

Environmental conditions and biotic interactions influence ecosystem structure and function in a drying stream

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Abstract Benthic consumers influence stream ecosystem structure and function, but these interactions depend on environmental context. We experimentally quantified the effects of central stoneroller minnows (*Campostoma anomalum* (Rafinesque)) and Meek's crayfish (*Orconectes meeki meeki* (Faxon)) on benthic communities using electric exclusion quadrats in Little Mulberry Creek before (June) and during (August) seasonal stream drying. Unglazed ceramic tiles were deployed in June and August to measure periphyton and invertebrate abundance, and leafpack decomposition and primary production were also measured in August. Relationships between stoneroller and crayfish density and the size of consumer effects were evaluated with multiple linear regression models. Average chlorophyll *a* abundance was greater on exposed than exclusion tiles in August, but not in June. Sediment dry mass, periphyton ash-free dry mass (AFDM), and chironomid densities on tiles did not

differ among treatments in either period. Leaf packs decayed faster in exposed than exclusion treatments ($k_{\text{exposed}} = 0.038 \pm 0.013$, $k_{\text{exclusion}} = 0.007 \pm 0.002$), but consumer effects were stronger in some pools than others. Leafpack invertebrate biomass and abundance and tile primary productivity did not differ among treatments. Consumer effects on chlorophyll *a* were related to crayfish and stoneroller density, and effects on chironomid density were related to stoneroller density. These results contrast with a previous exclusion experiment in Little Mulberry Creek that demonstrated strong consumer effects. The influence of stream drying on consumer effects appears to have been reduced by strong spates, underscoring the importance of conducting multi-year studies to determine the magnitude of variability in ecological interactions.

Keywords Meek's crayfish (*Orconectes meeki meeki*) · Central stonerollers (*Campostoma anomalum*) · Periphyton · Algae · Electric exclusions · Intermittent streams

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Introduction

Benthic consumers can alter stream ecosystem structure and function by modifying the abundance and composition of biofilm and invertebrate communities and by processing detritus (Gelwick & Matthews, 1992; Flecker, 1996; Schofield et al., 2001). Through

these interactions, stream consumers influence primary production, decomposition, nutrient cycling, and energy flow to downstream habitats (e.g., Peterson et al., 2001). In many streams in central and eastern North America, crayfish (e.g. *Orconectes spp.*) and central stoneroller minnows (*Campostoma anomalum*) are dominant benthic consumers and interact strongly with benthic communities (Power et al., 1985; Gelwick & Matthews, 1992; Whitlege & Rabeni, 1997; Creed & Reed, 2004). Omnivorous stonerollers and crayfish can strongly affect periphyton, sediment, and invertebrate abundance as well as rates of primary production and detrital decomposition (Power et al., 1988; Gelwick & Matthews, 1997; Usio & Townsend, 2002). Foraging activities dislodge and resuspend deposited sediment (Gelwick et al., 1997; Statzner et al., 2003). Consumption of invertebrate grazers may benefit algal production (Charlebois & Lamberti, 1996; Usio & Townsend, 2000), but omnivorous stonerollers and crayfish may dilute trophic cascades by directly depleting periphyton biomass (Usio, 2000).

Studies in other aquatic systems have demonstrated that consumer effects are often context dependent (Power & Matthews, 1983; Flecker, 1997; Power et al., 2008), and predicting when consumers will alter rates of ecosystem function is complex. If bottom-up factors (e.g., nutrient concentrations and light) permit high rates of primary production, algal abundance can outpace grazing. Alternatively, production can be so low that algal abundance is minimal even in the absence of grazers (McCormick, 1994; Mallory & Richardson, 2005). Top-down factors, like predator distributions, modify the abundance and foraging activity of fish and crayfish (Power et al., 1985; Magoulick, 2004). However, there is currently no framework for predicting when consumers will affect stream functioning, and despite the recognized need (Gelwick et al., 1997; Creed & Reed, 2004; Boogert et al., 2006), we have a limited understanding of the relationship between environment and consumer effects in streams and how these relationships vary in space and time. Climate and land use changes are reshaping stream ecosystems (Lake et al., 2000), making it all the more critical that we understand how environmental forces influence the effects of dominant stream consumers.

In the Ozark Mountains, seasonal drying periodically transforms stream habitats (Magoulick, 2000)

and provides an excellent opportunity to investigate how environmental conditions alter the effects of consumers on stream ecosystem structure and function (Ludlam & Magoulick, 2009). In drying streams, high temperatures, evapotranspiration, and sporadic summer rainfall result in reduced flows, habitat, and resource availability (Magoulick, 2000; Magoulick & Kobza, 2003), while infrequent but intense rainfall can cause high-flow disturbances that scour benthic habitats. Algae can recolonize dried or scoured substrates within weeks (Dodds et al., 1996) but disturbance alters algal composition and succession (Ledger et al., 2008). Drying can reduce the abundance of larger, long-lived invertebrates (Chadwick & Huryn, 2007) but drying can also benefit invertebrates by reducing the abundance of fish (Dorn, 2008). Drying concentrates organisms in shrinking disconnected pools where competition for resources can increase (Magoulick & Kobza, 2003), and drying also exposes organisms to increased predation by bass, herons, mink, and otter (Gelwick et al., 1997; Magoulick & Kobza, 2003).

Drying and consumer identity likely interact to mediate stream function. Several studies have indicated that stonerollers and the crayfish *Orconectes nais* (Faxon) and *Orconectes neglectus* (Faxon) consume similar resources but may perform different roles in stream communities (Evans-White et al., 2001, 2003; Bengtson et al., 2008). As drying increases exposure to predators, differential behavioral responses to predation risk (crayfish burrow construction, reduced foraging, and shifts in distribution) may cause stonerollers and crayfish to have different effects (e.g., Gelwick, 2000). In addition, crayfish (e.g., *Orconectes spp.*) use their chelae to process leaf litter and filamentous algae and to crush the shells of snails, whereas the inferior mouth and cartilaginous lower lip of stonerollers is well suited for grazing diatoms and other attached algae (Robison & Buchanan, 1988; Evans-White et al., 2003). These morphological differences may alter the relative efficiency of fish and crayfish foraging on different resources.

Ludlam and Magoulick (2009) measured effects of stonerollers and Meek's crayfish (*Orconectes meeki meeki*, hereafter *O. meeki*) on algal, sediment, and invertebrate abundance in an Ozark stream (Little Mulberry Creek) during early drying and after extended drying in 2006. Stonerollers and Meek's

crayfish (consumers) significantly reduced the abundance of chironomids, algae, and sediment on ceramic tiles, and effects were stronger during extended than early stream drying (Ludlam & Magoulick, 2009). This experiment suggested benthic fish and crayfish have the potential to strongly affect stream ecosystem processes (e.g., primary production and decomposition) in Little Mulberry Creek, and flow-related disturbance may intensify the role of these consumers in stream functioning.

We tested these hypotheses by experimentally measuring effects of fish and crayfish on net primary production and detrital decomposition, as well as algal, sediment, and invertebrate abundance. Consumer effects were measured as the difference between paired consumer enclosure and exposed quadrats. Stream pools were randomly selected from a longer reach than the 2006 study (3 vs. 1 km) to include a wider array of stream pools. We predicted that (1) crayfish and stonerollers would reduce benthic periphyton, sediment, and invertebrate abundances and net primary productivity, but increase biomass-specific primary productivity and leafpack decomposition and (2) the magnitude of consumer effects would increase as drying constricted pool habitats. Additionally, we used multiple linear regression models to evaluate the importance of benthic consumer identity in mediating the strength of consumer effects during stream drying.

Materials and methods

Study site

This study was conducted in a 3-km reach of Little Mulberry Creek, Arkansas, USA (Madison County; lat 35.768°N, lon 93.589°W), a second order stream in the heavily forested Boston Mountain ecoregion (described in Ludlam & Magoulick, 2009). Central stonerollers and Meek's crayfish were dominant benthic consumers in Little Mulberry Creek. Northern hog suckers (*Hypentelium nigricans* Lesueur) were present in some pools in low densities. Insectivorous orangethroat, fantail, and greenside darters (*Etheostoma spectabile* Agassiz, *Etheostoma flabellare* Rafinesque, and *Etheostoma blennioides* Rafinesque) were moderately abundant in riffles and pools. Fish predators included smallmouth and spotted bass

(*Micropterus dolomieu* Lacépède and *Micropterus punctulatus* Rafinesque), and longear and green sunfish (*Lepomis megalotis* Rafinesque and *Lepomis cyanellus* Rafinesque). Snails were observed infrequently on the periphery of pools and insect grazers (mostly Ephemeroptera, Trichoptera, and Coleoptera) were also low in abundance during the summer in pools (Ludlam, personal observations).

Experimental design

All pools in the main channel that were ≥ 60 cm deep in April 2007 were considered as possible sites. Pools with extensive bedrock bottoms were excluded because equipment could not easily be anchored to solid rock. One pool was excluded due to a confluence with a small tributary that occasionally scoured the pool. From the 19 pools identified based on these criteria 15 pools were randomly selected for study sites. We conducted an a priori power analysis that indicated six replicate pools would provide sufficient power ($\beta > 0.8$) to detect differences between treatments given effect sizes and variances for chlorophyll *a* and periphyton AFDM observed in a previous exclusion experiment (Ludlam & Magoulick, 2009). Within each pool paired electric exposed/exclusion quadrats (31 × 51 cm rectangles of 19 mm PVC pipe) were anchored to the substrate approximately 50 cm apart using metal stakes and cable ties. Electric exclusions excluded organisms $> \sim 1$ cm, and thus excluded most fish and crayfish (Pringle & Blake, 1994). The zone in which animals experienced electrical shock extended ~ 10 cm outside the quadrat. Visual observations confirmed that fish and crayfish strongly avoided electrified quadrats. Quadrat pairs were randomly located ≥ 1 m from the bank in the upstream third of each pool within zones of 60–70 cm depth and 0.1–0.2 m s⁻¹ flow at the time of selection (May 7–25, 2007). Within each exclusion quadrat, a cathode and two anodes of 12 gauge uninsulated copper wire were connected with insulated 12 gauge copper wire to a 6-V bank-mounted solar-powered electric fence charger (Parmak Model DF-SP-SS,¹ Parker McCrory Manufacturing Company, Kansas

¹ The use of trade, product, industry or firm names, or products is for informative purposes only and does not constitute an endorsement by the U.S. Government or the US Geological Survey.

City, Missouri, USA). Connecting wires were staked and buried beneath the substrate.

Unglazed ceramic tiles were used to measure consumer effects on periphyton, sediment, and invertebrate abundance. Ceramic tiles (11 × 11 cm) were fixed in each quadrat with cable ties, and collected after 30 days of exclusion. June tiles were allowed to colonize 46 days before the experiment started, and experimental exclusion ran from May 22 to June 21. August tiles colonized 54 days, and experimental exclusion ran from July 24 to August 23. Consumer effects on detrital decomposition and invertebrates within leafpacks were measured using leafpacks. Leafpacks were made from fresh sugar maple (*Acer saccharum*) leaves collected near Little Mulberry Creek, air dried to constant weight, and assembled into 3 g packs with plastic fasteners. Green leaves can be an important high-quality resource for stream detritivores during the summer (Kochi & Yanai, 2006). Six leafpacks (five collections plus a spare leafpack) were installed in each quadrat in June and August. A spate removed many June leafpacks and terminated the June decomposition experiment. August leaf packs were deployed from July 24 to September 4 and were collected on day 7, 15, 24, 34, and 42.

For collection, tiles and leafpacks were gently lifted and placed in plastic bags. When current was present, a 300- μ m mesh net was placed downstream to minimize loss of material. Bags were then put on ice, returned to the laboratory, and frozen for later analysis. Leafpacks were rinsed and invertebrates retained by a 250- μ m sieve were preserved in alcohol. Leafpacks were then dried at 50°C for 72 h, weighed, ashed at 550°C, wetted, redried, and weighed to determine ash-free dry mass. Leafpack decomposition was estimated as k , the slope of $\ln(\%$ remaining AFDM) versus time. Initial AFDM was estimated from 18 day 0 leafpacks. Invertebrates from day 34 (August 27) leafpacks were identified to family when possible, counted, and measured using an ocular micrometer on a dissecting scope. Day 34 leafpacks were used for invertebrate counts since two exposed Day 42 leafpacks had completely decayed. Invertebrate mass was estimated using length-weight regressions (Dumont et al., 1975; Benke et al., 1999). Mites, ostracods, and hydras were not included in counts due to rarity and small size, and a single snail was collected but not included in the analysis.

Before returning tiles to the laboratory in August, tiles were incubated in 4 L Ziploc[®] sacks filled with stream water to measure net primary productivity (NPP). Sacks were placed in the stream channel (depth = 15–20 cm) and incubated concurrently for 118–138 min in partial sun. Initial and final oxygen concentrations were measured with a YSI 85 dissolved oxygen meter and used to calculate NPP rates (μ g Oxygen $\text{h}^{-1} \text{cm}^{-2}$). Two sacks without tiles were incubated and changes in dissolved oxygen were used to correct for diffusion through sacks and non-benthic metabolism. This correction was on average <10% of production. Biomass-specific primary production (BSPP) was calculated as NPP/chlorophyll *a* abundance to estimate production per unit periphyton biomass.

Tile chironomid abundance was quantified as the number of chironomid cases on the tile surface. Periphyton on each tile was scraped with a razor blade, brushed with a nylon toothbrush, and rinsed into a beaker. Each periphyton sample was brought to 300–400 ml with water, mixed with a magnetic stir-plate, and two subsamples were filtered onto pre-ashed and weighed Whatman GF/F filters. One filter was dried for 24 h at 100°C to obtain sediment dry mass, weighed, ashed at 550°C for 1 h, rewetted, redried, and weighed for periphyton AFDM. The second was extracted in 96% EtOH and analyzed spectrophotometrically for chlorophyll *a* (Stich & Brinker, 2005; Wasmund et al., 2006).

Field measurements

Throughout the experiment, we visually observed tiles to confirm crayfish and fish exclusion was effective. Temperature/light loggers (Hobo Pendant UA-002-64, Onset Computer Corporation, Pocasset, Massachusetts, USA) were attached to stakes between quadrats on the stream bottom to record temperature and light intensity during the experiment. Sensors were frequently cleaned to prevent debris accumulation from blocking light. Current velocity was measured above the substrate with a Marsh-McBirney flowmeter (Flo-Mate 2000, Marsh-McBirney, Inc., Frederick, Maryland, USA) on the four corners of each quadrat in June (May 22, May 31, and June 13) and August (July 26, August 8, and August 22). Water turbidity over the quadrats was measured twice in June (May 31 and June 14) and three times in

August (July 24, August 8, and August 21) using a portable nephelometric turbidity meter (T-100, Oakton Instruments, Vernon Hills, Illinois, USA). Water depth over the quadrats was measured at least every 10 days (see “Results” section) with a meter stick. Dissolved oxygen and conductivity were measured with a YSI 85 meter on May 31, June 12, and July 26, and a YSI 60 meter recorded pH on July 24, August 8, and August 22 (YSI, Yellow Springs, Ohio, USA). Water nutrient samples were collected on June 12, July 24, and August 21, filtered with a Whatman GF/F filter and frozen for analysis of orthophosphate and nitrate. On June 13–14, July 26–27, and August 22–23, we determined pool area by measuring pool width every 10 m of pool length.

Fish and crayfish densities

Nocturnal surveys were used to estimate the density of active crayfish along transects in study pools (individuals (ind.) m^{-2}) on August 1–2 (Ludlam & Magoulick, 2009). Nocturnal surveys were used because crayfish were more active and less easily frightened at night. Crayfish were counted from 2200 to 0200 h on randomly located 0.92 m wide transects oriented at 45° angles to streamflow to avoid sampling along habitat gradients. A minimum of three transects with a total length ≥ 15 m were demarcated with twine along the stream bottom. Individual crayfish were recorded if they were on the transect and density was estimated as the number of individuals divided by the area sampled. Snorkeling gear was used to swim transects in deeper habitats, otherwise transects were slowly walked upstream while looking for crayfish. Young of year crayfish (< 18 mm carapace length) were not included in the density estimates, as they stayed mainly in riffles and pool margins. Care was taken not to disturb crayfish or count individuals multiple times.

Predator fish densities were estimated in daylight on August 7–8 by snorkeling upstream in each pool and counting predator fish (smallmouth bass, spotted bass, and green sunfish) ≥ 200 mm total length (TL). Lengths were estimated visually with the aid of a hand-held ruler. On August 8, active stoneroller abundance was visually estimated from the bank as the observer slowly walked the length of each pool. Counts were divided by the area surveyed to calculate density. Water turbidity was very low during the

study and provided clear viewing opportunities in the shallow pools surveyed. Visual sampling methods were used to reduce disturbance of pools during the experiment.

Data analysis

Statistical analyses were done with SYSTAT (version 11, Systat Software, Inc., San Jose, California). Several severe spates occurred during the study and high flows and uneven drying disrupted quadrats in some pools in both periods so that replication was reduced to 7 and 10 pools in June and August, respectively. Unfortunately, remaining pools were not always the same in June and August, so repeated measures analysis was not used. Differences between treatments for tile chlorophyll *a*, sediment dry mass, periphyton AFDM, and chironomid density were tested with paired *t*-tests separately for June and August. Likewise, differences between treatments were tested with paired *t*-tests for August tile NPP and BSPP and leafpack invertebrate abundance and biomass (day 34) and percent leafpack remaining as AFDM (day 42). Leafpack invertebrate abundance was $\log(x + 1)$ -transformed for homogeneity of variance.

Relationships between crayfish and stoneroller densities and the strength of consumer effects (the difference between exclusion and exposed treatments) on August chlorophyll *a*, periphyton AFDM, and chironomid density were evaluated with linear multiple regression models. Regression models are not presented for June because only seven pools were available. We compared three models: crayfish alone, stonerollers alone, and the combined effect of stonerollers and crayfish. Models were selected a priori and ranked using Akaike Information Criterion corrected for small sample size (AIC_c; Burnham & Anderson, 2002). The Akaike weight (w_i), an estimate of the relative likelihood of the model, was used to calculate the likelihood of a given model versus the best model (the evidence ratio (w_1/w_i); Burnham & Anderson, 2002). Models with evidence ratios < 8 were considered to have strong relative support (Royall, 1997), and models with no significant regression coefficients (95% confidence intervals that included 0) are not discussed. Periphyton AFDM was $\log(x + 1)$ -transformed to normalize data. Regressions were done with R (version 2.8.1, <http://www.r-project.org>).

Results

Environmental conditions

During experimental exclusions, Little Mulberry Creek gradually changed from a flowing stream to a series of disconnected and contracting pools. Average quadrat depth in pools decreased from June ($50 \text{ cm} \pm 2 \text{ SE}$) to August ($26 \text{ cm} \pm 3$), and pool area shrank from $553 \text{ m}^2 \pm 90$ (June 13) to $341 \text{ m}^2 \pm 54$ (August 22; Fig. 1). However, several substrate-shifting spates occurred during and between experimental periods (Fig. 2). Temperature, conductivity, nitrate, and light intensity increased between periods, phosphate levels remained similar, and dissolved oxygen concentrations and turbidity declined (Table 1).

Exclusion effects on tiles and leafpacks

We expected stonerollers and crayfish would negatively affect most tile and leafpack response variables, and that consumer effects would intensify with drying. However, chlorophyll *a* abundance was greater on exposed than exclusion tiles in August ($P = 0.037$), but was not significantly different in June ($P = 0.085$; Fig. 3a). June and August sediment dry mass, periphyton AFDM, and tile chironomid abundance did not differ between exposed and exclusion tiles ($P \geq 0.080$; Fig. 3b–d). August NPP

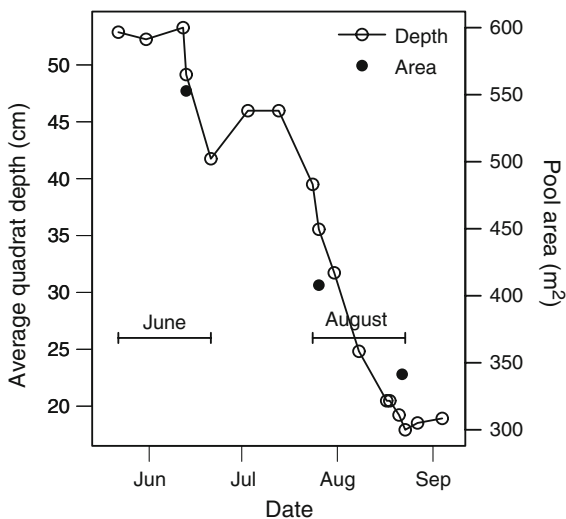


Fig. 1 Average quadrat depth (in cm, to left) as well as pool area (in m^2 , to the right) during the study period in Little Mulberry Creek, AR in 2007

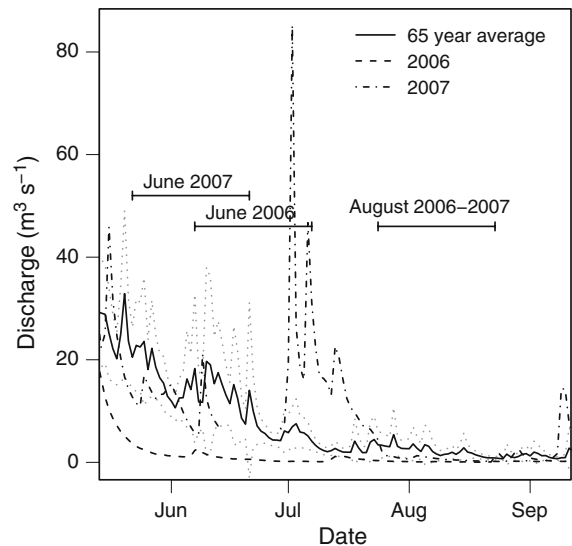


Fig. 2 Discharge ($\text{m}^3 \text{ s}^{-1}$) at USGS gauge on Mulberry River near Mulberry, AR. Data are shown for 2007 (study year), 2006, as well as for the 65 year average ($\pm 95\%$ confidence intervals; fine dotted lines)

Table 1 Mean ($\pm \text{SE}$) of study pool characteristics for June and August 2007 experimental periods

Variable	June	August
Quadrat depth (cm)	49.9 (2.2)	26.2 (3.0)
Pool area (m^2)	553 (90)	341 (54)
Water velocity (m s^{-1})	0.12 (0.04)	0.01 (0.01)
Temperature ($^{\circ}\text{C}$)	20.5 (0.06)	26.6 (0.26)
Light intensity (lux)	5060 (871)	6844 (1368)
Specific conductivity ($\mu\text{S cm}$)	36.60 (0.66)	56.17 (1.62)
pH	–	6.67 (0.08)
NO_3^- ($\mu\text{g l}^{-1}$)	22.9 (3.4)	43.9 (4.1)
PO_4^- ($\mu\text{g l}^{-1}$)	2 (0.2)	1 (0.1)
Dissolved oxygen (mg l^{-1})	8.57 (0.03)	6.67 (0.05)
Turbidity (NTU)	5.9 (0.1)	2.6 (0.1)

NTU nephelometric turbidity units

(exposed = 8.2 ± 0.8 , exclusion = 8.1 ± 0.7) and BSPP (exposed = 6.2 ± 0.8 , exclusion = 7.9 ± 0.6) were not significantly different between treatments ($P \geq 0.077$). Leaf packs decayed faster in exposed than exclusion treatments ($P = 0.008$, % AFDM remaining exposed = 47.2 ± 16.4 , exclusion = 80.6 ± 8.3 , $k_{\text{exposed}} = 0.038 \pm 0.013$, $k_{\text{exclusion}} = 0.007 \pm 0.003$), but results were not consistent among pools. Effects of exclusion on decomposition rates were observed in approximately half the pools but were not

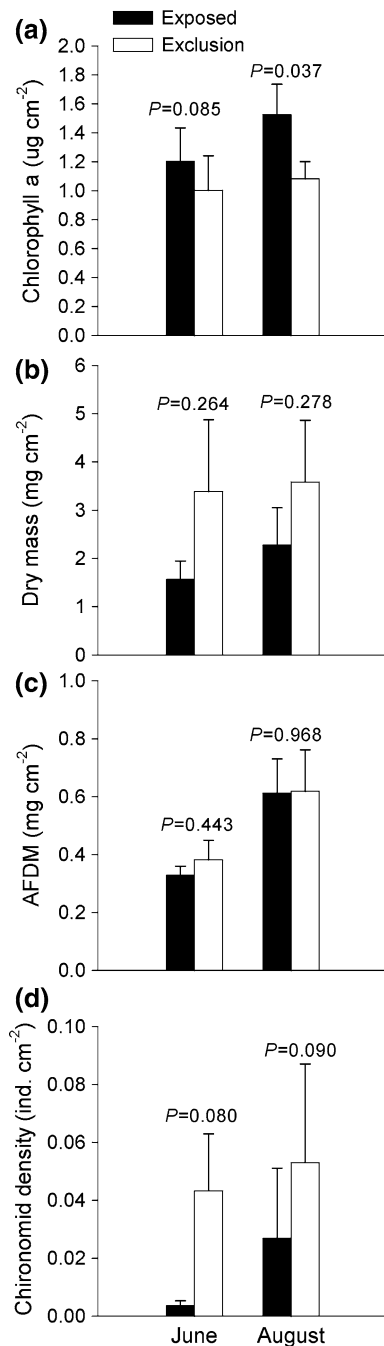


Fig. 3 Exclusion effects on tiles and leafpacks. Shown are response variables as mean (± 1 SE, June $n = 7$, August $n = 10$) **a** chlorophyll *a* ($\mu\text{g cm}^{-2}$), **b** sediment dry mass (mg cm^{-2}), **c** periphyton ash-free dry mass (AFDM, mg cm^{-2}), and **d** chironomid density (ind. cm^{-2}) of different treatments conducted in June and August 2007 in Little Mulberry Creek, AR. Black bars exposure, white bars exclusion

evident in the remainder. Invertebrate biomass (exposed = $9.8 \text{ mg} \pm 5.7$, exclusion = $10.7 \text{ mg} \pm 3.1$) and abundance (exposed = 52.8 ± 14.1 , exclusion = 110 ± 35.7) in leafpacks were not significantly different between treatments ($P \geq 0.089$).

Consumer effects on chlorophyll *a* were positively related to crayfish density and negatively related to stoneroller density (Table 2; Fig. 4). Consumer effects on tile chironomid density were positively related to stoneroller density, but consumer effects on periphyton AFDM had no models with regression coefficients significantly different from zero (Table 2).

Fish and crayfish density

Active crayfish density ranged from 0.13 to 1.66 ind. m^{-2} and averaged $0.90 \text{ ind. m}^{-2} \pm 0.16$. Central stoneroller density ranged from 0.03 to 0.64 ind. m^{-2} and averaged $0.24 \text{ ind. m}^{-2} \pm 0.07$. Smallmouth bass, spotted bass, and green sunfish were the only aquatic predators we observed $\geq 200 \text{ mm TL}$. On average, there were 1.6 ± 0.52 fish predators $\geq 200 \text{ mm TL}$ per pool.

Discussion

Previous studies have demonstrated that crayfish and benthic fish can have strong effects on benthic communities (e.g., Power & Matthews, 1983; Gelwick & Matthews, 1992; Creed, 1994; Usio & Townsend, 2002). We expected *O. meeki* and stonerollers would affect benthic stream structure and function and that the size of consumer effects would increase with stream drying. However, in our experiment consumer exclusion did not significantly affect primary production or the abundance of organic matter and invertebrates on tiles and consumer effects were largely similar before and during drying. Stoneroller and crayfish exclusion only had a significant effect on August chlorophyll *a*, when chlorophyll was more abundant on exposed than exclusion tiles.

Both the size of consumer effects on tile resources and average exclusion abundances of algae and sediment differed markedly from a previous exclusion experiment conducted in Little Mulberry Creek

Table 2 Model selection based on Akaike Information Criterion (AIC_c) for linear regression relating the strength of consumer effects (exclusion-exposed) on algae, organic material, and Chironomids on tiles to predictor variables in August 2007

Response	Model	SSE	No. of parameters	Δ_i	w_i	Evidence ratio (w_i/w_j)	Predictor variable	B_i	Lower CI	Upper CI
Chlorophyll <i>a</i>	Crayfish	1.41	2	0	0.47	1	Crayfish	0.800	0.178	1.422
	Stonerollers	1.52	2	0.8	0.32	1.47	Stonerollers	-0.170	-0.313	-0.027
	Crayfish + Stonerollers	0.91	3	1.6	0.21	2.25	Crayfish Stonerollers	0.566 -0.113	-0.050 -0.249	1.182 0.023
AFDM	Crayfish	1.44	2	0	0.5	1	Crayfish	0.121	-0.509	0.750
	Stonerollers	1.46	2	0.1	0.48	1.04	Stonerollers	-0.022	-0.162	0.118
Chironomids	Crayfish + Stonerollers	1.44	3	6	0.03	19.68				
	Stonerollers	0.01	2	0	0.93	1	Stonerollers	0.015	0.005	0.024
	Crayfish + Stonerollers	0.01	3	5.9	0.05	19.05				
	Crayfish	0.01	2	8	0.02	54.01				

Regression coefficients (B_i ; with 95% confidence intervals [CI]) are shown for models with evidence ratios < 8 . SSE model error sum of squares, *periphyton* AFDM ash-free dry mass, Δ_i difference between minimum AIC_c and model AIC_c. Minimum AIC_c: Chlorophyll *a* = -9.59, AFDM = -9.35, Chironomids = -63.73

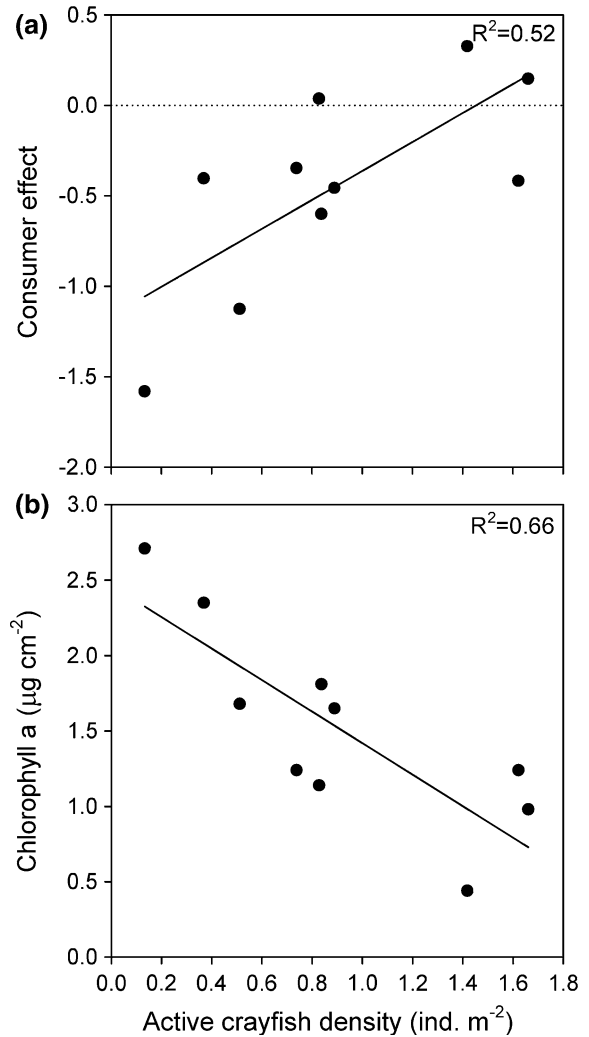


Fig. 4 Linear regression of active crayfish density (ind. m⁻²) versus **a** size of consumer effects (exclusion-exposed) on chlorophyll *a* and **b** chlorophyll *a* abundance (µg cm⁻²) on exposed tiles in August 2007

(Ludlam & Magoulick, 2009). In June and August 2006, *O. meeki* and stonerollers significantly reduced periphyton and chironomid abundance on exposed tiles by at least 1.5 to 3 times compared with enclosures, and consumer effects increased from June to August as stream drying intensified. In addition, exclusion abundances of periphyton differed between years; chlorophyll *a*, periphyton AFDM, and sediment dry mass in enclosures were 1.5–2 times greater in 2006 than in 2007.

Hydrologic differences between years may have contributed to observed variation in consumer effects. Water levels dropped rapidly in June 2006 and

consistently remained below the long-term average, while in 2007 several severe spates scoured the streambed. These high flows may have reduced accumulated periphyton and sediment (Lohman et al., 1992) and minimized the influence of benthic consumers. Thus, drying may intensify consumer effects only in the absence of severe summer spates. In contrast to our results (weaker consumer effects following spates), Bertrand et al. (2009) found grazing and water-column consumers such as southern redbelly dace (*Phoxinus erythrogaster*) and red shiners (*Cyprinella lutrensis*) altered recovery of periphyton communities in mesocosms following a simulated spate. Additionally, time since disturbance altered or reversed consumer effects. Consumers did not alter recovery in stream enclosures, perhaps because enclosures were not large enough for consumers to affect nutrient cycling (Bertrand et al., 2009). Additional long-term studies are needed to assess how different environmental disturbances like spates and drying interact to influence ecological interactions in streams (e.g., Power et al., 2008).

In contrast to weak effects on tiles, consumers significantly increased leafpack decomposition rates. Exposed leafpacks were shredded from the periphery suggesting crayfish were responsible for increased leafpack decomposition. This observation is supported by mesocosm enclosures of stonerollers and fish that demonstrated stonerollers had no significant effect on leafpack decomposition (Ludlam, unpublished data). Both the exposed and exclusion leafpack decomposition rates in our study were within the range reported in the literature. For instance, Schofield et al. (2001) reported decomposition of pre-conditioned *Rhododendron maximum* leafpacks ranging from $k = 0.018_{\text{summer}}$ to $k = 0.037_{\text{fall}}$ when exposed to the crayfish *Cambarus bartonii* (Fabricius). In contrast, in the presence of the crayfish *Paranephrops zealandicus* (White) decomposition rates of *Schefflera digitata* leafpacks were much higher ranging from $k = 0.082$ to $k = 0.091$ (Usio, 2000).

Unexpectedly, periphyton chlorophyll *a* was more abundant on exposed than exclusion tiles in August. Our data suggest that crayfish may have been stimulating algal abundance, but only for low crayfish densities. Thus, exposed sites had higher chlorophyll abundances than exclusion sites for crayfish densities <1.5 crayfish m^{-2} . Chlorophyll *a* on exposed tiles was negatively related to crayfish density, suggesting

that as crayfish density increased, consumption canceled out any stimulatory effects.

In addition to effects of crayfish on benthic resources, regression results indicated that stoneroller density was negatively related to the size of consumer effects on chlorophyll *a*, although the regression coefficient was small relative to the effects of crayfish. Stoneroller density was positively related to consumer effects on chironomid density, suggesting that the beneficial effect of stonerollers on algal abundance occurred through a reduction of chironomid herbivores.

Many studies have shown that consumers reduce algal abundance directly through consumption (Power et al., 1988; Creed, 1994; Gelwick & Matthews, 1997). Positive effects of consumers on periphyton are less well documented (but see Charlebois & Lamberti, 1996; Geddes & Trexler, 2003), but consumers can stimulate periphyton production through several mechanisms. Consumers may have benefitted algal abundance by reducing the density of chironomid herbivores on exposed tiles as mentioned above (e.g., Charlebois & Lamberti, 1996), although chironomid densities were very low in both exposed and exclusion treatments in this study. Additionally, other studies have demonstrated that nutrient excretion by consumers can reduce nutrient limitation (Flecker et al., 2002; Geddes & Trexler, 2003), feeding and foraging movements can reduce light limitation by decreasing sediment deposition (Flecker et al., 2002), and grazing may stimulate production by altering algal composition (Abe et al., 2007).

Conclusion

Stonerollers and crayfish can have strong effects on benthic structure and function in Little Mulberry Creek (e.g., leafpack decomposition (this study), periphyton and invertebrates (summer 2006, Ludlam & Magoulick, 2009)). However, consumer effects, especially effects on periphyton and sediment were surprisingly variable over both short spatial and temporal scales (i.e., summer 2006) and between years (2006 vs. 2007). Our results suggest that both biotic (e.g., consumer density) and abiotic factors (drying and spates) contributed to this variation. The dramatic differences in results between years should promote caution in interpreting the results of short-term studies on effects of consumers in benthic

habitats. Streams are complex, variable, and heterogeneous environments. Interactions between benthic consumers and stream structure and function reflect this complexity and highlight the critical need for long-term spatially replicated studies. In particular, future studies should investigate how multiple disturbances, like drying and spates, interact to alter stream systems. Without such studies, it might be difficult to accurately assess the causes and consequences of variation in ecological interactions in lotic ecosystems.

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References

- Abe, S. I., K. Uchida, T. Nagumo & J. Tanaka, 2007. Alterations in the biomass-specific productivity of periphyton assemblages mediated by fish grazing. *Freshwater Biology* 52: 1486–1493.
- Bengtson, J. R., M. A. Evans-White & K. B. Gido, 2008. Effects of grazing minnows and crayfish on stream ecosystem structure and function. *Journal of the North American Benthological Society* 27: 772–782.
- Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18: 308–343.
- Bertrand, K. N., K. B. Gido, W. K. Dodds, J. N. Murdock & M. R. Whiles, 2009. Disturbance frequency and functional identity mediate ecosystem processes in prairie streams. *Oikos* 118: 917–933.
- Boogert, N. J., D. M. Paterson & K. N. Laland, 2006. The implications of niche construction and ecosystem engineering for conservation biology. *Bioscience* 56: 570–578.
- Burnham, K. P. & D. R. Anderson, 2002. *Model Selection and Inference: a practical information-theoretic approach*, 2nd ed. Springer, New York.
- Chadwick, M. A. & A. D. Huryn, 2007. Role of habitat in determining macroinvertebrate production in an intermittent-stream system. *Freshwater Biology* 52: 240–251.
- Charlebois, P. M. & G. A. Lamberti, 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* 15: 551–563.
- Creed, R. P., 1994. Direct and indirect effects of crayfish grazing in a stream community. *Ecology* 75: 2091–2103.
- Creed, R. P. & J. M. Reed, 2004. Ecosystem engineering by crayfish in a headwater stream community. *Journal of the North American Benthological Society* 23: 224–236.
- Dodds, W. K., R. E. Hutson, A. C. Eichen, M. A. Evans, D. A. Gudder, K. M. Fritz & L. Gray, 1996. The relationship of floods, drying, flow and light to primary production and producer biomass in a prairie stream. *Hydrobiologia* 333: 151–159.
- Dorn, N. J., 2008. Colonization and reproduction of large macroinvertebrates are enhanced by drought-related fish reductions. *Hydrobiologia* 605: 209–218.
- Dumont, H. J., I. Vandavelde & S. Dumont, 1975. Dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75–97.
- Evans-White, M., W. K. Dodds, L. J. Gray & K. M. Fritz, 2001. A comparison of the trophic ecology of the crayfishes (*Orconectes nais* (Faxon) and *Orconectes neglectus* (Faxon)) and the central stoneroller minnow (*Camptostoma anomalum* (Rafinesque)): omnivory in a tallgrass prairie stream. *Hydrobiologia* 462: 131–144.
- Evans-White, M. A., W. K. Dodds & M. R. Whiles, 2003. Ecosystem significance of crayfishes and stonerollers in a prairie stream: functional differences between co-occurring omnivores. *Journal of the North American Benthological Society* 22: 423–441.
- Flecker, A. S., 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* 77: 1845–1854.
- Flecker, A. S., 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. *Journal of the North American Benthological Society* 16: 286–295.
- Flecker, A. S., B. W. Taylor, E. S. Bernhardt, J. M. Hood, W. K. Cornwell, S. R. Cassatt, M. J. Vanni & N. S. Altman, 2002. Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. *Ecology* 83: 1831–1844.
- Geddes, P. & J. C. Trexler, 2003. Uncoupling of omnivore-mediated positive and negative effects on periphyton mats. *Oecologia* 136: 585–595.
- Gelwick, F. P., 2000. Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. *Oecologia* 125: 573–583.
- Gelwick, F. P. & W. J. Matthews, 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. *Ecology* 73: 1630–1645.
- Gelwick, F. P. & W. J. Matthews, 1997. Effects of algivorous minnows (*Camptostoma*) on spatial and temporal heterogeneity of stream periphyton. *Oecologia* 112: 386–392.
- Gelwick, F. P., M. S. Stock & W. J. Matthews, 1997. Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. *Oikos* 80: 382–398.
- Kochi, K. & S. Yanai, 2006. Shredder colonization and decomposition of green and senescent leaves during summer in a headwater stream in northern Japan. *Ecological Research* 21: 544–550.
- Lake, P. S., M. A. Palmer, P. Biro, J. Cole, A. P. Covich, C. Dahm, J. Gibert, W. Goedkoop, K. Martens & J. Verhoeven, 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. *Bioscience* 50: 1099–1107.
- Ledger, M. E., R. M. L. Harris, P. D. Armitage & A. M. Milner, 2008. Disturbance frequency influences patch

- dynamics in stream benthic algal communities. *Oecologia* 155: 809–819.
- Lohman, K., J. R. Jones & B. D. Perkins, 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1198–1205.
- Ludlam, J. P. & D. D. Magoulick, 2009. Spatial and temporal variation in the effects of fish and crayfish on benthic communities during stream drying. *Journal of the North American Benthological Society* 28: 371–382.
- Magoulick, D. D., 2000. Spatial and temporal variation in fish assemblages of drying stream pools: the role of abiotic and biotic factors. *Aquatic Ecology* 34: 29–41.
- Magoulick, D. D., 2004. Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia* 527: 209–221.
- Magoulick, D. D. & R. M. Kobza, 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48: 1186–1198.
- Mallory, M. A. & J. S. Richardson, 2005. Complex interactions of light, nutrients and consumer density in a stream periphyton-grazer (tailed frog tadpoles) system. *Journal of Animal Ecology* 74: 1020–1028.
- McCormick, P. V., 1994. Evaluating the multiple mechanisms underlying herbivore algal interactions in streams. *Hydrobiologia* 291: 47–59.
- Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory & D. D. Morrall, 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292: 86–90.
- Power, M. E. & W. J. Matthews, 1983. Algae-grazing minnows (*Camptostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia* 60: 328.
- Power, M. E., W. J. Matthews & A. J. Stewart, 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* 66: 1448–1456.
- Power, M. E., M. S. Parker & W. E. Dietrich, 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs* 78: 263–282.
- Power, M. E., A. J. Stewart & W. J. Matthews, 1988. Grazer control of algae in an Ozark Mountain stream: effects of short-term exclusion. *Ecology* 69: 1894–1898.
- Pringle, C. M. & G. A. Blake, 1994. Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1443–1450.
- Robison, H. W. & T. M. Buchanan, 1988. *Fishes of Arkansas*. The University of Arkansas Press, Fayetteville, AR.
- Royall, R. M., 1997. *Statistical Evidence: A Likelihood Paradigm*. Chapman and Hall, London.
- Schofield, K. A., C. M. Pringle, J. L. Meyer & A. B. Sutherland, 2001. The importance of crayfish in the breakdown of rhododendron leaf litter. *Freshwater Biology* 46: 1191–1204.
- Statzner, B., O. Peltret & S. Tomanova, 2003. Crayfish as geomorphic agents and ecosystem engineers: effect of a biomass gradient on baseflow and flood-induced transport of gravel and sand in experimental streams. *Freshwater Biology* 48: 147–163.
- Stich, H. B. & A. Brinker, 2005. Less is better: uncorrected versus pheopigment-corrected photometric chlorophyll-*a* estimation. *Archiv für Hydrobiologie* 162: 111–120.
- Usio, N., 2000. Effects of crayfish on leaf processing and invertebrate colonisation of leaves in a headwater stream: decoupling of a trophic cascade. *Oecologia* 124: 608–614.
- Usio, N. & C. R. Townsend, 2000. Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey. *New Zealand Journal of Marine and Freshwater Research* 34: 557–567.
- Usio, N. & C. R. Townsend, 2002. Functional significance of crayfish in stream food webs: roles of omnivory, substrate heterogeneity and sex. *Oikos* 98: 512–522.
- Wasmund, N., I. Topp & D. Schories, 2006. Optimising the storage and extraction of chlorophyll samples. *Oecologia* 48: 125–144.
- Whitledge, G. W. & C. F. Rabeni, 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2555–2563.