Effects of organic matter availability on the life history and production of a top vertebrate predator (Plethodontidae: *Gyrinophilus palleucus*) in two cave streams

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SUMMARY

1. Surface ecosystems provide the primary source of organic matter to many cave communities. Variation in the strength of connectivity to the surface suggests that some caves may be more resource-limited than others. To test this, we examined diet, prey availability and production of an obligate cave salamander *Gyrinophilus palleucus* (Plethodontidae), a top predator, in two south-eastern U.S.A. caves with different levels of organic matter (Tony Sinks cave, 165 g AFDM m^{-2}; Bluff River cave, 62 g AFDM m^{-2}).
2. We quantified density, biomass, growth rate, production and diet of *G. palleucus* monthly for 21 months. Diet composition, differences in prey communities and seasonal patterns in prey consumption were also analysed.
3. Salamander density, biomass and secondary production were significantly greater in the high organic matter cave (0.10 m^{-2}, 0.18 g AFDM m^{-2}, 0.12 g AFDM m^{-2} year^{-1}) than in the low organic matter cave (0.03 m^{-2}, 0.03 g AFDM m^{-2}, 0.01 g AFDM m^{-2} year^{-1}). Although growth rates were not statistically different between the two cave salamander populations, low recaptures probably influenced this result.
4. Isopoda prey were the major contributor to salamander production in the high organic matter cave (69%). In the low organic matter cave, production was provided by isopods (41%) and oligochaetes (20%). The lower number of prey taxa contributing to salamander production in the high organic matter cave suggests the ability to forage more selectively.
5. The differences in foraging strategy, density, biomass and secondary production were probably related to differences in the strength of surface connectivity, which controls organic matter supply. Links between basal resource level and top predator performance show the importance of bottom-up limitation in the food webs of caves and other detritus-based ecosystems.

Keywords: bottom-up control, resource limitation, salamander, secondary production, trophic basis of production

Introduction

The relative strength of bottom-up and top-down control of community structure has been long debated

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(Power, 1992). Bottom-up control suggests that the rate of supply of basal resources (e.g. nutrients and detritus) determines community structure (Polis & Strong, 1996). Top-down control, on the other hand, is the direct or indirect control of community structure by consumers (Polis & Strong, 1996). It appears, however, that most systems are ultimately controlled by bottom-up rather than top-down forces (especially on a community

scale), because top-down control requires very specific conditions (Polis, 1999), such as predators that are remarkably efficient at obtaining prey relative to resource levels (Power, 1992). Factors such as parallel trophic linkages (web-like structure rather than chain-like), competition for resources other than food (e.g. shelter) and the ability of prey to evade predation all suggest that conditions necessary for top-down pressure are relatively rare (Power, 1992).

In freshwater ecosystems, and especially in detritus-based headwater streams, bottom-up control is thought to be the primary factor influencing community structure. Detrital manipulations have certainly supported this view. For example, experimental exclusion of leaf litter in a surface stream resulted in decreased abundance, biomass and production of the benthic community (Wallace *et al.*, 1997, 1999; Hall, Wallace & Eggert, 2000; Johnson & Wallace, 2005). Furthermore, the experimental addition of nutrients (nitrogen and phosphorus) to surface streams has increased microbial decomposition rates, which ultimately have stimulated invertebrate growth, abundance, biomass and production (Cross *et al.*, 2006; Suberkropp *et al.*, 2010).

The studies above examined the factors controlling community dynamics in surface streams. A few studies (e.g. Simon & Benfield, 2001; Simon, Benfield & Macko, 2003), however, have quantified the factors affecting community structure in aquatic environments belowground. Because of the lack of sunlight, photosynthetic organisms cannot directly support cave stream food webs (Poulson & Lavoie, 2000). Therefore, with a few exceptions, consumers in these systems rely on organic matter transported from the surface. Caves with low connectivity with surface systems (e.g. those lacking sinkholes or large bat colonies) thus contain low quantities of organic matter (Hüppop, 2000; Graening & Brown, 2003). These features have led to the assumption that cave streams are energy-limited systems with bottom-up control. It has been suggested that such energy limitation is an evolutionary pressure driving a suite of morphological, physiological and behavioural adaptations (e.g. reduced pigmentation, endurance to starvation and lowered metabolic rates) that are common to most obligate cave-dwelling organisms (stygobionts; Hüppop, 2000).

One organism that shows adaptations to cave ecosystems is the Tennessee cave salamander (*Gyrinophilus palleucus* McCrady), a top predator in many south-eastern U.S.A. cave food webs. For example, *G. palleucus* has a metabolic rate that is low compared to its surface-dwelling sister species *Gyrinophilus porphyriticus* (Green), which is suggested to be an adaptation to the energy limitation of cave ecosystems (Cooper & Cooper, 1968). With the exception of studies that have documented its generalist feeding habits (Lazell & Brandon, 1962; Brandon, 1967; Miller & Niemiller, 2007), however, little other information on the ecology of *G. palleucus* is available. No studies have compared populations of *G. palleucus* between caves with different resource availability.

The goal of this study was to determine the effect of resource level (quantity of organic matter) on the life history of *G. palleucus*. We tested a series of predictions about the role of organic matter in its feeding ecology and population attributes. We predicted (i) that caves with high levels of organic matter would have more abundant prey populations than caves with low levels of organic matter, (ii) salamanders in caves with high organic matter would exhibit a more specialised diet than those in caves with low organic matter, (iii) salamanders in caves with high organic matter will have higher growth rates than those in caves with low organic matter, and (iv) salamander secondary production will be higher in caves with high organic matter and be based upon fewer prey species than salamander production in caves with low organic matter.

Methods

Study sites

Two cave systems in north-eastern Alabama, U.S.A., were chosen for this study: Tony Sinks and Bluff River caves (Jackson County, Alabama). Tony Sinks was approximately 40 km south-west of Bluff River. Each cave contains a stream with alternating riffle-pool habitats and substrata ranging from limestone bedrock to fine gravel, sand and silt. The study reach in both caves was defined by all accessible, continuous stream passage. The stream reach in Tony Sinks cave (2094 m²) was smaller than the study reach in Bluff River cave (4132 m²). Stream area measurements were only taken during low flow because access to cave streams during high flows was too dangerous. These caves were chosen for study on the basis of

preliminary observations indicating higher amounts of organic matter stored in the Tony Sinks cave stream (which has a sink-hole at its entrance) compared to the Bluff River cave stream (no sink-hole). The pleth-odontid salamanders *Eurycea cirrigera* (Green) and *G. palleucus* are common in both Bluff River and Tony Sinks. *Gyrinophilus porphyriticus*, *Desmognathus fuscus* (Green) and *Pseudotriton ruber* (Latreille) were observed only in Tony Sinks. All salamanders (besides *G. palleucus*) were most abundant near the entrances of both caves, while rarely seen deeper in the cave (where the study reaches were located). Both caves supported two crayfish species. The facultative cave species *Cambarus tenebrosus* (Hay) occurred in both caves. The obligate cave species *Cambarus hamulatus* (Cope) occurred only in Bluff River, and the obligate cave crayfish *Orconectes australis* (Rhoades) occurred only in Tony Sinks.

Organic matter storage and water nutrient concentrations

Organic matter was estimated from 15 random samples from both cave streams during March 2009, July 2009, November 2009 and Feb 2010 using a 22.5-cm diameter corer, a hand-powered guzzler pump and an aquarium net fitted with 250-μm mesh. Organic matter was collected to a depth of 4 cm or until bedrock was reached and placed in plastic bags and returned to the laboratory where it was subsequently dried to a constant mass at 60 °C (~2 weeks), weighed to estimate dry mass (DM) and then ashed at 500 °C for 6 h to estimate ash mass. Ash-free dry mass (AFDM) was estimated by subtracting ash mass from DM.

Water for nutrient analysis was collected during March 2009, July 2009 and Nov 2009. On each date, a total of 14 water samples were collected at the downstream end of each stream reach. Water samples were filtered through a glass-fibre filter, placed in acid rinsed Nalgene® bottles and frozen. Water samples were later analysed for NH_4-N, NO_3-N and soluble reactive phosphorus (SRP). Ammonium was measured using the orthophthaldialdehyde fluorometric (OPA) method (Holmes *et al.*, 1999 as modified by Taylor *et al.*, 2007). SRP was measured using the ascorbic acid method (Murphy & Riley, 1962), and nitrate was measured using ion chromatography (Dionex ICS 2000 Ion Chromatograph; APHA, 2005). Water temperature was recorded every 30 min in each

cave using data loggers (Solinst BaroLogger, George-town, ON, Canada).

Salamander abundance, density and biomass

Gyrinophilus palleucus was sampled in Bluff River from 30 November 2008 to 15 November 2010, and in Tony Sinks from 4 January 2009 to 1 September 2010. Salamanders were sampled at monthly intervals by surveying on foot and capturing all salamanders found with a dip net. Sampling was confined to only the wetted channel because metamorphosed *G. palleucus* are rare in nature and no salamanders were found out of water during this study. Captured salamanders were anesthetised using tricaine methyl-sulfonate (MS-222, 1 g L^{-1} of water with 1 g L^{-1} $NaHCO_3$ added as a pH buffer; Kinkead, Lanham & Montanucci, 2006). Once unresponsive to touch, salamanders were measured from snout to the posterior angle of the vent (SVL), weighed (±0.1 g) and marked with alphanumeric tags (1.0 × 2.5 mm; North-west Marine Technology, Shaw Island, WA, U.S.A.). Tags were injected into the base of the tail with a small amount of visible implant elastomer (Northwest Marine Technology) to prevent tag loss and to assist in identification (Kinkead *et al.*, 2006; Spickler *et al.*, 2006). Salamanders were allowed to recover in containers of fresh stream water and were then returned to the point of capture.

Salamander abundance (total number per study area) was estimated using Program MARK (White & Burnham, 1999) and mark–recapture data on monthly intervals from January 2009 to January 2010. This estimate was based on the assumption of a closed population. Although our monthly sampling interval violates the assumption of strict closure (because of the potential for migration and immigration during the 30-day release period), this violation could be relaxed as *G. palleucus* is a relatively sedentary organism (Miller & Niemiller, 2007). Each model produced during our analysis was ranked based on Akaike's information criterion (AIC), where the lowest AIC value was the best fit model for our data (Akaike, 1973; Burnham & Anderson, 2002). Salamander abundance was converted to density by dividing by the wetted stream area. Population densities were combined with estimates of size distribution and converted to g AFDM m^{-2} using the following length–mass relationship:

$$M = a\mathrm{SVL}^b \tag{1}$$

where M is the body mass for a salamander (g AFDM individual^{-1}), a is the y-intercept, SVL is the snout-vent length (cm), and b is the slope of the relationship.

Prey consumption

Stomach contents were collected from anesthetised salamanders (January 2009 to April 2010) using gastric lavage (Cecala, Price & Dorcas, 2007). Stomach contents were preserved in 10% formalin. The density of potential prey was estimated using invertebrates that were separated from organic matter samples (see '*Organic matter storage and water nutrient concentrations*' above) and preserved in 10% formalin. Invertebrates removed from stomachs and benthic samples were identified to the lowest taxonomic level possible (Thorp & Covich, 2001; Merritt, Cummins & Berg, 2008), and their lengths were measured to the nearest 0.5 mm using 1-mm transparent graph paper placed on a dissecting microscope stage. Dry mass was estimated using regression equations from Leeper & Taylor (1998), Benke *et al.* (1999), Lemke & Benke (2004), and A. D. Huryn (unpubl. data).

A relativised electivity index (E^*) was used to compare the proportion of prey taxa in the stomachs of salamanders to the proportion of prey taxa available (Vanderploeg & Scavia, 1979). Values for E^* range from 1 to −1, where positive numbers indicate utilisation of a prey taxon and negative numbers indicate a lack of use of that taxon. A value of 0 indicates neither positive nor negative utilisation (i.e. neutral use). Although generally suitable for analysing the diets of predators consuming multiple prey taxa, this index is less reliable in cases where large numbers of prey taxa are available or when some taxa are rare in either the stomachs or the environment (Lechowicz, 1982). Consequently, only prey taxa that accounted for ≥1% of stomach content or benthos were entered into the analyses (see Parker, 1994). Because neither crayfish nor salamander populations were adequately sampled with the benthic corer and were found in stomach contents, these taxa were also excluded from electivity analyses. All benthic samples from Tony Sinks cave were taken the same date that salamander stomach contents were collected. In Bluff River cave, all benthic samples were taken within 15 days of the collection of salamander stomach contents.

Body condition and growth rates

A salamander body condition index (BCI) was calculated monthly (May 2009 to July 2010) using the following equation:

$$\mathrm{BCI} = \frac{\text{Body mass}}{a\mathrm{SVL}^b} \tag{2}$$

where body mass is the wet mass of a salamander, SVL is its snout-vent length and a and b are the intercept (a) and slope (b) of a length–wet mass relationship derived for salamanders for each cave. Salamander growth rates were estimated as the difference between the initial SVL and the SVL of recaptured individuals divided by days elapsed. These estimates were then multiplied by 30 to produce a monthly growth estimate. An equation describing size-specific growth rate (SGR) was derived by regressing monthly growth rates against mean SVL. This equation formed the basis of population-specific growth models that provided estimates of size-at-age. The regression models were seeded with an individual with a SVL of 10 mm (estimate based on the smallest individual of *G. palleucus* found during the study) and iterated over monthly intervals until the size of the largest individuals was attained. This procedure allowed the estimation of the expected size of salamanders for different year-classes (size-at-age) as well as an estimate of longevity. Confidence limits (95% CI) for these estimates were provided by a bootstrapping technique (Efron & Tibshirani, 1993; Whitmore & Huryn, 1999).

Snout-vent lengths at each age class were converted to ash-free dry mass (AFDM) using population-specific length–mass relationships:

$$\text{Mass (g AFDM individual}^{-1}) = 0.0022\,\mathrm{SVL}^{3.0}$$
$$(r^2 = 0.98) \tag{3}$$

where SVL is snout-vent length in cm.

To estimate annual instantaneous growth rate, G (g AFDM year^{-1}), the following equation was used:

$$G = \ln(W_{\mathrm{fn}}) - \ln(W_{\mathrm{in}}) \tag{4}$$

where W_{in} is the initial AFDM and W_{fn} is the final AFDM of a salamander of age class n.

Secondary production and trophic basis of production

Annual salamander production was estimated using the instantaneous growth method following Whitmore & Huryn (1999) with the exception of the treatment of population density. In our case, the estimate of variance provided by Program MARK was used to construct a normal distribution from which population estimates were randomly drawn and entered into the matrix of bootstrapped variables. This approach allowed the calculation of annual production for different year-classes that was then summed to estimate total annual production. Production attributed to the consumption of different prey taxa was estimated following Benke & Wallace (1980). The relative amount of production contributed by each prey taxon (F_i) was calculated as follows:

$$F_i = (G_i \times AE_i \times NPE) \tag{5}$$

where G_i is the proportion of prey taxon i consumed, AE_i is the assimilation efficiency of prey taxon i, and NPE_i is the net production efficiency of the salamander.

Salamander assimilation efficiencies (AE) were calculated using Conover's (1966) equation:

$$AE = \frac{F - E}{(1 - E) \times F} \times 100 \tag{6}$$

where F is the AFDM to DM ratio of ingested food and E is the AFDM to DM ratio of the faeces. Fifteen salamanders of varying sizes were placed in separate containers, housed in a dark, constant-temperature cabinet at 13 °C (±1 °C) and fed a known biomass of chironomid larvae. Prey and faecal matter were dried at 60 °C to estimate DM and were then ashed at 500 °C to estimate ash mass. AFDM (nearest 0.1 μg) was estimated by subtracting ash mass from DM. A reliable NPE was not obtained in this study, so a published value of 48% for *Plethodon cinereus* (Green) was used (Fitzpatrick, 1973).

Statistical analyses

A two-way ANOVA was used to compare square root transformed basal resource levels (g AFDM organic matter m^{-2}) between caves and seasonal variability among sampling dates. A one-way ANOVA was used to compare log +1 transformed prey biomass (both as the benthos and as stomach contents) between salamander populations. Linear regression was used to account for potential gape-limitation in salamander foraging. Biomass of stomach contents were log transformed (only salamanders that had prey items in stomachs were included) and regressed against salamander SVL in both caves. Multivariate techniques were used to compare stomach contents between salamander populations and to test for seasonal patterns in prey consumption. Analysis of similarities (ANOSIM), non-metric multidimensional scaling (NMDS) and similarity percentages (SIMPER) were all conducted using the PRIMER software package (Version 6; Plymouth Marine Labs, Plymouth, U.K.; Clarke & Warwick, 2001). Log +1 transformed prey biomass estimates were used for these analyses. Full details of each analysis are outlined in Bixby *et al.* (2009).

Results

Organic matter storage and water nutrient concentration

The annual average of organic matter in Tony Sinks cave (165.1 ± 33.1 g AFDM m^{-2}) was significantly greater than that in Bluff River (61.8 ± 20.0 g AFDM m^{-2}, $P = 0.04$, $F = 4.18$, Fig. 1). However, there was no evidence of a significant seasonal effect on organic matter availability ($P = 0.58$, $F = 0.72$). There was little difference between the two cave streams in nutrient concentrations (Table 1). There was also little difference in stream temperature between the two caves (Table 1). Temperatures in both cave streams were relatively constant for the duration of the study.

Salamander density and biomass

The area of stream reaches sampled ranged from 2094 m^2 in Tony Sinks cave to 4132 m^2 in Bluff River cave. More salamanders were tagged in Tony Sinks than Bluff River (111 and 82, respectively), and there were fewer recaptures in Tony Sinks than Bluff River (15 and 25, respectively). Consequently, mark–recapture estimates showed that salamander densities were significantly higher in Tony Sinks cave (0.10 individuals m^{-2}; Table 2) compared with Bluff River
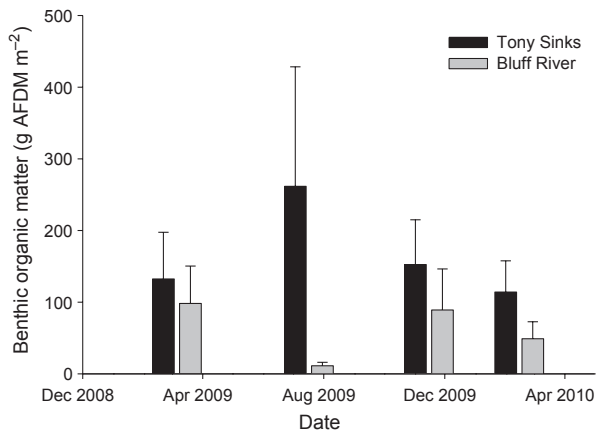
Fig. 1 Estimated benthic organic matter storage for each sampling date in Tony Sinks cave (TS) and Bluff River cave (BR), northeastern Alabama, U.S.A. Data are means ± 1 SE. Ash-free dry mass is abbreviated as AFDM.

Table 1 Abiotic characteristics of Tony Sinks and Bluff River caves in north-eastern, Alabama, U.S.A. Temperature data are daily means and nutrient data are means across three sampling dates (two in Tony Sinks for NH_4^+-N)

	Tony Sinks	Bluff River
Temperature (°C)	13.55 (0.03)	13.82 (0.03)
NH_4^+-N ($\mu g\ L^{-1}$)	15.3 (14.0)	7.0 (4.2)
NO_3^--N ($\mu g\ L^{-1}$)	292 (37)	268 (64)
SRP ($\mu g\ L^{-1}$)	6.3 (2.8)	6.7 (1.5)

Standard errors are in parentheses. SRP, soluble reactive phosphorus.

cave (0.03 individuals m^{-2}; Table 2) based on a lack of overlap in 95% confidence intervals. Also, the lack of overlap in 95% confidence intervals indicated that salamander population biomass was significantly higher in Tony Sinks cave (0.18 g AFDM m^{-2}; Table 2) than in Bluff River cave (0.03 g AFDM m^{-2}; Table 2).

Salamander prey consumption and prey biomass

Potential prey biomass was significantly higher in Tony Sinks cave (435.6 ± 97.6 mg DM m^{-2}) compared to Bluff River cave (111.6 ± 20.3 mg DM m^{-2}, $P = 0.001$, $F = 11.67$, Table 3). This difference was paralleled by differences in the stomach contents of the two salamander populations. Salamanders in Tony Sinks cave had higher prey abundances and biomass per stomach ($n = 5.7 ± 1.2$ items stomach^{-1}, 8.4 ± 2.3 mg dry mass

Table 2 Population size, salamander density, mean annual biomass, mean annual production and the ratio of production to biomass (P/B) of salamanders from Tony Sinks and Bluff River caves, north-eastern Alabama, U.S.A. Mean annual production and biomass estimates are in grams ash-free dry mass (g AFDM)

	Tony Sinks	Bluff River
Population size	215 (128–302)	109 (77–141)
Salamander density (individuals m^{-2})*	0.10 (0.06–0.14)	0.03 (0.02–0.03)
Mean annual biomass (g AFDM m^{-2})*	0.18 (0.14–0.22)	0.03 (0.02–0.03)
Mean annual production (g AFDM m^{-2} year^{-1})*	0.12 (0.09–0.16)	0.01 (0.00–0.02)
P/B	0.66 (0.54–0.78)	0.40 (0.13–0.67)

Upper and lower bounds of the 95% confidence intervals are in parentheses. Significant differences between caves are indicated by '*', which are based on lack of overlap in 95% confidence intervals.

stomach^{-1}) than Bluff River ($n = 2.8 ± 0.5$ items stomach^{-1}, 3.7 ± 2.3 mg DM stomach^{-1}), although these differences were not significant ($P = 0.34$, $F = 1.25$, Table 4). There was also no evidence of a relationship between salamander SVL and biomass of gut contents in either the Tony Sinks ($P = 0.62$, $R^2 = 0.005$, d.f. = 54) or Bluff River salamander population ($P = 0.77$, $R^2 = 0.001$, d.f. = 45), suggesting that gape-limitation did not influence differences in foraging activity between salamander sizes in either cave.

Mean prey biomass per stomach in the Tony Sinks population was highest during January–April (Fig. 2a). Mean BCI generally followed this pattern with BCI being highest early in the year (Fig. 2b). Similar patterns were observed for the salamander population in Bluff River (Fig. 2c,d). Prey biomass consumed was dominated by *Lirceus* (Isopoda) in Tony Sinks (5.5 ± 2.0 mg DM stomach^{-1}) and *Caecidotea* (Isopoda) in Bluff River (1.6 ± 0.5 mg DM stomach^{-1}; Table 4). The next highest contributors to prey biomass in both caves were oligochaetes and larvae of leptophlebiid mayflies (Table 4).

ANOSIM indicated no significant differences between taxonomic composition of either salamander stomach contents or the benthos from the two caves (R-statistic 0.019 and 0.081, respectively). ANOSIM indicated a significant seasonal pattern of prey consumption only in Bluff River cave (ANOSIM R-statistic = 0.52, Fig. 3). SIMPER analysis suggested that the first major grouping between January and February 2010 was driven primarily by a high abundance of oligochaetes and the occurrence of crane fly

Taxon	BR		TS	
	Mean abundance	Mean biomass	Mean abundance	Mean biomass
Nematoda	9.2 (3.4)	0.0 (0.0)	23.7 (3.7)	0.0 (0.0)
Bivalvia	3.9 (3.9)	0.1 (0.1)	52.7 (36.2)	2.5 (1.9)
Oligochaeta	38.7 (27.8)	1.1 (0.7)	164.0 (103.0)	6.5 (2.1)
Mites	0.5 (0.5)	0.01 (0.0)	8.2 (3.9)	0.2 (0.1)
Ephemeroptera				
Ephemerellidae	10.6 (6.9)	1.7 (1.2)	45.0 (4.0)	13.5 (5.1)
Leptophlebiidae	99.2 (71.1)	6.4 (6.0)	105.9 (37.0)	8.8 (6.4)
Plecoptera				
Capniidae	–	–	2.4 (2.4)	3.4 (3.4)
Chloroperlidae	0.5 (0.5)	0.02 (0.02)	3.9 (2.7)	18.9 (18.9)
Leuctridae	–	–	0.48 (0.48)	5.14 (5.14)
Nemouridae	1.0 (1.0)	0.6 (0.6)	–	–
Coleoptera				
Elmidae	–	–	1.0 (1.0)	1.3 (1.3)
Diptera				
Chironomidae pupae	24.8 (4.5)	6.8 (6.8)	4.5 (2.25)	0.2 (0.2)
Non-Tanypodinae	209.4 (56.3)	77.8 (25.3)	1102.8 (347.9)	331.3 (86.3)
Tanypodinae	37.7 (9.2)	5.7 (1.9)	105.9 (32.8)	16.0 (3.5)
Empididae	–	–	0.48 (0.48)	0.04 (0.04)
Tipulidae	–	–	1.0 (1.0)	1.1 (0.6)
Ostracoda	4.4 (1.8)	0.1 (0.1)	39.7 (11.3)	0.5 (0.2)
Cyclopoida	36.3 (22.6)	0.1 (0.04)	84.6 (41.0)	0.2 (0.1)
Harpacticoida	3.9 (1.8)	0.01 (0.01)	35.8 (11.0)	0.1 (0.02)
Amphipoda				
Crangonyx	2.9 (2.3)	0.8 (0.8)	1.0 (1.0)	0.1 (0.1)
Gammarus	–	–	3.4 (1.5)	2.9 (1.4)
Isopoda				
Caecidotea	16.9 (4.4)	11.2 (4.3)	6.8 (3.4)	3.1 (2.7)
Lirceus	–	–	120.9 (51.5)	41.8 (22.5)
Total	400.9 (64.9)[A]	111.6 (20.3)[C]	1594.9 (423.4)[B]	435.6 (97.6)[D]

Table 3 Mean abundance (individuals m^{-2}) and mean biomass (mg dry mass m^{-2}) of invertebrates in benthic core samples from Bluff River (BR) and Tony Sinks (TS) caves, north-eastern Alabama, U.S.A.

Standard errors are in parentheses. One-way analysis of variance was used to test for significant differences between caves. Different superscript letters indicate significant differences between the two caves in either mean total abundance or mean total biomass at an α-level of 0.05.

(Diptera: Tipulidae) larvae. A second February–March 2009 grouping was driven by leptophlebiid mayfly nymphs.

Nine prey taxa were analysed for E^* in Bluff River and only eight prey taxa in Tony Sinks (Fig. 4). Positive E^* values for four prey taxa and negative values for five were shown for salamanders from Bluff River cave (Fig. 4). The analysis of salamanders from Tony Sinks cave indicated positive E^* values for two prey categories while six were negative (Fig. 4).

Secondary production and trophic basis of production

Growth rates of salamanders in Tony Sinks cave were higher than those in Bluff River, although this differ- ence was not significant based on a conservative comparison of 95% CIs (Fig. 5). There were few recaptures of salamanders in both Bluff River cave ($n = 25$, two of which were recaptured twice) and Tony Sinks cave ($n = 15$, two of which were cap- tured twice), which resulted in low statistical power (Fig. 5).

Mean annual production of salamanders was sig- nificantly higher in Tony Sinks cave (0.12 g AFDM m^{-2} year^{-1}; Table 2) than Bluff River cave (0.01 g AFDM m^{-2} year^{-1}; Table 2) based on lack of overlap in 95% CIs. Turnover rates (production/biomass, P/B) were also higher for salamanders in Tony Sinks cave (0.66; Table 2) than Bluff River cave (0.40; Table 2), although not significant based on 95% CIs.

Table 4 Mean abundance (individuals stomach^{-1}) and mean biomass (mg dry mass stomach^{-1}) of invertebrates in stomach contents from Bluff River (BR) and Tony Sinks (TS) *Gyrinophilus palleucus* populations, north-eastern Alabama, U.S.A.

Taxon	BR		TS	
	Mean abundance	Mean biomass	Mean abundance	Mean biomass
Nematoda	0.01 (0.01)	0.0 (0.0)	–	–
Oligochaeta	0.5 (0.3)	1.3 (0.6)	0.7 (0.2)	1.8 (0.8)
Hirudinea	–	–	0.1 (0.03)	0.0 (0.0)
Ephemeroptera				
Ephemerellidae	0.1 (0.03)	0.1 (0.04)	0.1 (0.04)	0.2 (0.04)
Leptophlebiidae	0.4 (0.1)	0.3 (0.1)	0.2 (0.1)	0.4 (0.3)
Plecoptera				
Leuctridae	0.03 (0.02)	0.01 (0.01)	0.1 (0.04)	0.1 (0.03)
Chloroperlidae	–	–	0.02 (0.02)	0.01 (0.01)
Coleoptera				
Elmidae	0.01 (0.01)	0.02 (0.02)	0.01 (0.01)	0.02 (0.02)
Diptera				
Chironomidae pupae	0.2 (0.1)	0.03 (0.01)	0.04 (0.02)	0.02 (0.01)
Non-Tanypodinae	0.2 (0.1)	0.1 (0.03)	0.4 (0.1)	0.2 (0.1)
Tanypodinae	0.1 (0.04)	0.1 (0.03)	0.2 (0.1)	0.2 (0.1)
Tipulidae	0.1 (0.04)	0.1 (0.1)	–	–
Ostracoda	–	–	0.01 (0.01)	0.0 (0.0)
Cyclopoida	0.01 (0.01)	0.0 (0.0)	0.1 (0.04)	0.0 (0.0)
Harpacticoida	0.01 (0.01)	0.0 (0.0)	0.01 (0.01)	0.0 (0.0)
Amphipoda				
Crangonyx	0.1 (0.1)	0.1 (0.1)	0.03 (0.03)	0.01 (0.01)
Gammarus	–	–	0.04 (0.03)	0.04 (0.04)
Isopoda				
Caecidotea	1.1 (0.2)	1.6 (0.5)	0.1 (0.03)	0.1 (0.02)
Lirceus	–	–	3.7 (1.1)	5.5 (1.9)
Decapoda				
Cambarus hamulatus	0.1 (0.03)	–	–	–
Orconectes australis	–	–	0.1 (0.03)	–
Salamanders				
Eurycea	0.01 (0.01)	0.1 (0.1)	0.03 (0.02)	16.0 (14.6)
Total	2.8 (0.5)	3.7 (0.8)	5.7 (1.2)	8.4 (2.2)

Standard errors are in parentheses. Salamanders were not included in the totals.

The average AE of salamanders fed larval chironomids was 55.0 ± 1.7%. Based on this bioenergetic statistic, the majority of production for both populations was attributable to Isopoda (Tony Sinks = 69%, Bluff River = 41%; Fig. 6). Oligochaetes and Chironomidae accounted for 23% of salamander production in Tony Sinks with the balance of production being attributable to four other taxa (Fig. 6). Salamander production in Bluff River cave was based primarily upon oligochaetes and Chironomidae, with mayfly larvae making a lesser but substantial contribution (Fig. 6).

Discussion

The detrital pathway is an integral component of the structure and function of headwater streams.

Resource manipulations of surface streams have shown that the quantity and quality of detritus in headwater streams can directly influence the abundance, growth and productivity of most trophic levels in the aquatic food web (Wallace *et al.*, 1997, 1999; Hall *et al.*, 2000; Johnson & Wallace, 2005; Cross *et al.*, 2006). In cave stream ecosystems, the lack of primary production suggests that detrital inputs are probably the major factor controlling life history characteristics of obligate cave inhabitants (Poulson & White, 1969; Hüppop, 2000). Since different cave systems show large contrasts in organic matter inputs and storage, we hypothesised that these differences would influence the life history and production of *G. palleucus*, a top predator in cave food webs of the south-eastern U.S.A. On the basis of our hypothesis, we used the salamander populations inhabiting streams in Tony
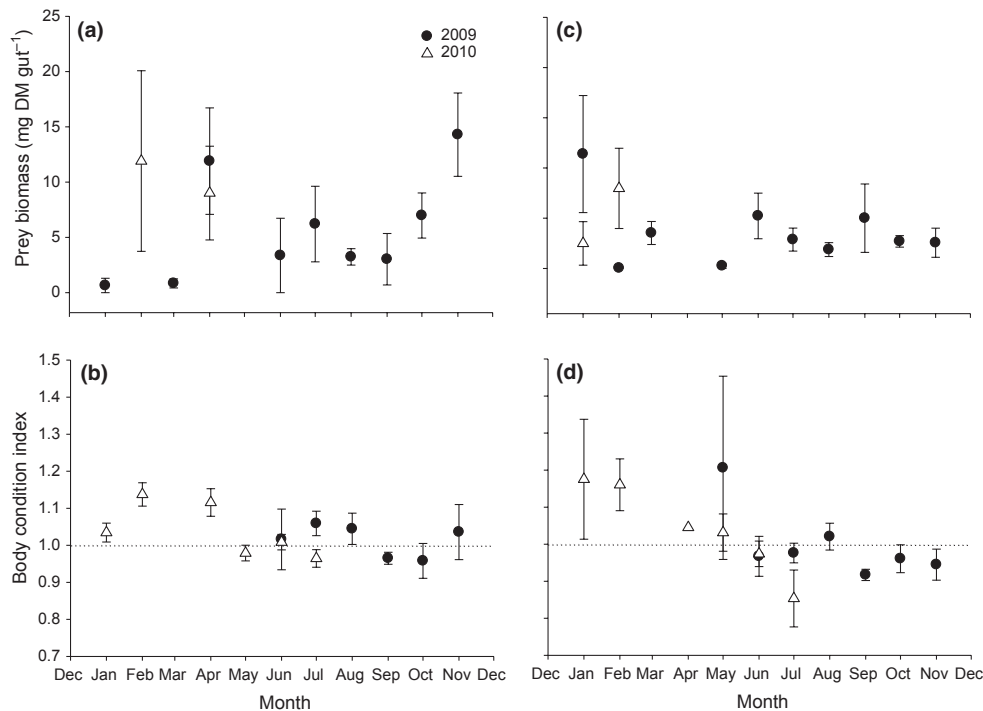
Fig. 2 Seasonal patterns of (a) mean prey biomass consumed (b) and mean body condition index, for *Gyrinophilus palleucus* in Tony Sinks cave, northeastern Alabama, U.S.A. and (c) mean prey biomass consumed and (d) mean body condition index for *G. palleucus* in Bluff River cave, northeastern Alabama, U.S.A. Data are means ± 1 SE. Points above and below the dashed line in (b) and (d) represent *G. palleucus* body mass that is higher and lower, respectively, than that predicted by the species-specific length-mass regression. Prey biomass in (a) and (c) is in milligrams dry mass per stomach (mg DM stomach^{-1}).

Sinks (high organic matter, 165 g AFDM m^{-2}) and Bluff River (low organic matter, 62 g AFDM m^{-2}) caves to test four *a priori* predictions.

Prediction 1 – Cave streams with high stores of organic matter have more abundant prey populations than caves with low stores of organic matter

This prediction was supported by the finding that the Tony Sinks cave stream contained about 4 × more prey biomass per m^2 than the Bluff River cave stream. Prey biomass consumed by salamanders (i.e. mass of stomach contents) in Tony Sinks cave was also greater than consumption in Bluff River cave, but this difference was not statistically significant. Johnson & Wallace (2005) showed a similar result for *Eurycea bislineata wilderae* Dunn in two Appalachian mountain surface streams, one of which was subject to a detritus exclusion treatment (low organic matter) with the other used as a reference (high organic matter). In contrast to our findings, however, they showed that prey community composition was different between the two reaches, with the stomach contents of salamanders from the high organic matter stream having stomach contents composed of higher-quality prey (based on caloric densities).

The month-to-month pattern of body condition generally reflected prey biomass consumed, with both body condition and prey biomass consumed being greatest during January through April. This pattern is probably attributed to seasonal variability in precipitation, as the mid-winter to early spring seasons at the study sites receive the greatest amount of precipitation seasonally. A link between precipitation and consumption has been found elsewhere. In a study by Petranka & Sih (1986), for example, greater volumes of prey were found in the stomachs of larvae of *Ambystoma texanum* (Mathes) during floods. The high discharge of streams entering caves during storms contributes large inputs of organic matter and prey to subterranean ecosystems and is an important factor controlling the temporal variability of the strength of surface-subterranean connections (Brandon, 1967). The potential effect of seasonal precipitation patterns on overall prey availability in our study was shown by changes in the abundance of potential prey taxa.
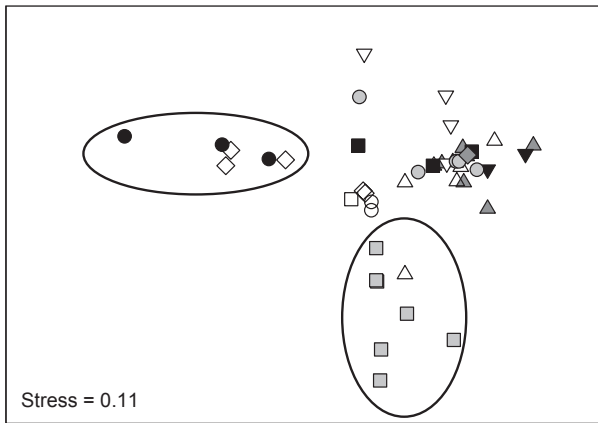
Fig. 3 Non-metric multidimensional scaling ordination plot based on log +1 transformed invertebrate biomass in the stomachs of *Gyrinophilus palleucus* from Bluff River cave, northeastern Alabama, U.S.A. Circled groupings indicate sources of dissimilarity between sampling dates January 11, 2009 (closed black circles) and February 21, 2010 (open diamonds), and March 21, 2009 (closed gray squares) from all other sampling dates based on ANOSIM analyses (see text).
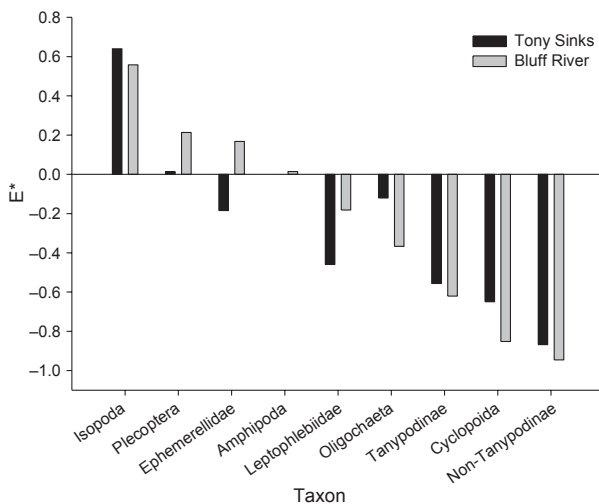

Fig. 5 Longevity growth model based on the snout-vent lengths (SVL) in centimeters (cm) and age in months of *Gyrinophilus palleucus* populations from Tony Sinks (TS) and Bluff River (BR) caves, northeastern Alabama, U.S.A. Dashed lines represent upper and lower bounds of the 95% confidence intervals.

Prediction 2 – Salamanders in caves with high organic matter have a more specialised diet than those in caves with low organic matter

Although a few differences were observed between caves in prey communities in the benthos (the occurrence of the isopod *Lirceus* in Tony Sinks but not Bluff River cave was probably the most striking with regard to actual prey consumed), the composition of prey taxa actually consumed by salamanders varied substantially. Stomach contents of salamanders in Tony Sinks cave were dominated by fewer prey taxa than Bluff River cave salamanders. The isopod *Lirceus* sp. was the major prey item consumed by Tony Sinks salamanders (>60% of total biomass consumed), while in Bluff River the isopod *Caecidotea* sp. contributed about 40% to total prey biomass and oligochaetes contributed >35%. Other cave salamanders have been shown to consume similar prey items to those we found. The cave salamander *Typhlotriton spelaeus* (Stejneger) was found to consume approximately 96% isopods from a Missouri cave (Smith, 1948). Brandon (1967) also found that isopods (*Caecidotea* sp.) constituted a majority of the diet of *G. palleucus*, in addition to earthworms, salamanders and crayfishes.

Salamanders from the Bluff River cave stream consumed three invertebrate taxa in proportions greater than their relative abundance among the benthos (i.e. positive *E** values – Isopoda, Plecoptera and Ephemerellidae), while in Tony Sinks cave, only

Fig. 4 Prey electivity index (*E**) for Bluff River cave (BR) and Tony Sinks cave (TS), in northeastern Alabama, U.S.A. Amphipoda were not included for Tony Sinks cave because too few animals were found in stomachs from that cave site.

Strong seasonal changes in the representation of different taxa among stomach contents, for example, were driven by oligochaetes and mayflies, which are apparently flushed into these systems during storms. Parker (1994) observed higher earthworm abundances in stomachs of salamanders after storms, which is also consistent with our results.
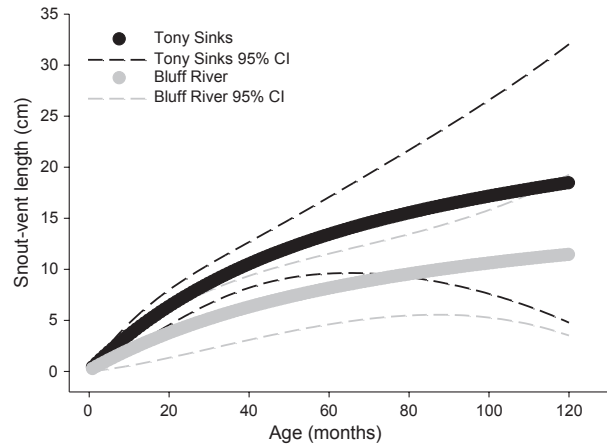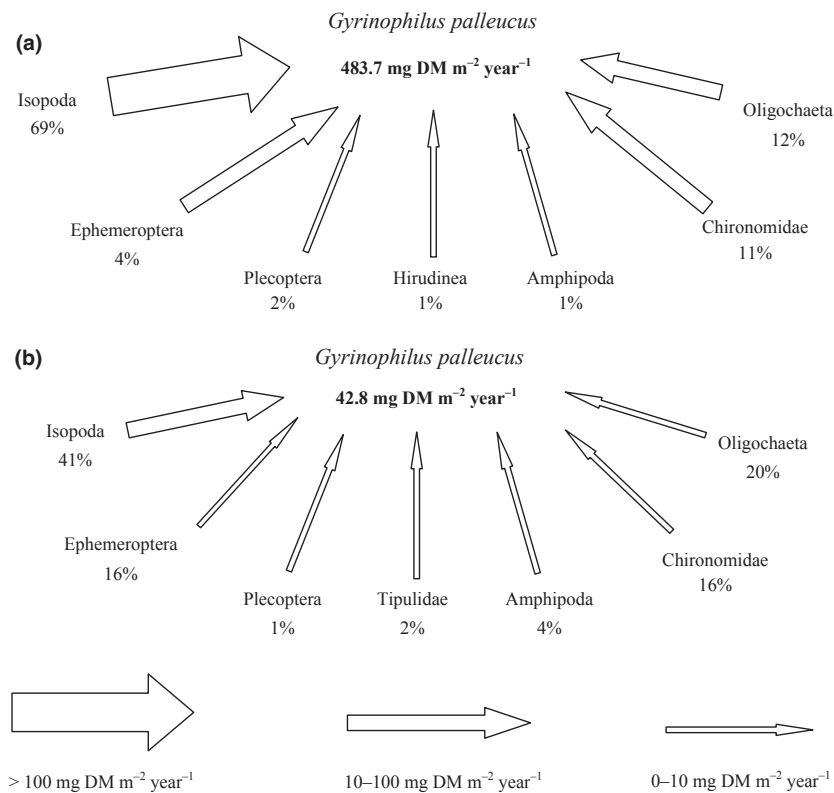
(a)

Gyrinophilus palleucus

483.7 mg DM m^{-2} year^{-1}

Isopoda
69%

Oligochaeta
12%

Ephemeroptera
4%

Plecoptera
2%

Hirudinea
1%

Amphipoda
1%

Chironomidae
11%

(b)

Gyrinophilus palleucus

42.8 mg DM m^{-2} year^{-1}

Isopoda
41%

Oligochaeta
20%

Ephemeroptera
16%

Plecoptera
1%

Tipulidae
2%

Amphipoda
4%

Chironomidae
16%

> 100 mg DM m^{-2} year^{-1}

10–100 mg DM m^{-2} year^{-1}

0–10 mg DM m^{-2} year^{-1}

Fig. 6 Organic matter flow webs for *Gyrinophilus palleucus* from Tony Sinks (a) cave and Bluff River (b) cave, northeastern Alabama, U.S.A. The units for organic matter flow are mg dry mass m^{-2} year^{-1}. Percentages indicate the amount of salamander production contributed by that prey item. Numbers in bold indicate total amount of prey biomass consumed to support salamander production.

isopods were consumed in greater proportion relative to their abundance within the prey community. Apparent 'selectivity' by *G. palleucus* is probably attributed to habitat selection on the part of the prey rather than active selection by salamanders. In our study, most of the prey taxa with positive E^* values are relatively active organisms while those having negative E^* values – such as chironomids – are generally burrowers (Thorp & Covich, 2001; Merritt *et al.*, 2008). A similar pattern was shown by Parker (1994), who found that chironomid larvae were underrepresented in the diet of the Pacific giant salamander [*Dicamptodon tenebrosus* (Baird & Girard)].

Prediction 3 – Salamanders in caves with high organic matter will have higher growth rates than those in caves with low organic matter

Resource supply has been shown to contribute directly to growth rates of predators through bottom-up control (Ballinger & Congdon, 1980; Wallace *et al.*, 1997; Johnson & Wallace, 2005; Johnson *et al.*, 2006). Based on these studies, we hypothesised that *G. palleucus* from Tony Sinks cave would have faster growth rates than those from Bluff River. Although

Tony Sinks salamanders did grow faster than those in Bluff River cave, comparison of the 95% CIs between caves indicated that this difference was not significant. Regardless, even minor differences in growth rates could have important implications for differences in reproductive success between the salamander populations. Dent & Kirby-Smith (1963) estimated male *G. palleucus* to reach reproductive maturity in approximately 2 years (later for females). Based on our longevity estimates, 2-year-old salamanders in Tony Sinks cave would be much larger than those in Bluff River cave (about 4 cm SVL in Bluff River and 7 cm SVL in Tony Sinks). This is significant because large-bodied salamanders have been shown to have higher fitness than small salamanders because of a greater allocation of energy towards egg production (Kusano, 1982; Petranka & Sih, 1986).

Prediction 4 – Salamander production will be higher in high organic matter caves and be supported by fewer prey species than salamander production in caves with low organic matter

Salamander population densities in the Tony Sinks cave stream were significantly higher than those in the

Bluff River cave stream. These estimates, however, were based on closed population models and thus violate strict assumptions of closure. Violations of this assumption are based on four potential parameters: birth, death, immigration and emigration. Although births may contribute to the lack of closure in this study, the low number of small salamanders (<4 cm SVL) captured during the study ($n = 3$ in Tony Sinks cave, $n = 1$ in Bluff River cave) suggests that the effect of recruitment is minimal. Violations based on death within populations may also have a minimal effect. Based on our longevity estimates, salamanders in both populations live longer than 6 years, which potentially relaxes violations due to high death rates. This leaves immigration and emigration (e.g. mobility) as potential sources of a closure violation. A study by Miller & Niemiller (2007) indicated that *G. palleucus* is relatively sedentary. Our mark–recapture study, however, yielded few recaptures, suggesting either that these animals are more mobile than originally believed or were difficult to locate due to habitat heterogeneity. Violation of the assumption of low mobility would result in an overestimate of population sizes because of reductions in recapture rate. Ultimately, comparisons between the two cave systems are probably valid, because populations were analysed similarly. However, we stress that any comparison of our results with those of other studies should be made with caution.

Like density, the biomass and production of *G. palleucus* were significantly greater in Tony Sinks cave compared with Bluff River cave, a result that is consistent with studies that have experimentally altered organic matter supply in surface streams (Wallace *et al.*, 1997; Hall *et al.*, 2000; Johnson & Wallace, 2005). Our estimates of production for *G. palleucus* (0.03–0.12 g AFDM m^{-2} year^{-1}) were intermediate to published estimates for other species of aquatic salamanders. Production of *Ambystoma* species assemblages in three Illinois ponds, for example, ranged from 0.35 to 7.4 g AFDM m^{-2} year^{-1} (Regester, Lips & Whiles, 2006), while estimates for *Eurycea bislineata wilderae* in Appalachian Mountain surface streams were <0.01 g AFDM m^{-2} year^{-1} (Johnson & Wallace, 2005). The latter study, however, was based on larval salamanders only. If adult production had been accounted for, the production estimates for *E. b. wilderae* may have exceeded those of *G. palleucus* at our study sites, further indicating extreme resource limitation in cave systems.

Diet analyses suggested that salamanders from the two systems consumed similar prey. However, the contribution of these prey taxa to salamander production was allocated differently between the two cave systems. In Tony Sinks cave, the majority of production was attributed to fewer species and, in particular, one group accounted for the majority of salamander production (Isopoda). In Bluff River cave, isopods were less important, so more prey items contributed to production. These differences in production were most likely due both to the relative availability of prey items and the life history characteristics of prey taxa. Most major prey categories were at higher densities and biomass in the high organic matter cave. However, salamanders from Tony Sinks cave were more selective foragers than those in Bluff River, suggesting that *G. palleucus* may consume higher-quality resources at higher proportions under conditions of higher basal resource availability. These results conform to optimal foraging theory, in that resource availability seems to influence foraging decisions of *G. palleucus* populations.

In our two cave systems, energy availability was based on organic matter and associated prey assemblages, which were both shown to be higher in Tony Sinks cave. Higher resource availability suggests that less energy is expended searching for prey items and travelling between resource patches (Charnov, 1976). That Tony Sinks cave was more energetically favourable than Bluff River cave was supported by higher biomass estimates, growth rates and production estimates for its salamander population. Organic matter in many headwater streams has been shown to be a limiting factor controlling the productivity of most trophic levels (Wallace *et al.*, 1997). Such bottom-up constraints have been suggested to 'cascade up' trophic levels of the associated food web (Hunter & Price, 1992). In cave systems, ambient resource levels vary greatly from cave to cave, with the potential to influence the structure of food webs and the life history of organisms within them. Our study of the productivity and carbon flow through a top predator in cave stream food webs is consistent with the notion of bottom-up control 'cascading up' successive trophic levels of food webs.

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(Manuscript accepted 29 March 2011)