Relating carrion breakdown rates to ambient resource level and community structure in four cave stream ecosystems

Brock M. Huntsman[1], **Michael P. Venarsky**[2], AND **Jonathan P. Benstead**[3]

Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487 USA

Abstract. Detrital inputs into ecosystems vary in quantity and quality (e.g., plant litter vs carrion). Variability in detrital quantity and quality potentially affects consumer biomass and rates of organic matter (OM) breakdown. We used cave streams to test 2 linked hypotheses regarding the influence of total detrital inputs on consumer biomass and the breakdown of high-quality carrion detritus. First, we hypothesized that cave systems with higher total OM availability would support a higher biomass of consumers. Second, we predicted that higher consumer biomass would cause faster carrion breakdown rates. To test these hypotheses, we quantified macroinvertebrate biomass and breakdown rates (k, d^{-1}) of carrion (mouse carcasses, *Mus musculus*) in 4 cave streams in northeastern Alabama and southeastern Tennessee (USA) that varied in total OM storage. We estimated carrion breakdown rates in coarse- and fine-mesh packs (10-mm and 500-µm mesh size) to isolate the influence of scavenging by crayfish. Macroinvertebrate biomass (excluding crayfish) in carrion packs was positively correlated with OM storage, but neither macroinvertebrate biomass (excluding crayfish) nor OM storage were strong predictors of carrion breakdown rates. Crayfish biomass was not correlated with total OM storage but was positively correlated with coarse-mesh breakdown rates. Our study illustrates the influence of community structure and consumer biomass on detrital breakdown rates in cave ecosystems. However, determining how detrital inputs structure cave communities will require further study.

Key words: bottom-up, *Cambarus*, cave, decomposition, karst, *Orconectes*, scavenging.

Community structure in ecosystems is influenced by a combination of bottom-up and top-down forces. The relative strength of these forces is ecosystem dependent (Hunter and Price 1992). For example, in detritus-based headwater streams, experimental manipulations have shown that both detrital and nutrient inputs (e.g., bottom-up forces) are major factors controlling microbial, invertebrate, and vertebrate consumer production (Wallace et al. 1997, 1999, Hall et al. 2000, Johnson and Wallace 2005, Cross et al. 2006, Suberkropp et al. 2010). These studies also have illustrated how changes in community structure can subsequently affect ecosystem function, such as detrital breakdown rates. Stimulating microbial activity via nutrient additions increased detrital breakdown rates (Suberkropp et al. 2010), whereas decreas-

ing shredder biomass via detrital exclusion decreased litter breakdown rates (Eggert and Wallace 2003).

Many cave streams have a community structure similar to that of surface streams (Simon et al. 2003), but relatively little is known about how these cave stream communities are structured or how their structure influences cave ecosystem function (Simon and Benfield 2001). Nearly all cave stream ecosystems, except those based on chemolithoautotrophy (Sarbu et al. 1996), are wholly dependent on allochthonous inputs of surface detritus to support in situ productivity (Poulson and White 1969). Low connectivity with surface systems typically reduces detrital inputs to cave ecosystems (Hüppop 2000, Graening and Brown 2003), but substantial variability in detrital inputs can exist among caves. Cave systems that are well connected to the surface (e.g., via entrances and sinkholes) can receive large detrital inputs, whereas systems with few connections typically have reduced detrital inputs. Energy limitation (e.g., limited detrital inputs) has been considered the primary factor influencing cave community structure, evolution, and ecosystem-level processes (Poulson

[1] Present address: Division of Forestry and Natural Resources, West Virginia University, Morgantown, West Virginia 26506 USA. E-mail: brockhunts@gmail.com

[2] E-mail addresses: mpvenarsky@crimson.ua.edu

[3] jbenstead@bama.ua.edu

and White 1969, Simon and Benfield 2001, Huntsman et al. 2011). However, how gradients in detrital availability affect the structure and function of cave communities is poorly understood. Only a few investigators have examined such questions. Simon and Benfield (2001) observed a direct link between leaf-litter breakdown and surface-to-cave stream connectivity. They suggested that higher breakdown rates were the result of higher densities of shredding species, facilitated by direct surface connections and consequently higher inputs of organic matter (OM). Leaf-litter breakdown was significantly slower in disconnected streams that had low OM storage and lacked a well developed shredder community (Simon and Benfield 2001). Similarly, biomass and production of a top cave predator, the Tennessee cave salamander (*Gyrinophilus palleucus*) was higher in a cave system with high OM availability than in a nearby system with lower OM (Huntsman et al. 2011). These studies illustrate the potential roles that energy availability plays in cave ecosystem processes.

The quality of detritus varies in any ecosystem. In caves, inputs of detritus typically are heterogeneous and range from very refractory wood to relatively high-quality carrion. The vast majority of studies of detritus processing in cave and surface systems were focused on refractory plant material, which typically dominates inputs. In contrast, breakdown of carrion has received far less attention, and consequently, its importance for food webs may be underestimated (Wilson and Wolkovich 2011). Rat carrion added as part of an experimental manipulation in cave terrestrial environments was colonized by invertebrates faster than leaf litter and supported 4× the invertebrate biomass (Schneider et al. 2011). Detrital breakdown rates were not measured, but the rate at which rat carrion had to be replenished to maintain a constant level was much faster than that of leaf litter.

The studies to date in cave and surface streams illustrate how detrital quantity and quality can influence community structure and ecosystem processes. We examined the links between OM availability, invertebrate community structure, and the breakdown rate of high-quality carrion detritus in 4 cave systems with varying amounts of benthic OM. We chose mouse carrion as a representative high-quality detritus. We consider it an appropriate surrogate for the many vertebrate taxa (cave- and noncave-adapted, including fish, amphibians, reptiles, and mammals) that might enter the detrital food web as carrion (Poulson and Lavoie 2000, Poly 2001). We tested 2 linked hypotheses. First, we hypothesized that cave consumer biomass would be positively related to ambient OM storage because ambient level of detritus

is a factor influencing consumer biomass in cave and surface aquatic ecosystems. Second, we hypothesized that higher consumer biomass would directly influence carrion breakdown rates because consumer biomass affects litter breakdown rates in cave and surface ecosystems.

Methods

Study sites

We chose 4 cave streams in the southeastern USA: 2 in Jackson County, Alabama (Jess Elliot and Tony Sinks), 1 in Madison County, Alabama (Hering), and 1 in Grundy County, Tennessee (Big Mouth). Stream substrates varied among caves. Jess Elliot substrates were composed mainly of silt, fine sediments, and bedrock, whereas Tony Sinks had mostly large cobble. Hering was dominated by sandy substrate, and Big Mouth was composed of large rocks and bedrock. The experimental reaches (length = 70 m for Tony Sinks, Big Mouth, and Hering, and 85 m for Jess Elliot) were pool habitats in the dark zone of each cave. Average areas of the experimental reaches over the course of the study were 251 ± 5 m^2 in Jess Elliot, 328 ± 6 m^2 in Tony Sinks, 374 ± 6 m^2 in Hering, and 282 ± 3 m^2 in Big Mouth. Crayfish assemblages were similar among caves, but vertebrate taxa differed slightly. All 4 caves were inhabited by the obligate cave crayfish *Orconectes australis* and the facultative cave crayfish *Cambarus tenebrosus*. Three of the 4 caves (all except Hering) had populations of the Tennessee cave salamander *Gyrinophilus palleucus*. The southern cave fish *Typhlichthys subterraneus* occurred in 2 of the 4 caves (Big Mouth and Hering), and the mottled sculpin (*Cottus bairdi*), a surface species, was observed in Hering.

Carrion breakdown rate

We used juvenile mice, *Mus musculus* (2.8–7.4 g wet mass; www.rodentpro.com) as the carrion type. We constructed coarse-mesh carrion packs by wrapping individual mice in bird netting (1-cm mesh), and we used zip-ties to attach an individual to the inside of a 10×10-cm mesh pack (1-cm mesh). We used bird netting for coarse-mesh packs to assist in carrion retention while allowing macroconsumer (e.g., crayfish) access. We constructed fine-mesh packs with 500-μm mesh, but we did not use the bird netting. On 10 April 2010, we placed 5 sand bags in each cave stream (10 m apart). We attached 10 carrion packs (5 coarse-mesh and 5 fine-mesh) to each sand bag with nylon string at 1-m intervals (total = 50 mice/cave). On days 5, 12, 19, 28, and 36, we removed 1 fine- and 1 coarse-mesh pack from each sand bag ($n = 10$ packs cave^{-1}

d^{-1}, $n = 40$ packs/d). We transported carrion packs to the laboratory on ice and processed them the next day. In the laboratory, we rinsed each mouse over a 250-µm sieve to remove invertebrates, which were preserved in 5% buffered formalin. We identified invertebrates to the lowest possible taxonomic level with keys in Thorp and Covich (2001) and Merritt et al. (2008).

We estimated initial dry mass (DM) and ash-free dry mass (AFDM) of each mouse as follows. We thawed 5 mice of varying size classes and blotted them dry with paper towels. Mice were weighed (wet mass), dried at 60°C for 1 wk and reweighed to obtain DM. We regressed wet mass against DM to obtain the linear equation: $y = 0.372x - 0.296$ ($R^2 = 0.99$). We then combusted mice at 500°C for 12 h in a muffle furnace and weighed them to obtain AFDM. We regressed DM against AFDM to obtain the linear equation: $y = 0.929x - 0.010$ ($R^2 = 0.99$). We calculated carrion breakdown rate (k, d^{-1}) for each cave by regressing ln(% AFDM remaining + 1) against sampling date.

Dissolved nutrient sampling

We sampled on 6 primary sampling dates, with 2 consecutive days per primary sampling date. For example, the 1st sampling period included 3 and 4 April 2010. On the 1st day of each primary sampling period, we filtered water samples from each stream through glass-fiber filters and froze them until analysis. We collected water samples for NH_4^+-N, NO_3^--N, total dissolved N (TDN), soluble reactive P (SRP), and dissolved organic C (DOC) analyses ($n = 5$ for each analyte). We used the orthophthaldialdehyde fluorometric method to measure NH_4^+-N (Holmes et al. 1999, as modified by Taylor et al. 2007). We used the ascorbic acid method to measure SRP (Murphy and Riley 1962). We used a Shimadzu TOC analyzer (Shimadzu, Columbia, Maryland) to measure DOC and TDN and ion chromatography (ICS 2000 Ion Chromatograph; Dionex, Sunnyvale, California; APHA 2005) to measure NO_3^--N. We measured discharge in each primary sampling period with a Marsh–McBirney velocity meter (Marsh–McBirney, Frederick, Maryland). Stream velocity was too low to measure with the Marsh–McBirney meter in Jess Elliot and Big Mouth caves, so we were unable to estimate discharge. We used data loggers (Solinst Barologger, Georgetown, Ontario) to record water temperature every 30 min in each cave.

Invertebrate biomass

We estimated crayfish biomass on each primary sampling date, beginning 3 April 2010, by scanning each reach 3 times and collecting all crayfish encountered with aquarium dip nets. We measured ocular carapace lengths (±1 mm) with calipers and released all crayfish at their point of capture. We converted measurements to AFDM with ocular carapace length–mass regressions for the 2 crayfish species encountered during our study (*C. tenebrosus*: g AFDM = 0.000006 ocular carapace length $[mm]^{3.693}$, $R^2 = 0.98$; *O. australis*: g AFDM = 0.00003 ocular carapace length $[mm]^{3.175}$, $R^2 = 0.96$; MPV, unpublished data). We estimated DM of all other macroinvertebrates with linear regression equations developed by Leeper and Taylor (1998), Benke et al. (1999), Lemke and Benke (2004), and A. D. Huryn (University of Alabama, unpublished data).

OM storage

We estimated benthic OM on 4 April 2010. In a previous study, no seasonal pattern in benthic OM was found in Tony Sinks, Big Mouth, or Jess Elliot (MPV, unpublished data). We used a 400-cm² corer ($n = 10$ in each cave) to collect 2 random samples around each sand bag in each cave stream. We collected OM samples to a depth of 4 cm or bedrock, depending on which was reached first. We collected all large fragments of OM (e.g., large pieces of wood) from the corer first. Then we disturbed the substrate and swept a 250-µm mesh net through the corer 10 times to collect the remaining OM. We pooled all OM for each sample, dried it at 60°C, and combusted it at 500°C to determine AFDM.

Data analysis

We used 1-way analysis of variance (ANOVA) and a Bonferroni post hoc analysis to compare benthic OM among cave streams. We used a 2-way ANOVA and a Bonferroni post hoc analysis to examine the effect of cave site and mesh size on carrion breakdown rates. We used linear regression to test for relationships between benthic OM and invertebrate biomass (in carrion packs), crayfish biomass and carrion breakdown rates among caves, and the influence of invertebrate and crayfish biomass on carrion breakdown rates.

We used multivariate techniques to investigate differences among cave invertebrate communities sampled from carrion packs. We ran analysis of similarities (ANOSIM), nonmetric multidimensional scaling (NMDS), and similarity percentages (SIMPER) in the PRIMER software package (version 6; Plymouth Marine Labs, Plymouth, UK; Clarke and Warwick 2001). We used log($x + 1$)-transformed biomass data from fine-mesh packs (few coarse-mesh packs in Hering and Big Mouth had carrion remaining upon

TABLE 1.   Daily means (SE) for abiotic characteristics of the 4 cave streams in northern Alabama and southern Tennessee, USA. Discharge was too low to measure in Big Mouth or Jess Elliot. DO = dissolved O_2, TDN = total dissolved N, SRP = soluble reactive P, DOC = dissolved organic C.

Variable	Tony Sinks	Big Mouth	Hering	Jess Elliot
Temperature (°C)	12.7 (0.04)	13.0 (0.07)	13.3 (0.06)	13.5 (0.01)
Discharge (m^3/s)	0.11 (0.05)	–	0.43 (0.15)	–
DO (mg/L)	9.13 (0.23)	8.74 (1.86)	9.85 (0.07)	9.39 (0.53)
NH_4^+-N (μg/L)	3 (1)	8 (2)	2 (0)	3 (1)
NO_3^--N (μg/L)	302 (26)	308 (16)	432 (62)	310 (78)
TDN (μg/L)	312 (21)	370 (35)	464 (41)	376 (73)
SRP (μg/L)	18 (1)	18 (2)	22 (4)	21 (1)
DOC (mg/L)	2.6 (0.6)	3.1 (0.8)	2.6 (0.3)	3.2 (0.6)

retrieval) for all multivariate analyses. We assessed differences in community structure among caves with ANOSIM, with cave as the factor. SIMPER analysis enabled us to quantify the % contribution of each taxon to the observed differences in community composition between each pair of caves. We used NMDS to provide a graphical representation of patterns in the invertebrate community data (see Clarke and Warwick 2001 for details of these analyses).

Results

Nutrients

Abiotic characteristics were generally similar among all caves during the study period (Table 1). Nutrient concentrations ranged from 2 to 8 μg/L NH_4^+-N, 302 to 432 μg/L NO_3^--N, 18 to 22 μg/L SRP, 2.6 to 3.2 mg/L DOC, and 312 to 464 μg/L TDN. Discharge could be measured only at Tony Sinks (0.11 ± 0.05 m^3/s) and
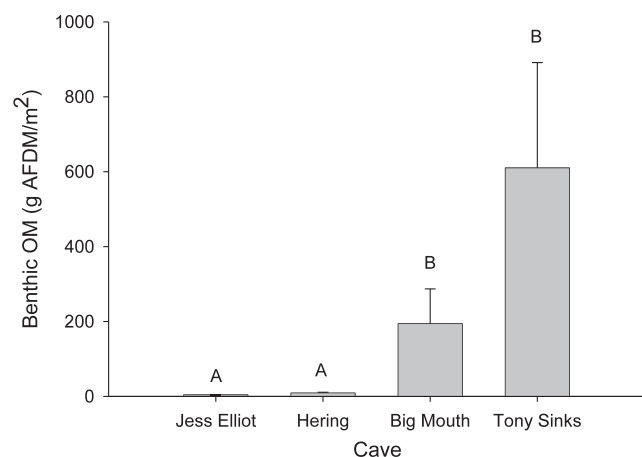

FIG. 1.   Mean (±1 SE) benthic organic matter (OM) in 4 cave streams in northern Alabama and southern Tennessee, USA. SE bars are small but present in Jess Elliot and Hering. Bars with the same letter are not significantly different. AFDM = ash-free dry mass.
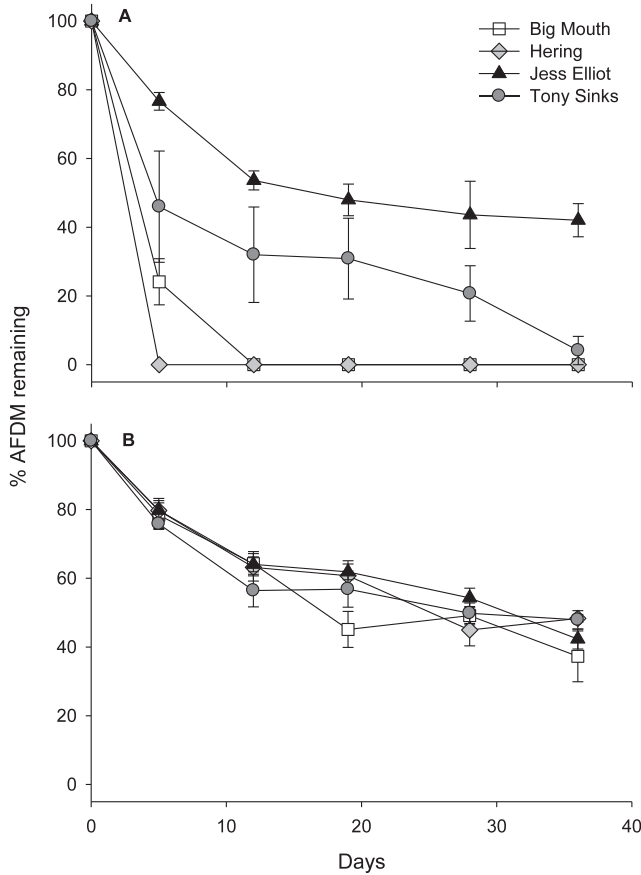
Hering (0.43 ± 0.15 m^3/s). Water temperature was constant in each cave. The highest (13.5 ± 0.01°C) and lowest (12.7 ± 0.04°C) daily average temperatures were recorded in Jess Elliot and Tony Sinks, respectively.

OM

Average benthic OM varied significantly among the cave streams. Tony Sinks had the highest benthic OM and Jess Elliot had the lowest (Fig. 1). Tony Sinks and Big Mouth had significantly higher amounts of benthic OM than Jess Elliot and Hering (F = 15.67, $p < 0.05$). Large standard errors in Big Mouth and Tony Sinks indicated that OM was patchily distributed in these caves, whereas the very small standard error bars in Hering and Jess Elliot showed that OM was consistently low in these caves (Fig. 1).

Carrion breakdown rate

Carrion breakdown rates in both fine- and coarse-mesh packs fit an exponential relationship (Fig. 2A, B). Percent remaining AFDM in coarse-mesh packs at the end of the study was lowest in Hering (0 ± 0%) and highest in Jess Elliot (42.0 ± 4.8%; Fig. 2A). Percent remaining AFDM in fine-mesh packs was highest in Hering (48.3 ± 1.1%) and lowest in Big Mouth (37.3 ± 7.4%; Fig. 2B). Breakdown rates in coarse-mesh packs were fastest in Hering and slowest in Jess Elliot, and breakdown rates in fine-mesh packs were fastest in Big Mouth and slowest in Tony Sinks (Table 2). Breakdown rates differed significantly between fine- and coarse-mesh packs in all caves except Jess Elliot (Table 2). Breakdown rates in coarse-mesh packs were significantly lower in Jess Elliot than in all other caves, whereas breakdown rates in fine-mesh packs were similar among all caves (Table 2). Breakdown rates in coarse-mesh packs were lowest in caves at both ends of the benthic OM spectrum (Fig. 3).

Cave	Fine-mesh (k, d^{-1})	Coarse-mesh (k, d^{-1})
Tony Sinks[a]	0.0081 (0.0003)[A]	0.1397 (0.0623)[B]
Big Mouth[a]	0.0118 (0.0014)[A]	0.4976 (0.1064)[B]
Hering[a]	0.0098 (0.0014)[A]	0.9230 (0.0000)[B]
Jess Elliot[b]	0.0093 (0.0006)[A]	0.0247 (0.0053)[A]

dominated biomass estimates. The lowest total biomass was found in Jess Elliot (0.45 ± 0.06 mg DM/pack), where the community was dominated by Tanypodinae chironomids (0.26 mg DM/pack).

The differences among cave invertebrate communities were reflected by the ANOSIM (indicated by the relatively large R-statistic = 0.43, $p = 0.001$) and can be seen in the NMDS plot (Fig. 4). Tony Sinks was distinguished from the other 3 caves by its high isopod biomass. Jess Elliot differed from the other caves because of relatively high Tanypodinae biomass, whereas high non-Tanypodinae biomass separated Big Mouth and Hering from the other 2 caves (SIMPER analysis).

Invertebrate biomass/pack and OM storage were significantly related (fine-mesh invertebrate biomass only; $R^2 = 0.84$, $p = 0.05$), but invertebrate biomass and carrion breakdown rate were not significantly

Fig. 2. Mean (±1 SE) mass loss of mouse carrion in 4 cave streams in northern Alabama and southern Tennessee, USA in coarse- (A) and fine-mesh (B) packs. SE bars are small but present in Big Mouth and Hering. AFDM = ash-free dry mass.

Invertebrate colonization of carrion

Biomass (excluding crayfish) and taxonomic structure (biomass differences were based on all carrion packs that had carrion remaining on retrieval date) of the macroinvertebrate community that colonized carrion differed among caves. The highest mean total biomass encountered over the duration of the study occurred in Tony Sinks (7.2 ± 1.42 mg DM/pack; Table 3). In this cave, isopods had the highest biomass (5.46 mg DM/pack), followed by *Gammarus* amphipods (1.86 mg DM/pack). The cave with the next highest biomass estimates was Hering, in which only 1.49 ± 0.49 mg DM were found in carrion packs. The dominant taxon by biomass in Hering cave was non-Tanypodinae chironomids (1.45 mg DM/pack). The cave with the 3rd highest biomass was Big Mouth (1.06 ± 0.52 mg DM/pack). Community composition in Big Mouth was similar to that in Hering, in that non-Tanypodinae chironomids (0.91 mg DM/pack)
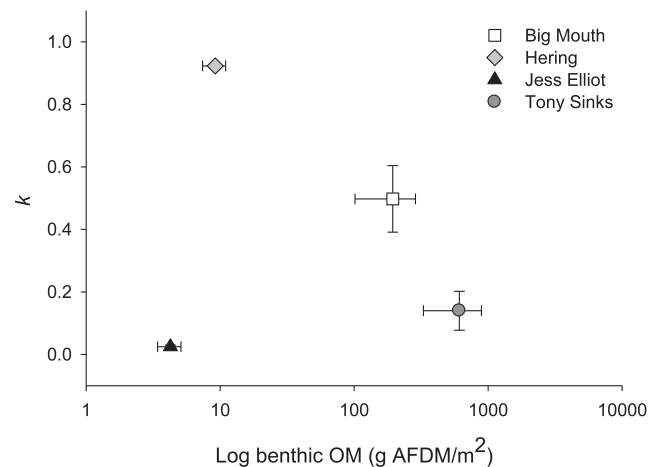

Fig. 3. Regression of benthic organic matter (OM) vs carrion breakdown rates (k, d^{-1}) in coarse-mesh packs in 4 cave streams in northern Alabama and southern Tennessee, USA. SE bars are small but present in Jess Elliot and Hering. AFDM = ash-free dry mass.

TABLE 3. Mean (SE) biomass (mg dry mass/pack) of invertebrates found in coarse- and fine-mesh carrion packs placed in 4 cave streams in northern Alabama and southern Tennessee, USA. Values are based only on packs that contained carrion upon retrieval (Tony Sinks, $n = 42$; Big Mouth, $n = 30$; Hering, $n = 25$; Jess Elliot, $n = 50$).

Taxon	Tony Sinks	Big Mouth	Hering	Jess Elliot
Amphipoda				
Gammarus	1.86 (0.51)	–	–	–
Crangonyx	0.14 (0.13)	0.03 (0.03)	–	–
Chironomidae				
Non-Tanypodinae	0.79 (0.24)	0.91 (0.51)	1.45 (0.49)	0.07 (0.01)
Tanypodinae	0.10 (0.03)	0.02 (0.02)	0.00 (0.00)	0.26 (0.04)
Cyclopoida	0.00 (0.00)	–	–	–
Ephemeroptera				
Ephemerellidae	0.01 (0.01)	–	–	–
Leptophlebiidae	0.01 (0.01)	–	–	–
Isopoda				
Caecidotea	0.00 (0.00)	0.10 (0.04)	0.04 (0.04)	0.05 (0.01)
Lirceus	5.46 (1.40)	–	–	0.03 (0.00)
Nematoda	0.00 (0.00)	–	–	–
Oligochaeta	0.47 (0.30)	–	–	–
Ostracoda	0.00 (0.00)	–	–	–
Plecoptera				
Leuctra	0.03 (0.02)	–	–	–
Trichoptera				
Lepidostomatidae	0.11 (0.08)	–	–	0.04 (0.01)
Total	7.23 (1.42)	1.06 (0.52)	1.49 (0.49)	0.45 (0.06)

related (fine-mesh carrion breakdown and fine-mesh invertebrate biomass only; $R^2 = 0.19$, $p = 0.32$).

Average crayfish biomass was greatest in Hering (70.9 mg AFDM/m^2) and lowest in Jess Elliot (6.4 mg AFDM/m^2). In Hering and Tony Sinks caves, *C. tenebrosus* contributed most crayfish biomass (Table 4),

whereas *O. australis* dominated crayfish biomass estimates in Big Mouth and Jess Elliot caves (Table 4). Hering and Big Mouth caves contained significantly
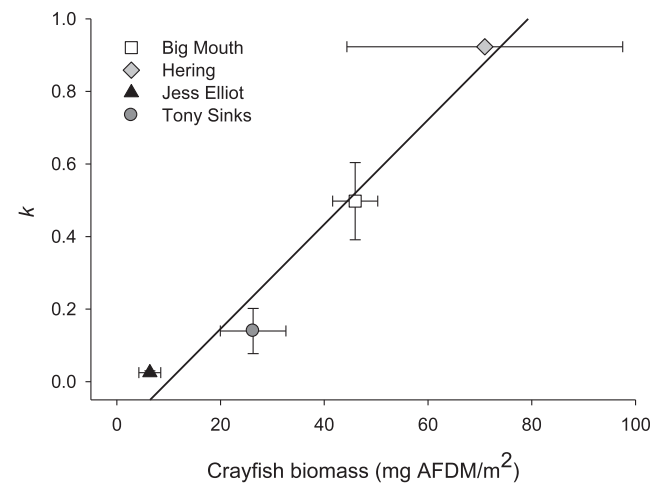

FIG. 4. Nonmetric multidimensional scaling (NMDS) ordination plot based on log($x + 1$)-transformed invertebrate biomass in fine-mesh carrion packs from 4 cave streams in northern Alabama and southern Tennessee, USA.

FIG. 5. Regression of mean (± 1 SE) crayfish biomass vs mean carrion breakdown rate (k, d^{-1}) in coarse-mesh packs in 4 cave streams in northern Alabama and southern Tennessee, USA. SE bars for breakdown rate are small but present in Jess Elliot and Hering. The fitted line is a linear relationship ($y = 0.014x - 0.142$, $p = 0.02$, $R^2 = 0.98$).

TABLE 4. Mean (SE) biomass and density estimates for *Orconectes australis* and *Cambarus tenebrosus* crayfishes in 4 cave streams in northern Alabama and southern Tennessee, USA. Estimates are based on each sampling period and are corrected for stream area (mg ash-free dry mass/m^2 and individuals/m^2). Values with the same letter are not significantly different.

| | *O. australis* | | *C. tenebrosus* | | Total | |
Cave	Biomass	Density	Biomass	Density	Biomass	Density
Tony Sinks	1.4 (0.4)	0.0049 (0.0014)	25.4 (6.2)	0.0106 (0.0028)	26.8 (6.3)[B]	0.0155 (0.0031)
Big Mouth	29.8 (3.4)	0.1058 (0.0102)	16.1 (3.7)	0.0066 (0.0009)	46.0 (4.4)[A]	0.1125 (0.0101)
Hering	5.6 (1.6)	0.0117 (0.0032)	65.3 (25.4)	0.0127 (0.0044)	70.9 (26.6)[A]	0.0244 (0.0073)
Jess Elliot	6.3 (2.1)	0.0157 (0.0046)	0.1 (0.1)	0.0006 (0.0006)	6.4 (2.1)[B]	0.0162 (0.0047)

more crayfish biomass than Tony Sinks or Jess Elliot ($F = 4.76$, $p < 0.05$; Table 4). No significant relationship was detected between crayfish biomass and benthic OM, but crayfish biomass and carrion breakdown rate were strongly related in coarse-mesh packs ($R^2 = 0.98$, $p = 0.02$; Fig. 5).

Discussion

Absence of photosynthetic activity makes use of detritus the dominant energetic pathway in cave ecosystems. In addition, low connectivity with surface environments typically restricts detrital inputs to many cave systems and can limit biological productivity. Carrion is a frequently ignored element of the detrital pathway (Wilson and Wolkovich 2011), but can be a significant and high-quality component of detrital inputs in caves, freshwater streams of the Pacific northwest, oligotrophic lakes, and deep-sea ecosystems (Bilby et al. 1998, Jones et al. 1998, Wipfli et al. 1998, Janssen et al. 2000, Premke et al. 2003, 2010, Chidami and Amyot 2008, Schneider et al. 2011). We hypothesized that caves with relatively high amounts of total OM would support higher biomass of consumers. We also hypothesized that higher consumer biomass would directly influence carrion breakdown rates.

We found some support for our 1st hypothesis. Invertebrate biomass in fine-mesh packs was related to benthic OM across the 4 caves, a result suggesting that the production of small invertebrates may be limited by energy resources in the cave systems we studied. However, crayfish dominated total invertebrate biomass, and their biomass was not related to benthic OM across the 4 cave systems. Support for our 2nd hypothesis was found in the positive relationship between carrion breakdown rates and crayfish biomass and in differences in carrion breakdown rates between fine- and coarse-mesh packs (in all caves except Jess Elliot). Fine mesh did not prevent smaller invertebrates, such as early instars of Chironomidae, from colonizing carrion, but it excluded crayfish. The important role of macroconsumers in carrion process-

ing has been observed in previous studies. For example, breakdown rates of rainbow trout (*Oncorhynchus mykiss*) carcasses were faster when rainbow trout carcasses were not placed in fine-mesh packs (Minshall et al. 1991, Fenoglio et al. 2010). Crayfish have been observed near carrion packs in many studies (Parmenter and Lamarra 1991, Garman 1992, Schneider 1998), an observation suggesting that these omnivores may greatly influence carrion breakdown rates in the ecosystems they inhabit. However, to our knowledge, our study is the first in which the relationship between crayfish biomass and carrion breakdown rates has been quantified in any ecosystem.

Resource availability is a dominant factor controlling ecosystem functions, including consumer secondary production and detrital breakdown rate (Wallace et al. 1997, Simon and Benfield 2001, Eggert and Wallace 2003). In a few studies in caves, resource availability was a key driver of ecosystem function (Simon and Benfield 2001, Schneider et al. 2011), but carrion breakdown rates did not follow a simple relationship with OM storage in our study. The caves with the highest (Tony Sinks) and lowest (Jess Elliot) amount of benthic OM had the slowest carrion breakdown rates, results suggesting that different mechanisms may control community structure and ecosystem function at opposite ends of the OM-storage spectrum. When OM inputs are too low to support high consumer biomass, rare and patchily distributed resources can be found and used only slowly. This fact might explain the slow breakdown rates in Jess Elliot cave, where crayfish biomass was lowest and carrion breakdown rates did not differ significantly between coarse- and fine-mesh carrion packs. The pattern observed at the high end of the OM input gradient (i.e., Tony Sinks) is more difficult to explain. In our study, carrion breakdown rates could be predicted from crayfish biomass alone, a result suggesting that breakdown efficiency by crayfish was constant across the 4 cave systems. Thus, why we found no positive relationship between total OM storage and crayfish biomass is an

important question. Total crayfish biomass was almost 3× higher in Hering cave (mean OM storage = 9.20 ± 1.80 g AFDM/m^2) than in Tony Sinks (mean OM storage = 610.10 ± 281.16 g AFDM/m^2), a result indicating that total OM storage is a poor predictor of crayfish biomass. In addition to total OM availability, unknown factors (e.g., resource quality, top-down forces, dispersal from surface streams) might be important controls on the success of cave crayfish populations. For example, substrate type greatly influenced crayfish production in the James River (Mitchell and Smock 1991). Substrate type is a potential explanation for the lack of a relationship between crayfish biomass and OM availability in our cave streams. These factors should be studied further because energy limitation is widely accepted as the most likely factor controlling trophic-level biomass and ecological processes in caves (Poulson and White 1969, Simon and Benfield 2001).

Our data invite comparison with those from other systems, including deep-sea areas, where food webs are relatively energy-limited. For example, consumption of tuna (*Thunnus* sp.) carrion was more rapid in less productive than in highly productive areas (Janssen et al. 2000). Janssen et al. (2000) suggested that relatively productive systems may support taxa that need not use rare food patches efficiently because resources are abundant. We found no evidence for resource saturation at the highest-OM site in our study (Tony Sinks). Carrion broke down at a rate that was predictable based on crayfish biomass alone, and this biomass was lower than at sites with less OM. However, cave systems and deep-sea environments are similar in that resources are low and distributed patchily in both habitats. Both environments are home to very efficient scavenging species that use chemosensory strategies to locate and use rare food patches quickly (Jones et al. 1998, Janssen et al. 2000, Premke et al. 2003, Kemp et al. 2006). Crayfish use chemical olfaction to locate carrion resources (Willman et al. 1994). Our results indicate that crayfish play a pivotal role in carrion breakdown in cave systems, and such adaptations probably enhance their competitive advantage in exploiting carrion resources.

The role of carrion and scavengers in food webs is receiving increasing theoretical and experimental attention (Wilson and Wolkovich 2011). Input of carrion and its consumption by facultative scavengers, such as crayfish, may be particularly important in cave food webs because of their donor-controlled dynamics. However, consumption of natural inputs of carrion is difficult to track. Carrion usually disappears rapidly and consequently is observed only rarely in cave streams (BMH and MPV, personal observations). Further experimental work is needed. Studies should include large-scale manipulations that test for whole-system effects of carrion on ecosystems (e.g., Schneider et al. 2011), something our study was not designed to do. Such work probably will illustrate further the potentially important links among carrion, scavenging, and interactions with other consumers and basal resources in caves and in other ecosystems (Wilson and Wolkovich 2011). Experimental carrion work will inform more than foodweb theory. Wilson and Wolkovich (2011) pointed out that scavenging of carrion is likely to interact with future aspects of global change, including climate warming, emerging diseases, and species invasions. For example, effects of white-nose syndrome on bat populations in the eastern USA have drastically modified inputs of carrion to caves, at least in the short term (Frick et al. 2010). Improved understanding of the ecological consequences of such changes is sorely needed.

Cross-system comparisons can complement experimental studies of the role of carrion. Carrion breakdown rates in coarse-mesh packs in caves with high crayfish biomass measured in our study were faster than in almost all systems from which comparable data are available (Table 5). Faster rates were measured only in a study of eastern mosquitofish carrion in the subtropical Florida Everglades, USA (Stevenson and Childers 2004; Table 5). The breakdown rates in Table 5 are from a diverse group of habitats and carrion types, and this diversity complicates comparisons. However, the data suggest that the energy and nutrients bound by carrion are used faster in caves with relatively high amounts of crayfish biomass than in many surface systems. This result may indicate high efficiency of cave communities in exploiting such resources.

In conclusion, use of carrion in resource-limited cave ecosystems may be directly influenced by community structure, specifically crayfish biomass. Benthic OM might have affected carrion breakdown rates indirectly by supporting invertebrate production, but total OM storage did not influence cave ecosystem processes in predictable ways in our study. Community structure, rather than total OM availability, was of overriding importance in predicting carrion breakdown rates. We found no simple relationship between total OM storage and consumer biomass, an outcome suggesting that other factors also are important controls on trophic-level biomass in cave ecosystems. The fate and role of carrion in cave ecosystems, including the consequences of increased inputs linked to mortality from newly emerging bat disease (Frick et al. 2010, Wilson and

Table 5. Published breakdown rates (k, d^{-1}) for different carrion types in various aquatic habitats. Breakdown rates are ranked from fastest to slowest.

Taxon	k	Habitat	Mesh Size	Citation
Eastern mosquitofish (*Gambusia holbrooki*)	1.7700	Wetland (summer)	1-mm mesh	Stevenson and Childers (2004)
Eastern mosquitofish (*G. holbrooki*)	1.3400	Wetland	1-mm mesh	Stevenson and Childers (2004)
House mouse (*Mus musculus*)	**0.9230**	**Cave stream: high crayfish biomass**	**10-mm mesh**	**This study**
Larval spotted salamander (*Ambystoma maculatum*)	0.7580	Woodland pond	1.5-mm mesh	Regester and Whiles (2006)
Egg clutches of *A. maculatum*	0.0750	Woodland pond	5-mm mesh	Regester and Whiles (2006)
Rainbow trout (*Oncorhynchus mykiss*)	0.0610	Marsh	1-mm mesh	Parmenter and Lamarra (1991)
Pintail duck (*Anas acuta*)	0.0580	Marsh	1-mm mesh	Parmenter and Lamarra (1991)
Rainbow trout (*O. mykiss*)	0.0570	Stream	10-mm mesh	Fenoglio et al. (2005)
Rainbow trout (*O. mykiss*)	0.0479	Stream (summer)	Nylon string tether	Minshall et al. (1991)
Pink salmon (*Oncorhynchus gorbuscha*)	0.0330	Stream	50-mm mesh	Chaloner et al. (2002)
Alewife (*Alosa pseudoharengus*)	0.0290[b]	Pond microcosm	No mesh	Durbin et al. (1979)
Bluegill (*Lepomis macrochirus*)	0.0260[b]	Lake	Perforated plastic containers	Kitchell et al. (1975)
House mouse (*Mus musculus*)	**0.0247**	**Cave stream: low crayfish biomass**	**10-mm mesh**	**This study**
Rainbow trout (*O. mykiss*)	0.0210	Stream	10-mm mesh	Fenoglio et al. (2010)
Rainbow trout (*O. mykiss*)	0.0174	Boreal lake at ~1 m depth	Tethered	Chidami and Amyot (2008)
Rainbow trout (*O. mykiss*)	0.0170	Stream	0.25-mm mesh	Fenoglio et al. (2010)
Rainbow trout (*O. mykiss*)	0.0155	Stream (winter/spring)	Nylon tether	Minshall et al. (1991)
Pink salmon (*O. gorbuscha*)	0.0100[b]	Stream microcosm	Monofilament tether	Wipfli et al. (1998)
House mouse (*M. musculus*)	**0.0097[a]**	**Cave stream**	**0.5-mm mesh**	**This study**
Rainbow trout (*O. mykiss*)	0.0004	Boreal lake at ~11 m depth	Tethered	Chidami and Amyot (2008)

[a] Mean of all breakdown rates from the study
[b] Values calculated by Regester and Whiles (2006) from data in the cited study

Wolkovich 2011), are likely to be linked tightly to the structure of the scavenger communities. Predicting the structure of cave communities from resource level alone probably is too simplistic. Such predictions could be improved by considering other factors, such as hydrology and the dispersal of organisms, particularly from surface source populations.

Acknowledgements

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