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Quantitative food web analysis supports the energy-limitation hypothesis in cave stream ecosystems

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Abstract Energy limitation has long been the primary assumption underlying conceptual models of evolutionary and ecological processes in cave ecosystems. However, the prediction that cave communities are actually energy-limited in the sense that constituent populations are consuming all or most of their resource supply is untested. We assessed the energy-limitation hypothesis in three cave streams in north-eastern Alabama (USA) by combining measurements of animal production, demand, and resource supplies (detritus, primarily decomposing wood particles). Comparisons of animal consumption and detritus supply rates in each cave showed that all, or nearly all, available detritus was required to support macroinvertebrate production. Furthermore, only a small amount of macroinvertebrate prey production remained to support other predatory taxa (i.e., cave fish and

salamanders) after accounting for crayfish consumption. Placing the energy demands of a cave community within the context of resource supply rates provided quantitative support for the energy-limitation hypothesis, confirming the mechanism (limited energy surpluses) that likely influences the evolutionary processes and population dynamics that shape cave communities. Detritus-based surface ecosystems often have large detrital surpluses. Thus, cave ecosystems, which show minimal surpluses, occupy the extreme oligotrophic end of the spectrum of detritus-based food webs.

Keywords Bioenergetics · Detritus · Bottom-up control · Trophic basis of production · Subterranean

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Introduction

The goal of many ecological studies has been to gain an understanding of how resources (bottom-up) and consumers (top-down) interact to control species biomass, productivity, and food web complexity (Power 1992; Menge 2000; Dyer and Letourneau 2003; Gripenberg and Roslin 2007). Studies of food webs based on herbivory have clarified how bottom-up and top-down interactions influence community structure (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981; Power 1992), and subsequent efforts have explored how these processes also shape detritus-based ecosystems (Wallace et al. 1999; Chen and Wise 1999; Rosemond et al. 2001; Moore et al. 2004). Although different types of detrital ecosystems have been studied (e.g., forested streams and soil habitats), few have quantitatively explored the extreme oligotrophic end of the detritus-supply spectrum found in cave ecosystems.

Cave ecosystems represent an endpoint along several ecological continua. Lack of light prevents photosynthesis, causing nearly all cave communities (except those based on

chemolithoautotrophy; see Sarbu 2001; Engel et al. 2004; Roach et al. 2011) to be completely reliant on inputs of detritus from surface ecosystems (i.e., 100 % donor-controlled; sensu Polis and Strong 1996; Poulson and Lavoie 2001; Simon et al. 2007). Limited surface connectivity reduces detritus supply to caves and detritus quality is generally low due to biological processing along transport pathways (i.e., through soil horizons, epikarst, and aquifers). Collectively, the low quantity and quality of detritus in caves underlies the assumption that these ecosystems are energy-limited (Hüppop 2001).

The bottom-up constraint of energy limitation has been identified as the principal evolutionary force in the development of many traits common to most obligate cave species, including low metabolic rates, increased starvation resistance, and K-selected life-history traits (e.g., long life span, slow growth rate, and reduced fecundity; see Hüppop 2001; Venarsky et al. 2012a). Similarly, the low levels of species diversity and abundance often reported for caves have been attributed to limited energy availability (Hüppop 2001).

Despite a long history of research in caves, studies have only recently begun to assess how energy availability influences cave population and community dynamics (see Datry et al. 2005; Cooney and Simon 2009; Huntsman et al. 2011a; Schneider et al. 2011). Collectively, these studies suggest that detritus quality and quantity limit consumer productivity (i.e., microbes and animals). Although these studies each address the energy-limitation hypothesis, they have not placed the energetic and material demands (e.g., consumption and growth) of cave communities within the context of ecosystem energetics (e.g., resource supply and consumption rates). Consequently, it is not known if cave communities are actually energy-limited in the sense that their constituent populations are consuming all or a large proportion of the available resources.

We tested the energy-limitation hypothesis in three cave streams receiving varying supplies of detritus. We predicted that biomass and production of benthic macroinvertebrates, including the omnivorous cave-obligate southern cave crayfish *Orconectes australis*, would be positively correlated with detritus and prey biomass. Second, we used the trophic basis of production approach (sensu Benke and Wallace 1980) to compare the energetic demands (i.e., consumption and growth) of animals to detritus supply rates and prey production. Guided by the energy-limitation hypothesis, we predicted that animal energetic demands would be equivalent to detrital supply rates and prey production in each cave.

Materials and methods

Study sites

Three cave streams in northeastern Alabama (Jackson County, USA) were chosen for study. These streams drain

Hering, Limrock, and Tony Sinks caves. Stream reaches ranging from 327 to 1,202 m in length (1,298–5,323 m²) and containing a series of riffle and pool habitats with sand, gravel, and bedrock substrata were sampled in each cave. Mean daily water temperature, measured from June 2007 to July 2011 within these stream reaches, was 13 °C and showed little annual variation (SD of average daily water temperature: ± 1 °C; Venarsky et al. 2012b). All three caves contain populations of *O. australis* and similar assemblages of other macrofauna, including the cavespring crayfish *Cambarus tenebrosus*, a facultative cave-dwelling species, and the Tennessee cave salamander *Gyrinophilus palleucus*, an obligate cave taxon. The southern cavefish (*Typhlichthys subterraneus*) and mottled sculpin (*Cottus bairdii*) occurred only in Limrock and Hering caves. During our 5+ year mark-recapture study (Venarsky et al. 2012a), *O. australis* represented >95 % of the total number of large (i.e., macroscopic) animals encountered on each sampling date.

Unlike Limrock and Hering caves, Tony Sinks Cave has well-developed ceiling fissures, below which are deposits of terrestrial detritus (i.e., dead terrestrial vegetation). Additionally, its recharge area contains several vertical and horizontal entrances that intersect intermittent stream channels that supply detritus during floods. Large deposits of detritus were not observed in either Limrock or Hering caves. Although bats (eastern pipistrelle, *Perimyotis subflavus*) occurred in each cave, their populations were small (e.g., <20 individuals observed per visit), and accumulations of guano were never evident.

Detritus and non-crayfish macroinvertebrates

On each of four dates (March, July, and November 2009 as well as February 2010), 15 samples of benthic detritus (primarily decomposing wood particles) and non-crayfish macroinvertebrates were collected from each cave using a 22.5-cm diameter corer. The core was inserted into the stream bottom, large detritus was removed, and the substrate was disturbed to a maximum depth of 4 cm. Remaining suspended detritus was sampled via ten sweeps of the water column with a 250- μ m mesh net. Samples were returned to the laboratory on ice and processed within 48 h. Processing consisted of rinsing the sample through a 250- μ m sieve followed by the removal and preservation (5 % formalin) of macroinvertebrates. The remaining detritus was dried at 60 °C for ~2 weeks, weighed, combusted at 500 °C for 6 h, and then weighed again to estimate ash-free dry mass (AFDM). Non-crayfish macroinvertebrates were identified to the following levels: family or tribe for insects, family or genus for crustaceans, and class for annelids. Dry mass was estimated using published length–mass relationships (Calow 1975; Culver et al. 1985; Leeper and Taylor 1998; Benke et al. 1999; Lemke and Benke 2009; Doroszuk et al. 2007). Macroinvertebrate dry mass was converted

to AFDM assuming AFDM is 93 % of dry mass (Benke and Wallace 1980). A nonparametric Kruskal–Wallis test in R (R Core Team 2013) was used to examine differences in detritus and non-crayfish macroinvertebrate biomass among caves because transformation could not normalize detrital standing crop to meet the assumptions of parametric statistics.

Crayfish

Sampling for crayfish began in November 2005 in Hering, January 2006 in Limrock, and July 2006 in Tony Sinks caves, and was conducted semi-monthly (conditions permitting) until August 2011. On each visit, study reaches were surveyed by two observers, and all crayfish encountered along each reach were collected using dip-nets. Captured crayfish were marked using both internal tags [Visible Implant Alpha Tags (VIAT), Northwest Marine Technology, Shaw Island, WA, USA] and Visible Implant Elastomer (VIE; Northwest Marine Technology). VIATs are small (1.0×2.5 mm), fluorescent, uniquely numbered tags that were placed beneath the abdominal cuticle. The VIE was injected directly posterior to the VIATs and was used to assess tag loss, which was infrequent. Once an individual was marked, its ocular carapace length (OCL; posterior margin of ocular cavity to posterior center-margin of carapace) was measured (± 0.1 mm) with dial calipers and it was released near the point of capture. OCL was used rather than total carapace length to avoid errors due to damage to the acumen following release (Venarsky et al. 2012b).

Crayfish growth rates

Annual crayfish growth rates (G) were estimated as

$$G = \frac{\ln(W_{\text{fn}}/W_{\text{in}})}{\text{yr}},$$

where W_{fn} is g AFDM upon recapture, W_{in} is g AFDM at initial marking, and yr is years elapsed. Length–AFDM equations for *O. australis* are given in Huntsman et al. (2011b). Since growth increments are “episodic” due to the molting cycle, annual growth increments were only calculated for individuals recaptured over intervals of 350 days or longer to allow for molting to occur between recapture events. For crayfish recaptured multiple times, the annual growth increment was calculated using the recapture date closest to the 350-day minimum (Venarsky et al. 2012b). Annual growth increments were regressed against mean crayfish biomass (g AFDM) to estimate the size-specific annual growth rate.

Crayfish abundance and biomass

We used the POPAN open-population Jolly–Seber formulation in Program MARK to estimate crayfish abundance in

each stream (Schwarz and Arnason 1996). Crayfish abundance was estimated from March 2009 to February 2010 for each population (i.e., the 12-month period during which we quantified benthic detrital and non-crayfish macroinvertebrate biomass). Model parameters of ϕ (apparent survival probability) and β (probability of entrance) were constrained to be either time-variant or constant. We modeled capture probabilities to be time-variant in each model because of high variability in the number of crayfish captured across sampling dates at each site. We used program RELEASE in MARK to assess the fit of our most parameterized model to Cormack–Jolly–Seber (CJS) assumptions. Chi-squared analysis indicated that the most parameterized model (i.e., all parameters time-dependent) for all three sites showed an adequate model fit (Hering $\chi^2 = 17.72$, $p = 0.82$; Limrock $\chi^2 = 15.51$, $p = 0.69$; Tony Sinks $\chi^2 = 17.49$, $p = 0.42$). All models were ranked using Akaike’s information criterion corrected for a small sample size (AICc; Burnham and Anderson 2002), and superpopulation abundance estimates were estimated using model averaging from the candidate model set.

Crayfish abundance was converted to biomass by first distributing the total population size acquired from Program MARK among the observed size classes in a cumulative size–frequency distribution of carapace lengths for each cave. Biomass was then calculated using the geometric mean of each size class. Estimates of abundance and biomass were standardized to area using wetted stream area estimates. To determine if the cumulative size–frequency distribution for each cave was representative of all sampling years, we constructed yearly size–frequency distributions and then compared for annual variability within each cave using pair-wise Kolmogorov–Smirnov (K–S) tests in R (R Core Team 2013).

Crayfish production

Annual crayfish production for each size class was estimated using the following formula:

$$P = G \times \bar{B},$$

where G is a annual instantaneous growth rate (g g^{-1} AFDM year^{-1}) and \bar{B} is a mean biomass (g AFDM m^{-2} ; Hury and Wallace 1987). Uncertainty in both growth rates and biomass were estimated by bootstrapping (Efron and Tibshirani 1993; Benke and Hury 2006).

To estimate \bar{B} , the estimated variance for the population sizes provided by Program MARK was entered into the Normal Distribution function in Microsoft Excel 2010 and 1,000 random population sizes were generated. Each randomly generated population was then distributed among size classes using the cumulative size–frequency distribution.

This approach allowed the calculation of annual production for different year classes, which were then summed to estimate the total annual production. Estimates of P and \bar{B} were compared among caves using pairwise two-sample randomization tests (Manly 1991; Benke and Huryn 2006).

Crayfish diet

Fifteen to 20 specimens of *O. australis* were collected from each cave during November 2012 and flash-frozen in liquid nitrogen for stomach content analysis. We assumed that this single sample of crayfish provided an unbiased assessment of their diet, as previous studies suggest that the number of food types at our study sites is relatively limited and that their availability and diversity (e.g., animal prey taxa) exhibit little annual variation (Venarsky et al. 2012b; Venarsky, unpublished data). The contents of the cardiac and pyloric stomachs were thawed and removed in the laboratory, rinsed on a 100- μm sieve, and filtered onto 25-mm 1.2- μm polycarbonate membrane filters. These filters were placed on microscope slides, dried at 60 °C, and cleared with immersion oil. Random fields on each filter were observed at 40 \times until a minimum of 100 particles was counted. Particles were classified as either detritus or animal tissue. Animal tissue was invariably in the form of chironomid head capsules or crustacean body parts. Because detritus dominated stomach contents, the entire filter was also scanned following the randomized procedure to determine if additional animal particles were present. Stomachs containing only crayfish carapace were presumed to be from newly molted individuals that had recently ingested their own exoskeleton and so were excluded from further analysis.

Stable isotope analyses

Samples of detritus, potential crayfish prey (non-Tanypodinae Chironomidae), and *O. australis* were collected from each cave in November 2012 and transported to the laboratory on ice. Non-Tanypodinae Chironomidae were chosen as a representative primary consumer and prey item because this group was both relatively abundant in the cave streams and prevalent in crayfish stomachs. Samples were lyophilized, ground, and stored at -20 °C until stable isotope analysis (Analytical Chemistry Laboratory, University of Georgia, Athens, GA, USA). We estimated the relative contributions of detritus and animal prey to *O. australis* production by combining $\delta^{15}\text{N}$ and stomach content data in a mixing model (R package SIAR; Parnell et al. 2010; Parnell and Jackson 2011; R Core Team 2013). We did not use $\delta^{13}\text{C}$ data because of uncertain contributions of inorganic carbon from crayfish carapace in our whole-body samples. SIAR uses a Bayesian framework that incorporates uncertainty in all input data, as well as the optional use of prior information,

to produce robust probability distributions of source contributions to biomass production. Our mixing model incorporated uncertainty in the $\delta^{15}\text{N}$ of *O. australis* and two diet categories (non-Tanypodinae Chironomidae larvae and wood, which was used as a proxy for detritus), as well as the variance associated with the % N content of the two diet categories and the category-specific trophic fractionation of N isotopes ($\Delta\delta^{15}\text{N}$). To our knowledge, only two rather disparate estimates of $\Delta\delta^{15}\text{N}$ for crayfish have been published (Rudnick and Resh 2005; Veliscek Carolan et al. 2012). Consequently, we used three different fractionation scenarios to examine the effect of $\Delta\delta^{15}\text{N}$ on SIAR output: $+2.54 \pm 0.11$ ‰ SD for both diet categories (i.e., the mean trophic fractionation value from Vanderklift and Ponsard 2003); $+2.69 \pm 0.11$ and 0.53 ± 0.11 ‰ SD for animal and detritus material, respectively (i.e., the mean values for carnivores and detritivores from Vanderklift and Ponsard 2003); and $+2.62$ to $+3.2$ and 3.72 to $+4.0$ ‰ (± 0.11 SD) for animal and detritus material, respectively [i.e., diet-dependent discrimination factors (DDDFs) for each cave; Caut et al. 2009]. Finally, we corrected the mean (± 1 SD) proportions of detritus and animal material in stomach contents for assimilation using assimilation efficiencies of 0.1 and 0.85, respectively (see Table 1) before entering them as priors in the mixing model run for each cave. Each SIAR run consisted of 500,000 iterations (burn-in of 50,000 iterations) with the output thinned by a factor of 15.

Resource supply and demand

Detritus supply rate ($\text{g AFDM m}^{-2} \text{ year}^{-1}$) and non-crayfish macroinvertebrate production were estimated assuming that (i) detritus and non-crayfish macroinvertebrate biomass did not vary over time, and (ii) resources that were either consumed or lost via downstream export were replaced (i.e., steady-state conditions). These assumptions are reasonable due to the low amount of variation in monthly estimates of detritus and non-crayfish macroinvertebrate biomass reported for caves in the study area (Venarsky et al. 2012a; Venarsky, unpublished data).

Given these assumptions, detritus supply rate was estimated as the product of mean annual detritus biomass and average annual breakdown rate of wood. Wood, rather than leaf, breakdown rates were used to estimate detritus supply rate because few leaves were observed during the processing of core samples. Wood breakdown rates from both surface and cave streams were acquired from Simon and Benfield (2001) ($k = 1.5\text{--}2.4 \text{ year}^{-1}$) and Spänhoff and Meyer (2004) ($k = 0.02\text{--}3.1 \text{ year}^{-1}$). Annual production of crayfish prey (e.g., non-crayfish macroinvertebrates) was estimated by first assuming that ash-free dry mass (AFDM) was 93 % of dry mass and then multiplying AFDM biomass by an annual production:biomass (P:B) relationship

Table 1 Assimilation efficiencies (AE) and net production efficiencies (NPE) for several decapods that were used to estimate resource demand by *Orconectes australis* in Hering, Limrock, and Tony Sinks caves

Habitat	Species	AE	NPE	References
Cave	<i>Orconectes inermis</i>	Leaf material—0.10		Weingartner (1977)
		Chironomid—0.85		
Surface	<i>Panulirus homarus</i> (spiny lobster)		0.43–0.66	Rathinam et al. (2009) (Table 3) ^a
	<i>Procambarus clarkii</i>		0.39–0.74	Gutiérrez-Yurrita and Montes (2001) (Table 2) ^a
	<i>Cherax tenuimanus</i>		0.54–0.81	Villarreal (1991) (Table 4) ^a
	Various (8 crayfish species)		0.09–0.75	Momot (1995) (Table 3)

^a NPE calculated following Benke and Wallace (1980)

of 5 (Benke and Huryn 2006). An annual P:B of 5 was used on the basis of (1) the findings of Benke and Huryn (2006), who examined annual P:Bs for 58 stream communities and found that 54 % had P:Bs <6, 28 % had P:Bs of 6–10, and only 18 % had P:Bs >11, and (2) the expectation that the low quality of detritus available in the cave streams results in relatively slow growth rates (e.g., Ward and Cummins 1979), which would result in low annual P:Bs.

We used the trophic basis of production approach (sensu Benke and Wallace 1980) to estimate resource demand for non-crayfish macroinvertebrates. We assumed that the non-crayfish macroinvertebrate diet consisted solely of detritus. Non-crayfish macroinvertebrate demand for detritus was estimated by dividing macroinvertebrate annual production by the product of assimilation efficiency (AE) and net production efficiency (NPE; Benke and Wallace 1980). Estimates of AE (0.10) and NPE (0.33) for non-crayfish macroinvertebrates were based on literature estimates for aquatic detritivores (Benke and Wallace 1980). For *O. australis*, the relative contributions of detritus and animal prey to production were acquired from the SIAR mixing-model results (1,000 estimates from the output were sampled at random for use in the bootstrapping analysis). Demands for detritus and animal prey were estimated by dividing the proportion of annual production of *O. australis* attributable to each resource by the product of diet-specific (i.e., detritus or macroinvertebrate prey) AE and NPE. Estimates of AE and NPE for crayfish were acquired from the literature for both surface and cave species (Table 1). Because information concerning phenological changes in energetic efficiencies is lacking for crayfish (and rare for macrocrustaceans in general), we assumed that AE and NPE were constant. This assumption is supported by Ross (1982b), who studied the energetics of North Pacific krill (*Euphausia pacifica*) and concluded that AE (of carbon) was not related to age or body mass, and by Ross (1982a, b), who provided data indicating that NPE was similarly unrelated to age and body mass. In the latter case, the NPE contributing to somatic tissue growth of juveniles was not significantly different from the NPE contributing to both growth and reproduction by adults.

Uncertainty in estimates of NPE, detritus standing crop, non-crayfish macroinvertebrate biomass and production, and mean detritus breakdown rates was estimated by bootstrapping (see above). To assess whether resource surpluses existed, the bootstrapped data sets estimating crayfish consumption were subtracted from the bootstrapped data sets for detritus supply rates and non-crayfish macroinvertebrate prey production. To assess the effect on our results of violations of our assumption regarding the annual P:B (i.e., 5) for non-crayfish macroinvertebrates, we conducted a sensitivity analysis of the effect of varying annual P:B (5, 10, 20) on estimates of the trophic basis of production.

Results

Detritus and non-crayfish macroinvertebrate biomass

Detritus standing crop was highest in Tony Sinks Cave (mean = 133; median = 20 g AFDM m⁻²) and lowest in Hering Cave (mean = 22; median = 10 g AFDM m⁻²), but no significant difference was found among caves ($\chi^2 = 4.2$, $df = 2$, $p = 0.12$; Fig. 1). Non-crayfish macroinvertebrate biomass was also highest in Tony Sinks Cave (mean = 346; median = 146 mg AFDM m⁻²) and lowest in Hering Cave (mean = 29; median = 4 mg AFDM m⁻²), but was significantly different among caves ($\chi^2 = 52.5$, $df = 2$, $p < 0.05$; Online Resource 1 of the Electronic supplementary material, ESM; Fig. 1).

Crayfish production

A total of 3,812 crayfish were marked in Hering (919 individuals), Limrock (943), and Tony Sinks (1,950) caves over the course of our 5+ year mark–recapture study. Growth models were constructed using 78 (37 males and 41 females) crayfish in Hering Cave, 112 (47 males and 65 females) crayfish in Limrock Cave, and 97 (46 males and 51 females) crayfish in Tony Sinks Cave. Monthly capture rate was highest in Tony Sinks Cave and lowest in Hering Cave. Recapture

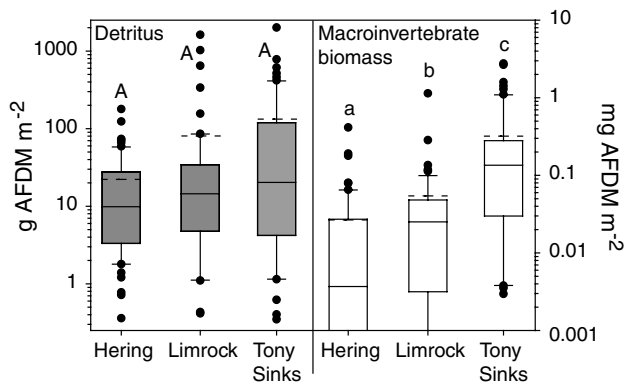


Fig. 1 Box and whisker plot of detritus (left y-axis; $n = 60$ all caves) and macroinvertebrate biomass (right y-axis; $n = 60$ for Hering and Tony Sinks; $n = 58$ for Limrock) in Hering, Limrock, and Tony Sinks caves. Gray boxes are the 25th and 75th percentiles and whiskers are the 5th and 95th percentiles. The dashed and solid lines within each box are the mean and median, respectively. AFDM ash-free dry mass. Significant differences ($p < 0.05$) are indicated by different letters. Note that different letters with different cases do not indicate significant differences, and that a log scale is used

rates for crayfish were highest in Limrock Cave and lowest in Tony Sinks Cave (Table 2). Crayfish abundance was highest in Tony Sinks Cave and lowest in Hering Cave (Table 2; see Online Resource 2 of the ESM for rankings of Cormack–Jolly–Seber mark–recapture models generated in Program MARK). Crayfish biomass, production, and biomass turnover rates (i.e., P:B year⁻¹) were highest in Tony Sinks Cave (Table 2). Size-structured distributions of crayfish were similar among caves and years of the study (K–S test, $p > 0.05$), indicating that the population structure was stable over the 5-year study and did not differ among caves.

Stomach contents and stable isotope analyses

Detritus dominated stomach contents of *O. australis* in all caves (≥ 97 % of particles; Table 3). After correcting for

Table 2 Mean capture rate (range), % crayfish recaptured (range), modeled average superpopulation size (error), biomass (95 % confidence interval), production (95 % confidence interval), and

	Hering	Limrock	Tony Sinks
Capture rate (individuals month ⁻¹)	35 (13–67)	43 (9–90)	71 (28–126)
% Crayfish recaptured (month ⁻¹)	35 (11–60)	39 (8–62)	20 (3–43)
Population size (individuals)	700 (95)	938 (121)	3492 (891)
Biomass (mg AFDM m ⁻²)	70 (51–89) ^A	54 (40–68) ^A	596 (297–895) ^B
Production (mg AFDM m ⁻² year ⁻¹)	20 (14–26) ^a	14 (10–18) ^a	232 (107–357) ^b
Production:biomass (year ⁻¹)	0.28 (0.25–0.31) ^Y	0.27 (0.24–0.30) ^Y	0.39 (0.32–0.46) ^Z

Significant differences among caves are indicated by different letters
AFDM ash-free dry mass

Table 3 Mean (standard error) percent detritus and animal particles found in the stomachs of *Orconectes australis* collected from Hering ($n = 11$), Limrock ($n = 8$), and Tony Sinks ($n = 16$) caves

	Hering	Limrock	Tony Sinks
Crayfish stomachs			
% Detritus	97 (3)	98 (2)	99 (3)
% Animal	3 (3)	2 (2)	1 (3)
$\delta^{15}\text{N}$ (‰)			
Wood	1.1 (0.1)	1.0 (0.1)	0.2 (0.1)
Chironomidae	4.7 (0.3)	4.4 (0.3)	2.8 (0.2)
<i>Orconectes australis</i>	7.1 (0.6)	6.5 (0.6)	4.9 (0.3)

Mean (standard error) natural abundance values of $\delta^{15}\text{N}$ for wood ($n = 3$ all caves), Chironomidae ($n = 3$ all caves), and *Orconectes australis* ($n = 5$ all caves) collected from Hering, Limrock, and Tony Sinks caves

differences in AE between animal prey and detritus, mean proportions of detritus that entered into the SIAR models as a Dirichlet prior distribution ranged between 80 and 92 %. The three caves differed in their $\delta^{15}\text{N}$ values for wood (0.2–1.0 ‰), non-Tanyptodinae Chironomidae (2.8–4.7 ‰), and *O. australis* (4.9–7.1 ‰; see Table 3). Inclusion of priors based on stomach contents greatly constrained the probability distribution functions of detrital contributions (5–95th percentiles of 65–84, 76–91, and 76–92 % in Hering, Limrock, and Tony Sinks Caves, respectively). Choice of trophic fractionation factors had only minimal effects on the estimated contributions of detritus and animal prey to crayfish production. In Hering Cave, mean contributions of detritus were 74–76 % for all three scenarios, while mean contributions of detritus were 84–85 % in Limrock Cave. Only in Tony Sinks Cave did estimates of detritus contribution differ with fractionation estimate: the single (+2.54 ‰) and diet-specific fractionation values (2.69 and 0.53 ‰ for animal prey and detritus, respectively) from Vanderklift and Ponsard (2003) yielded mean values of 83 and 84 %, while use of the DDDF (Caut et al. 2009)

production:biomass (year⁻¹; 95 % confidence interval) of *Orconectes australis* within Hering, Limrock, and Tony Sinks caves

Table 4 Estimates of mean detritus supply rates, macroinvertebrate production, *O. australis* and macroinvertebrate demand, and detritus and macroinvertebrate surplus in Hering, Limrock, and Tony Sinks caves

	Hering	Limrock	Tony Sinks
Detritus supply rate	13 (7–19)	48 (5–91)	79 (27–131)
Macroinvertebrate production	0.13 (0.05–0.21)	0.26 (0.24–0.28)	1.61 (0.9–2.32)
Macroinvertebrate detritus demand	4.03 (1.65–6.41)	8.03 (2.1–13.96)	48.7 (27.18–70.22)
Crayfish detritus demand	0.33 (0.2–0.46)	0.27 (0.18–0.36)	4.32 (1.77–6.87)
Crayfish macroinvertebrate demand	0.01 (0–0.02)	0.01 (0.006–0.014)	0.09 (0–0.18)
Detritus surplus	9 (2–16)	40 (–4 to 84)	26 (–30 to 82)
Macroinvertebrate surplus	0.12 (0.04–0.2)	0.26 (0.06–0.46)	1.51 (0.79–2.23)

All values are g ash-free dry mass m⁻² year⁻¹. Numbers in parentheses are 95 % confidence intervals

increased the estimated mean detrital contribution to 94 %. Based on the generally low effect of trophic fractionation value, we used results from SIAR runs based on the value of +2.54 ‰ for both diet categories in subsequent calculations of resource demand. Using this fractionation estimate, the 95 % credible intervals for detritus contributing to *O. australis* production were 62–86 % in Hering Cave, 73–93 % in Limrock Cave, and 75–94 % in Tony Sinks Cave, with the balance in each cave consisting of animal prey.

Resource supply

The mean wood breakdown rate used to estimate detritus supply was 0.6 year⁻¹ (0.4–0.8 year⁻¹; 95 % CI). Estimates of detritus supply rates were highest for Tony Sinks Cave and lowest for Hering Cave (Table 4). Based on an annual P:B of 5, mean non-crayfish macroinvertebrate production was highest in Tony Sinks Cave and lowest in Hering Cave (Fig. 2a; Table 4). The large amount of spatial variability in resource biomasses translated into relatively wide confidence intervals in resource supply rates (Figs. 1, 2a).

Resource demand

After accounting for total animal demand for detritus, a small surplus was estimated for Hering Cave. Consumer demand in Limrock and Tony Sinks caves was not significantly different from the detritus supply rate (Fig. 2b; Table 4). After accounting for crayfish demand for animal prey, a surplus of prey production was estimated for all caves (Fig. 2b; Table 4). Detritus demand by non-crayfish macroinvertebrates (i.e., potential animal prey) was lowest in Hering Cave and highest in Tony Sinks Cave (Fig. 2a; Table 4). The mean NPE used to estimate energetic demands by *O. australis* was 0.46 (0.38–0.54; 95 % CI). Both detritus and animal prey demand by *O. australis* were lowest in Limrock Cave and highest in Tony Sinks Cave (Fig. 2a; Table 4).

Our results were based on the assumption that non-crayfish macroinvertebrates had an annual P:B of 5. We

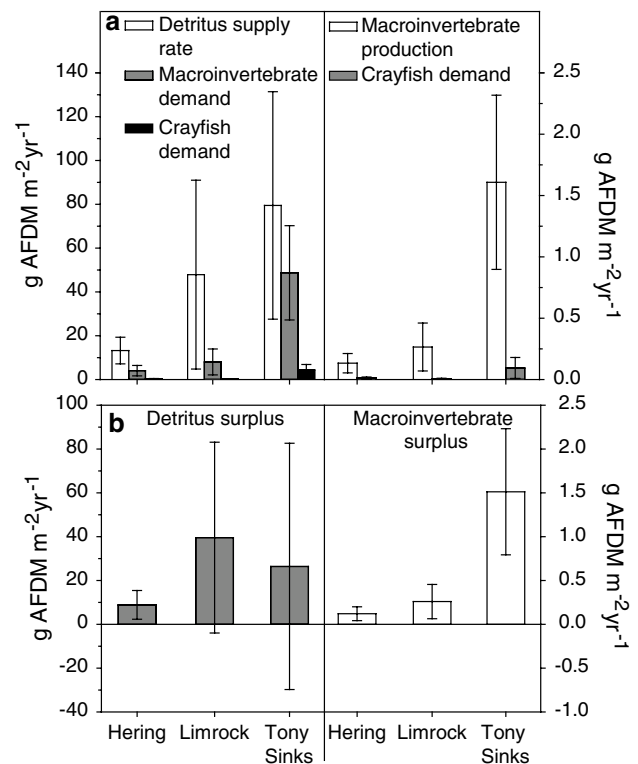


Fig. 2 Detritus supply rate and macroinvertebrate and *Orconectes australis* detritus demand in Hering, Limrock, and Tony Sinks caves (a, left). Macroinvertebrate production and crayfish macroinvertebrate demand in Hering, Limrock, and Tony Sinks caves (a, right). b Detritus (left) and macroinvertebrate (right) surpluses in Hering, Limrock, and Tony Sinks caves. AFDM ash-free dry mass. Bars are 95 % confidence intervals

assessed the effect of violations of this assumption by estimating the trophic basis of production for non-crayfish macroinvertebrates in each cave stream using annual P:Bs of 5, 10, and 20. The results of these analyses indicated that our estimates of resource surpluses were relatively insensitive to variation in non-crayfish macroinvertebrate P:B. Detritus and crayfish prey surpluses in Hering and Limrock

caves, for example, did not significantly differ among annual P:Bs ranging from 5 to 20 (Online Resource 3 in the ESM). Using an annual P:B of 20 for Tony Sinks Cave, however, resulted in detritus surpluses that were significantly lower than those estimated using P:Bs of 5 and 10, and were also not significantly different from zero.

Discussion

The energy-limitation hypothesis and cave ecosystems

Placing the energetic demands of a cave stream community within the context of energy supply rates provided a robust test of the energy-limitation hypothesis because the presence or absence of resource surpluses was quantified. Using this approach, we showed that the cave-stream communities included in this study consumed nearly all available resources on an annual basis. Additionally, after accounting for consumption by crayfish, only a small amount of macroinvertebrate production was apparently available to support the production of other predatory cave taxa, such as cave fish and salamanders. Huntsman et al. (2011b), for example, estimated prey consumption by the cave-obligate Tennessee cave salamander (*Gyrinophilus palleucus*) in Tony Sinks Cave. Consumption of prey by salamanders ($0.45 \text{ g AFDM m}^{-2} \text{ year}^{-1}$; we assumed AFDM is 93 % of dry mass) in this cave, in addition to crayfish consumption, would reduce our estimates of the annual prey surplus by ~33 %, and would cause the surplus of prey to decline to almost zero. The inclusion of estimates of salamander consumption in our trophic basis of production analyses thus suggests that nearly all non-crayfish animal prey production in Tony Sinks Cave is necessary to support production of macropredators. Collectively, our analyses suggest that the carrying capacity for animal productivity has been reached in Tony Sinks Cave and likely in each of the two additional cave stream communities studied, which have similar macrofaunal communities.

Although our data provide strong support for the energy-limitation hypothesis in caves, it is important to consider the effects of several potentially important energy flow-paths that were not included in our conceptual model of cave-stream energetics, such as cyclical coprophagy by macroinvertebrates (e.g., Strayer 1988; Grimm 1988), subsidies in the form of potential invertebrate prey drifting into the caves from surface streams (Huntsman et al. 2011a; Venarsky et al. 2012b) and, perhaps most significantly, the production of particulate organic matter in the form of fungal and bacterial biomass via the uptake of dissolved organic carbon (DOC). Microbial production resulting from the assimilation of DOC is an important component of both cave and surface stream food webs (Hall and

Meyer 1998; Hall et al. 2000; Simon et al. 2003). Studies of cave streams, however, indicate that rates of bacterial production are relatively low (Hendricks 1996; Cooney and Simon 2009), presumably due to the low DOC concentrations characterizing karst aquifers ($1\text{--}3 \text{ mg L}^{-1}$; Strayer 1994; Simon et al. 2003). Extrapolating these estimates (Hendricks 1996; Cooney and Simon 2009) to an annual timescale suggests that $\sim 3 \text{ g C m}^{-2} \text{ year}^{-1}$ could potentially be provided to animals via bacterial production, which represents approximately 4–19 % of detritus inputs. Thus, including additional bacterial carbon would not significantly increase our estimates of detritus surplus. However, bacterial production and associated exopolymers could be relatively important to some animal taxa within caves because they provide high-quality (i.e., high assimilation efficiency) food (Hall and Meyer 1998).

Energy-limitation and cave species evolution and community structure

The energy-limitation hypothesis forms the historical foundation for conceptual models of evolutionary and ecological processes in cave ecosystems (Culver 1982; Culver et al. 1995; Poulson and Lavoie 2001; Hüppop 2001). Previous studies have tested this hypothesis by tracking changes in microbial or animal abundance or shifts in the biomass of cave communities. Our analyses go beyond a simple test of the energy-limitation hypothesis because they explore limitation from an explicitly energetic perspective. These analyses quantified the mechanism (e.g., limited energetic surplus) that likely influences both the evolution and maintenance of the K-selected life histories and reduced metabolic rates found in many obligate cave species.

Previous studies have reported shifts in cave community structure following organic pollution episodes in various types of groundwater ecosystems (e.g., karst and gravel aquifers; Sinton 1984; Smith et al. 1986; Madsen et al. 1991; Notenboom et al. 1994; Simon and Buikema 1997; Sket 1999, 2005; Wood et al. 2002; Culver and Pipan 2009). In particular, many of these studies reported that obligate cave species were replaced by facultative taxa adapted to energy-rich surface environments. The facultative taxa quickly exploit the additional resources and out-compete obligate cave species. Our study provides support for this potential mechanism. The combination of evolutionary adaptations (K-selected life histories) and minimal energetic surpluses allows obligate cave species to compete in low-energy cave environments, even if resident animal biomass is dominated by facultative taxa. However, when energetic surpluses increase, facultative taxa appear more capable of monopolizing the additional resources for growth and reproduction than do cave-obligate taxa. Thus,

minimal energetic surpluses appear to be important in structuring cave communities because changes in organic matter quantity or quality can induce significant shifts in cave community structure.

Cave ecosystems offer the opportunity to exploit “natural manipulations” of key ecosystem drivers—light and detritus supply—that are otherwise difficult to alter experimentally at large spatial scales. As cave streams represent the extreme oligotrophic end of the detritus-supply spectrum, the quantitative analysis of their energetic pathways provides a useful context for understanding ecosystem processes occurring in their surface counterparts. The severely energy-limited food webs assessed in our study, for example, essentially processed the entire detritus supply on an annual basis. Similarly, detritus availability in detritus-rich surface streams limits the productivity of both prey and predators; the latter trophic group can consume nearly all prey production in these ecosystems (Dobson and Hildrew 1992; Wallace et al. 1999; Hall et al. 2000, 2001). Nevertheless, detritus supply typically exceeds consumer demand in surface ecosystems regardless of apparent resource limitations (Smock and Roeding 1986; Wallace et al. 1999; Stagliano and Whiles 2002; Cross et al. 2007; Hall et al. 2000, 2001), indicating that the almost complete consumption of detritus documented for the severely energy-limited cave streams we studied represents an unusually high level of consumer efficiency.

Although support for the energy-limitation hypothesis in the caves used in this study is compelling, the generalization of our conclusions is limited due to a regional focus and the small number of caves studied. Small energy surpluses may not be a universal characteristic of all cave ecosystems. Some caves receive large seasonal inputs of energy-rich bat guano, which support high species diversity and levels of abundance (Culver and Pipan 2009). Additionally, basal resources are not donor-controlled in every cave ecosystem because populations of chemolithoautotrophic bacteria are significant primary producers in some caves (Sarbu 2001; Tobler et al. 2006; Engel 2007; Porter et al. 2009). Applying an energetic approach to assess resource supply and demand in a greater diversity of cave ecosystems will provide a more robust assessment of the role that energy limitation plays in the evolutionary and ecological processes that shape cave communities.

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