

Assessing ecological responses to catastrophic amphibian declines: Patterns of macroinvertebrate production and food web structure in upland Panamanian streams

Checo Colón-Gaud and Matt R. Whiles

Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901

Susan S. Kilham

Department of Biosciences and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104-2875

Karen R. Lips

Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901

Cathy M. Pringle and Scott Connelly

Institute of Ecology, University of Georgia, Athens, Georgia 30602

Scot D. Peterson

Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901

Abstract

As part of the Tropical Amphibian Declines in Streams (TADS) project, we estimated macroinvertebrate production and constructed quantitative food webs for four headwater stream reaches in the Panamanian uplands: two that had experienced massive amphibian declines and two with unaffected amphibian populations. As expected for forested headwaters, allochthonous materials were the dominant energy source. Total macroinvertebrate biomass and production ranged from 231 to 360 mg ash-free dry mass m^{-2} and from 3.1 to 4.4 g ash-free dry mass $m^{-2} yr^{-1}$, respectively, and did not appear influenced by the presence or absence of amphibians. However, macroinvertebrate functional structure differed between pre- and post-decline sites, with shredder production significantly higher in pre-decline sites and scrapers significantly higher in post-decline sites. Taxonomic differences between pre- and post-decline sites were also evident. There was a shift in scrapers from smaller-bodied taxa (e.g., *Psephenus*) in pre-decline sites to larger-bodied groups (e.g., *Petrophila*) in post-decline sites. Detrital pathways were dominant in these systems, with shredders and collectors accounting for most energy flow. However, scrapers were well-represented and they were food-limited in these systems, particularly in the presence of larval amphibians at pre-decline sites. Ecological effects of catastrophic amphibian declines ranged from subtle shifts in taxonomic composition and functional structure of remaining consumers to changes in the availability and relative importance of autochthonous energy sources.

There is growing concern over the loss of biodiversity and potential effects on the structure and functioning of ecosystems, particularly given the rate at which these losses are now taking place (Chapin et al. 2000; Loreau et al. 2001). Much of our current understanding of relationships between biodiversity and ecosystem functioning is based on small-scale manipulations or assembled communities (Petchey et al. 2004), and studies often produce conflicting

results (Chapin et al. 2000). Further, although many studies have focused on producer communities, only a few have examined the loss of consumers (Duffy 2002), and most of these have focused on a single consumer group (Jonsson and Malmqvist 2000; Cardinale et al. 2002). One of the primary reasons for the knowledge gaps regarding the consequences of declining consumer diversity is that large-scale declines or extinction events generally occur over long time periods and/or are unexpected, and thus they are difficult to study and design experiments around, particularly at the ecosystem scale. Hence, the few studies that have quantified ecosystem responses to losses of consumer groups in natural systems are of great value for understanding the consequences of declining biodiversity (Taylor et al. 2006).

Over the last 25 yr, amphibian declines have been recorded throughout the world, particularly in upland regions of the tropics (Young et al. 2001; Lips et al. 2003). Although there is great concern regarding the loss of amphibian populations and diversity, there is little information on the ecological consequences of these losses

Acknowledgments

The Smithsonian Tropical Research Institute and Parque Nacional General de División Omar Torrijos Herrera provided logistical support for this project. We thank R. Brenes, S. Arce, C. Espinosa, J. L. Bonilla, H. Ross, A. Colón-Millan, and F. Quezada for assistance with fieldwork and D. A. Walther, A. D. Huryn, C. K. Meyer, J. D. Reeve, S. G. Baer, M. Sears, and R. Hopkins for valuable advice and support. We also thank H. Maurice Valett and two anonymous reviewers for comments and editorial advice that greatly improved this manuscript. Funding for this project was provided by National Science Foundation grants DEB 0234386 and DEB 645875.

(Ranvestel et al. 2004; Whiles et al. 2006; Connelly et al. 2008). In Central America, these declines are occurring rapidly and in a predictable fashion along a moving disease front (Lips et al. 2006), a situation that affords the rare opportunity to quantify the ecological consequences of the loss of an entire consumer group occurring over a relatively short timescale (Whiles et al. 2006).

Stream-breeding amphibians are abundant and diverse in upland regions of the neotropics, and they may be important to the structure and function of these systems for a variety of reasons. For one, amphibians represent an energetic link between aquatic and terrestrial systems because of their complex life cycles. Many amphibian larvae develop in freshwater habitats and then transfer energy and nutrients acquired in aquatic habitats into terrestrial food webs (Regeister et al. 2006). Likewise, adults return to the aquatic habitats to reproduce, depositing energy-rich eggs (Regeister et al. 2006). In addition, many stream-dwelling tadpoles graze on periphyton and associated organic accumulations (Flecker et al. 1999; Ranvestel et al. 2004), and may facilitate other scrapers by removing sediments and exposing underlying algae (Ranvestel et al. 2004). Although few studies have examined the importance of tadpole grazing in lotic systems (Flecker et al. 1999; Ranvestel et al. 2004), significant increases in sedimentation and changes in the composition of algal and insect communities have been found when other large, dominant grazers such as fish (Flecker 1996; Pringle and Hamazaki 1998) and shrimp (Pringle et al. 1993; Pringle and Blake 1994) are excluded.

Many stream-dwelling tadpole taxa graze periphyton, but others have different functional roles (Altig et al. 2007). Despite the abundance and functional diversity of tadpoles in some systems, little is known about their potential direct or indirect interactions with other consumers. In neotropical streams, abundant grazing tadpoles may influence basal resources by reducing the amount of food available to other primary consumers, but they may also enhance periphyton resources via nutrient excretion, contribute to fine particulate organic matter (FPOM) and seston pools via egestion, and remove sediments overlying periphyton (Ranvestel et al. 2004; Whiles et al. 2006). Tadpoles can reach high densities in neotropical headwaters (Lips 1999; Ranvestel et al. 2004), and thus likely compete for space and resources with macroinvertebrates, the other dominant consumers in these systems. Considering the myriad potential possible interactions with other consumers, losses of tadpole assemblages from neotropical streams likely result in measurable changes in system structure and function.

Secondary production is a robust measure of the importance and success of consumers because it incorporates various components of ecological performance, including density, biomass, growth, reproduction, and survivorship (Benke and Huryn 2006). Secondary production estimates provide a link between populations and ecosystems and also allow for a better characterization of community structure and function than density or biomass estimates alone. Production estimates have been important for understanding dynamics of energy flow in streams

(Benke 1993), and there are a fair number of studies of macroinvertebrate production from temperate streams (Benke 1993; Huryn and Wallace 2000). However, production estimates are generally lacking for streams in the tropics (Ramirez and Pringle 1998; Dudgeon 1999). Given the lack of information on these systems, production studies will provide valuable new information on the structure and function of neotropical stream systems. Furthermore, production estimates represent a powerful means for examining community and ecosystem-level responses to changes such as the sudden loss of amphibians.

As part of the Tropical Amphibian Declines in Streams (TADS) project, our primary objective was to quantify responses of stream ecosystems to catastrophic amphibian declines. To accomplish this, we quantified resource pools, macroinvertebrate production, associated energy flow, and food web structure in unaffected stream reaches in upland regions of Panama and compared them to similar streams that had experienced massive amphibian declines in the past decade. In doing so, we also developed a comprehensive pre-decline dataset that will allow for eventual pre- and post-extirpation comparisons following predicted declines in our unaffected sites.

Methods

Study sites—We studied four 100-m headwater stream reaches in the Panamanian uplands: two that at the time of the study had unaffected, diverse amphibian populations (El Copé 1 and El Copé 2) and two (Fortuna 1 and Fortuna 2) that had experienced massive amphibian declines associated with the fungal pathogen *Batrachochytrium dendrobatidis* in 1996 and had not recovered (Lips 1999; Whiles et al. 2006). Prior to the decline at Fortuna, both El Copé and Fortuna had similar amphibian assemblages, with over 40 species of riparian anurans, ~20 of which had stream-dwelling tadpole stages (Lips et al. 2003; Ranvestel et al. 2004). Bimonthly intensive amphibian surveys during the study period produced no tadpoles in Fortuna streams, compared to densities of up to 30 individuals m^{-2} (average = 11 individuals m^{-2}) in El Copé streams. At the time of this study, a *B. dendrobatidis* disease front was located between Fortuna and El Copé, moving east towards El Copé (Fig. 1).

El Copé 1 and El Copé 2 are second-order reaches of the Río Guabal located in Parque Nacional G. D. Omar Torrijos H., El Copé, Coclé, Panama, on the eastern extreme of the Cordillera Central (8°40'N, 80°35'W) at approximately 700 m above sea level. Fortuna 1 and Fortuna 2 are located in the Reserva Forestal Fortuna, Chiriquí, Panama, which is ~200 km west of El Copé (8°42'N, 80°14'W) at approximately 1200 m above sea level. Fortuna 1 is a reach of Quebrada Chorro, a second-order stream draining directly into the Río Chiriquí. Fortuna 2 is part of Tube stream, a first-order stream draining into Río Hornito and adjacent to the Smithsonian Tropical Research Institute's field station at Fortuna. All four study reaches are low-order, heavily forested, high-gradient streams typical of this region. Physicochemical characteristics of the study streams are summarized in Table 1.

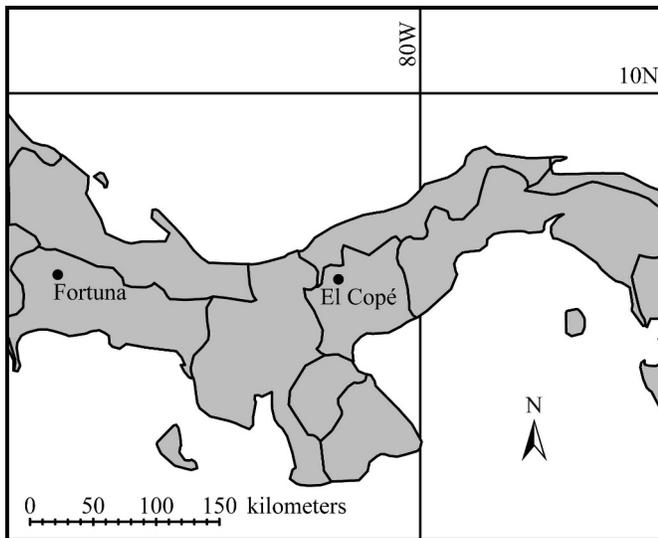


Fig. 1. Map of Panama indicating study sites at Fortuna (affected by amphibian declines) and El Copé (unaffected by amphibian declines).

Physical and chemical characteristics—We estimated stream habitat composition, percent canopy cover, mean width, mean depth, and streambed area for each stream reach in October 2003 and March 2004. Stream substrate composition for each reach was quantified in August 2004 and April 2005. For these analyses, transects were established every 5 m along the entire length of the study reach. Habitat composition was estimated for each 5-m section of the stream reach and summed to calculate the proportion of each major habitat type (erosional, depositional). We quantified canopy cover by taking 100 readings

along the entire length of the study reach with a densitometer (Geographic Resource Solutions). Substrate composition was estimated by measuring substrate particle sizes at three to five points on every 5-m transect for the length of the study reach. Substrate categories were based on a modified Wentworth scale (Stagliano and Whiles 2002). Water temperature was recorded continuously at each site during the entire duration of the study with HOBO temperature data loggers (Onset Corporation). Discharge was measured at least monthly during the study at the base of each reach. Water chemistry (dissolved oxygen [mg L^{-1}], conductivity [$\mu\text{S cm}^{-1}$], and pH) was measured monthly at the base of each study reach with a Hydrolab Quanta[®] (Hydrolab Corporation).

Resource pools—We used quantitative estimates of organic matter inputs, primary production, benthic organic matter (BOM) standing stocks, and organic seston fluxes to estimate resource availability to functional groups. Net primary production was estimated from values generated during a concurrent study at two of the study reaches (El Copé 1 and Fortuna 1) during June and September 2003 using unglazed tiles that were placed in the stream (Connelly et al. 2008). Direct and lateral litter inputs were estimated from materials collected in litter traps placed along two of the study reaches (El Copé 1 and Fortuna 1) for 1 yr starting in July 2004 (Colón-Gaud et al. 2008). Although for logistical reasons litter inputs and primary production were only measured in one reach at each of the two sites, study reaches at each site are physically and chemically very similar, are bordered by similar vegetation, and are in close proximity to each other. It is thus unlikely that primary production or litter inputs would vary appreciably between them.

Table 1. Physicochemical characteristics of the El Copé and Fortuna study stream reaches.

Characteristic	El Copé 1	El Copé 2	Fortuna 1	Fortuna 2
Stream order	2	2	2	1
Mean width (m)	3.28	3.55	3.37	2.01
Mean depth (m)	0.12	0.15	0.15	0.11
Streambed area (m^2)	328	355	337	201
Canopy cover (%)	74	67	68	74
Habitat composition (%)				
Erosional	74	48	60	83
Depositional	26	52	40	17
Substrate composition (%)				
Cobble and larger	25	23	23	25
Pebble	25	24	22	28
Gravel	20	18	16	21
Sand	10	12	30	8
Silt	20	23	9	18
Mean annual water temp ($^{\circ}\text{C}$)	20.7	21.0	17.4	18.1
Dissolved oxygen (mg L^{-1})	6.5	6.9	7.0	7.3
Conductivity ($\mu\text{S cm}^{-1}$)	0.035	0.032	0.014	0.021
Mean annual pH	8.2	8.3	8.3	8.4
Mean annual discharge (L s^{-1})	78	113	88	31
Mean annual rainfall (cm)	350	350	450	450

BOM standing stocks (coarse particulate organic matter [CPOM], >1 mm; FPOM, <1 mm, >250 μm ; very fine particulate organic matter [VFPO], <250 μm , >1.6 μm) were estimated from samples collected monthly from all stream reaches for 1 yr beginning in June 2003 (Colón-Gaud et al. 2008, and macroinvertebrate methods below). Organic seston concentrations (particles ranging from 1.6 to 754 μm) in all four study reaches were estimated based on samples collected at base flow or near base flow conditions about two to three times per month for 1 yr beginning in June 2003 (Colón-Gaud et al. 2008). We estimated organic seston fluxes by dividing the product of the mean annual concentration of organic seston and mean annual discharge by the streambed area of each reach.

Macroinvertebrate biomass and production—We quantified macroinvertebrate biomass and production in all four study reaches to estimate consumer standing stocks and turnover rates. Benthic macroinvertebrate samples were collected monthly from all four streams for 1 yr beginning in June 2003. On each sampling date, three samples were collected from depositional habitats (pools) using a stovepipe benthic corer (sampling area = 314 cm^2) and four were collected from erosional habitats (riffles and runs) using a Surber sampler (sampling area = 930 cm^2 ; 250- μm mesh). For cores, we removed all materials enclosed in the sampler to a depth of ~ 10 cm or until bedrock was contacted and placed them in a bucket. Cobbles were scrubbed with a stiff brush in the bucket and then discarded. Organic materials were elutriated from mineral portions and collected on a 250- μm sieve. We collected Surber samples in a similar manner, except that substrata were disturbed and larger particles scrubbed in the flowing water at the entrance of the collecting net. Materials retained on sieves were placed in plastic bags and preserved in $\sim 8\%$ formalin solution containing Phloxine B stain to facilitate sorting.

In the laboratory, samples were washed through nested 1-mm and 250- μm sieves to separate large (>1 mm) and fine (<1 mm, >250 μm) materials. Large fractions were processed entirely, whereas fine fractions were often subsampled (one-half to one-eighth of total) using a Folsom splitter (Wildlife Supply Company) prior to invertebrate removal. Macroinvertebrates were sorted from other organic materials, identified to the lowest possible taxonomic level (usually genus), measured (total body length) to the nearest 1 mm, and counted. Size-specific ash-free dry mass (AFDM) was estimated using published length-mass relationships (Benke et al. 1999) or our own relationships developed during this study using procedures of Benke et al. (1999). Secondary production was estimated using different methods according to information available for each taxon. For most taxa, production was estimated using the size-frequency method (Benke and Huryn 2006) corrected for the cohort production interval. Cohort production intervals were derived from published estimates for macroinvertebrates in similar Central American systems (Jackson and Sweeney 1995) or by constructing size-frequency plots of individual taxa. The instantaneous growth method (Benke and Huryn 2006) was used for taxa

with short development times (i.e., chironomid midges, blackfly larvae, and small mayflies). Size-class-specific growth rates for Chironomidae, Leptophlebiidae, Leptohyphidae, and Baetidae were estimated during November 2004 and April 2005 using in situ growth chambers following the methods of Huryn (1996a, 2002). Instantaneous growth rates (IGRs) were then estimated from changes in average individual biomass over a given time interval using the following equation:

$$\text{IGR} = \ln(W_f/W_i)/t_i \quad (1)$$

where W_i is the average individual mass at the beginning and W_f the average individual mass at the end of the time interval (t_i). Instantaneous growth rates for Simuliidae were estimated using the relationship developed by Hauer and Benke (1987):

$$\text{IGR} = 0.016T - 0.161 \quad (2)$$

where T = mean annual water temperature ($^{\circ}\text{C}$) in the study reach. This regression was developed from blackfly larva growth trials conducted at different ambient temperatures simulating base flow conditions of a subtropical blackwater river. According to Hauer and Benke (1987), no size-specific adjustment in IGR is required, because no relationship was found between size and growth rate. Production of taxa that were rarely collected in samples was estimated by applying a model developed by Benke (1993) that estimates P:B ratios based on the relationships between individual weight and water temperature:

$$\log P:B = a + cT + d \log W_m \quad (3)$$

where P = mean annual production (mg AFDM m^{-2} yr^{-1}), B = mean annual biomass (mg AFDM m^{-2}), T = mean annual water temperature ($^{\circ}\text{C}$), W_m = maximum individual weight (mg AFDM), and a , c , and d are fitted constants that vary for each insect order (Benke 1993).

We estimated habitat-specific biomass and production by multiplying values from each major habitat type (erosional and depositional) by the proportion of the habitat type available in a study reach and then summing the values. Biomass and production values of individual taxa were summed into their respective functional feeding groups, based on assignments by Merritt and Cummins (2007) and natural abundance stable isotope composition data from recent studies in these streams and similar upland streams in Panama (Verburg et al. 2007). The shrimp *Macrobrachium* sp. and the crab *Ptychophallus* spp. are present in these streams, but they are not appropriately sampled with the gear we used and we thus did not include them in our production estimates.

We constructed 90% confidence intervals to compare mean annual biomass and production estimates using bootstrap techniques (Efron and Tibshirani 1993). Bootstrapped data sets were generated by randomly resampling individual data sets with replacement 1000 times. Differences in mean biomass and secondary production between communities, functional groups, and individual taxa were estimated by comparing the degree of overlap of confidence intervals (Benke and Huryn 2006). We considered values

Table 2. Primary production, benthic organic matter (BOM) standing stocks, and suspended particulate organic matter fluxes (SPOM) for the El Copé and Fortuna study reaches from June 2003 to May 2004. AFDM, ash-free dry mass; CPOM, coarse particulate organic matter (>1 mm); FPOM, fine particulate organic matter (1 mm–250 μm); VFPOM, very fine particulate organic matter (250 μm –1.6 μm). Wood includes woody materials collected in samples and thus does not include large woody debris in the channel.

Variable	El Copé 1	El Copé 2	Fortuna 1	Fortuna 2
Inputs (g AFDM $\text{m}^{-2} \text{yr}^{-1}$)				
Net primary production*	0.5	–	2.0	–
Total allochthonous inputs†	1258	–	1020	–
Direct litter fall†	1080	–	887	–
Lateral litter inputs†	178	–	133	–
Organic matter (g AFDM m^{-2})				
Total CPOM (>1 mm)	51	96	65	96
Leaves	12	10	14	24
Wood	22	48	28	44
Reproductive	2	7	2	6
Miscellaneous	15	31	21	22
FPOM	10	17	16	11
VFPOM	47	72	48	39
Total BOM	108	185	129	146
Organic matter fluxes (g AFDM $\text{m}^{-2} \text{yr}^{-1}$)				
SPOM (1.6–754 μm)	19,499	22,084	33,763	26,264

* Primary production estimates based on data from Connelly et al. (2008).

† Allochthonous input estimates based on data from Colón-Gaud et al. (2008).

with nonoverlapping confidence intervals significantly different at an a priori $\alpha = 0.10$. This approach has been used in similar studies to assess differences in production estimates of aquatic macroinvertebrate communities (Huryn 1996b) and individual taxa (Huryn 2002).

Macroinvertebrate community structure—We used non-metric multidimensional scaling (NMDS) to compare macroinvertebrate community structure between pre- and post-decline sites (El Copé vs. Fortuna) and dominant macrohabitats (erosional vs. depositional). Nonmetric scaling is an ordination technique that uses ranked distances to linearize relationships between distances measured in species space and distances in environmental space, thus providing a biologically meaningful view of the data that displays the strongest fit (Clarke 1993). We used estimates for macrohabitats by stream reach as sampling units ($n = 8$) where macroinvertebrate community composition was based on mean monthly estimates of biomass or annual estimates of secondary production (total taxa = 49), and we standardized the output to unit maxima. We calculated dissimilarities using the Bray-Curtis Index (Bray and Curtis 1957) and performed the analysis in one to four dimensions using 100 random starting configurations.

We used analysis of similarity (Clarke 1993) to detect differences between a priori groups of samples (pre-decline vs. post-decline) for both macroinvertebrate biomass and production. Analysis of similarities (ANOSIM) is calculated as:

$$R = \frac{r_B - r_W}{M/2} \quad (4)$$

where r_B = the rank similarity between groups, r_W = the rank similarity within groups, and $M = n(n - 1)/2$, where n = the number of sampling units. Values in ANOSIM were generated using the Gower metric to obtain an R value

ranging from -1 to 1 . R approaches 1 if samples are more similar within groups than among groups. As with production estimates, we tested for significance at $\alpha = 0.10$.

We performed vector fitting (Faith and Norris 1989; Kantvilas and Minchin 1989) to examine correlations between macroinvertebrate community composition and the following potential explanatory variables: amphibian (pre-decline = 1, post-decline = 0); amounts of CPOM, FPOM, VFPOM, and total BOM (monthly standing stock values); and net primary production (NPP). We used the DECODA software package (Minchin 1989) for ordination, ANOSIM, and vector fitting procedures.

Food web structure—Macroinvertebrate functional feeding group consumption was estimated by dividing annual production values by gross production efficiencies (GPEs), estimated as the product of assimilation efficiencies (AE) and net production efficiencies. The following GPE values were estimated from Lawton (1970), Perry et al. (1987), and Benke and Wallace (1980) and applied to macroinvertebrate functional feeding groups: shredders = 0.049, gatherers = 0.033, scrapers = 0.15, filterers = 0.05, predators = 0.35. Macroinvertebrate egestion was estimated as the product of consumption and $(1 - \text{AE})$.

Results

Resource pools—Net primary production on experimental tiles was highest at Fortuna study reaches where tadpole grazers were absent (Table 2). Allochthonous litter inputs, measured in a concurrent companion study, ranged from 1020 to 1258 g AFDM $\text{m}^{-2} \text{yr}^{-1}$ and varied little between Fortuna and El Copé sites. Organic matter standing stocks in all four streams were dominated by CPOM (>50% of total), mostly in the form of leaves and wood, and VFPOM

Table 3. Mean annual biomass (mg AFDM m⁻²), production (mg AFDM m⁻² yr⁻¹), and production to biomass (P:B) ratios of macroinvertebrates in the El Copé and Fortuna study reaches. Habitat-weighted estimates reflect the relative contributions of each erosional and depositional habitat to totals. Ranges presented below means are 90% confidence intervals.

Site	Erosional			Depositional			Habitat-weighted		
	Biomass	Production	P:B	Biomass	Production	P:B	Biomass	Production	P:B
El Copé 1	209 ^a	2865 ^a	13.7	295 ^{ab}	3754 ^{ab}	12.7	231 ^a	3096 ^a	13.4
	185–233	2616–3114		244–353	3110–4487		208–255	2833–3361	
El Copé 2	302 ^b	3355 ^{ac}	11.1	413 ^a	5306 ^b	12.8	360 ^b	4370 ^b	12.1
	268–335	2897–3770		324–500	4471–6185		312–406	3870–4859	
Fortuna 1	338 ^b	4231 ^b	12.5	364 ^{ab}	2763 ^a	7.6	348 ^{bc}	3644 ^{ab}	10.5
	292–385	3880–4586		167–557	2178–3329		269–432	3332–3969	
Fortuna 2	253 ^{ab}	3890 ^{bc}	15.4	232 ^b	3706 ^a	16.0	249 ^{ac}	3858 ^{ab}	15.5
	199–306	3245–4583		183–280	3109–4331		204–295	3323–4457	

^{a-d} Superscripted letters denote differences between sites at $\alpha=0.10$.

(27–44% of total). Fluxes of suspended particulate organic matter (SPOM) were highest at Fortuna, with the highest rate at Fortuna 1 and the lowest at El Copé 1 (Table 2).

Macroinvertebrate biomass and production—Habitat-weighted macroinvertebrate biomass ranged from 231 to 360 mg AFDM m⁻² and production ranged from 3.1 to 4.4 g AFDM m⁻² yr⁻¹ across the study reaches. However, variability in habitat-weighted values among sites did not appear to be linked to amphibian declines. Habitat-weighted community P:B values ranged from 10.5 to 15.5 (Table 3). Macroinvertebrate mean annual biomass, production, and P:B estimates in erosional and depositional habitats varied among the study reaches, but differences were not consistent with the presence or absence of amphibians (Table 3).

Functional structure, based on habitat-weighted biomass and production estimates, varied significantly between pre- and post-decline sites (Table 4). Production in El Copé 1 was dominated by shredders and filter-feeders (60% of total) and El Copé 2 was dominated by shredders and predators (61%). Production in Fortuna 1 was dominated by predators and filter-feeders (56%), and filter-feeders (53%) were the major contributors to production in Fortuna 2.

Functional group biomass and production estimates varied between major habitats for some groups (Table 4). Scraper biomass and production were generally higher in erosional habitats (~2–6× higher than depositional), whereas predator biomass and production were generally higher in depositional habitats. Habitat-specific patterns of filterer biomass and production varied between pre- and post-decline sites, with somewhat higher values in depositional habitats of the El Copé reaches, but 23–32× higher biomass and 19–61× higher production in erosional habitats compared to depositional in the Fortuna sites.

Habitat-weighted shredder biomass and production were significantly (>2×) higher in El Copé sites compared to Fortuna. The ptilodactylid beetle *Anchytarsus* was the dominant shredder in all four study reaches, but was much more abundant and productive in El Copé reaches, where it accounted for >80% of shredder production (see Web Appendix 1, www.aslo.org/lo/toc/vol_54/issue_1/0331a1.pdf). Shredder biomass in erosional habitats was highest

in El Copé 2, and both El Copé 1 and El Copé 2 were significantly higher than Fortuna sites. Shredder production in erosional habitats was also significantly higher in El Copé sites compared to Fortuna. In depositional habitats, shredder biomass and production were significantly higher in El Copé sites compared to Fortuna sites.

Scrapers accounted for 8–16% of total habitat-weighted macroinvertebrate production across all sites. Scraper biomass in erosional habitats and habitat-weighted values in Fortuna 1 were significantly higher than in El Copé reaches, and habitat-weighted scraper production was significantly higher in Fortuna streams compared to El Copé. Contributions of individual taxa to scraper biomass and production also varied across study reaches, with smaller-bodied taxa, including leptophlebiid mayflies (*Farrododes* and *Thraulodes*) and the water penny beetle *Psephenus*, contributing most at El Copé (Web Appendix 1). *Baetodes* and *Dactylobaetis* (Baetidae), the lepidopteran *Petrophila*, and the leptophlebiid *Farrododes* were dominant in Fortuna sites.

Collector-gatherers represented 10–12% of total habitat-weighted biomass, and values did not vary consistently between El Copé and Fortuna. Gatherer production was highest at Fortuna 2, where gatherers accounted for ~21% of total production. Collector-gatherer chironomids and elmid beetle larvae were dominant contributors to gatherer biomass across all study reaches, whereas small mayflies (*Tricorythodes*, *Baetis*) along with chironomids contributed most to production in all study reaches (Web Appendix 1).

Habitat-weighted filter-feeder biomass was significantly higher in Fortuna 2 than in all but one other study reach (El Copé 2) and filter-feeder production was significantly higher in Fortuna 2 than in all other sites. Hydropsychid caddisflies (*Leptonema* and *Macronema*) were the dominant filterers at El Copé study reaches, accounting for ~90% of total biomass and ~80% of annual production of filter-feeders (Web Appendix 1). *Macronema* were productive in depositional habitats at El Copé, accounting for the relatively large contributions of depositional habitats to filter feeder production at El Copé compared to Fortuna. *Leptonema* was also a dominant contributor at Fortuna, but the black fly *Simulium* accounted for 62% of total filter-feeder production at Fortuna 1 and 42% at Fortuna 2. In

Table 4. Mean annual biomass (mg AFDM m⁻²), production (mg AFDM m⁻² yr⁻¹), and production to biomass (P : B) ratios of macroinvertebrate functional feeding groups in the El Copé and Fortuna study reaches. Habitat-weighted estimates reflect the relative contributions of each erosional and depositional habitat to totals. Ranges presented below means are 90% confidence intervals. FFG, functional feeding group.

FFG	Site	Erosional			Depositional			Habitat-weighted		
		Biomass	Production	P : B	Biomass	Production	P : B	Biomass	Production	P : B
Shredder	El Copé 1	80 ^b (61–99)	931 ^a (727–1143)	11.6	134 ^a (110–161)	1429 ^a (1139–1770)	10.7	94 ^b (78–110)	1060 ^b (890–1238)	7.6
	El Copé 2	140 ^a (114–166)	1275 ^a (874–1651)	9.1	170 ^a (114–233)	2054 ^a (1405–2752)	12.1	156 ^a (124–191)	1680 ^a (1302–2054)	10.8
	Fortuna 1	47 ^c (36–60)	409 ^b (329–502)	8.7	41 ^b (24–59)	416 ^b (295–540)	10.1	44 ^c (35–54)	412 ^c (343–488)	9.4
	Fortuna 2	18 ^d (14–22)	158 ^c (126–195)	8.8	72 ^b (40–106)	753 ^b (410–1108)	10.5	27 ^d (20–34)	259 ^d (193–331)	9.6
Scraper	El Copé 1	24 ^b (21–27)	402 ^c (358–448)	16.8	7 ^b (5–10)	99 ^b (70–127)	14.1	20 ^b (18–22)	324 ^c (290–358)	16.2
	El Copé 2	31 ^b (27–34)	522 ^b (455–585)	16.8	11 ^{ab} (8–13)	170 ^{ab} (126–211)	15.5	20 ^b (18–22)	339 ^c (298–374)	17.0
	Fortuna 1	48 ^a (40–56)	886 ^a (755–1001)	18.5	9 ^{ab} (5–14)	131 ^b (91–181)	14.6	33 ^a (28–37)	584 ^a (507–655)	17.7
	Fortuna 2	26 ^b (22–30)	467 ^c (401–530)	18.0	15 ^a (11–20)	276 ^a (205–354)	18.4	24 ^{ab} (21–28)	435 ^b (379–490)	18.1
Gatherer	El Copé 1	22 ^b (19–25)	382 ^b (332–439)	17.4	26 ^b (22–30)	353 ^c (311–392)	13.6	23 ^c (21–26)	375 ^c (336–418)	16.3
	El Copé 2	25 ^b (22–28)	399 ^b (352–443)	16.0	61 ^a (48–75)	935 ^b (726–1173)	15.3	44 ^a (37–51)	678 ^{ab} (571–810)	15.4
	Fortuna 1	34 ^a (30–38)	535 ^a (473–604)	15.7	38 ^{ab} (29–48)	713 ^b (560–885)	18.8	35 ^{ab} (31–40)	606 ^b (535–688)	17.3
	Fortuna 2	22 ^b (18–26)	612 ^a (538–689)	27.8	70 ^a (44–97)	1717 ^a (1280–2217)	24.6	30 ^{bc} (25–36)	800 ^a (705–896)	26.7
Filterer	El Copé 1	44 ^{bc} (33–57)	674 ^c (566–792)	15.3	88 ^a (43–138)	1127 ^a (565–1781)	12.8	55 ^b (41–72)	792 ^b (624–976)	14.4
	El Copé 2	29 ^c (20–39)	530 ^c (391–674)	18.3	91 ^a (37–152)	797 ^a (396–1261)	8.8	61 ^{ab} (32–92)	669 ^b (446–905)	11.0
	Fortuna 1	70 ^b (50–92)	1459 ^b (1215–1762)	20.8	3 ^b (0–6)	24 ^c (6–43)	8.0	43 ^b (31–57)	885 ^b (741–1066)	20.6
	Fortuna 2	161 ^a (109–213)	2449 ^a (1803–3145)	15.2	5 ^b (3–8)	127 ^b (78–184)	24.5	134 ^a (91–178)	2054 ^a (1516–2634)	15.3
Predator	El Copé 1	39 ^c (30–50)	477 ^c (413–543)	12.2	39 ^b (31–49)	745 ^b (631–856)	19.1	39 ^c (32–47)	547 ^b (491–603)	14.0
	El Copé 2	78 ^b (59–98)	629 ^b (560–706)	8.1	80 ^a (51–109)	1350 ^a (1028–1679)	16.9	79 ^b (61–96)	1004 ^a (833–1182)	12.7
	Fortuna 1	138 ^a (99–179)	942 ^a (750–1131)	6.8	273 ^a (79–472)	1478 ^a (939–2056)	5.4	192 ^a (118–278)	1157 ^a (902–1412)	6.0
	Fortuna 2	27 ^c (12–48)	204 ^d (152–264)	7.6	70 ^{ab} (47–97)	833 ^{ab} (607–1065)	11.9	34 ^c (21–51)	311 ^c (257–373)	9.1

^{a-d} Superscripted letters denote differences between sites at $\alpha=0.10$.

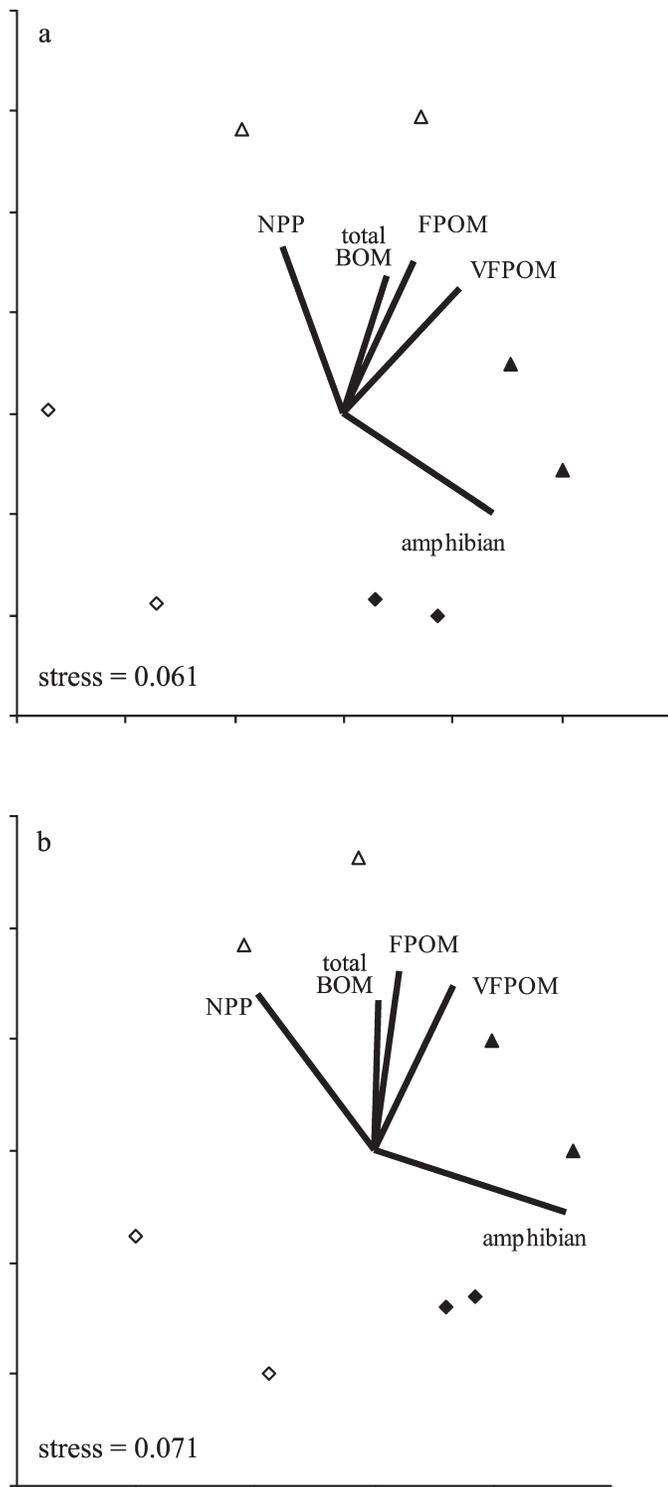


Fig. 2. Two-dimensional NMDS ordination plots of macroinvertebrate community structure for each macrohabitat type in the El Copé (filled symbols) and Fortuna (open symbols) study reaches. Analyses (ANOSIM comparing El Copé and Fortuna sites) were performed on (a) taxa-specific mean monthly biomass ($R = 0.52$, $p = 0.03$) and (b) production ($R = 0.24$, $p = 0.21$) estimates. Diamonds = erosional habitats; triangles = depositional habitats. Significantly correlated environmental variables are shown as vectors. NPP = net primary production; total BOM

contrast, *Simulium* contributed only 14–17% of total filter-feeder production in the El Copé sites. *Simulium* also had some of the highest turnover rates among all taxa, with annual P:B values of ~ 64 (Web Appendix 1).

Predator biomass and production varied across study reaches, but patterns were not consistent between Fortuna and El Copé (Table 4). Habitat-weighted predator biomass was significantly higher at Fortuna 1 than at all other stream reaches and production was significantly higher in Fortuna 1 compared to all other sites except El Copé 2. Flatworms (Tricladida) and predatory chironomids (Tanyptodinae) were the dominant predators at both El Copé study reaches and Fortuna 2, whereas the odonate *Neurocordulia* contributed most to predator biomass and production at Fortuna 1 (Web Appendix 1).

Macroinvertebrate community structure—Two-dimensional NMDS ordinations were used for both taxa-specific macroinvertebrate biomass and production by macrohabitat ordinations (Fig. 2). ANOSIM results showed significant differences in community composition based on biomass ($R = 0.52$, $p = 0.03$), but did not reflect differences based on production ($R = 0.24$, $p = 0.21$). In the biomass ordination, fitted vectors of maximum correlation with primary production ($R^2 = 0.87$, $p = 0.01$), FPOM ($R^2 = 0.82$, $p = 0.03$), VFPOM ($R^2 = 0.81$, $p = 0.05$), total BOM ($R^2 = 0.70$, $p = 0.04$), amphibians ($R^2 = 0.85$, $p = 0.06$), and CPOM ($R^2 = 0.60$, $p = 0.06$) were significant (Fig. 2a). In the production ordination, fitted vectors of maximum correlation with NPP ($R^2 = 0.85$, $p = 0.01$), FPOM ($R^2 = 0.81$, $p = 0.04$), VFPOM ($R^2 = 0.81$, $p = 0.04$), total BOM ($R^2 = 0.67$, $p = 0.05$), amphibians ($R^2 = 0.85$, $p = 0.06$), and CPOM ($R^2 = 0.56$, $p = 0.08$) were significant (Fig. 2b).

Food web structure—Consumption estimates based on macroinvertebrate production indicated that collector-gatherers, scrapers, and predators consumed sizable portions of their available food resources, whereas shredders and filterers were not resource-limited (Table 5). In particular, scrapers consumed more periphyton production than estimates indicated was available. This pattern was most pronounced in the pre-decline sites at El Copé, where scraper consumption estimates exceeded available periphyton production by $4\times$. Estimates at Fortuna indicated scraper consumption exceeded periphyton production by $\sim 1.5\times$ (Table 5; Fig. 3).

Quantitative food webs indicated that most energy flow in both El Copé and Fortuna study reaches was through allochthonous pathways (Fig. 3), and shredders and collector-filterers consumed small portions of their respective available resources in all four study reaches ($<3\%$ in all sites). In El Copé, dominant energy transfers were from litter to shredders, from FPOM and VFPOM to gatherers, and from SPOM to filterers (Fig. 3a). Dominant energy

←

= total benthic organic matter; FPOM = fine particulate organic matter; VFPOM = very fine particulate organic matter; Amphibian = pre- or post-decline sites.

Table 5. Functional feeding group production and resource consumption (g AFDM m⁻² yr⁻¹) in the El Copé and Fortuna study reaches. Food availability for gatherers is from mean annual FPOM+VFPOM standing stocks (g AFDM m⁻²); all other values are annual rates (g AFDM m⁻² yr⁻¹) of allochthonous inputs (shredders), primary production (scrapers), SPOM transport (filterers), and total macroinvertebrate production (predators).

Functional group	Production	Consumption	Available food resources	% consumed
El Copé 1				
Shredders	1.1	22.4	1258	2
Gatherers	0.4	12.1	57	21
Scrapers	0.3	2.0	0.5	400
Filterers	0.8	16.0	19,499	<1
Predators	0.5	1.4	2.8	50
El Copé 2				
Shredders	1.7	34.7	1258*	3
Gatherers	0.7	21.2	99	21
Scrapers	0.3	2.0	0.5*	400
Filterers	0.7	14.0	22,084	<1
Predators	1.0	2.9	4.4	66
Fortuna 1				
Shredders	0.4	8.2	1020	1
Gatherers	0.6	18.2	64	28
Scrapers	0.6	4.0	2	200
Filterers	0.9	18.0	33,763	<1
Predators	1.2	3.4	4.1	83
Fortuna 2				
Shredders	0.3	6.1	1020*	1
Gatherers	0.8	24.2	50	48
Scrapers	0.4	2.6	2*	130
Filterers	2.1	42.0	26,264	<1
Predators	0.3	0.9	3.9	23

* Primary production and litter input estimates are from El Copé 1 and Fortuna 1 study reaches.

transfers in Fortuna study reaches were consumption of FPOM and VFPOM by gatherers and of SPOM by filterers (Fig. 3b). Macroinvertebrate predators removed at least 50% of total invertebrate production at all but one study reach (Fortuna 2; 23%).

Discussion

Predicted catastrophic amphibian declines occurred at El Copé following our study (Lips et al. 2006). Based on densities observed during our study (Connelly et al. 2008), and densities measured during prior investigations in our study streams (Lips et al. 2003; Ranvestel et al. 2004), larval amphibians were an abundant and diverse consumer group in these systems and they undoubtedly interacted with other consumers in a variety of direct and indirect ways. In particular, many of the dominant tadpole taxa that were once abundant in these systems are grazers (Ranvestel et al. 2004), and thus responses to their losses might be most evident in other consumer groups that feed on periphyton.

Our study, combined with results from prior studies in these same streams, suggests that the loss of larval amphibians resulted in increased algal biomass and production and consequent changes in community structure of grazing invertebrates (i.e., scrapers), and overall increased production of scrapers. Smaller-scale experimen-

tal manipulations at El Copé showed that tadpole feeding activities reduced the amount of algal primary production available to other consumers (Ranvestel et al. 2004; Connelly et al. 2008). Our quantitative food webs indicate that algal production is a limited resource in neotropical headwaters, particularly when tadpoles are present. The limited availability of primary production likely results in more generalist feeding behavior by scrapers in these systems, and this is also a plausible explanation for our estimates indicating that more than the available resources were consumed. Some similar studies of consumer production and resource use have also produced estimates of consumption that exceed availability of food resources, and these apparent paradoxes have been attributed to underestimates of the turnover rates of food resources, selective feeding on more nutritious components of the resource, and/or omnivory (Fisher and Gray 1983; Stagliano and Whiles 2002).

Our study suggests that macroinvertebrate scraper communities shift in response to the loss of tadpoles. In particular, smaller-bodied grazers may be most affected by amphibian declines. Smaller taxa such as *Psephenus* contributed ~2× the amount of biomass and production in our El Copé sites, where amphibians were present, compared to Fortuna (Web Appendix 1). *Thraulodes*, a small grazing mayfly, also had much higher production (>2× higher) in the pre-decline streams compared to

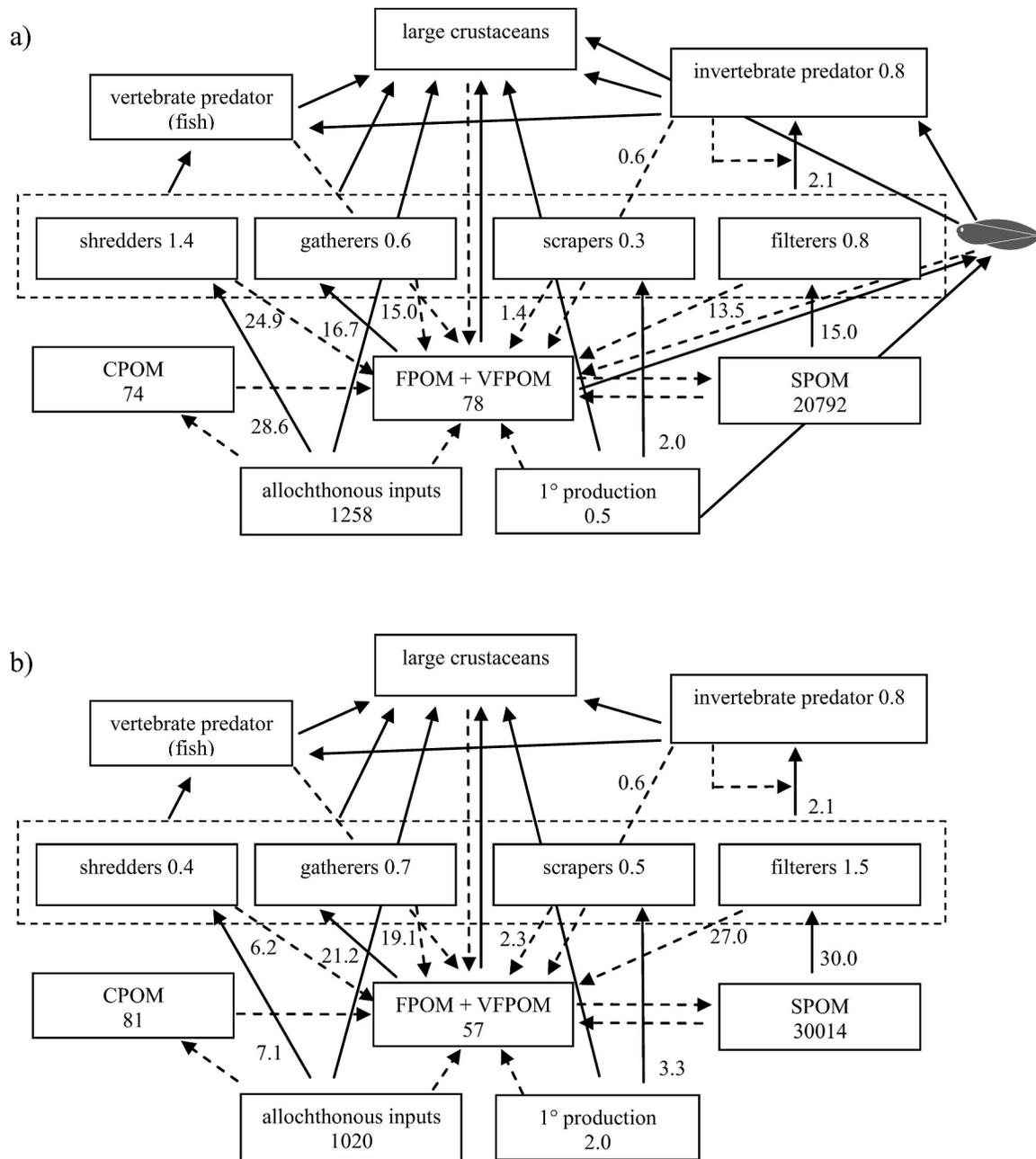


Fig. 3. Community food web and energy flow pathways for the (a) El Copé and (b) Fortuna study reaches. Values in each diagram are averages for the two study reaches at each site. Functional group values represent annual production (g AFDM m⁻² yr⁻¹). Resource pool values are annual rates (g AFDM m⁻² yr⁻¹), except for coarse particulate organic matter (CPOM) and fine and very fine particulate organic matter (FPOM + VFPOM), which are mean annual standing stocks (g AFDM m⁻²). Arrows entering consumer boxes indicate consumption (g AFDM m⁻² yr⁻¹) and those entering organic matter pools indicate estimated replenishment of the pool. Dashed arrows exiting boxes indicate nonconsumptive losses or, in the case of consumers, egestion (g AFDM m⁻² yr⁻¹). Arrows with no numbers were not quantified in this study.

Fortuna (Web Appendix 1). In contrast, a larger grazer, *Petrophila*, was much more productive (>2× higher) at Fortuna sites. These patterns are consistent with small-scale experimental manipulations in these same streams that indicated that small-bodied grazers benefit from tadpole feeding because tadpoles remove fine organic and inorganic sediments from substrata (Ranvestel et al. 2004) and can increase periphyton production per unit biomass

(Connelly et al. 2008). Consistent with this pattern, *Tricorythodes*, a small-bodied gathering mayfly, also had 3.7–6.6× higher production in the pre-decline streams during our study (Web Appendix 1). However, *Baetis*, another small-bodied gatherer, and one that showed a positive response to tadpole grazing in prior manipulative experiments in these systems, showed no consistent patterns across pre- and post-decline sites, suggesting that

mechanisms behind responses, or lack thereof, for individual groups and taxa vary. Similar patterns were observed for several small-bodied mayflies (i.e., *Farrodus*, *Baetodes*, *Dactylobaetis*) that obtained higher estimates for biomass and production at one study stream, but not consistently across pre- or post-decline sites. Likewise, macroinvertebrate responses to the presence or absence of amphibians may vary with spatial scale; small-bodied insects may be attracted to tadpole-grazed areas of substrata on a patch scale, but their populations may ultimately be unaffected by amphibians at the reach scale.

Increased primary production and algal biomass following amphibian declines may also influence other consumer groups that we did not examine in this study. In particular, densities of the freshwater crab, *Ptychophallus* spp., were consistently higher at the post-decline Fortuna study reaches compared to El Copé throughout the study period (C. Colón-Gaud unpubl.). These crabs are omnivorous, and thus may have responded positively to increased algal resources or, alternatively, to increased scraper production.

Larval amphibians may influence the quantity and quality of resource pools via excretion and egestion (Whiles et al. 2006; Colón-Gaud et al. 2008). Colón-Gaud et al. (2008) showed that seston in the El Copé study stream reaches had a lower C:N than in Fortuna, and hypothesized that this was linked to tadpole feeding and egestion at El Copé. This suggests that materials exported from headwaters with unaffected amphibian populations are of higher quality than those from streams where amphibians have declined. This pattern of lower-quality seston in post-decline streams might be expected to negatively influence filter-feeding macroinvertebrates. However, our results indicate the opposite; we observed generally higher production of filterers in Fortuna stream reaches, particularly in Fortuna 2. This pattern was related to taxonomic differences in filterer communities between sites. Filterer production in Fortuna 2 mainly consisted of *Simulium*, which filter at a much finer scale, even at the level of individual bacterial cells, than many other larger filterers (i.e., hydroptychid caddisflies) (Wallace and Webster 1996), and thus may be indifferent to changes in the quality of larger size fractions of particles that include tadpole feces.

Differences in filterer biomass and production in post-decline streams compared to unaffected sites could be related to the quantity, rather than the quality, of exported materials, as Colón-Gaud et al. (2008) found that seston concentrations were consistently higher in Fortuna stream reaches compared to El Copé. Whiles and Dodds (2002) found positive relationships between filter-feeding macroinvertebrates and organic seston concentrations, particularly among hydroptychid caddisflies, in a Great Plains drainage network. Hydroptychid caddisflies (*Leptonema* and *Macronema*) were common filterers in our study streams. *Leptonema*, for example, was substantially more productive in stream reaches at Fortuna than at El Copé, accounting for >50% of the total filterer production at Fortuna 2, where SPOM export was highest (Web Appendix 1). *Macronema* was the only filterer that was consistently more productive in the El Copé reaches, and was most productive in depositional habitats. *Macronema* are often associated with large wood in streams, and they feed on very small particles (Wallace and Sherberger 1974). Thus,

patterns of *Macronema* production may have been more related to habitat type than SPOM quantity or quality.

Although seston concentrations and export are heavily influenced by hydrology, they may also be influenced by scrapers and other consumers through egestion and bioturbation (Wallace and Webster 1996). Taylor et al. (2006) found that experimental removal of a dominant detritivorous fish, *Prochilodus mariae*, altered ecosystem metabolism by increasing primary production and decreasing downstream transport of organic carbon in a Venezuelan river. Results of our study and prior investigations in the same streams (Ranvestel et al. 2004; Connelly et al. 2008) indicate that loss of *Prochilodus* and loss of tadpoles influence primary production similarly. However, the loss of larval amphibians at Fortuna did not appear to influence SPOM export as observed for *Prochilodus*. Tadpoles undoubtedly contribute to local SPOM pools, but factors such as hydrology likely supersede their influence in the high gradient headwaters that we examined.

Our results suggest that shredders are more productive in streams with tadpoles, because shredder biomass and production, in this case mostly *Anchytarsus*, were significantly higher in pre-decline sites, even though litter inputs and CPOM standing stocks were similar among all reaches. Although these differences in shredder biomass and production could be linked to a variety of habitat features of these streams, they could also reflect the influence of larval amphibians on the quality of detrital resources (e.g., local replenishment of nutrients for microbes associated with detritus from tadpoles grazing in pools and/or living in CPOM accumulations). In particular, glass frog tadpoles (Centrolenidae) are almost exclusively found in CPOM accumulations in these systems and were abundant in the El Copé reaches during our study. Centrolenids and other tadpoles inhabiting leaf litter and debris accumulations may stimulate microbial activity and thus nutritional quality of detrital resources via excretion and may thus positively influence shredder production. Increased nutrient availability has been shown to positively influence shredder feeding, biomass, and production in temperate forested headwaters (Cross et al. 2007).

Overall, our production estimates are low compared to estimates from other similar-size streams (range 4.1–135 g dry mass m⁻² yr⁻¹; Benke 1993; Huryn and Wallace 2000), but higher than those from a low-altitude, fish-dominated, third-order stream in Costa Rica (0.4 g AFDM m⁻² yr⁻¹; Ramirez and Pringle 1998). Hence, our results support prior observations that macroinvertebrate production is relatively low in neotropical streams in general, but that production is higher in upland headwaters where fish are absent or in low abundance.

Relatively low production in our study streams compared to headwaters in other regions may be related to the hydrology of these systems. In particular, frequent high-discharge events scour these systems, reducing food resources and likely displacing invertebrates. Colón-Gaud et al. (2008) showed that although litter inputs in these same streams are relatively high compared to forested headwaters in other regions, BOM standing stocks are low because of frequent scouring and a general lack of retentive

structures such as large woody debris. Scouring events also reduce biofilms and periphyton (Grimm and Fisher 1989; Dodds et al. 1996), and similar relationships with flood frequency have been reported in tropical lowland streams in Costa Rica (Pringle and Hamazaki 1997; Ramirez and Pringle 1998) and highland streams in Puerto Rico (Pringle and Blake 1994).

Based on NMDS and related analyses, differences in macroinvertebrate communities between sites and between habitats within sites were related to amounts of basal resources and the presence or absence of amphibians. Significant and autocorrelated vectors for detrital resources reflected a predictable pattern of differing amounts of fine and coarse particulate organic materials in depositional and erosional habitats, and macroinvertebrates obviously responded. In contrast, vectors for the presence or absence of amphibians and NPP were opposing, reflecting higher periphyton production in post-decline sites, and linked differences in communities based on biomass estimates. The production-based ANOSIM analysis was not significant, but NMDS plots showed nearly identical community patterns based on biomass and production estimates.

Our results, along with those of related studies in these same systems, suggest that although amphibians can clearly influence ecosystem processes and function in numerous ways (e.g., reducing algal biomass and increasing production per unit biomass [Ranvestel et al. 2004; Connelly et al. 2008] and enhancing nutrient recycling and seston quality [Whiles et al. 2006; Colón-Gaud et al. 2008]), some aspects of structure and function that we examined (e.g., total macroinvertebrate production and production of some functional groups) showed little or only subtle responses to their loss, and there may be some degree of functional redundancy in these systems (e.g., production of some invertebrates increasing with primary production). However, the long-term responses and consequences of these losses remain to be seen, and ecosystem responses to change can sometimes be slow (Slavik et al. 2004). Further, other potential consequences of these sudden, dramatic declines in consumer diversity are yet to be examined. For example, stability and resistance and resilience to disturbance and vulnerability to invasion by exotic species have all been linked to biodiversity (Chapin et al. 2000; Loreau et al. 2001), and could thus be altered in streams following amphibian extirpations.

This study represents the first investigation of the responses of in-stream consumers to amphibian declines and related changes in food webs and energy flow. Our study was constrained by the logistics of intensively sampling sites in remote regions of Central America, and thus low replication of pre- and post-decline streams. However, continued studies at both sites (now that amphibians at El Copé have declined) will allow for more robust assessments of patterns we observed in this study. Our results suggest that losses of larval amphibians can affect consumer communities, resource pools, and food web structure in a variety of ways. Whether these shifts will persist, or other changes will occur over longer timescales, is unknown. However, there is no indication that amphibians will recover at sites that have declined (Lips et al. 2006).

References

- ALTIG, R., M. R. WHILES, AND C. L. TAYLOR. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshw. Biol.* **52**: 386–395.
- BENKE, A. C. 1993. Concepts and patterns of invertebrate production in running waters. *Verh. Int. Ver. Theor. Angew. Limnol.* **25**: 15–38.
- , AND A. D. HURYN. 2006. Secondary production of macroinvertebrates, p. 691–709. *In* F. R. Hauer and G. A. Lamberti [eds.]. 2007. *Methods in stream ecology*, 2nd ed. Academic Press.
- , ———, L. A. SMOCK, AND J. B. WALLACE. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J. N. Am. Benthol. Soc.* **18**: 308–343.
- , AND J. B. WALLACE. 1980. Trophic basis of production among net spinning caddisflies in a Southern Appalachian stream. *Ecology* **61**: 108–118.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27**: 325–349.
- CARDINALE, B. J., M. A. PALMER, AND S. L. COLLINS. 2002. Species diversity enhances ecosystem functioning. *Nature* **415**: 426–429.
- CHAPIN, F. S., AND OTHERS. 2000. Consequences of changing biodiversity. *Nature* **405**: 234–242.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**: 117–143.
- COLÓN-GAUD, C., S. D. PETERSON, M. R. WHILES, S. S. KILHAM, K. R. LIPS, AND C. M. PRINGLE. 2008. Allochthonous litter inputs, organic matter standing stocks, and organic seston dynamics in upland Panamanian streams: Potential effects of larval amphibians on organic matter dynamics. *Hydrobiologia* **603**: 301–312.
- CONNELLY, S., AND OTHERS. 2008. Changes in stream primary producer communities resulting from large-scale catastrophic amphibian declines: Can small scale experiments predict effects of tadpole loss? *Ecosystems* **11**: 1262–1276.
- CROSS, W. F., J. B. WALLACE, AND A. D. ROSEMOND. 2007. Nutrient enrichment reduces constraints on material flows in a detritus-based food web. *Ecology* **88**: 2563–2575.
- DODDS, W. K., R. E. HUSTON, A. C. EICHEM, M. A. EVANS, D. A. GUDDER, K. M. FRITZ, AND L. J. GRAY. 1996. The relationship of floods, drying, flow and light to primary production and producer biomass in a prairie stream. *Hydrobiologia* **333**: 151–159.
- DUDGEON, D. 1999. Patterns of variation in secondary production in a tropical stream. *Arch. Hydrobiol.* **144**: 271–281.
- DUFFY, J. E. 2002. Biodiversity and ecosystem function: The consumer connection. *Oikos* **99**: 201–219.
- EFFRON, B., AND R. TIBSHIRANI. 1993. An introduction to the bootstrap. *Monographs on statistical and applied probability* **57**. Chapman and Hall.
- FAITH, D. P., AND R. H. NORRIS. 1989. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biol. Conserv.* **50**: 77–98.
- FISHER, S. G., AND L. J. GRAY. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* **64**: 1217–1224.
- FLECKER, A. S. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* **77**: 1845–1854.

- , B. P. FEIFAREK, AND B. W. TAYLOR. 1999. Ecosystem engineering by a tropical tadpole: Density-dependent effects on habitat structure and larval growth rates. *Copeia* **1999**: 495–500.
- GRIMM, N. B., AND S. G. FISHER. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *J. N. Am. Benthol. Soc.* **8**: 293–307.
- HAUER, F. R., AND A. C. BENKE. 1987. Influence of temperature and river hydrograph on black fly growth rates in a subtropical blackwater river. *J. N. Am. Benthol. Soc.* **6**: 251–261.
- HURYN, A. D. 1996a. Temperature dependent growth and life cycle of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in two high-country streams in New Zealand. *Freshw. Biol.* **36**: 351–361.
- . 1996b. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnol. Oceanogr.* **41**: 243–252.
- . 2002. River-floodplain linkage determines production dynamics of detritivorous and predacious mayflies (Ephemeroptera) in a sedge-meadow wetland. *Arch. Hydrobiol.* **155**: 455–480.
- , AND J. B. WALLACE. 2000. Life history and production of stream insects. *Annu. Rev. Entomol.* **45**: 83–110.
- JACKSON, J. K., AND B. W. SWEENEY. 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. *J. N. Am. Benthol. Soc.* **14**: 115–130.
- JONSSON, M., AND B. MALMQVIST. 2000. Ecosystem process rate increases with animal species richness: Evidence from leaf-eating, aquatic insects. *Oikos* **89**: 519–523.
- KANTVILAS, G., AND P. R. MINCHIN. 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio* **84**: 99–112.
- LAWTON, J. H. 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrosoma nymphula* (Sulz.) (Odonata: Zygoptera). *J. Anim. Ecol.* **40**: 385–423.
- LIPS, K. R. 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conserv. Biol.* **13**: 117–125.
- , J. D. REEVE, AND L. R. WITTERS. 2003. Ecological traits predicting amphibian population declines in Central America. *Conserv. Biol.* **17**: 1078–1088.
- , AND OTHERS. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proc. Natl. Acad. Sci. USA* **103**: 3165–3170.
- LOREAU, M., AND OTHERS. 2001. Ecology—biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **294**: 804–808.
- MERRITT, R. W. AND K. W. CUMMINS [EDS.]. 2007. An introduction to the aquatic insects of North America, 4th ed. Kendall/Hunt.
- MINCHIN, P. R. 1989. DECODA user's manual. Research School of Pacific Studies, Australian National Univ., Canberra.
- PERRY, W. B., E. F. BENFIELD, S. A. PERRY, AND J. R. WEBSTER. 1987. Energetics, growth, and production of a leaf-shredding aquatic insect in an Appalachian Mountain stream. *J. N. Am. Benthol. Soc.* **6**: 12–25.
- PETCHY, O. L., A. L. DOWNING, G. G. MITTELBACH, L. PERSSON, C. F. STEINER, P. H. WARREN, AND G. WOODWARD. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* **104**: 467–478.
- PRINGLE, C. M., AND G. A. BLAKE. 1994. Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: Use of electricity for experimental exclusion. *Can. J. Fish. Aquat. Sci.* **51**: 1443–1450.
- , ———, A. P. COVICH, K. M. BUZBY, AND A. FINLEY. 1993. Effects of omnivorous shrimp in a montane tropical stream: Sediment removal, disturbance of sessile invertebrates, and enhancement of understory algal biomass. *Oecologia* **93**: 1–11.
- , AND T. HAMAZAKI. 1997. Effects of fishes on algal response to storms in a tropical stream. *Ecology* **78**: 2432–2442.
- , AND ———. 1998. The role of omnivory in structuring a neotropical stream: Separating diurnal versus nocturnal effects. *Ecology* **79**: 269–280.
- RAMIREZ, A., AND C. M. PRINGLE. 1998. Structure and production of a benthic insect assemblage in a neotropical stream. *J. N. Am. Benthol. Soc.* **17**: 443–463.
- RANVESTEL, A. W., K. R. LIPS, C. M. PRINGLE, M. R. WHILES, AND R. J. BIXBY. 2004. Neotropical tadpoles influence stream benthos: Evidence for the ecological consequences of decline in amphibian populations. *Freshw. Biol.* **49**: 274–285.
- REGISTER, K. J., K. R. LIPS, AND M. R. WHILES. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia* **147**: 303–314.
- SLAVIK, K., B. J. PETERSON, L. A. DEEGAN, W. B. BOWDEN, A. E. HERSHEY, AND J. E. HOBBI. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* **85**: 939–954.
- STAGLIANO, D. M., AND M. R. WHILES. 2002. Macroinvertebrate production and trophic structure in a tallgrass prairie headwater stream. *J. N. Am. Benthol. Soc.* **21**: 97–113.
- TAYLOR, B. W., A. S. FLECKER, AND R. O. HALL. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* **313**: 833–836.
- VERBURG, P., S. S. KILHAM, C. M. PRINGLE, K. R. LIPS, AND D. L. DRAKE. 2007. A stable isotope study of a neotropical stream food web prior to the extirpation of its large amphibian community. *J. Trop. Ecol.* **23**: 643–653.
- WALLACE, J. B., AND F. F. SHERBERGER. 1974. The larval retreat and feeding net of *Macronema carolina* banks (Trichoptera: Hydropsychidae). *Hydrobiologia* **45**: 177–184.
- , AND J. R. WEBSTER. 1996. The role of macroinvertebrates in stream ecosystem function. *Annu. Rev. Entomol.* **41**: 115–139.
- WHILES, M. R., AND W. K. DODDS. 2002. Relationships between stream size, suspended particles, and filter-feeding macroinvertebrates in a Great Plains drainage network. *J. Environ. Qual.* **31**: 1589–1600.
- , AND OTHERS. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Front. Ecol. Environ.* **4**: 27–34.
- YOUNG, B. E., AND OTHERS. 2001. Population declines and priorities for amphibian conservation in Latin America. *Conserv. Biol.* **15**: 1213–1223.

Edited by: H. Maurice Valett

Received: 23 April 2008

Accepted: 26 August 2008

Amended: 4 September 2008