pond to be an independent unit and analyzed the experimental design as a replicated (3 sites) regression across 4 dates. We used the means for the 3 containers of each treatment taken out of each pond on each date to avoid pseudo-replication. We tested for differences in CPOM and FPOM between treatments through time by specifying day of sampling (day), treatment, and their interaction as fixed effects and caddisfly density nested within pond as a random effect. When the interaction between time and treatment was significant, we performed post-hoc tests on the different treatments individually. For these post-hoc tests, we assigned day as a fixed factor and caddis density (nested within pond) as a random factor. We also performed post-hoc tests by modeling the relationship between CPOM remaining and day separately for each pond. These analyses used the amount of CPOM in each container in each pond, instead of the average within a pond. Here, we used treatment and day as fixed factors and container within ponds as a random factor.

RESULTS

Detritivore species composition and biomass

Larvae of 6 species of limnephilid caddisflies (*G. lorettae* Denning, *L. externus* Hagen, *L. tarsalis* Banks, *L. secludens* Banks, *L. sublunatus* Provancher, and *L. picturatus* McLachlan) were present in the 3 study ponds at the start of the experiment (Fig. 2A, B). Total caddisfly biomass and density were highest in pond K1 (Fig. 2A, B), mainly because of the high abundance of *L. externus* and *L. sublunatus* in that pond (see Table S1). Phenological differences in caddisfly life cycles led to shifts in assemblage composition during the experiment. For example, before the start of the experiment in early June, *L. externus*, which develops latest in the season, made up only 10 to 15 % of the biomass in these ponds, but this proportion increased as earlier-developing species (e.g., *L. tarsalis*, *L. secludens, L. picturatus*, *L. sublunatus, G. lorettae*) pupated and emerged. By the end of the experiment, 100% of the caddisfly biomass in each pond was *L. externus*.

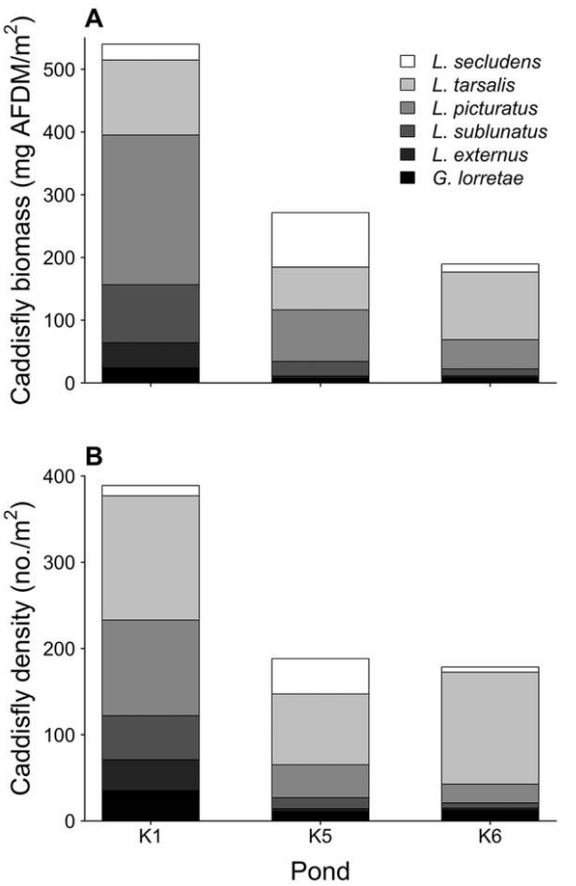


Figure 2. Mean biomass (mg AFDM/m^2) (A) and densities (no./m^2) (B) of 6 limnephilid caddisfly species in the 3 study ponds.

Caddisfly diets

Coarse particulate organic matter (CPOM; >1 mm) derived from vascular plant material was present in the diets of all caddisfly species and ranged from >70 to 22% in *L. externus* and *L. tarsalis*, respectively (Fig. 3). Fine particulate organic matter (FPOM; <1 mm) accounted for most of the rest of gut contents of all caddisflies (Fig. 3). The presence of cell walls indicated that nearly all of the fine detritus also originated from vascular plants. Together, coarse and fine vascular plant material comprised 75–95% of the diets of the 6 caddisfly species. Chitinous animal fragments derived from epibenthic crustaceans (cladocerans, copepods, ostracods) and chironomid head capsules represented <10% of the diet of all species except *L. secludens*, which comprised 23% of the diet of this species (Fig. 3). Algal cells were present in the diets of all species, but made up <5% of their diet by volume.

Test for mesh size effects

At the end of the experiment, no difference in litter biomass existed between mesh treatments placed inside of the larger exclusion cage (20-mm-mesh: mean [±1 SD] = 3.84 ±

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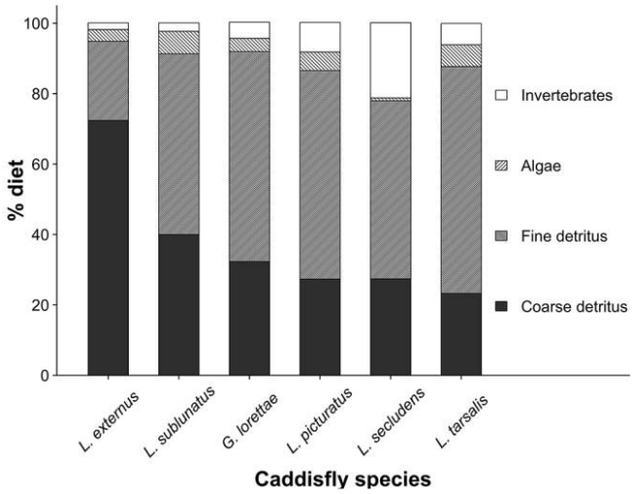


Figure 3. Percent abundance of coarse particulate organic matter (CPOM > 1 mm) and fine particulate organic matter (FPOM < 1 mm), algae, and animal (chitinous) material in the diets of the 6 limnephilid caddisflies in the 3 study ponds.

0.07; 2-mm-mesh: mean [±1 SD] = 3.87 ± 0.04; Student's *t*, $p = 0.37$). Thus, effects of mesh size that might be associated with either microbial processes or spillage do not explain our experimental results.

Presence and absence of animal detritivores and detritus breakdown

The manipulation created the expected contrast in detritivore abundance. At the end of the experiment, caddisflies were present inside the caddis treatment containers along with several other taxa of aquatic invertebrates including a few snails and chironomids, dytiscid beetle larvae, and epibenthic crustaceans. There were no Chorus Frog tadpoles inside any of the containers. No macroinvertebrates, including chironomids, were present in any of the no-caddis exclosures. We suspect that the absence of chironomids in the fine-mesh enclosures was related to the timing of chironomid generations in these short-lived ponds—i.e., early-season cohorts had already developed and emerged, and late-season cohorts had not colonized by the end of the experiment.

In each pond, sedge detritus broke down faster in the presence than in the absence of caddisflies (Fig. 4, Table 1). Decay slopes were 2 to 3× steeper in containers with caddisflies (0.09 g to 0.11 g/d) than without caddisflies (~0.04 g/d) (Fig. 4, Table 1). On the final sample date, ~1 g of detritus remained in caddis treatments compared with 3–4 g in no-caddis treatments (Fig. 4). Furthermore, across all ponds, the steep decline in CPOM in caddis treatments was associated with a steep increase in FPOM (Fig. 5, Table 2). On the final sampling date, the caddis treatments had twice as much FPOM as did the no-caddis treatments (Fig. 5).

DISCUSSION

Detritus is an important primary energy source for food webs in ponds, wetlands, and other shallow standing-water habitats with abundant emergent vegetation (Batzer et al. 2014). Lentic ecologists have often assumed that the stream paradigm regarding the relative importance of animal detritivores and microbes to litter processing (e.g., Wallace et al. 1997, Graça et al. 2001, Hieber and Gessner 2002) also applies to standing-water habitats. The stream paradigm typically invokes the sequential importance of conditioning by microbial decomposers (fungi and bacteria) and subsequent shredding of the microbial-detritus complex by animal detritivores that obtain their energy and nutrients from this complex. The degree to which animal detritivores play a similarly important role in standing-water habitats is poorly documented in lentic habitats where shredders are often minor components of the fauna (Batzer et al. 2014). Here, we found that detritus breakdown during the short mon-

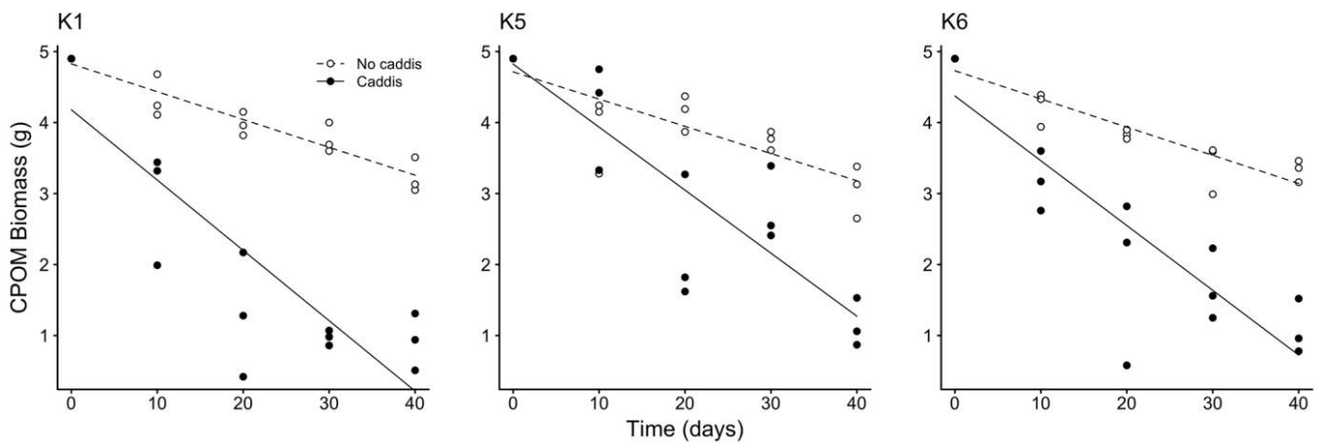


Figure 4. Coarse particulate organic matter (CPOM) mass in individual caddis and no-caddis containers in each pond and on each sample day.

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Table 1. Results of mixed-effects model analyses on relationships between coarse particulate organic matter (CPOM), time (day), treatment (caddis or no-caddis), and their interaction for individual ponds (K1, K5, and K6). Sampling site within the pond is a random effect in all models. df (degrees of freedom) is expressed as treatment, total degrees of freedom. r^2 (marg) is the marginal r^2 (coefficient of determination) of the model without the random variables, and r^2 (cond) is the conditional r^2 of the model including random variables.

Variable	*F*-test	df	*p*	r^2 (marg)	r^2 (cond)
K1 CPOM (g/m^2)				0.85	0.85
day	77.56	1,24	<0.001		
caddisfly treatment	68.93	1,24	<0.001		
day × caddisfly treatment	14.54	1,24	<0.001		
K1 CPOM (g/m^2) caddis				0.75	0.75
day	42.17	1,11	<0.001		
K1 CPOM (g/m^2) no-caddis				0.89	0.89
day	111.61	1,11	<0.001		
K5 CPOM (g/m^2)				0.78	0.78
day	71.33	1,24	<0.001		
caddisfly treatment	17.86	1,24	<0.001		
day × caddisfly treatment	11.23	1,24	0.003		
K5 CPOM (g/m^2) caddis				0.76	0.76
day	44.68	1,11	<0.001		
K5 CPOM (g/m^2) no-caddis				0.68	0.68
day	29.33	1,11	<0.001		
K6 CPOM (g/m^2)				0.84	0.84
day	90.64	1,24	<0.001		
caddisfly treatment	50.78	1,24	<0.001		
day × caddisfly treatment	14.04	1,24	0.001		
K6 CPOM (g/m^2) caddis				0.78	0.78
day	49.49	1,11	<0.001		
K6 CPOM (g/m^2) no-caddis				0.85	0.88
day	99.57	1,11	<0.001		

tane growing season in temporary wetlands is 2–3× faster when animal detritivores have access to detritus than when they do not (Fig. 4). We detected this strong detritivore effect in open wetlands against the backdrop of natural densities of detritivores and natural volumes of detritus, indicating that at least in these particular habitats, shredders play a comparable role to that in headwater streams (McKie et al. 2008).

The sedge (*C. aquatilis*) detritus used in the experiment is the dominant emergent vascular plant in and along the shorelines of montane and subalpine wetlands at our study sites (Wissinger et al. 1999), and in high-elevation wetlands in general (Wissinger et al. 2016). The preponderance of detritus (vascular plant CPOM+FPOM) in the diets of all 6 species of caddisflies (Fig. 3) is consistent with dietary data from previous micro- and mesocosm studies in which limnephilid caddisflies accelerated detritus breakdown (Wissinger et al. 1996, Jannot et al. 2008, Klemmer et al. 2012). Caddisflies are likely to be the major detritus shredders in these habitats because they make up 30–70% of the total invertebrate biomass (Wissinger et al. 1999). Some other animals that are omnivorous could have contributed to detritus breakdown in this experiment by grazing epidetrital biofilms and ingesting CPOM fragments (Altig et al. 2007, Brady and Turner 2010, Stoler et al. 2016b). Such an effect is likely in ponds and wetlands in general because omnivory is prevalent in food webs, and especially common in freshwater food webs (Thompson et al. 2007, 2012). However, in ponds in which we conducted these experiments, caddisflies are often >50% of the macroinvertebrate biomass (SAW, unpublished data) and likely to be the primary animal consumers of detritus.

Where they are abundant, limnephilid caddisflies should accelerate detritus breakdown, given that detritus is their primary food source. Limnephilid caddisflies are widely distributed in the northern hemisphere at high latitudes and elevations (e.g., Winterbourn 1971, Otto 1976, Wiggins et al. 1980, Berté and Pritchard 1986, Higgins and Merritt 1999, Whiles et al. 1999), and in those regions, should be important detritivores. However, our dietary data provide the ca-

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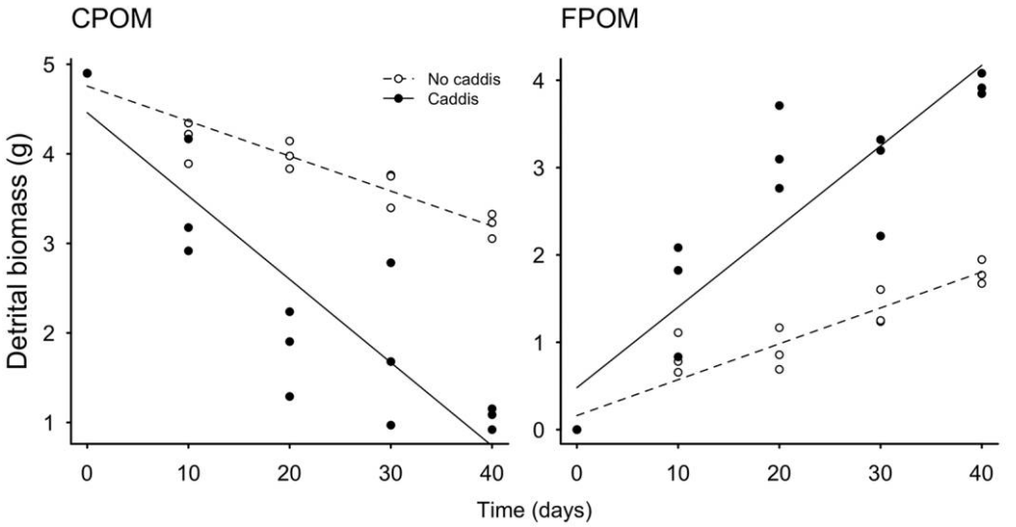


Figure 5. Mean mass of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) by pond and day in the caddis and no-caddis containers.

veat that the presence of high densities of limnephilids does not necessarily mean they will play a role in detritus breakdown; i.e., some species are omnivores that might gain most of their nutrition from FPOM and meiofauna (e.g., *L. secludens* and *L. tarsalis*; Fig. 3). We cannot distinguish from this study whether FPOM detritus from vascular plants (with plant cell walls) in caddisfly diets was ingested as FPOM or was generated during CPOM digestion. Thus, we do not know whether the shredding activity of some caddisfly species generates FPOM resources for other caddisfly species.

The in situ influence of animal detritivores on detritus breakdown in our study ponds might be high relative to other types of shallow, lentic habitats for at least 2 reasons. First, the limnephilid caddisflies that are the primary detritivores in these ponds are extremely abundant (200–400 caddisflies/m^2 and 5–6 g biomass/m^2). Second, detrital inputs

Table 2. Results of the mixed-effects model analyses on the overall relationships between coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) and time (day), caddisfly treatment (caddis or no-caddis), and their interaction across all ponds. Caddisfly density nested within pond is a random effect variable in all models. df (degrees of freedom) is expressed as treatment, total degrees of freedom. r^2 (marg) is the marginal r^2 (coefficient of determination) of the model without the random variable, and r^2 (cond) is the conditional r^2 of the model including the random variable.

Variable	*F*-test	df	*p*	r^2 (marg)	r^2 (cond)
CPOM (g/m^2)				0.86	0.87
day	111.66	1,24	<0.001		
caddisfly treatment	60.59	1,24	<0.001		
day × caddisfly treatment	18.62	1,24	<0.001		
CPOM (g/m^2) caddis				0.80	0.84
day	70.43	1,11	<0.001		
CPOM (g/m^2) no-caddis				0.90	0.90
day	121.12	1,11	<0.001		
FPOM (g/m^2)				0.86	0.86
day	110.18	1,24	<0.001		
caddisfly treatment	55.89	1,24	<0.001		
day × caddisfly treatment	16.23	1,24	<0.001		
FPOM (g/m^2) caddis				0.80	0.82
day	64.33	1,11	<0.001		
FPOM (g/m^2) no-caddis				0.87	0.87
day	96.62	1,11	<0.001		

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in these relatively nutrient-poor, high-elevation ponds are modest (see Wissinger et al. 1999) compared with those in low-elevation, eutrophic wetlands (e.g., Inkley et al. 2008, Bush and Wissinger 2016). Thus, it remains an open question whether animal detritivores play a significant or trivial role in detritus breakdown in lentic habitats that either receive higher detrital inputs or have fewer shredders than in this study (Batzer et al. 2005; Batzer and Ruhí 2013).

A full accounting of the roles of animal detritivores and microbial decomposers in wetlands in general will require experiments over the entire annual cycle of a pond. In permanent habitats, the role of invertebrates will depend on how long detritus remains above the aerobic–anaerobic boundary in the sediment. Below this boundary, detritus breakdown will be dominated by the anaerobic microbial processes associated with the early stages of peat formation (Clymo et al. 1998, Boon et al. 2015, Bonaiuti et al. 2017). Moreover, fungi that colonize dead standing emergent macrophytes before they become submerged (Verma et al. 2003, Keuhn and Suberkropp 1998, Kuehn et al. 2011) will also be important contributors to the overall contribution of microbial decomposers.

In temporary lentic habitats, hydroperiod, or degree of permanence and schedule of filling and drying (Wissinger 1999), will affect the relative importance of microbial decomposers and animal detritivores for overall detritus breakdown. Long-term monitoring indicates that the basins in this study typically remain dry from late summer through the end of winter when they fill with melt water from the 1 to 3 m of overlying snow (billy barr, Rocky Mountain Biological Laboratory, unpublished data). These species of caddisflies overwinter in these ponds as diapausing eggs (Wissinger et al. 2003), and like other aquatic invertebrates should play little or no role in litter breakdown when ponds dry and benthic organic matter is rapidly mineralized by aerobic fungi and bacteria (Bärlocher et al. 1977, Battle and Golladay 2007, Fuell et al. 2013, Boon et al. 2015).

Ultimately, a general model that summarizes the relative importance of microbial decomposers and animal detritivores to detritus breakdown in shallow, lentic freshwater habitats will need to account for: 1) microbial processing of emergent vegetation above the waterline and during dry phases of temporary habitats, 2) the time detritus is available to detritivores before it is buried in anaerobic sediments in permanent habitats, and 3) the abundance and diversity of detritivorous taxa relative to the volume of detrital inputs.

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