Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations

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SUMMARY

1. Few studies have assessed the role of tadpoles in tropical streams, although they are often abundant and conspicuous components of these systems. Moreover, amphibian populations are declining around the globe, particularly stream-dwelling species in tropical uplands, and the ecological consequences of these losses are not understood.

2. We chose a stream in the central Panamanian highlands, which has an intact fauna of stream-breeding anurans, to examine the ecological consequences of amphibian losses. This site differs dramatically from sites in nearby western Panama and Costa Rica where anuran diversity and abundance have declined greatly in the last two decades.

3. We used an underwater electric field to create tadpole exclosures in runs, so that we could evaluate their influence on sediment dynamics and the abundance and community structure of algae and aquatic insects. Tadpoles reduced total sediments and both organic and inorganic fractions on substrata. Tadpoles also reduced algal abundance on substrata by approximately 50% and decreased algal biovolume. Gut content analyses showed that tadpoles consumed algae and sediments and we could see that algae and sediments were also displaced through bioturbation.

4. *Atelopus zeteki*, *Rana warszewitschii*, and *Hyla* spp. were the dominant larval anurans responsible for the effects observed. Visual surveys indicated that the densities of these taxa ranged from 23 (*R. warszewitschii* and *Hyla* spp. combined) to 43 m^{-2} (*A. zeteki*) in runs.

5. The abundance of baetid mayflies was lower in tadpole exclosures compared with controls, and this was attributed to tadpoles facilitating mayfly feeding by removing sediments and exposing underlying periphyton.

6. Tadpoles affect the abundance and diversity of basal resources and other primary consumers, and thus influence food web dynamics and energy flow in these tropical streams. Catastrophic decline in stream-breeding anuran populations will influence the structure and function of neotropical stream ecosystems.

Keywords: bioturbation, grazing, periphyton, tropical stream, tadpole

Introduction

Although they are diverse and abundant in some streams, the importance of tadpoles in the structure and function of lotic ecosystems has received little attention hitherto (e.g. Lamberti *et al.*, 1992;

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Kupferberg, 1997; Flecker, Feifarek & Taylor, 1999). In contrast, the importance of other consumer groups, such as macroinvertebrates and fish, is well documented. Manipulative field studies have shown that macroinvertebrate consumers influence stream ecosystem processes in streams, such as decomposition and organic particle formation (e.g. Cuffney, Wallace & Lugthart, 1990; Wallace *et al.*, 1991; Chung, Wallace & Grubaugh, 1993; Whiles, Wallace & Chung, 1993) and primary production (e.g. Rosemond, Pringle & Ramírez, 1998; Hillebrand, 2002; Taylor, McIntosh & Peckarsky, 2002), and similar patterns are evident for fishes (e.g. Power, 1984, 1990; Gido & Matthews, 2001). Consumer groups in streams can also indirectly influence organic and inorganic sediment dynamics through bioturbation (Flecker, 1992; Wallace *et al.*, 1993; Pringle & Blake, 1994; March *et al.*, 2002; Statzner, Peltret & Tomanova, 2003). Where tadpoles are abundant, it is likely they will have similar effects.

Amphibians are an abundant and diverse component of terrestrial and aquatic food webs in the humid tropics, and they are thus likely to be important at the ecosystem level. For example, estimates of amphibian species richness at neotropical sites range from 81 anuran species at a site in Ecuador (Crump, 1974) to at least 74 species at a mid-elevation site in central Panamá (Lips, Reeve & Witters, 2003). In these regions, adult and larval amphibians can be found in many aquatic habitats including streams, ponds, wetlands, canopy epiphytes that hold water, and tree holes (Inger, Voris & Frogner, 1986; Alford, 1999; McDiarmid & Altig, 1999), and they are often the most abundant vertebrates in these systems (Stebbins & Cohen, 1995; Duellman, 1999). Lips *et al.* (2003) documented densities of adult anurans as high as 1.35 individuals m^{-2} in riparian habitats in Panama and Stewart & Woolbright (1996) found densities of the terrestrial frog *Eleutherodactylus coqui* Thomas as high as 2.48 m^{-2} in a Puerto Rican forest. Despite their abundance and diversity in many systems, few studies have quantified the ecosystem-level significance of amphibians (but see Burton & Likens, 1975a,b).

Most aquatic tadpoles are primary consumers that metamorphose into insectivorous, terrestrial adults thus transferring energy acquired in aquatic habitats to terrestrial food webs (Wassersug, 1975). Given the number of habitats occupied and the diversity of larval body forms and feeding structures, different species of larval anurans probably use a variety of food resources including periphyton and detritus. However, the true trophic status of most tadpoles is not known (Altig & Johnston, 1989). Although streams in some temperate regions can harbour abundant insectivorous larval salamanders, herbivorous tadpoles are most abundant and diverse in lotic systems in the tropics (McDiarmid & Altig, 1999).

Amphibian populations are declining around the world (Alford & Richards, 1999; Houlahan *et al.*, 2000). The loss of tropical anurans could affect both terrestrial and aquatic systems. At least 13 Latin American countries have reported population declines and/or losses in the last 20 years, especially in upland areas (Young *et al.*, 2001). For example, Lips (1998, 1999) and Lips *et al.* (2003) described losses of 50% of the anuran species and 80% of anuran individuals in the mountains of southern Costa Rica and adjacent western Panamà. These studies also found that species associated with streams were more likely to disappear than more terrestrial species.

To assess the consequences of losses of anurans from tropical streams, we excluded tadpoles from substrata within an upland stream in Panamá. This stream is in a region that has not yet experienced a decline in amphibian populations, but is ecologically and geologically similar to other Latin American sites where declines have occurred. We predicted that tadpoles could control algal periphyton, and thus that exclusions would result in increased algal standing crop and species diversity. We also hypothesised that tadpole exclusion would result in an increase in the accumulation of sediment on the substratum because of reduced bioturbation, and that the abundance of grazing macroinvertebrates would be higher in the absence of tadpoles.

Methods

Study site

We conducted this study in a headwater tributary of the Río Guabal in Parque Nacional Omar Torríjos Herrera, El Copé, Coclé, Panamá (8°40′04.0″N, 80°35′35.6″W). This cloud forest is approximately 700 m a.s.l. on the continental divide and represents a transitional climatic zone between the wetter rainforests of the Atlantic slope and the drier forests of the Pacific slope. The study reach is one of several

headwater streams that flow into the Río Guabal (Pacific drainage), all of which are high gradient streams characterised by distinct sequences of pools, runs and riffles, with occasional waterfalls and plunge pools. The substratum is generally coarse, consisting mainly of pebbles and gravel with abundant cobbles and boulders and a few sandy deposits. Canopy cover is uniformly dense (>70%), with occasional treefall gaps.

We conducted this study from May to July 2001 during the early rainy season. During this period, mean daily rainfall was 5.6 mm (range 0–70 mm), daily air temperature was 21°C (range 16–30°C), daily stream temperature was 23–25°C, and stream pH was 6.7–7.0. On day 38 of the experiment, 70 mm of rain fell in <3 h, resulting in a spate that scoured most organic material, inorganic material and insects from the experimental plots and tiles. Thus, for some analyses, we focused on data from the sampling date just prior to this scouring event (day 31, see below).

Although nearby regions of western Panamá and Costa Rica have recently experienced widespread and massive losses of amphibian populations (Lips, 1998, 1999; Young *et al.*, 2001; Lips *et al.*, 2003), the El Copé study site still supports an abundant and diverse amphibian community. Over 70 amphibian species are known from El Copé, and at least 40 live in riparian habitats; 23 of these have stream-dwelling tadpoles (Lips *et al.*, 2003). Stream-dwelling species vary in their use of habitats; *Rana warszewitschii* and most hylid tadpoles live in pools, glassfrog tadpoles prefer leaf packs, *Colostethus* tadpoles burrow in detritus accumulations in marginal pools, and *Atelopus zeteki* adhere to large rocks in erosional habitats. Amphibians at this site are abundant throughout the year, with average capture rates of 0.36 (±0.05 SE) adult anurans per metre of stream and 0.13 adults (±0.004) per metre of terrestrial trail (Lips, unpublished data). Tadpoles are the only vertebrate grazers present in the headwaters of the Río Guabal (Ranvestel, 2002).

Tadpole densities and diets

In addition to visual surveys of tadpoles on tiles (see below), we estimated ambient tadpole densities in habitats along a 1 km stretch that encompassed our study reach, using both visual surveys ($n = 29$ run, riffle and pool sites) and removal sampling ($n = 11$ pool sites). Visual surveys were performed by count-

ing tadpoles observed on the substratum in randomly selected sections of erosional and depositional habitats. Removal sampling involved repeated dip netting in isolated pools until three consecutive sweeps of a 0.5 mm mesh net produced no further tadpoles. Following both procedures, the surface area of a sampled area was measured and numbers observed or collected were converted to density. Visual surveys counted only obvious tadpoles found on the substratum surface (e.g. *R. warszewitschii* (Schmidt), *Atelopus zeteki* Dunn, *Hyla* spp.), while removal sampling also captured interstitial species (e.g. *Hyla* spp., *Colostethus* spp.). It is difficult to distinguish between *R. warszewitschii* and *Hyla* spp. during visual surveys, so we combined the density of these two species.

To verify that tadpoles were ingesting diatoms, we quantified the gut contents of five individuals of each of two common species, *R. warszewitschii* and *Hyla colymba* Dunn, collected in 2000. A total of 3 cm of gut (1 cm foregut and 2 cm hindgut) was removed from each tadpole and contents were placed in glycerine and homogenised. Gut contents were then placed in a 40 mL beaker with 10 mL water and sonicated for 15–60 s to further break up the contents. Depending on the abundance of particles, either the entire sample or a subsample was filtered onto a gridded Metricel® (Pall Corporation, East Hills, NY, U.S.A.) filter (Gelman 0.45 μm), to obtain 10–15 particles per square. Filters were allowed to dry for 2 h at ambient temperature, cleared with Type A immersion oil, fitted with a cover slip, and sealed with clear enamel nail polish. Slides were examined with a stereoscope at 10× attached to a computer running Image Pro Plus 3.0.1 (Media Cybernetics, Silver Spring, MD, U.S.A.). The entire slide was reviewed, then two intersecting transects were selected for close examination and quantification. Twenty to 30 particles on transects were photographed, identified (plant particles, amorphous detritus, fungi, diatoms, filamentous green algae, or animal matter), and the area of each was measured.

Tadpole exclusion experiment

We conducted a 52-day experiment that began on 24 May 2001. Electric exclosure devices, similar to those described by Pringle & Hamazaki (1997), were used to exclude grazing tadpoles from artificial substrata placed in the stream. Exclosures consisted of a 0.5 × 0.5 m polyvinyl chloride (PVC) frame fitted with

two concentric loops of 12-gauge copper wire and were powered by 12 V, solar-powered electric fence chargers. Every 1–2 s, the fence charger supplied the copper wire with a pulse of electricity creating an electrified field that excluded tadpoles and other large macroconsumers, but allowed unrestricted access by small aquatic insects that were not affected (e.g. Pringle & Blake, 1994; March *et al.*, 2001).

We established five experimental plots within a representative 100-m section of stream. Each plot included one exclosure and one adjacent control. Runs were selected because water depth and velocity were less variable there than in riffles or pools. Current velocity (0.11–0.26 m s^{-1}), depth (5–13 cm), and canopy cover (>90%) were similar among all experimental plots and representative of stream conditions in this region. We anchored control and exclusion frames to large boulders on the stream bottom with monofilament nylon fishing line. Binder clips were attached to each end of six unglazed ceramic tiles (7.6 × 15.2 cm) and tiles were secured to PVC frames with monofilament nylon line and nylon cable ties. To verify that macroconsumers other than tadpoles (i.e. shrimps, crabs, fishes) were not interfering with experimental tiles, and to quantify tadpole visits to the tiles, we observed each pair of frames for 5 min on each of 10 days and 10 nights over the study period.

At approximately weekly intervals (days 16, 27, 31, 38, 45 and 52), we removed at random one tile per frame. We placed a dip net downstream of the tile as it was removed to collect any drifting macroinvertebrates. Each tile and the contents of the dip net were placed into a plastic bag and returned to the laboratory where we rinsed the tile and the contents of the bag into an enamel pan. We used a stiff toothbrush to remove any material remaining on the tile and this was added to the pan. We collected all macroinvertebrates from tiles and preserved them in 7% formalin. We poured the remainder of the sample into a graduated beaker and diluted it to a known volume. We preserved 15 mL subsamples of this homogenate with 2% formalin for determination of algal species composition and biovolume. We also filtered a 20–100 mL subsample of each homogenate onto a preashed and weighed glass fibre filter (0.7 μm). Filters were dried at 55°C for 48 h, weighed to the nearest 0.0001 g, ashed at 500°C for at least 2 h, and reweighed to obtain ash-free dry mass (AFDM) and inorganic mass (IM).

We also compared diatom species composition and abundance between the five control and five experimental tiles collected on day 31. We removed 5 mL subsamples from the formalin-preserved homogenate and boiled them for 1 h in 30% hydrogen peroxide to oxidise organic material. We rinsed the samples six times with distilled water to remove by-products and poured samples into small evaporating chambers similar to those designed by Battarbee (1973). We used a smaller than standard chamber size to concentrate the sample density. Coverslips were mounted on microscope slides with Naphrax™ (PhycoTech, St Joseph, MI, U.S.A.). We counted a minimum of 500 valves along transects of a coverslip using a Zeiss Universal research microscope (Carl Zeiss, Thornwood, NY, U.S.A.) with brightfield oil immersion optics (numerical aperture (NA) = 1.25) at 1000×. In two control replicates, counts were terminated after 14 transects because of extremely low diatom abundances. Diatoms were identified to the lowest taxonomic level (usually species) using standard taxonomic references (Hustedt, 1930; Patrick & Reimer, 1966; Krammer & Lange-Bertalot, 1986, 1988, 1991) and published neotropical flora (Hagelstein, 1938; Bourrelly & Manguin, 1952; Foged, 1984; Silva-Benavides, 1996). Identifiable fragments were mathematically reconstituted to whole valve units when possible and included in the total count. We calculated biovolume for each taxon using published estimates (Lowe & Pan, 1996; Alverson, Courtney & Luttenton, 2001) or, where published estimates were not available, by measuring dimensions of 10 cells and using BIOVOL software, version 2.1 (http://www.msu.edu/~kirschte/ biovol). These biovolume estimates were summed for all taxa and converted to total biovolume per square metre (mm^3 m^{-2}). We also calculated diatom species diversity (H') using the Shannon index (Pielou, 1966).

After the final tile was removed on day 52, we used a Surber sampler (Wildco, Buffalo, NY, U.S.A.) to collect benthic insects from beneath all treatment and control frames. Samples were preserved in approximately 7% formalin and macroinvertebrates were identified to family or genus where possible.

Statistical analyses

We used multivariate RM-ANOVA for a randomised block design to compare overall differences in AFDM, IM and macroinvertebrate abundance among
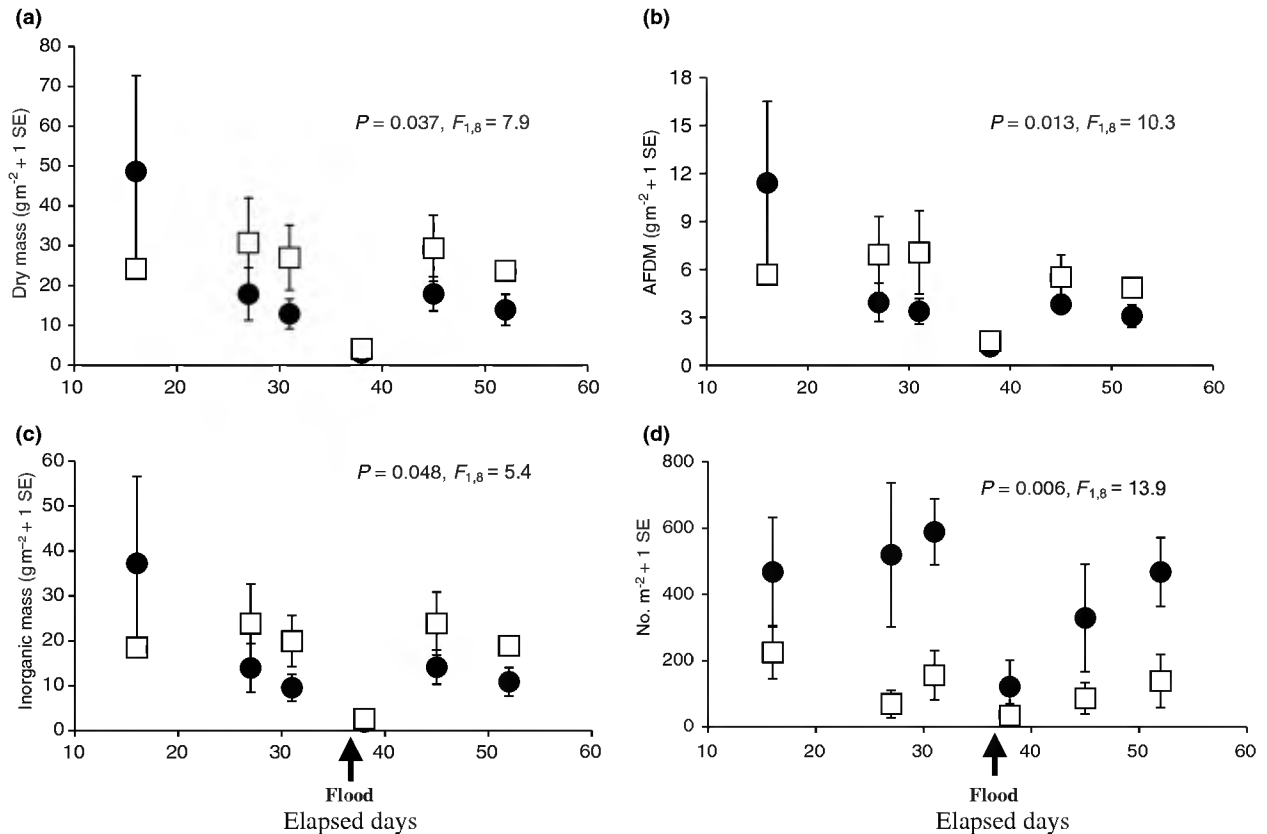
Fig. 1 Total dry mass (a), ash-free dry mass (AFDM) (b), inorganic mass (c), and baetid mayfly densities (no. m^{-2}) (d) on experimental tiles on each sampling date. Closed circles indicate control treatments and open squares indicate tadpole exclusions. Note consistent drop for all values in control and exclusion plots following the scouring flood that preceded the fourth sampling date (indicated by arrow).

treatments. For macroinvertebrates, we focused on baetid mayflies because they were the only grazers that were consistently abundant on tiles. On the first day that tiles were collected (day 16), one control tile had unusually high amounts of sediments on it (greater than three times any other tiles) because it was in a spot with lower flow (see day 16 data points on Fig. 1a–c). Because of this, we did not include this initial date in our statistical analyses of AFDM and IM on tiles. We log-transformed AFDM and IM values before analysis to correct for the non-homogeneity of variances. We compared algal community structure and biovolume between treatments at day 31 (last date when tiles were collected prior to the scouring flood on day 38) and total insect abundance between treatments at day 52 (end of the experiment) with a two-way ANOVA without replication. Correspondence analysis (CA) was used to investigate periphyton community structure in response to tadpole exclusion. Relative diatom abundance and

biovolume were compared by calculating the mean CA Axis 1 and 2 scores of exclosure and control replicates using a one-way ANOVA and Bonferroni *post hoc* testing (Peterson & Stevenson, 1992; Verb, Casmatta & Vis, 2001). All statistical analyses were performed with JMP (SAS, 2000) using $\alpha = 0.05$.

Results

Tadpole densities and feeding habits

Dominant tadpole taxa were abundant in most habitats in the study stream, but distributional patterns varied. *Atelopus zeteki* tadpoles were most abundant in erosional habitats [43.3 ± 5.1 m^{-2} (mean ± 1 SE) in runs and 60.0 ± 17.4 m^{-2} in riffles], but were absent from 95% of pools examined. In contrast, *R. warszewitschii* and *Hyla* spp. were abundant in both erosional (run = 23.6 ± 3.1 m^{-2}, riffle = 28.3 ± 0.3 m^{-2}) and pool habitats (36.7 ± 7.9 m^{-2}).

Gut contents analysis of five *R. warszewitschii* and five *H. colymba* tadpoles confirmed that both fed on periphyton; 31% (range 19–49%) of *R. warszewitschii* and 36% (range 17–54%) of *H. colymba* gut contents were diatoms. Unidentified, amorphous detrital material comprised nearly 50% of the gut contents of both species. Only one individual of each species had ingested filamentous green algae (1–3% of total contents), although nine of the 10 individuals had ingested pieces of terrestrial plant leaves (7–10%).

Algae, sediments and macroinvertebrates on tiles

Tadpoles were the most abundant macroconsumers in the study reach and on tiles. During 8.33 h of diurnal observation, only tadpoles and some insects were observed on tiles. During 8.33 h of nocturnal observations one small crab and two small *Macrobrachium* shrimps were the only non-anuran macroconsumers observed on control tiles.

We observed tadpoles on control tiles throughout the experiment. Visual surveys indicated that the density of tadpoles on control tiles ranged from 15.0–34.1 m^{-2} (mean = 26.3 ± 2.1, n = 10 observations) during the day, and from 5.8–46.2 m^{-2} (mean = 21.7 ± 4.4, n = 10 observations) at night, similar to the ambient density in the stream. Electric excluders effectively deterred most tadpoles from the frames, as tadpole density was 0–2.9 m^{-2} in the electrified plots by day (mean = 0.63 ± 0.29, n = 10 observations) and was 0 at night (n = 10 observations). Additionally, tadpoles in control plots represented the full range of body sizes observed in the field, while only the smallest tadpoles (i.e. <1 cm total length) were ever observed in exclosures.

Tadpoles significantly reduced the amount of total, organic and inorganic sediments on experimental tiles (Fig. 1a–c). Tiles in exclosures had 41% more AFDM (P = 0.013, $F_{1,8}$ = 10.29) and 43% more inorganic mass (P = 0.048, $F_{1,8}$ = 5.44) than tiles exposed to tadpole grazing for all sample periods combined. This pattern was established after day 16 of the experiment and persisted until the scouring flood of day 38 (Fig. 1a–c).

On day 31, we found a 61% greater biovolume of diatoms in exclosures compared to controls (P = 0.0395, $F_{1,4}$ = 9.075; Table 1). While relative biovolumes of the entire communities were not significantly different between control and exclusion

Table 1 Mean diatom genera biovolume (mm^{3}m^{-2} ± 1 SE) from experimental tiles collected on day 31 of the experiment. Exclusion indicates tiles from tadpole exclusion plots. Asterisk indicates mean control and exclusion values are significantly different (P = 0.0395, $F_{1,4}$ = 9.07)

	Treatment	
Taxa	Control	Exclusion
Achnanthidium	5.59 ± 2.06	13.39 ± 2.74
Amphipleura	3.95 ± 2.52	19.84 ± 10.23
Amphora	0.01 ± 0.01	0.01 ± 0.01
Anomoeoneis	0.01 ± 0.01	0.00 ± 0.00
Brachysira	0.13 ± 0.07	0.47 ± 0.17
Caloneis	0.01 ± 0.01	0.05 ± 0.03
Cocconeis	2.74 ± 1.10	1.61 ± 0.29
Cymbella	0.00 ± 0.00	0.02 ± 0.02
Diploneis	0.02 ± 0.02	0.06 ± 0.04
Eunotia	5.82 ± 1.64	12.31 ± 3.31
Frustulia	0.21 ± 0.14	0.57 ± 0.21
Fallacia	0.22 ± 0.10	0.24 ± 0.09
Gomphonema	0.41 ± 0.16	1.26 ± 0.13
Gyrosigma	1.43 ± 0.80	3.86 ± 1.73
Navicula	1.46 ± 0.52	2.91 ± 0.47
Nitzschia	0.25 ± 0.13	1.41 ± 0.73
Orthoseira	0.01 ± 0.01	0.00 ± 0.00
Pinnularia	0.07 ± 0.04	0.19 ± 0.05
Planothidium	0.03 ± 0.02	0.03 ± 0.03
Rhopalodia	0.03 ± 0.03	0.48 ± 0.15
Stauroneis	0.07 ± 0.07	0.00 ± 0.00
Synedra	0.54 ± 0.32	0.99 ± 0.44
Terpsinoe	0.90 ± 0.46	0.82 ± 0.48
*Total	23.92 ± 0.19	60.51 ± 0.29

treatments (P = 0.765, $F_{1,8}$ = 0.10), large species like *Amphipleura lindheimerii* Grun. and *Gyrosigma acuminatum* (Kutz.) Rabh. accounted for a large portion of the biovolume differences between treatments. Cell densities ranged from 553.1 to 4470.7 cells mL^{-1} on the control tiles and 2685.6–7007.6 cells mL^{-1} on the exclusion tiles. Average diatom abundance on control tiles (2372 ± 807 cells mL^{-1}) was approximately 50% less than that of exclusions (4328 ± 814 cells mL^{-1}), and this difference was marginally significant (P = 0.092, $F_{1,8}$ = 3.65).

We found a total of 103 diatom taxa representing 23 genera on the 10 tiles collected on day 31 of the experiment (Table 1). Twenty-five diatom taxa were unique to the control tiles, 33 were unique to the exclusion tiles, and 45 occurred in both treatments. Species composition showed a shift from a community of both adnate taxa and larger, upright taxa such as *G. acuminatum* and *A. lindheimerii* on exclusion tiles to primarily smaller, adnate taxa (*Achnanthidium* spp.,

Table 2 Mean number of aquatic insects (±1 SE) collected per tile from all experimental tiles on all sample dates. Exclusion indicates tiles from tadpole exclusion plots

Taxa	Control	Exclusion
Baetidae	24.00 ± 3.95	6.17 ± 1.19
Chironomidae	2.00 ± 0.68	2.67 ± 1.02
All others	1.00 ± 0.68	0.33 ± 0.21
Total insects	27.00 ± 4.40	9.17 ± 1.76

Table 3 Mean number of aquatic insects per square metre (±1 SE) collected in Surber samples from substrata beneath control and exclosure treatments on the last day of the experiment (day 52)

Taxa	Control	Exclosure
Ptilodactylidae	3.00 ± 2.28	1.60 ± 0.93
Hydropsychidae	3.00 ± 0.45	1.40 ± 0.93
Calamoceratidae	1.40 ± 0.93	0.60 ± 0.24
All others	0.60 ± 0.40	0.60 ± 0.40
Total insects	8.00 ± 2.41	4.20 ± 1.77

Cocconeis spp. and *Eunotia* spp.) on control tiles, but these differences were not significant based on CA and a one-way ANOVA ($P = 0.3072$, $F_{1,8} = 1.19$). There were also no significant differences in species richness between control and exclusion tiles ($P = 0.196$, $F_{1,8} = 1.98$). Diversity was approximately 30% higher on tiles from exclusions ($H' = 3.0$) compared with controls ($H' = 2.0$).

Aquatic insects on tiles consisted almost exclusively of baetid mayflies and chironomids (Table 2). Baetid mayflies were present on tiles at all sites throughout the experiment, but were 76% more abundant in control than exclusion treatments for all dates combined ($P = 0.006$, $F_{1,8} = 13.59$; Fig. 1d; Table 2). Mayfly abundance decreased sharply after the high discharge event on day 38 but rebounded to previous values by the next sample date 7 days later. Surber samples from beneath control and treatment frames suggested that treatment did not have an effect on the abundance of benthic aquatic insects ($P = 0.27$, $F_{1,4} = 1.6$; Table 3).

Discussion

Tadpole feeding and bioturbation

Our study demonstrates that tadpoles can influence algae and sediment dynamics in tropical streams.

Where tadpole grazing and associated bioturbation were excluded, we found a significant increase in both benthic sediments and algal biovolume. Few studies have examined tadpoles in streams, but similar patterns have been observed for other grazers such as mayflies, fishes and shrimps (e.g. Pringle & Blake, 1994; Flecker, 1996, 1997; Pringle & Hamazaki, 1997, 1998; Pringle *et al.*, 1999; March *et al.*, 2002). The few other tadpole exclusion studies (e.g. Lamberti *et al.*, 1992; Flecker *et al.*, 1999) have found reduced AFDM, chlorophyll *a* and algal abundance on stream substrata subject to tadpole grazing. In particular, Flecker *et al.* (1999) found that *Rana palmipes* Spix tadpoles at densities as low as 10 m^{-2} were capable of removing up to 100% of accrued sediment from the substratum in a lowland Venezuelan stream. Natural densities of tadpoles in all habitats at our site were as much as six times greater than those in the Flecker *et al.* (1999) study, suggesting that the numerous tadpoles in upland streams such as ours may have relatively large impacts on benthic processes and communities.

Bioturbation associated with foraging by a variety of grazers may alter sediment dynamics and algal communities. Snails (Hawkins & Furnish, 1987; Harvey & Hill, 1991), tadpoles (Kiffney & Richardson, 2001) and fishes (Flecker, 1992) have all been referred to as the 'bulldozers' of the benthic world because they disturb deposited sediments as they forage. Analysis of gut contents and our observations in the field confirm that the common tadpoles in our system fed on periphyton and associated organic sediments. In addition to direct consumption, however, bioturbation by tadpoles appeared to reduce sedimentation on tiles. We frequently observed *R. warszewitschii* and *A. zeteki* feeding on our tiles and on the natural substratum throughout the stream. Wherever tadpoles were feeding, cleared trails were evident in the sediments because, as tadpoles flick their tails to move, they suspend plumes of sediment in the water column which are then easily entrained.

Grazing effects on diatom communities

Our results indicate that grazing by tadpoles can alter periphyton biomass and possibly community structure and diversity. The lack of significant differences in cell densities between treatments may have been related to the relatively small sample size used (five replicates per treatment and one sampling date) and/

or spatial heterogeneity of periphyton. Spatial heterogeneity also may have been a reason for the lack of periphyton removal by tadpoles on some of the control tiles, as there was marked variation in cell densities among tiles, especially among control tiles. Overall, there was a trend of more diatom individuals and species in the exclosures than the controls, and tadpole grazing shifted species composition from a community of mostly tall, stalked and erect or loosely attached taxa such as *Gomphonema* spp., *G. acuminatum*, and *A. lindheimerii* to a more cropped community of adnate, understory taxa dominated by *Achnanthidium* and *Cocconeis* species. In contrast to the upright species, these smaller, adnate taxa are able to grow under grazing pressure and may also be more resistant to scouring (Hill & Knight, 1987; Stevenson, 1990). The shift in species composition that we found is similar to the effects of grazing by snails (Hill, Boston & Steinman, 1992; Rosemond, Mulholland & Elwood, 1993), fishes (Pringle & Hamazaki, 1997), shrimps (Pringle, 1996) and aquatic insects (Steinman *et al.*, 1987; Walton, Welch & Horner, 1995).

Growth form also explains the difference in biovolume between the exclosure and control tiles that we observed. The larger taxa present in the exclosure tiles, like *A. lindheimerii* and *G. acuminatum*, accounted for a larger percentage of the total biovolume on the exclusion tiles. Tadpoles removed these larger, upright cells and reduced the overall biovolume by decreasing the average cell size of diatoms. This reduction in total biovolume is similar to the decreases in biovolume associated with grazing by a temperate tadpole, *Rana boylii* Baird, which decreased diatom biovolume on *Cladophora* by 56% (Kupferberg, 1997). Overall biovolume in both the control and exclosure treatments in our study was considerably lower compared with other work in the neotropics (e.g. 1200 $mm^3 m^{-2}$ in unshaded Costa Rican streams; Pringle & Hamazaki, 1997), probably because of light limitation in our heavily shaded streams. We anticipate that the influence of grazing tadpoles in less heavily shaded neotropical streams (e.g. larger, lowland systems or logged areas) would be even more pronounced than observed here.

Tadpole interactions with other grazers

The dense canopy cover and steep topography of our study site limited sunlight penetration to a few hours at midday in most reaches. As a result, litterfall is probably the major energy source for this and similar streams in the region (e.g. Vannote *et al.*, 1980), and low rates of primary production may lead to competition among grazers. However, we found that tadpole grazing increased the abundance of other grazers such as baetid mayflies. Although this result seems counterintuitive, some other studies have also shown positive relationships where grazers enhanced the quality or availability of food resources for others (Feminella & Resh, 1991; Gelwick & Matthews, 1992; Pringle *et al.*, 1993; Creed, 1994; Flecker, 1996; March *et al.*, 2002). However, unlike ours, many of these studies also showed negative impacts of grazing macroconsumers on smaller taxa, where macroconsumers probably displaced smaller-bodied grazers through exploitative or interference competition (Flecker, 1984, 1992; McAuliffe, 1984; Dudgeon & Chan, 1992).

Grazers can facilitate algal growth and production by removing sediment and epiphytic diatoms (e.g. Power, 1990; Rosemond, 1993a; Kupferberg, 1997), and we hypothesise that tadpoles indirectly facilitated baetid mayflies during our study by clearing sediment from the substratum, through both ingestion and bioturbation, and exposing underlying algal food resources. Baetid mayflies are grazers and collector-gatherers that feed on fine detritus and diatoms, and they can recognise and colonise food-rich patches (Kohler, 1984, 1985; Richards & Minshall, 1988). In a recent ^{15}N tracer experiment, baetids were more highly labelled with ^{15}N than the average of any single potential food resource in the stream, indicating they were selectively feeding on highly active material at a fine scale (Dodds *et al.*, 2001). By disturbing and removing sediments during our study, tadpoles exposed underlying diatoms and mayflies responded positively to these relatively sediment-free, food-rich patches.

Although baetid mayflies were abundant on our tiles, they were not a dominant component of adjacent substrates based on our samples of natural substrates from beneath the tiles. It is likely that we under-sampled baetids on natural substrates because they are very active and mobile insects that likely swam or drifted while the Surber sampler frame was being placed on the substrates. It is also possible that baetids were attracted to the periphyton on the relatively stable and flat tiles and thus were concentrated there.

While other macroconsumers such as large crustaceans were present in our stream, for several reasons we attribute differences in the amount of sediments on tiles to tadpoles rather than to these other taxa. First, we rarely observed *Macrobrachium* shrimp or crabs on tiles whereas tadpoles were nearly always present. Secondly, stable isotope analyses conducted at this same stream site from May to August 2000 indicated that both *Macrobrachium* and crabs feed at a higher trophic level than tadpoles (S. Kilham, C. Pringle, K. Lips, D. Drake & T. Ranvestal unpublished data). Finally, these results are in agreement with diet analyses and feeding observations conducted at other sites in the tropics, where *Macrobrachium* are considered to be predators and stream-dwelling crabs are omnivores feeding on invertebrates, fruits and seeds (Abele & Blum, 1977; Covich & McDowell, 1996).

As with the large crustaceans, there is ample evidence that fish did not influence the results of our study. Both species of fish at this site are predators and were never observed on our experimental tiles. Gut contents of 15 individuals of *Brachyraphis roswithae* Meyer & Etzel indicated that they were opportunistically feeding on terrestrial, aerial and drifting insects, and thus had minimal interaction with benthic algae, sediment or insects (Ranvestel, 2002). The fossorial catfish *Trichomycterus striatus* Meek & Hildebrand, which is very rare at our site, feeds almost exclusively on benthic insects in the interstitial spaces of riffles (Power *et al.*, 1988).

Consequences of the decline in amphibian populations

The decline in amphibian populations of the magnitude recently documented in many upland tropical sites (e.g. Pounds *et al.*, 1997; Lips, 1998, 1999; Lips *et al.*, 2003) would be expected to produce cascading effects throughout aquatic and terrestrial food webs. At the least, adult and larval amphibians represent a large pool of available prey in tropical streams and a substantial decline in abundance would be expected to affect predator populations, such as the diverse guild of tropical frog-eating snakes that depend on them (Cadle & Greene, 1993; Pounds, 2000).

Along with the loss of prey for snakes and other predators, the results of this study and others (e.g. Lamberti *et al.*, 1992; Kupferberg, 1997; Flecker *et al.*, 1999) indicate that the catastrophic decline and extinc-tion of amphibians that is currently occurring will influence stream food web dynamics and energy flow in a variety of other ways. The severe reduction of stream macroinvertebrates significantly decreased litter decomposition and generation and export of fine particle organic material (FPOM) in Appalachian mountain streams (Wallace, Webster & Cuffney, 1982; Cuffney *et al.*, 1990; Chung *et al.*, 1993; Whiles *et al.*, 1993), and we predict that the loss of grazing tadpoles will have similar, ecosystem-level effects in these headwater neotropical streams. Specifically, our results suggest several top-down responses to tadpole extinctions, including increased algal biomass, altered algal community structure, increased accumulation of organic and inorganic sediments on the substratum (and thus less export to downstream reaches), and possible shifts in distribution and/or feeding patterns of grazing insects. In the light of the continuing decline in amphibians, we need future studies of their role in ecosystem structure and function before they disappear.

Acknowledgments

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