Ecosystems (2008) 11: 1262–1276
DOI: 10.1007/s10021-008-9191-7

ECOSYSTEMS

Changes in Stream Primary Producer Communities Resulting from Large-Scale Catastrophic Amphibian Declines: Can Small-Scale Experiments Predict Effects of Tadpole Loss?

Scott Connelly,[1]* Catherine M. Pringle,[1] Rebecca J. Bixby,[2] Roberto Brenes,[3] Matt R. Whiles,[3] Karen R. Lips,[3] Susan Kilham,[4] and Alexander D. Huryn[5]

[1]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602, USA;* [2]*Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA;* [3]*Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901-6501, USA;* [4]*Department of Bioscience and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104, USA;* [5]*Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA*

Abstract

Global declines of amphibian populations are well documented, yet effects of these declines on freshwater ecosystem structure and function are poorly understood. Here we examine responses of algal primary producers to tadpole extirpation over differing spatial and temporal scales. We experimentally excluded tadpoles from artificial substrata within localized areas (0.25 m^2) of two streams. One stream had an intact community of frogs (*frog* stream), and the other had recently experienced a catastrophic decline (*frogless* stream), leaving virtually no tadpoles. In the *frog* stream, there were significantly greater levels of chlorophyll *a* (+111%, $P = 0.009$), ash-free dry mass (AFDM) (+163%, $P = 0.02$), inorganic sediments (+114%, $P = 0.001$), and higher mean algal cell biovolume in tadpole exclusion treatments than in the tadpole access treatments. Correspondingly, overall AFDM-specific net primary production (NPP) increased by 38% ($P = 0.001$) and chlorophyll *a*-specific NPP increased by 29% ($P = 0.001$) in tadpole access treatments compared to tadpole exclusion treatments. Areal-specific NPP did not differ between treatments. There were no significant differences in chlorophyll *a*, AFDM, inorganic sediments, algal cell biovolume, or biomass-specific NPP between treatments in the *frogless* stream. Fifteen months after our experiments, a massive amphibian decline associated with a fungal pathogen occurred in the *frog* stream, resulting in the extirpation of over 90% of tadpoles. This extirpation was followed by significant increases in levels of chlorophyll *a* (269%, $P = 0.001$), AFDM (+220%, $P < 0.001$), and inorganic sediments (+140%, $P = 0.001$). Reach-scale NPP increased from −1587 to −810 mg DO m^{-2} d^{-1}. Additionally, algal community composition shifted from a dominance of small adnate diatoms (pre-decline) to a dominance of large upright algal species (post-decline). Our experimental results, combined with algal monitoring at the reach scale, indicate that

Received 7 January 2008; accepted 19 May 2008; published online 23 September 2008

Author Contributions: S.C., C.M.P., M.R.W., K.R.L., and S.K. designed the study, S.C., C.M.P., R.B., M.R.W., K.R.L., and A.D.H. performed research, S.C., C.M.P., R.J.B., M.R.W., and A.D.H. analyzed data. S.C., C.M.P., and R.J.B. wrote the paper.

*Corresponding author; e-mail: scottcon@uga.edu

over the course of our study catastrophic amphibian losses have significant effects on stream ecosystem structure and function. Ecosystem-level impacts of tadpole extirpations were more dramatic than results from our small-scale, short-term experiments, which predicted the direction of change in response variables but underestimated the magnitude. However, the long-term stream ecosystem responses remain unknown.

Key words: tadpoles; amphibian declines; Panama; tropical streams; primary production; grazing; periphyton.

Introduction

Biodiversity is declining on a global scale and across taxonomically diverse groups (Chapin and others 1998). Many freshwater taxa, such as fishes, mussels, crayfishes, and amphibians, are disproportionately imperiled (Ricciardi and Rasmussen 1999). A burgeoning literature exists to address effects of biodiversity change on ecosystem structure and function, and there is increasing evidence of significant changes in ecosystems where these losses are occurring (for example, Tilman and Downing 1994; Hooper and others 2005; Hector and Bagchi 2007; McIntyre and others 2007). However, few studies have quantified the effects of species loss in situ during an actual extirpation event.

What are the effects of widespread losses of entire taxonomic groups of consumers on stream ecosystems? This is a key question with respect to amphibians, which are suffering global catastrophic losses (Lips and others 2006; Whiles and others 2006). As many as 120 species of amphibians have become extinct since 1980, and currently one-third of known amphibian species are threatened (Stuart and others 2004). Amphibians are often an abundant and diverse component of both terrestrial and aquatic ecosystems. They are the most common land vertebrate throughout parts of the Neotropics (Stebbins and Cohen 1995), with densities of adult frog populations as high as 1.35 individuals m^{-2} in riparian habitats in Panama (Lips and others 2003). Continued widespread catastrophic declines of amphibians are expected to alter ecosystems across the globe because of the linkages that they create between aquatic and terrestrial systems (for example, Regester and others 2006), and their potential role as keystone species (Holomuzki and others 1994; Wissinger and others 1999).

In this study, we focus on effects of this biotic impoverishment (that is, the loss of the entire frog assemblage) on algal primary producers in Neotropical streams. Although the importance of other grazing taxa, such as invertebrates and fishes, is well documented in lotic systems (for example, Rosemond and others 1993; Pringle and Hamazaki 1997; March and others 2002), the ecological role of tadpoles in streams is less studied. Experiments have shown that grazing amphibian larvae can influence the abundance and community composition of periphyton and insect assemblages (Lamberti and others 1992; Ranvestel and others 2004). However, the influence of tadpoles on ecosystem function (for example, primary production) has rarely been studied (but see Kupferberg 1997), and the extent to which tadpoles alter periphyton communities can be difficult to predict, as their influence on periphyton can be the result of complex interactions among a number of biotic and abiotic variables (Mallory and Richardson 2005). Moreover, experimental studies quantifying the influence of tadpoles on primary producers have been conducted on relatively small spatial scales and for short periods of time (for example, Flecker 1996; Ranvestel and others 2004). Results of these studies have not been validated with comparisons to ecosystem response to widespread losses of tadpoles over greater spatial and temporal scales. Short-term, small-scale experimental tadpole exclusion studies have the potential to underestimate large-scale ecosystem responses to tadpole losses as there would possibly be a lack of sufficient time for algal community composition to change. Additionally, flat experimental tiles do not fully replicate the more complex structure of natural stream substata, which could result in higher rates of sloughing of periphyton from within our treatments than might be occurring in the stream.

The objective of our study was to quantify algal periphyton response to amphibian declines at different spatial and temporal scales. On a 'local' scale we experimentally manipulated the presence and absence of tadpoles, in situ, in two upland Panamanian streams. One stream had a healthy population of stream-dwelling tadpoles (at the onset of our studies), and the other had virtually no tadpoles as a result of a fungal pathogen-related amphibian population decline in 1996 (Lips 1999). We also examined algal community composition and biomass at the reach-scale within both study streams over a 2-year period, inclusive of the per-

iod during which the stream with the healthy frog population experienced a massive amphibian die-off. This extirpation provided the rare opportunity to interpret results of our short-term, small-scale exclusion experiments in the context of long-term, reach-scale responses. We hypothesized that tadpole-exclusion experiments in a stream with an intact amphibian community would: (1) result in algal standing crop and community composition similar to that found in a stream where tadpoles had been extirpated; and (2) predict the *direction*, but under-estimate the *magnitude*, of changes in algal standing crop and community composition resulting from whole-stream tadpole extirpation.

Methods

Study Sites

Research was conducted in two Panamanian headwater streams. The *frog* stream had an intact population of amphibians, whereas the *frogless* stream was essentially devoid of amphibians due to a catastrophic extirpation associated with the fungal pathogen *Batrachochytrium dendrobatidis* in 1996 (Lips 1999). The study streams are approximately 200 km apart, and are physically similar in terms of order, discharge, geology, temperature, canopy cover, and nutrient concentrations.

The *frog* stream (Rio Guabal) is located in the Parque Nacional G. D. Omar Torrijos Herrera, El Copé, Coclé, Panama (8°40′N, 80°35′W). The park is comprised of cloud forest and is situated on the continental divide at approximately 600 m a.s.l. Our study reach is part of a high gradient stream characterized by distinct pool-run-riffle sequences, with substrates consisting of pebbles and gravel, with frequent cobbles, boulders, and depositional sandy areas. Riparian canopy cover is generally dense (>80%), with occasional tree-fall gaps.

The *frog* stream drainage supports 74 documented species of amphibians, 40 of which live in the riparian zone. Of these, 23 have stream-dwelling larvae (Lips and others 2003). Adult frog abundance is high throughout the year, with mean capture rates of 0.36 (±0.05 SE) frogs m^{-1} of stream and 0.13 (±0.0004) m^{-1} of trail walked (K.R. Lips unpublished data). Tadpoles occur in all stream habitats: pools and runs support *Rana warszewitschii* and several treefrog (Hylidae) species; *Atelopus zeteki* (Bufonidae) frequent riffles and erosional areas; glass frogs (Centrolenidae) use leaf packs; and several species of *Colostethus* (Dendrobatidae) are found in detritus of marginal pools. Tadpoles of *R. warszewitschii, Hyla palmeri*, and *H. colymba* are numerous and prominent, achieving densities of up to 50 m^{-2}, and tadpoles are the only vertebrate grazers in this stream at this elevation (Ranvestel and others 2004). Two water column-feeding fish species (*Brachyrhaphis roswithae* and *Trichomycterus striatus*), one *Macrobrachium* shrimp species, one crab species (*Pseudothelphusa*), and 26 families of aquatic insects are found within park streams (Ranvestel 2002; Colon-Gaud and others unpublished data).

The *frogless* stream (Quebrada Chorro) drains the Reserva Forestal Fortuna, Chiriquí, Panama (8°42′N, 82°14′W). The site is approximately 200 km west of the *frog* stream, at about 1200 m a.s.l., and includes montane and lower montane rainforest and cloud forest habitat. The stream has a moderate gradient and, like the *frog* stream, is characterized by pool-run-riffle sequences and flows over mainly pebble, gravel, and sand substrates, with silt in depositional areas. The stream also has dense canopy cover (>80%).

Amphibian populations have been monitored at the *frogless* site since 1993 (Lips 1999; K.R. Lips unpublished data). Fifty-seven species were initially documented, of which 34 were riparian species and 22 of those with stream-dwelling tadpoles. The amphibian community once included the periphyton-grazing *R. warszewitschii*, *H. palmeri*, *H. colymba*, *Atelopus*, and other groups such as *Colostethus* and Centrolenids (Lips 1999) which were found in the the *frog* stream at the onset of our study. In 1996, Lips documented a mass mortality event and subsequent population decline of the amphibians in the *frogless* stream, and by 2000 only 23 species were found, 8 of which had stream-dwelling larvae. Stream tadpole densities were documented as high as 50 m^{-2} in 1993 (Lips 1999); however, virtually none (<0.01 tadpoles m^{-2}) have been seen since 2000. Stream fish and invertebrate communities are similar to those of the *frog* stream (de Sousa 1999).

Small-Scale Tadpole Exclusion Experiments

Tadpole exclusion experiments were run consecutively at each site during the rainy season, from June 12 to July 22, 2003 at the *frog* stream and from July 25 to September 3, 2003 at the *frogless* stream. Mean daily rainfall during the 40-day study at the *frog* site was 3.6 mm d^{-1} (range 0–49 mm d^{-1}), mean stream pH was 7.3, mean water temperature was 21.4°C, NO_3–N was 0.16 mg l^{-1} and PO_4–P was 0.02 mg l^{-1} (one-time nutrient concentrations measured during the experiment, at baseflow

conditions). At the *frogless* site, mean daily rainfall during the study was 2.7 mm d^{-1} (range 0–10.8 mm d^{-1}), stream pH was 8.1, mean water temperature was 18.5°C, NO_3–N was 0.12 mg l^{-1} and PO_4–P was 0.02 mg l^{-1}.

Electric exclusion devices (0.5 m^2 frames constructed of PVC tubing and concentric copper wire loops), modified from Pringle and Hamazaki (1997), were used to exclude tadpoles from artificial substrates placed on the stream bottom. Similar electric exclusion devices have been used effectively to exclude a variety of aquatic macroconsumers (for example, tadpoles, fishes, shrimps, and crayfishes) from habitat patches, while not affecting movements of small aquatic insects (Pringle and Blake 1994; Schofield and others 2001; March and others 2002; Ranvestel and others 2004). Within each stream, 10 treatment pairs (one electrified frame and one identical control frame without electricity) were placed within comparable 200 m reaches, with five pairs each in pools and riffles. Pools and riffles were selected based on similar current velocities (pools: ~0 m s^{-1}, riffles 0.15–0.33 m s^{-1}), depths (pools: 19–24 cm; riffles: 15–18 cm), and percent canopy cover (75–85%). Current velocity was measured with a Marsh McBirney current meter and canopy cover was measured with a spherical densiometer. The two PVC frames of each pair were situated at least 0.5 m apart and anchored to the stream bottom using tent stakes and cable ties. Eight unglazed ceramic tiles (7 × 15 cm) were secured within each frame using binder clips and monofilament fishing line, for a total of 80 tiles per treatment per stream. Each frame was observed for 3 min on each of 20 days and 20 nights during the course of the experiment, for a total of 40 h for all frames in each stream, to quantify tile visitation by tadpoles and to verify that other potential macroconsumer visitors (for example, fishes and shrimps) were not accessing control treatments. Grazing tadpoles were identified to species in the cases of *R. warszewitschii* and *A. zeteki*. Due to the difficulty of species-level identification in situ, tadpoles of the genus *Hyla* were identified only to genus.

One randomly selected tile was removed from each frame every 5 days over a 40-day period. Each tile was placed within a fine mesh dip net (to prevent the escape of invertebrates), slowly raised to the stream surface, and placed in a Ziploc® bag along with the contents of the dip net. Tiles were placed in a cooler and transported to the laboratory where each tile was scrubbed with a toothbrush and rinsed, along with the contents of the bag, into an enamel pan. Invertebrates were removed from the homogenate and preserved in 7% formalin for identification. The homogenate was transferred to a beaker and diluted to a known volume. While stirring, 20 ml was subsampled and preserved with 2% formalin for later analysis of algal species composition and biovolume. From the remaining homogenate two subsamples were obtained. The first 40–100 ml subsample was filtered onto a combusted and pre-weighed Whatman glass fiber filter (0.7 μm). These filters were dried at 60°C for 24 h, weighed to the nearest 0.0001 g, ashed at 500°C for 2 h, and reweighed to determine ash-free dry mass (AFDM) and inorganic sediments. The second 40–100 ml subsample was filtered onto a glass fiber filter (0.7 μm), placed in an aluminum-foil pouch, and frozen until analysis for chlorophyll *a*. Chlorophyll *a* was estimated using a Turner Designs model 10-AU fluorometer (Turner Designs, Inc., Sunnyvale, California, USA) using standard methods (APHA 1985).

Benthic invertebrates from control and experimental treatments were sampled using a Surber sampler after the final tiles were collected on day 40. Invertebrates were preserved in 7% formalin and identified to family or genus. Algal community composition and biovolume also was assessed on day 40 using a 20 ml formalin-preserved subsample. Densities of filamentous cyanobacteria were determined using a Palmer-Maloney counting chamber at 400× magnification (brightfield optics) on a Zeiss Universal microscope. Taxa were identified and enumerated along a transect(s) until 300 live cells/units were recorded. Some cyanobacterial filaments were counted in 10 μm lengths (one length = one unit). In samples with extremely low cell densities, a maximum of 10 transects were examined.

A 5-ml subsample for diatom identification was boiled in 30% hydrogen peroxide for 1 h to oxidize organic material. Samples were rinsed six times with distilled water to remove by-products and evaporated onto coverslips in 100 ml beakers to concentrate cell densities. Coverslips were mounted on microscope slides with Naphrax™ (PhycoTech, St. Joseph, Michigan, USA). A minimum of 500 valves were enumerated and identified along transects of the coverslip using a Zeiss Universal research microscope (Carl Zeiss, Thornwood, New York, USA) with brightfield oil immersion optics at 1000×. Identifiable valve fragments along each transect were categorized by size relative to whole valves (for example, 25%), and mathematically reconstituted to whole-valve units and fractions. Diatoms were identified to the lowest taxonomic level (usually species) using standard taxonomic references (Patrick and Reimer 1966; Krammer and Lange-Bertalot 1986; 1988; 1991) and published

Neotropical flora descriptions (Bourrelly and Manguin 1952; Foged 1984; Silva-Benavides 1996). We calculated the biovolume for each taxon by measuring dimensions of 10 cells and using published geometric equations to calculate cell biovolumes (Hillebrand and others 1999).

On a localized scale, net primary production (NPP), as measured by oxygen production, was measured on the final sampling dates (days 39 and 40; 10 tiles per treatment per stream). Each tile was placed in a custom-made Plexiglass metabolism chamber (Rapid Creek Research, Boise, Idaho, USA), which was filled with stream water. Air bubbles were removed, the container was sealed, and a 12-V electric re-circulating pump was used to simulate stream current at 2.4 cm s^{-1} within the chamber. Changes in dissolved oxygen over a period of 1 h were obtained from a small chamber port using a YSI Model 58 Dissolved Oxygen Meter (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio, USA) with a self-stirring probe. Each tile used in the metabolism chambers was processed as described above to determine the corresponding algal biomass estimates used for calculations of biomass-specific NPP.

Pre- and Post-Decline Comparisons

To characterize changes in algal standing crop and community composition over time, and to determine whether periphyton biomass and composition associated with experimental tiles were representative of the natural stream substratum, periphyton on rocks from both streams were sampled monthly over 24 months, beginning June 2003. A benthic sampler, modified after Loeb (1981), was used to quantitatively sample periphyton from a known area of these natural substrata. Five replicate samples of benthic algae and inorganic sediments were collected from rocks, during baseflow, in each of five pools and riffles along the same 200 m reach used for the exclusion experiment. The replicate samples from each pool or riffle were pooled and homogenized. A 20-ml subsample was preserved with formalin, and the remaining homogenate was analyzed for chlorophyll *a*, AFDM, and inorganic sediments following previously described methods. Subsamples from three pools and three riffles sampled from the *frog* stream were analyzed monthly for diatom and soft algae community composition. Densities were determined using a Palmer-Maloney counting chamber at 400× magnification (brightfield optics) on a Zeiss Universal microscope. We counted 300 cells, identified the nine largest diatoms to species level, quantified the filamentous cyanobacteria cells, and categorized the remaining smaller diatom species as a group. For samples with extremely low cell densities, a maximum of 10 transects were examined.

Tadpole abundance surveys were conducted monthly. Surveys began in June 2003 and continued through June 2005. Tadpoles in three randomly chosen pools were quantified with a stovepipe benthic corer (22-cm diameter) that was modified with external rubber flaps at the base, which helped seal the bottom of the sampler when substrate was irregular. The core sampler was pushed approximately 3 cm into the substrate, and tadpoles were removed with a dip net ($15 \times 10 \times 10$ cm^3), counted, identified, and released. Kick net sampling was used to quantify tadpoles in three randomly chosen riffles, according to methods described by Hauer and Resh (1996) and Heyer and others (1994).

We measured reach-scale metabolism in the *frog* stream on March 4–5, 2004 (pre-decline) and June 5–6, 2005 (post-decline), using the single-station method (Owens 1974). Prevailing weather (for example, temperature and rainfall), staff gage height, and discharge (39 l s^{-1}; baseflow conditions) were similar during the two sampling periods. Diel oxygen curves (readings at 10–12 min intervals for 24 h) were obtained at the upstream and downstream ends of the 100 m study reach during each sampling event using YSI 600 sondes. We used the single-station approach because diel changes in dissolved oxygen in this stream were too subtle to use an upstream–downstream, two-station method. Prior to sampling, sondes were calibrated in water-saturated air at sea level and oxygen saturation values were later corrected for altitude. Reaeration was estimated by measuring decline in dissolved propane concentrations along the study reach during a steady-state propane injection performed on each sample date (Marzolf and others 1994). A sodium chloride solution was added as a conservative tracer at the same time as the propane to account for dilution and to estimate reach travel time. Metabolism was calculated based on Marzolf and others (1994) using the corrected measure of oxygen flux via reaeration (Young and Huryn 1998). Reach-scale metabolism could not be measured at the *frogless* stream because of the discovery of a large groundwater source along the reach and adverse weather conditions during site visits.

Statistical Methods

Differences in chlorophyll *a*, AFDM, inorganic sediments, and invertebrates in the small-scale

exclusion experiments were assessed using repeated measures ANOVA. Chlorophyll *a*, AFDM, and inorganic sediments values were log-transformed prior to analysis to satisfy the assumption of normality of variances. Analyses were performed on SAS System for Windows, Version 8.0 (SAS Institute, Cary, North Carolina, USA) using $\alpha = 0.05$.

Indicator species analysis (ISA) (Dufrêne and Legendre 1997) was used to determine which algal taxa were characteristic of either control or exclusion treatments in the small-scale experiment. This analysis generates an indicator value [0 (not an indicator)−100 (perfect indicator)] for each taxon based on the product of relative frequency and abundance (based on cell numbers) of each taxon in each treatment. Monte Carlo tests (1500 randomizations) were run to determine if the indicator value is greater than expected by chance. Indicator species have both an indicator value above 25 and a p less than 0.05 (Dufrêne and Legendre 1997). This classification was calculated using PC-ORD software (Version 4.37, McCune and Mefford 1999).

Monthly whole-stream sampling was unreplicated (that is, one reference and one treatment stream). We used Randomized Intervention Analysis (RIA, Carpenter and others 1989) to detect pre- and post-decline changes in chlorophyll *a*, AFDM, levels of inorganic sediments, and tadpole abundance in the *frog* stream relative to the *frogless* stream. RIA tested the null hypothesis that no change occurred in these variables in the *frog* stream relative to the *frogless* stream following the decline in amphibian abundance.

Results

Small-Scale Tadpole Exclusion Experiments

Tadpole Densities

In the *frog* stream, tadpoles were abundant grazers throughout the experiment. Ambient stream densities of the most common species, *R. warszewitschii*, ranged from 6.4 to 39.2 m^{-2} (mean 27.6 ± 11.8) in pools and 0 to 28.1 m^{-2} (mean 14.2 ± 10.2) in riffles. *Hyla* spp. and *A. zeteki* were encountered less frequently than *Rana*, with *Hyla* more common in pools (range 1.8–5.4 m^{-2}, mean 3.4 ± 1.4) and *A. zeteki* found only in riffles (range 0–3.6 m^{-2}, mean 2.0 ± 0.9). No other macroconsumers (for example, crabs and shrimps) were observed within control treatments. Water column-feeding fishes were seen above tiles, but never in contact with tiles. The electric current effectively deterred tadpoles from exclusion treatments, and only five small tadpoles were observed in exclusion plots over 20 h of observation during the course of the experiment. No tadpoles were observed in control or exclusion treatments in the *frogless* stream.

Chlorophyll a, AFDM, and Sediments

Tadpoles significantly reduced the amount of chlorophyll *a* in control treatments in the *frog* stream over time in pools and riffles (Figure 1A). During the final 20 days of the experiment, after a major rain and scouring event (base flow increased from 25 to 135 l s^{-1}), control treatments in pools and riffles had 54 ($F_{1,8} = 11.62$, $P = 0.009$) and 35% ($F_{1,8} = 18.87$, $P = 0.0025$) less chlorophyll *a*, respectively, than exclusion treatments.

Organic mass (AFDM) and inorganic sediments followed similar trends to chlorophyll *a* (Figure 1B, C). During the final 20 days, AFDM in pools was 70% less ($F_{1,8} = 39.31$, $P = 0.002$) in controls than in exclusion treatments, and AFDM in riffles was reduced 53% ($F_{1,8} = 9.42$, $P = 0.02$) in control versus exclusion treatments. During this period, inorganic sediments in pools of control treatments were reduced 51% relative to exclusion treatments ($F_{1,8} = 22.81$, $P = 0.025$) and reduced 56% ($F_{1,8} = 26.71$, $P = 0.003$) in riffles (Figure 1C).

In contrast to results for the *frog* stream, in the *frogless* stream we found no differences in chlorophyll *a* between treatments in pools ($F_{1,8} = 1.18$, $P = 0.30$), or in riffles ($F_{1,8} = 0.00$, $P = 0.99$) (Figure 1A). Like the *frog* stream, the *frogless* stream experienced a high-discharge event prior to day 20, although of lesser intensity (personal observation). By day 35, levels of chlorophyll *a* on tiles in the *frogless* stream pools began to stabilize near 2.46 mg m^{-2}, similar to final levels measured in tadpole exclusion treatments in tadpole-dominated pools of the *frog* stream (mean 2.21 mg m^{-2}). Similarly, mean chlorophyll *a*, in both exclusion and control treatments in the *frogless* stream riffles by day 35, approximated mean levels of chlorophyll *a* in the exclusion treatment in the *frog* stream (1.53 versus 1.63 mg m^{-2}).

AFDM and sediment levels of control and exclusion treatments in the *frogless* stream were not statistically different (Figure 1B, C). Subsequent to the high-discharge event, AFDM and inorganics in exclusion and control treatments in the *frogless* stream pools and the tadpole exclusion treatments in the *frog* stream pools were similar (*frogless* stream exclusion = 7.31 ± 3.43 g AFDM m^{-2}, *frogless* stream control = 7.44 ± 3.89 g AFDM m^{-2}, and *frog* stream exclusion = 8.44 ± 5.65 g AFDM m^{-2}; inorganic sediments data not shown).

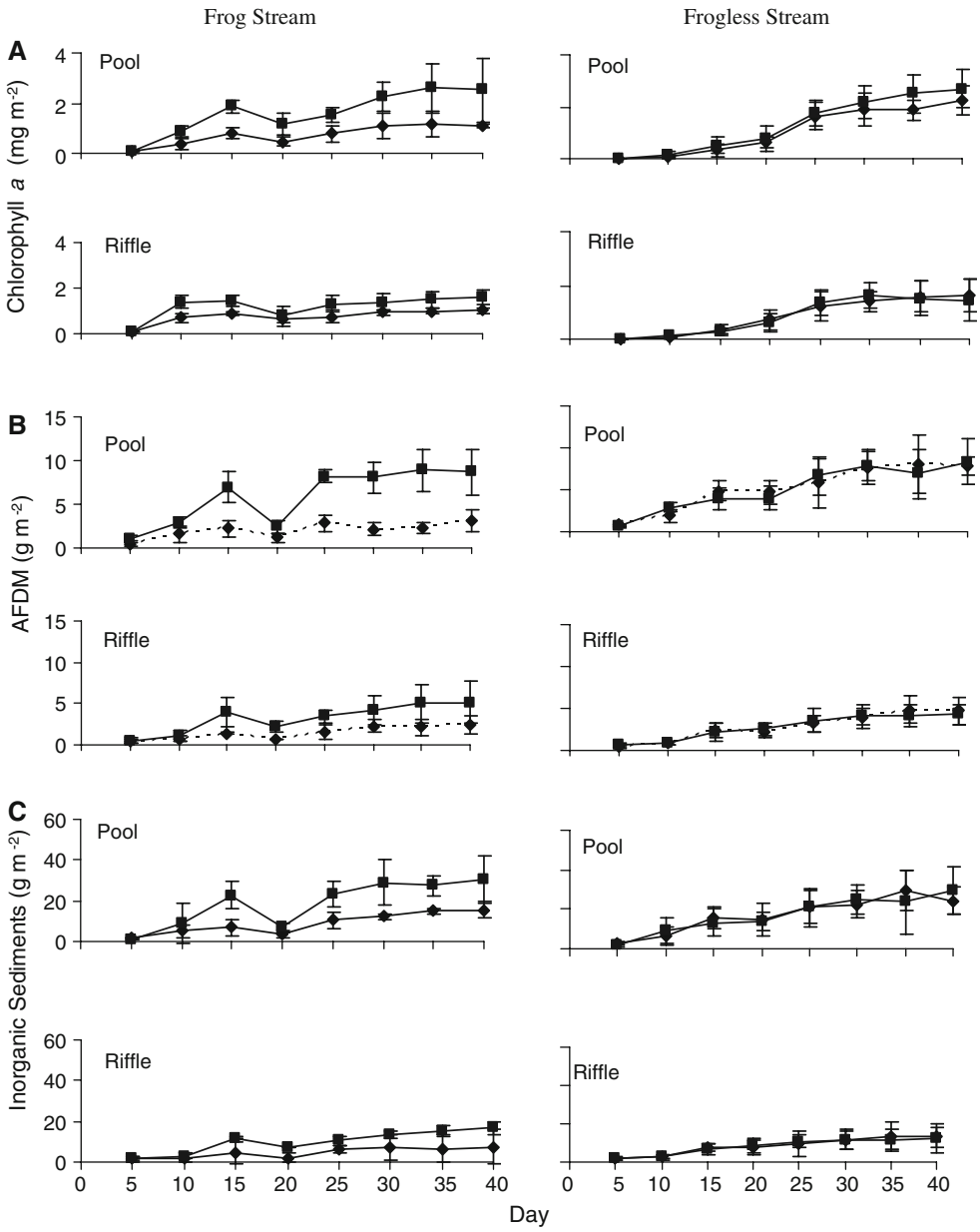

Figure 1. Mean (±1 SE). (**A**) chlorophyll *a*, (**B**) AFDM, and (**C**) inorganic sediments accrued on tiles in pools and riffles in the *frog* stream (tadpoles present) and the *frogless* stream (tadpoles absent) over a 40-day period. *Diamonds* represent controls (tadpole access) and *squares* represent tadpole exclusion treatments.

Algal Community Composition

We found a total of 132 diatom taxa (31 genera) in the *frog* stream on all tiles collected on day 40 of the exclusion experiment. Of the more dominant larger and motile taxa, such as *Gyrosigma sciotoense* (Sullivant and Wormley) Cl, *Navicula* sp., *Pinnularia butantanum* (Krasske) Metzeltin & Lange-Bert, and *Rhopalodia gibberula*, cell densities were greater in tadpole exclusion treatments relative to controls. Cell densities were 59% greater in the tadpole exclusion treatment, and this difference was greater in both pools and riffles. Mean diatom biovolume was 105% greater in pool habitat and 71% greater in riffle habitat where tadpoles were excluded relative to control treatments (Table 1). Of the genera present, *Achnanthes*, *Eunotia*, *Navicula*, *Nupela*, *Pinnularia*, *Synedra*, and *Terpsinöe* comprised 87.4% of the total biovolume on experimental tiles. In contrast, no significant differences in cell densities or biovolume were found between control and exclusion treatments in the *frogless* stream (Table 1).

ISA showed a shift in algal community composition between control and exclusion treatments within the *frog* stream. This analysis showed that mostly the small-celled *Diadesmis contenta* (Grun.) D.G. Mann (indicator value 70.9, $P = 0.0413$), *G. sciotoense* (Sullivant & Wormley) Cl.

Table 1. Mean Diatom Genera Biovolume ($mm^3\ m^{-2} \pm 1$ SE) from Experimental Tiles Collected from each Stream on Day 40 of the Experiment

Taxa	Frog stream (Rio Guabal)				Frogless stream (Rio Chorro)			
	Control pools	Tadpole exclusion pools	Control riffles	Tadpole exclusion riffles	Control pools	Tadpole exclusion pools	Control riffles	Tadpole exclusion riffles
Achnanthes	0.72 ± 0.51	22.73 ± 39.52	3.99 ± 4.12	1.66 ± 1.32	81.85 ± 135.36	41.15 ± 42.69	39.78 ± 34.91	19.97 ± 6.05
Achnanthidium	0.56 ± 0.22	1.07 ± 0.53	1.74 ± 2.72	2.64 ± 3.90	0.23 ± 0.17	0.09 ± 0.11	0.14 ± 0.08	0.05 ± 0.04
Amphipleura	2.65 ± 5.92	0.00 ± 0.00	4.36 ± 5.07	2.14 ± 3.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Caloneis	0.01 ± 0.02	0.51 ± 0.96	0.00 ± 0.00	0.00 ± 0.00	1.14 ± 0.90	1.63 ± 1.64	3.07 ± 3.74	1.37 ± 1.14
Cocconeis	3.23 ± 1.29	5.86 ± 5.15	2.16 ± 2.30	3.99 ± 2.85	4.81 ± 2.83	1.42 ± 1.70	1.04 ± 1.38	1.40 ± 1.13
Eunotia	59.47 ± 28.66	145.86 ± 182.65	39.10 ± 34.32	37.69 ± 22.57	17.69 ± 19.13	13.20 ± 11.06	34.82 ± 20.19	39.62 ± 23.59
Frustulia	0.25 ± 0.24	1.38 ± 1.69	0.55 ± 0.63	0.18 ± 0.41	2.16 ± 3.26	5.08 ± 5.79	3.19 ± 2.81	0.87 ± 1.33
Gyrosigma	0.48 ± 0.76	2.30 ± 1.82	0.37 ± 0.45	0.43 ± 0.42	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Luticola	0.61 ± 0.62	1.74 ± 2.69	0.65 ± 1.05	2.25 ± 1.99	0.00 ± 0.00	0.14 ± 0.31	0.04 ± 0.08	0.01 ± 0.03
Navicula	6.23 ± 1.82	13.33 ± 5.07	5.14 ± 4.42	10.50 ± 10.81	25.97 ± 33.34	19.65 ± 22.30	7.21 ± 8.17	7.80 ± 7.66
Nupela	14.37 ± 8.30	44.73 ± 30.87	17.33 ± 15.30	39.72 ± 42.22	22.81 ± 12.36	15.86 ± 6.40	17.26 ± 9.22	20.24 ± 12.34
Orthoseira	0.99 ± 2.21	6.33 ± 8.75	2.77 ± 3.85	1.05 ± 1.52	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.47 ± 3.28
Pinnularia	0.41 ± 0.92	17.17 ± 20.80	3.85 ± 6.62	13.98 ± 19.25	17.09 ± 28.07	3.53 ± 4.05	5.78 ± 4.15	4.31 ± 2.87
Planothidium	0.78 ± 0.68	2.82 ± 2.78	1.20 ± 1.90	3.04 ± 1.99	17.06 ± 11.17	13.31 ± 11.14	9.55 ± 6.40	13.93 ± 7.93
Rhopalodia	2.56 ± 1.70	5.58 ± 4.58	1.64 ± 1.66	2.66 ± 2.74	0.93 ± 2.07	1.11 ± 1.77	0.00 ± 0.00	0.08 ± 0.17
Stenopterobia	0.00 ± 0.00	0.27 ± 0.61	0.00 ± 0.00	0.67 ± 1.51	5.53 ± 5.27	3.03 ± 5.89	0.10 ± 0.22	0.12 ± 0.26
Synedra	2.34 ± 2.49	4.44 ± 6.83	0.70 ± 0.99	3.74 ± 3.67	40.18 ± 72.99	64.95 ± 18.35	26.92 ± 38.18	53.06 ± 22.36
Terpsinoe	47.24 ± 87.09	16.64 ± 18.36	7.23 ± 13.80	29.14 ± 43.48	0.00 ± 0.00	0.00 ± 0.00	9.38 ± 20.98	0.00 ± 0.00
Other	2.44 ± 0.13	4.53 ± 0.18	1.94 ± 0.16	6.05 ± 0.34	3.68 ± 0.31	2.28 ± 0.13	2.14 ± 0.17	1.13 ± 0.09
Total	145.35	297.28	94.71	161.54	241.12	186.44	160.40	165.42

Genera totaling $<2\ mm^3\ m^{-2}$ are grouped as ''other''.

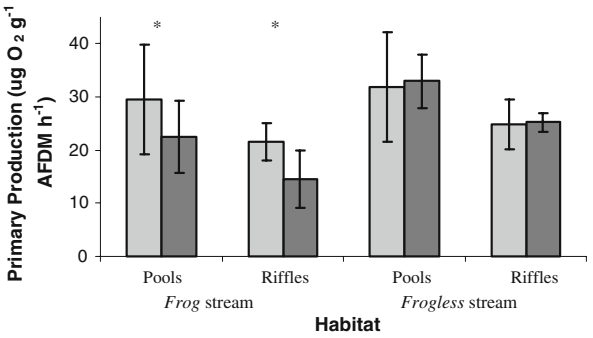

Figure 2. Mean (±1 SE) NPP, as measured by oxygen production, on a per-biomass basis from tiles collected on day 40 of the exclusion experiment. *Light bars* represent tiles from control treatments (tadpole access), *dark bars* represent experimental treatments (tadpoles excluded). *Asterisks above bars* indicate a significant difference between treatments ($P < 0.05$).

(56.0, $P = 0.0240$), *Navicula pseudoarvensis* Hust. (47.5, $P = 0.0553$), *Nitzschia clausii* Hantzsch (56.6, $P = 0.0267$), and *Nupela* sp. (67.7, $P = 0.0047$) were the indicators of control treatments with tadpole grazing; no taxa were indicators of the tadpole exclusion treatments. ISA showed no difference in algal community composition between control and exclusion treatments in the *frogless* stream.

Primary Production

AFDM-specific NPP measured at a small-scale (0.25 m^2) in the *frog* stream was 37% greater on tadpole-grazed tiles within pools ($t = 4.05$, $P = 0.015$) and 55% greater in riffles ($t = 2.72$, $P = 0.048$; Figure 2). Chlorophyll *a*-specific NPP was 36% greater on grazed tiles in pools ($t = 3.73$, $P = 0.02$), and 49% greater in riffles ($t = 2.86$, $P = 0.035$). However, small-scale *areal*-specific NPP was not significantly different between treatments in either pools or riffles. Biomass-specific NPP was not significantly different between control and exclusion treatments when normalized for AFDM, chlorophyll *a*, or area in either pools or riffles in the *frogless* stream.

Invertebrates

Invertebrates colonizing tiles consisted almost entirely of baetid mayflies (Ephemeroptera) and chironomids (Diptera) in both the *frog* and *frogless* streams. There were no treatment differences in invertebrate abundance between control and exclusion treatments (baetids $F_{1,18} = 0.19$, $P = 0.67$; chironomids $F_{1,18} = 0.15$, $P = 0.72$) in the *frog* stream or in the *frogless* stream (baetids $F_{1,18} = 0.13$, $P = 0.72$; chironomids $F_{1,18} = 0.06$, $P = 0.81$). There were also no differences in invertebrate communities (collected by Surber sampling) from control and experimental treatments on the final day of the electric exclusion experiments in the *frog* or *frogless* streams.

Pre- and Post-Decline Comparisons of Natural Substrate

Dead and dying frogs infected with a pathogenic chytrid fungus were first detected at the *frog* stream during September 2004. Subsequent adult frog mortality was high through January 2005, at which time the riparian amphibian abundance had become greatly reduced (Lips and others 2006). A mass reduction in tadpole abundance, compared with previously documented abundances, occurred nearly concurrently in the *frog* stream. During this time tadpole densities within pools declined from a mean of 8.2 to 1.3 tadpoles m^{-2} ($P = 0.042$, RIA). Tadpole densities in riffles declined from 0.9 to 0.0 tadpoles m^{-2} during this period, although the change was not significant ($P > 0.05$, RIA). We characterize the periods of June 2003 to September 2004 as 'pre-decline,' and February 2005 to June 2005 as 'post-decline.' The transitional period (October 2004–January 2005) was not used for our RIA analysis.

Chlorophyll a, AFDM, and Sediments

Following tadpole extirpation, mean monthly levels of chlorophyll *a* and AFDM in the *frog* stream increased significantly in both pools ($P = 0.001$ chlorophyll *a*, AFDM, and sediments, RIA) and riffles ($P < 0.001$ chlorophyll *a*; $P = 0.001$ AFDM and sediments, RIA; Figure 3A). Monthly chlorophyll *a* increased in pools by 2.6-fold (from 3.00 ± 1.31 to 8.31 ± 0.63 mg m^{-2}) and 5.9-fold (from 1.07 ± 1.27 to 6.74 ± 0.62 mg m^{-2}) in riffles post-decline (Figure 3A). AFDM showed a similar trend. Post-decline AFDM increased by 2.2-fold in pools (19.14 ± 5.04 to 41.95 ± 4.98 g m^{-2}) and increased by 2.3-fold in riffles (10.74 ± 7.32 to 24.25 ± 2.14 g m^{-2}). Post-decline inorganic sediments increased 1.6-fold in pools (47.54 ± 16.14 to 76.35 ± 25.98 g m^{-2}) and 1.4-fold in riffles (38.78 ± 16.62 to 54.25 ± 2.14 g m^{-2}).

In Rio Chorro, where tadpoles had been extirpated 8 years earlier, there were far less dramatic increases in chlorophyll *a* (+32% in pools, +68% in riffles; Figure 3B), AFDM (+22% in pools, +31% in riffles), and sediments (+17% in pools, +19% in riffles) between the same periods. RIA indicated significant increases in chlorophyll *a*, AFDM, and

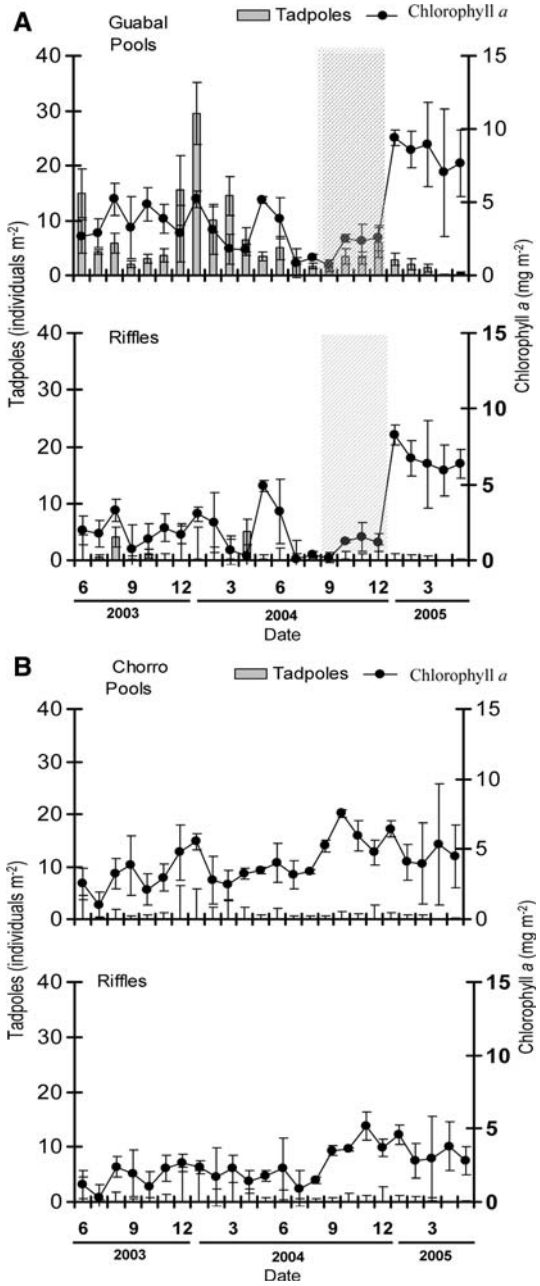

Figure 3. Mean tadpole density (*shaded bars*) and chlorophyll *a* (*black dots*) (±1 SE) sampled monthly from pools and riffles of the *frog* stream (**A**) and the *frogless* stream (**B**) over 24 months. September 2004 begins adult amphibian decline at the *frog* stream, and transitional period of tadpole decline is *shaded.*

sediments in the *frog* stream, relative to the *frogless* stream, following tadpole extirpation.

Algal Community Composition

The pre-decline algal community within the *frog* stream shifted from one dominated by small adnate diatom taxa, to a post-decline community with a higher percentage of large upright taxa, and included more filamentous cyanobacteria. Of the 132 diatom species identified in the *frog* stream, the nine largest species were between 1 and 3 orders of magnitude larger in biovolume than the smaller 123 species. As a group, these species increased in mean abundance from 10.1 % of total diatom abundance during the pre-decline period to a post-decline mean abundance of 20.6%. *P. butantanum* and *T. musica* accounted for the largest mean increase by biovolume, increasing 155 and 67%, respectively. Filamentous cyanobacteria cell density increased by 282%, from a pre-decline mean density of 214 cells mm^2 to a post-decline mean of 605 cells mm^2.

Reach-Scale Primary Production

Reach-scale NPP increased from a pre-decline mean of -1587 mg DO m^{-2} d^{-1}, in the presence of grazing tadpoles, to a post-decline mean of -810 mg DO m^{-2} d^{-1}. Reach-scale gross primary production increased from a pre-decline mean of 113 ± 12.5 to 238 ± 35.0 mg DO m^{-2} d^{-1} after tadpole extirpation. Community respiration dropped from a mean of 1700 ± 345.0 to 1048 ± 276.4 mg DO m^{-2} d^{-1}, and the ratio of production to respiration (P/R) increased from 0.07 to 0.23 over this period. During this time, tadpole density declined from a mean of 10.16 (March 2004) to 0.38 individuals m^{-2} (June 2005).

Discussion

Our results link declining amphibian populations to alterations in stream primary producers over two spatial and temporal scales. Tadpoles reduced algal standing crop and sediments, and altered diatom community composition at both small experimental and larger reach-scales. However, our post-decline studies in the *frog* stream indicated that tadpole-mediated changes that we observed on a short-term localized scale (that is, electric exclusion experiments) underestimated changes evident at larger spatial and temporal scales when tadpoles were extirpated from the entire stream. Our data offer insight into expected stream ecosystem changes resulting from the extirpation of amphibians with stream-dwelling larvae.

How do Tadpoles Affect Algal Standing Crop and Community Structure on a Local Scale?

Intact assemblages of grazing tadpoles can reduce algal standing crop and sediments as evidenced by

significantly greater chlorophyll *a*, AFDM, and inorganic sediments in exclusion versus control treatments in the *frog* stream. Observed treatment differences in the *frog* stream were not apparent in the *frogless* stream, where tadpoles were absent. This supports our assertion that treatment differences in the *frog* stream were due to tadpole grazing and not an artifact of electrical exclusion.

Treatment differences in response variables were greatest in pools, where tadpoles were not only in greatest abundance, but also tended to be larger in size. Grazing tadpoles can decrease algal standing crop and organic matter accrual by direct ingestion of the benthos, although bioturbation may also alter algal assemblages and sediments (Kiffney and Richardson 2001). As grazing tadpoles move over the substratum, inorganic matter and detritus (for example, decaying plant matter and fecal accumulations) are displaced in the water column and are subjected to a greater likelihood of being transported away from the grazed area. Effects of tadpole grazing on sediments were more evident in pools, as loose sediments prone to tadpole grazing would have been previously displaced by the higher current shear associated with riffle habitat. With or without tadpoles, amounts of chlorophyll *a* and organic and inorganic mass in both pools and riffles tended to plateau after day 35, likely the result of natural sloughing and regeneration of periphyton.

ISA of algal community structure suggests that the tadpoles were more efficient at ingesting the less abundant, but possibly easier-to-graze, larger diatom species, which resulted in a higher proportion of smaller diatom species in control versus exclusion treatments. These smaller taxa were almost always present in both treatments, displaying consistent relative *frequency* numbers (based on presence or absence); however, relative *abundances* of these taxa were higher in controls. It is this change in the relative abundance, rather than relative frequency, which is reflected in the ISA. The expectation of grazing-induced changes in the periphyton community is not likely to be reflected in presence/absence of taxa (that might be indicative of changing nutrient levels, for example), but rather in shifts in abundance as larger taxa are more likely to be removed or displaced from the upper canopy.

Although several studies have shown that tadpoles alter algal standing crop (for example, Dickman 1968; Bronmark and others 1991), their effects on community structure have rarely been addressed (but see Kupferberg 1997; Ranvestel and others 2004). The importance of diatoms as a tadpole food source was shown by Kupferberg (1997), who found that tadpoles metamorphosed earlier, and at a higher weight, when allowed to selectively graze epiphytic diatoms and detritus from the less palatable filamentous green alga *Cladophora glomerata*. Although tadpole ingestion may directly decrease overall mean algal size (that is, biovolume), tadpoles can also locally displace larger, unattached taxa (for example, *Terpsinöe* and *Amphipleura*) through bioturbation (Ranvestel and others 2004). It is unlikely that tadpoles are truly selective in their grazing, but they probably do have different consumption efficiencies for different algal growth forms (Steinman 1996). Digestibility of algae by tadpoles has been shown to differ among algal taxa. For example, Peterson and Boulton (1999) showed that some diatom taxa, such as the relatively large-celled *Synedra ulna*, are less prone to intact tadpole gut passage, suggesting that benthic algal community structure can be influenced by differential passage of smaller, viable diatoms. These intact diatoms could serve to recolonize the grazed substrata. Although biofilms are not necessarily stratified by growth form, tadpole feeding likely would remove the upper canopy, which is primarily composed of larger taxa with upright growth. This removal of upper canopy taxa may indirectly benefit smaller, more grazer-resistant algal species, as competition for space, light, and nutrients is reduced (McCormick and Stevenson 1989).

How Does Tadpole Grazing Affect Primary Production on Local and Reach Scales?

On a localized scale, we found biomass-specific primary production to be greater in control treatments in our experiments. Hence, although tadpole grazing decreased levels of algal standing crop, the remaining algal community was more productive on a per-unit biomass (AFDM and chlorophyll *a*) basis. It is likely that increased rates of biomass-specific NPP were partly in response to the ingestion or displacement of accumulated sediment by tadpoles, which exposed underlying algal communities to nutrients and light. Not only were feeding trails through sediments often apparent on tiles, we also observed bioturbation of accrued matter from substrate surfaces when tadpoles moved rapidly. We found no difference in areal-specific NPP between treatments, indicating that increased algal biomass, resulting from tadpole exclusion, compensated for declines in biomass-specific NPP in tadpole exclosures.

Both grazer density and size have been linked to beneficial effects of sediment removal on primary production (Power 1990). In the *frog* stream, we found differences in production to be greatest in pools, where *R. warszewitschii* and *Hyla* spp. (the largest of the tadpoles) were most abundant. The less obvious differences in NPP between control and exclusion treatments in riffles might be attributable to a combination of lower tadpole densities, smaller size of the dominant grazing tadpoles (that is, *A. zeteki*), and high stream flow that constantly removed sediment.

Previous experiments designed to assess tadpole-grazing effects on primary production have shown equivocal results. In an experimental manipulation of two tadpole species, Kupferberg (1997) found that both species reduced areal-specific NPP. However, one species decreased biomass-specific net productivity, whereas the other had no effect. Mechanisms proposed to explain increased biomass-specific NPP by grazers include the dislodgement of senescent algae through grazing (Lamberti and others 1989), and the stimulation of primary production through the mineralization of nutrients from ingested diatoms and detritus (Seale 1980).

Although net production on a per-biomass basis was lower on ungrazed than grazed tiles in the small-scale experiment, mean reach-scale NPP (measured on a *per-unit area* basis rather than on a *per-biomass* basis) increased dramatically from a pre-decline mean of -1587 mg DO m^{-2} d^{-1} to a post-decline mean of -810 mg DO m^{-2} d^{-1}. We found a much stronger effect of tadpole extirpation on whole-stream NPP than we found in the small-scale exclusion experiment. This result was not unexpected, given that the increase in overall stream productivity occurred simultaneously with a considerable increase in algal biomass associated with tadpole losses (Figure 3A). Accordingly, the P/R of the *frog* stream shifted toward a higher level of autotrophy as the tadpole decline proceeded (pre-decline P/R = 0.07; post-decline P/R = 0.23).

Do Tadpoles Account for Inter-Stream Differences in Algal Standing Crop and Community Structure Between Our Two Study Streams?

Unlike the *frog* stream, the *frogless* stream lost its historical assemblage of tadpole grazers approximately 8 years prior to our exclusion experiment, and can be viewed as a long-term, whole-stream tadpole exclusion experiment. Most of the same riparian frog species found at the *frog* stream were once found at the *frogless* stream, and sufficient time has passed to allow multiple generations of other organisms, such as aquatic invertebrates, to respond to this change. Because aquatic invertebrates were potentially released from competition for resources (for example, food and space) when tadpoles were extirpated, it is reasonable to hypothesize that their populations might increase, off-setting initial increases in algal standing crop that we observed post-decline in the *frog* stream. Ecosystem-level responses in algal community structure and function resulting from tadpole declines, therefore, might be ameliorated over time. We found response variables in the *frogless* stream, measured from both the exclusion experiment and monthly sampling, intermediate in comparison to the ranges of response variables from the *frog* stream. One hypothesis for this pattern is that tadpole losses contributed to long-term changes in the *frogless* stream's algal community, and although other functionally similar consumer communities (that is, invertebrates) may have responded, they did not completely replace the role of tadpoles. We also observed an increase in algal biomass in the *frogless* stream during late 2004 (many years after tadpoles had been extirpated from the stream), although of lesser magnitude relative to the *frog* stream during the same time period. This reflects the fact that our study streams are not structured entirely by tadpole presence/absence, but rather by a number of complex biotic and abiotic interactions (sensu Mallory and Richardson 2005).

Does Algal Response to Small-Scale and Short-Term Experimental Tadpole Exclusion Reflect Algal Response to Whole-Stream Tadpole Extirpation?

Little is known about the ecological consequences of extinction because of difficulties associated with studying species loss in natural settings. Small-scale manipulations, such as removal experiments, can provide insight into the consequences of species loss. However, because the spatial and temporal scales of many experiments are small and short in comparison to the size and duration of the impacts they attempt to predict, there are concerns about the usefulness of small-scale experiments in predicting whole-stream ecosystem change as a result of widespread species losses (for example, Kohler and Wiley 1997). For example, Sarnelle (1997) showed that short-term enclosure experiments underestimated results found over a longer term due to long response times of indirect effects. Additionally, small-scale experimental perturbations may underestimate large-scale stream response because of the exchange (of diatoms, for instance) between

treatment areas and the surrounding unmanipulated stream community. Ongoing and predictable extinctions of amphibian communities throughout Latin America provide a rare opportunity to compare the results of our experimental study to reach-scale effects of tadpole losses.

Our small-scale exclusion approach to assess ecosystem alteration accurately predicted the direction of reach-scale responses resulting from the loss of grazing tadpoles in the *frog* stream; each of our three primary response variables (that is, chlorophyll *a*, AFDM, and inorganic sediments) in control treatments showed significant decreases compared to tadpole-exclusion treatments. Our monthly sampling of natural stream substratum likewise showed that tadpoles reduced algal standing crop and inorganic sediments. However, subsequent to the tadpole decline, algal biomass increased similarly in both pools and riffles in the *frog* stream, despite the lower tadpole densities in riffles prior to extirpation. The extent to which algal biomass in riffles increased when tadpoles were extirpated from the stream was unexpected, given the tadpoles' relatively low pre-decline densities. It is plausible that actual tadpole densities were under-estimated using our riffle sampling techniques. Also, although a number of studies have shown that grazing herbivores can exert strong control over algal communities (Steinman 1996), much less is known about the extent to which stream grazers can influence algal communities across an environmental gradient, such as stream velocity. Our results suggest that potentially higher energetic costs associated with grazing in riffle habitat, in combination with different tadpole communities in riffle versus pool habitat, resulted in riffle tadpoles exerting a higher *per capita* influence on algal biomass and sediments. Additionally, the increased post-decline algal biomass in pools could have contributed toward the recolonization of riffle algal colonies. Overall, differences in our response variables resulting from whole-stream amphibian extirpations were dramatically more pronounced than predicted by small-scale exclusion.

We also found an altered diatom community that differed significantly in species composition after tadpoles had been extirpated. The effect of localized tadpole exclusion on diatom community structure underestimated differences we observed when tadpoles were extirpated from the entire stream, possibly because available sources of diatoms for the recolonization of grazed areas were restricted by stream-wide tadpole grazing pressure outside of exclusion treatments. However, subsequent to the amphibian decline, diatom communities were released from tadpole grazing pressure, and larger diatom species were more likely to repopulate grazed areas of the stream.

Past experiments have drawn varying conclusions regarding the ability of small-scale experiments to predict the direction of change at larger scales (Peckarsky and others 1997), and few studies have examined whether small-scale experiments can accurately predict the magnitude of response to ecosystem-level alteration (but see Sarnelle 1997; Kohler and Wiley 1997; Greathouse and others 2006). Whole-stream responses to extensive and permanent tadpole losses might be different than those changes detected with relatively short-term and small-scale manipulations for a number of reasons. A review of benthic grazers by Bronmark and others (1991) showed that periphyton removal rates increased with grazer biomass, so we might predict that algal standing crop would increase when abundant grazers (that is, tadpoles) are extirpated from an entire stream. However, other studies have shown that trade-offs may occur. For example, although grazing pressure by tadpoles (Osborne and McLachlan 1985) or invertebrates (Gresens 1995) can reduce algal standing crop, algae may benefit also from increased nutrient availability from grazer excretion, especially in nutrient-limited systems. We found that experimental tadpole exclusion predicted the direction of change in algal response that was evident over a reach-scale in the *frog* stream when tadpoles were extirpated; however, the magnitude of change in the algal periphyton community was significantly greater on a reach- versus local-scale.

The ecological consequences of consumer losses, such as those resulting from catastrophic amphibian declines, can be difficult to predict, in part due to the rapid loss of many species, potential synergisms, system complexity, and emergent properties of ecosystems (for example, Polis 1998; Michener and others 2001). Our results show strong linkages between the presence of tadpole grazers and certain stream ecosystem properties. Where abundant, Neotropical tadpoles significantly reduced algal standing crop and inorganic sediment accrual, and they also altered algal community composition. Tadpoles also have the potential to increase biomass-specific primary production but reduce overall reach-scale primary production. These influences on headwater streams are especially relevant in light of on-going, large-scale global declines and extinctions of amphibian species (Stuart and others 2004). We found that ecosystem-level impacts of amphibian extinctions were more dramatic than results obtained from our

small-scale, short-term exclusion experiments, which predicted the direction of change in response variables, but underestimated the magnitude of change. Nonetheless, our experimental results, combined with stream monitoring at the reach scale, indicate that tadpole losses have significant effects on stream ecosystem structure and function.

ACKNOWLEDGEMENTS

Funding for this project was provided by National Science Foundation grants DEB #0234386, DEB #0234149, DEB #0234179, DEB #0213851, and DEB #0130273. The Smithsonian Tropical Research Institute and Parque Nacional Omar Torrijos provided logistical support and fieldwork in Panamá. Special thanks to Jose Colon-Gaud for field assistance. Effie Greathouse and the Pringle and Rosemond lab groups provided critical comments on the manuscript. Two anonymous reviewers greatly improved earlier versions of the manuscript.

REFERENCES

APHA. 1985. Standard methods for the examination of water and wastewater, 16. Washington, DC: American Public Health Association.

Bourrelly P, Manguin E. 1952. Algues d'eau douce de la Guadeloupe et dépendances. Paris, France: Centre National de la Recherche Sientifique, Société d'Edition d Enseignement Supérieur.

Bronmark C, Rundle SD, Erlandsson A. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. Oecologia 87:8–18.

Carpenter SR, Frost TM, Heisey D, Kratz TK. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecology 70:1142–52.

Chapin FS III, Sala OS, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen WL, Tilman D. 1998. Ecosystem consequences of changing biodiversity. Science 48:45–52.

de Sousa F. 1999. Fortuna reserva biologica. Panama: Editorial Universitaria.

Dickman M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49:1188–90.

Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–66.

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–54.

Foged N. 1984. Freshwater and littoral diatoms from Cuba. Bibliotheca Diatomologica 5:1–243.

Greathouse EA, Pringle CM, McDowell WH. 2006. Do small-scale enclosure-exclosure experiments predict effects of large-scale extirpation of freshwater migratory fauna? Oecologia 149:709–17.

Gresens SE. 1995. Grazer diversity, competition and the response of the periphyton community. Oikos 73:336–46.

Hauer FR, Resh VH. 1996. Benthic macroinvertebrates. In: Hauer FR, Ed. Methods in stream ecology. New York: Academic Press, Inc. p 339–69.

Hector A, Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188–91.

Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Washington DC: Smithsonian Institute Press.

Hillebrand H, Durselen CD, Kirschtel D, Pollingher U, Zohany T. 1999. Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–24.

Holomuzki JR, Collins JP, Brunkow PE. 1994. Trophic cascades of fishless ponds by tiger salamander larvae. Oikos 71:55–64.

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge D, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35.

Kiffney PM, Richardson JS. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. Copeia 2001:422–9.

Kohler SL, Wiley MJ. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. Ecology 78:2164–76.

Krammer K, Lange-Bertalot H. 1986. Bacillariophyceae 1. Teil: naviculaceae. In: Ettl H, Ed. Süsswasserflora von Mitteleuropas, *2/1*. Jena: Gustav Fischer Verlag. p 1–876.

Krammer K, Lange-Bertalot H. 1988. Bacillariophyceae 2. Teil: bacillariaceae, epithemiaceae, surirellaceae. In: Ettl H, Ed. Süsswasserflora von Mitteleuropas, *2/2*. Jena: Gustav Fischer Verlag. p 1–596.

Krammer K, Lange-Bertalot H. 1991. Bacillariophyceae 3. Teil: centrales, fragilariaceae, eunotiaceae. In: Ettl H, Ed. Süsswasserflora von Mitteleuropas, *2/3*. Jena: Gustav Fischer Verlag. p 1–576.

Kupferberg S. 1997. Facilitation of periphyton production by tadpole grazing: functional differences between species. Freshw Biol 37:427–39.

Lamberti GA, Gregory SV, Hawkins CP, Wildman RC, Ashkenas LR, Denicola DM. 1992. Plant-herbivore interactions in streams near Mount St. Helens. Freshw Biol 27:237–47.

Lamberti GA, Gregory SV, Ashkenas LR, Steinman AD, McIntire CD. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70:1840–56.

Lips KR. 1999. Mass mortality and population declines of anurans at an upland site in western Panama. Conserv Biol 13:117–25.

Lips KR, Reeve J, Witters L. 2003. Ecological traits predicting amphibian population declines in Central America. Conserv Biol 17:1078–88.

Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, Carey C, Livo L, Pessier AP, Collins JP. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proc Natl Acad Sci U S A 103:3165–70.

Loeb SL. 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. Limnol Oceanogr 26:394–9.

Mallory MA, Richardson JS. 2005. Complex interactions of light, nutrients and consumer density in a stream periphyton-grazer (tailed frog tadpoles) system. J Anim Ecol 74:1020–8.

March JG, Pringle CM, Townsend MJ, Wilson AI. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshw Biol 47:377–90.

Marzolf ER, Mulholland PJ, Steinman AD. 1994. Improvements to the diurnal upstream–downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Can J Fish Aquat Sci 51:1591–9.

McCormick PV, Stevenson RJ. 1989. Effects of snail grazing on benthic algal community structure in different nutrient environments. J North Am Benthol Soc 8:162–72.

McCune B, Mefford MJ. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.37. Gleneden Beach, OR: MjM Software.

McIntyre PB, Jones LE, Flecker AS, Vanni MJ. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. Proc Natl Acad Sci 104:4461–6.

Michener WK, Baerwald TJ, Firth P, Palmer MA, Rosenberger JL, Sandlin EA, Zimmerman H. 2001. Defining and unraveling biocomplexity. Bioscience 51:1018–24.

Osborne PL, McLachlan AJ. 1985. The effect of tadpoles on algal growth in temporary, rain-filled rock pools. Freshw Biol 15:77–87.

Owens M. 1974. Measurements on non-isolated natural communities in running waters. In: Vollenweider RA, Ed. A manual on methods for measuring primary production in aquatic environments. Oxford, UK: Blackwell Scientific. p 111–9.

Patrick R, Reimer CW. 1966. The diatoms of North America exclusive of Alaska and Hawaii. Volume I. Monogr Acad Nat Sci Philadelphia 13:1–688.

Peckarsky BL, Cooper SD, McIntosh AR. 1997. Extrapolating from individual behavior populations and communities in streams. J North Am Benthol Soc 16:375–90.

Peterson CG, Boulton AJ. 1999. Stream permanence influences microalgal food availability to grazing tadpoles in arid-zone springs. Oecologia 118:340–52.

Polis GA. 1998. Stability is woven by complex webs. Nature 395:744–5.

Power ME. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. Ecology 71:897–904.

Pringle CM, Blake GA. 1994. Quantitative effects of Atyid shrimp (Decapoda), (Atyidae) on the depositional environment in a tropical stream – use of electricity for experimental exclusion. Can J Fish Aquat Sci 51:1443–50.

Pringle CM, Hamazaki T. 1997. Effects of fishes on algal response to storms in a tropical stream. Ecology 79:2432–42.

Ranvestel AW. 2002. The influence of grazing tadpoles on algal biovolume, sediment dynamics, and aquatic insects in a tropical stream. MS thesis, Southern Illinois University.

Ranvestel AW, Lips KR, Pringle CM, Whiles MR, Bixby RJ. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshw Biol 49:274–85.

Regester KJ, Lips KR, Whiles MR. 2006. Energy flow through early life history stages of ambystomatid salamanders in midwestern forest ponds. Oecologia 147:303–14.

Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. Conserv Biol 13:1220–2.

Rosemond AD, Mulholland PJ, Elwood JW. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology 74:1264–80.

Sarnelle OJ. 1997. *Daphnia* effects on microzooplankton: comparisons of enclosure and whole-lake responses. Ecology 78:913–28.

SAS, Version 8.0. SAS Institute, Cary, NC, USA.

Schofield KA, Pringle CM, Meyer JL, Sutherland AB. 2001. The importance of crayfish in the breakdown of rhododendron leaf litter. Freshw Biol 46:1–14.

Seale DB. 1980. The influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–50.

Silva-Benavides AM. 1996. The epilithic diatom flora of a pristine and polluted river in Costa Rica, Central America. Diatom Res 11:105–42.

Stebbins RC, Cohen NW. 1995. A natural history of amphibians. Princeton, NJ: Princeton University Press.

Steinman AD. 1996. Effects of grazers on freshwater benthic algae. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. Algal ecology: freshwater benthic ecosystems. New York: Academic Press. p 341–73.

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Waller RW. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–6.

Tilman D, Downing J. 1994. Biodiversity and stability in grasslands. Nature 367:363–5.

Whiles MR, Lips KR, Pringle CM, Kilham SS, Bixby RJ, Brenes R, Connelly S, Colon-Gaud JC, Hunte-Brown M, Huryn AD, Montgomery C, Peterson S. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Front Ecol Environ 4:27–34.

Wissinger SA, Whiteman HH, Sparks GB, Rouse GL, Brown WS. 1999. Foraging trade-offs along a predator-permanence gradient in subalpine wetlands. Ecology 80:2102–16.

Young RG, Huryn AD. 1998. Comment: improvements to the diurnal upstream downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Can J Fish Aquat Sci 55:1784–5.