

Recovery of a tropical stream after a harvest-related chlorine poisoning event

EFFIE A. GREATHOUSE, JAMES G. MARCH AND CATHERINE M. PRINGLE

Institute of Ecology, University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. Harvest-related poisoning events are common in tropical streams, yet research on stream recovery has largely been limited to temperate streams and generally does not include any measures of ecosystem function, such as leaf breakdown.
2. We assessed recovery of a second-order, high-gradient stream draining the Luquillo Experimental Forest, Puerto Rico, 3 months after a chlorine-bleach poisoning event. The illegal poisoning of freshwater shrimps for harvest caused massive mortality of shrimps and dramatic changes in those ecosystem properties influenced by shrimps. We determined recovery potential using an established recovery index and assessed actual recovery by examining whether the poisoned reach returned to conditions resembling an undisturbed upstream reference reach.
3. Recovery potential was excellent (score = 729 of a possible 729) and can be attributed to nearby sources of organisms for colonisation, the mobility of dominant organisms, unimpaired habitat, rapid flushing and processing of chlorine, and location within a national forest.
4. Actual recovery was substantial. Comparison of the reference reach with the formerly poisoned reach indicated: (1) complete recovery of xiphocaridid and palaemonid shrimp population abundances, shrimp size distributions, leaf breakdown rates, and abundances of oligochaetes and mayflies on leaves, and (2) only small differences in atyid shrimp abundance and community and ecosystem properties influenced by atyid shrimps (standing stocks of epilithic fine inorganic and organic matter, chlorophyll *a*, and abundances of chironomids and copepods on leaves).
5. There was no detectable pattern between any measured variables and distance downstream from the poisoning. However, shrimp size-distributions indicated that the observed recovery may represent a source-sink dynamic, in which the poisoned reach acts as a sink which depletes adult shrimp populations from surrounding undisturbed habitats. Thus, the rapid recovery observed in this study is consistent with results from other field studies of pulse chlorine disturbances, harvest-related fish poisonings, and recovery of freshwater biotic interactions, but it is unlikely to be sustainable if multiple poisonings deplete adult populations to the extent that juvenile recruitment does not offset adult shrimp mortality.

Keywords: Decapoda, macroinvertebrates, Puerto Rico, pulse disturbance, shrimps, toxic release

Correspondence: Effie A. Greathouse, Institute of Ecology,
University of Georgia, Athens, GA 30602, U.S.A.

E-mail: effieg@gmail.com

Present address: James G. March, Department of Biology,
Washington and Jefferson College, 60 South Lincoln Street,
Washington, PA 15301, U.S.A.

Introduction

Most studies of stream ecosystem disturbance and recovery have examined measures of ecosystem structure, such as species- or community-level indicators (Fisher, 1990; Yount & Niemi, 1990). In contrast,

there has been relatively little focus on recovery of ecosystem functions or processes, such as leaf litter breakdown, despite different advantages and disadvantages in using species/community-level versus process-level indicators in evaluating ecosystem recovery (Kelly & Harwell, 1990; Niemi, Detenbeck & Perry, 1993). Although indicators of ecosystem structure, such as species composition, may be sensitive and show a rapid response (Schindler, 1987), they generally give only a snapshot of current conditions and thus are difficult to use in evaluating potential future ecosystem dynamics (Kelly & Harwell, 1990). Process measures may be useful in evaluating recovery because they offer insight on ecosystem function. Ecosystem function may need to recover before species can respond, but it can be insensitive to changes in the system because of functional redundancy (Schindler, 1987; Kelly & Harwell, 1990). Thus, structural and functional measures should be evaluated in recovery studies (Kelly & Harwell, 1990), although few have done so (Yount & Niemi, 1990).

Ecosystem-wide effects of toxins, mediated through biotic interactions, are a critical area for research (Carlisle, 2000). Many stream studies of chemical releases have concentrated on consequences of reduced predators and competitors (e.g. Heckman, 1983; Wallace, 1990; Mackay, 1992), but there has been comparatively little research examining disturbance and recovery of herbivore–plant interactions (Gawne & Lake, 1996).

One little-studied type of chemical release with strong potential to alter ecosystem structure, function and biotic interactions is harvest-related poisoning of tropical streams. In Puerto Rico, illegal poisonings, using chlorine bleach to harvest freshwater shrimps, are believed to be relatively frequent in the Caribbean National Forest (E. García, U.S. Forest Service, personal communication) and in other parts of the island (I. Corujo, Puerto Rico Department of Natural Resources, personal communication). Chlorine poisonings are thought to be used primarily to harvest large numbers of adult *Macrobrachium*, which reach sizes >230 mm in length, to sell on local markets. Poisonings using chlorine, insecticides and traditional toxins to harvest fishes have also been reported in Africa (Victor & Ogbeibu, 1986), Costa Rica (E. Anderson, La Selva Biological Station, personal communication), and South America (Baksh, 1984). To our knowledge, however, the work of Victor & Ogbeibu

(1986) is the only published study of recovery following one of these tropical stream harvest-related poisonings.

Here we document the recovery of ecosystem structure, function and biotic interactions 3 months after a chlorine bleach poisoning in the Sonadora, a second-order stream draining the Luquillo Experimental Forest/Caribbean National Forest (LEF/CNF), Puerto Rico. The LEF is one of the largest old growth forests left in the Caribbean and the only tropical rainforest in the U.S. National Forest system. Data on illegal, harvest-related poisonings are few because they are difficult to detect. Yet LEF stream poisonings are important to study because these streams may be critical refugia for freshwater biota in the Caribbean. For example, LEF populations may be a source of colonists for downstream reaches and streams across the island affected by other human impacts.

The Sonadora and its tributaries are the main study sites for research conducted over the past 15 years on the ecological roles of freshwater shrimps (e.g. Pringle *et al.*, 1993, 1999; March *et al.*, 2001, 2002). In March 1999, the Sonadora was poisoned with chlorine bleach 140 m upstream of the bridge of Road 186 in the LEF (300 m a.s.l., Fig. 1). The poisoning was discovered by U.S. Forest Service personnel on 12 March and was estimated to have occurred on 10 March based on the condition of thousands of decaying shrimps observed along the approximately 500-m reach affected by the poisoning (N. Hemphill, National Park Service, and E. García, U.S. Forest Service, personal communication). Immediate effects of the poisoning were studied by E.A. Greathouse, C.M. Pringle, N. Hemphill, E. García, W.H. McDowell & A. Ramírez (unpublished data). In the poisoned reach, E.A. Greathouse *et al.* (unpublished data) found dramatically reduced abundances of shrimps which caused alterations in algae, fine particulate organic/inorganic matter, and nutrients that were consistent with previous *in situ* shrimp exclusion experiments conducted over small spatial scales (0.25 m²).

In this paper, our objective is to assess: (1) recovery potential, using an established recovery index (Cairns, 1990), and (2) whether the formerly poisoned reach returned to conditions resembling an undisturbed reference reach upstream (*sensu* Yount & Niemi, 1990). We examined several components of ecosystem structure (fine particulate inorganic and organic matter; algal, benthic invertebrate, shrimp and fish

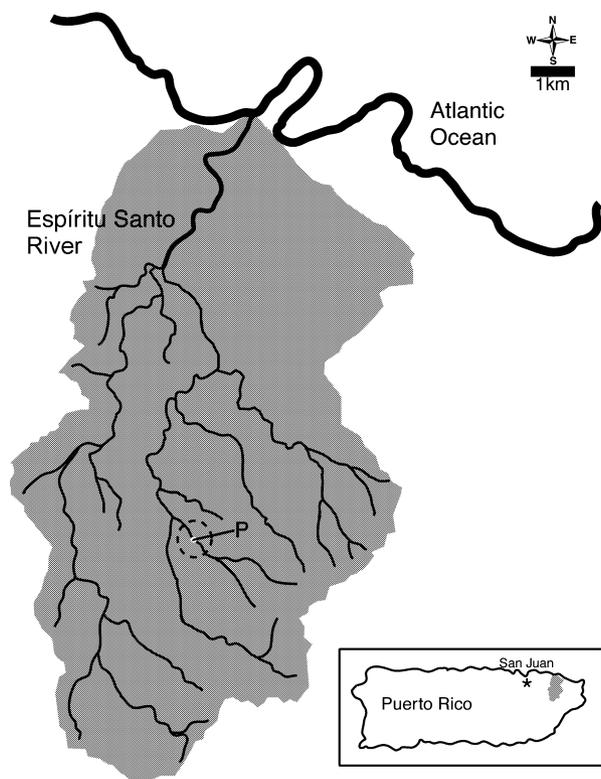


Fig. 1 Map of the Espiritu Santo watershed. 'P' indicates the location of the poisoning on the Sonadora. The dashed circle indicates the approximate location of the formerly poisoned reach and upstream reference reach used for our study of recovery. The inset shows the location of the Espiritu Santo watershed in Puerto Rico in relation to the capital city, San Juan.

abundances; shrimp size distributions) and function (leaf breakdown). We were also able to examine recovery of biotic interactions by measuring structural and functional components that we know represent important biotic interactions in the Sonadora based on our previous manipulative experiments of shrimps prior to the poisoning.

Study area

The Sonadora is a second order tributary (based on a 1 : 20 000 USGS map) of the Espiritu Santo River, which drains the LEF in north-eastern Puerto Rico (Fig. 1). Physical habitat of the Sonadora is characterised by large boulders with interstitial cobble and coarse gravel and a steep gradient with alternating pools and cascades. Vegetation at the study site is secondary rain forest dominated by tabonuco (*Dacryodes excelsa* Vahl). The LEF shows only slight seasonal variation in rainfall and allochthonous inputs (Covich

& McDowell, 1996). Flash floods occur throughout the year, with discharge increases of up to 10-fold in less than an hour (Covich & McDowell, 1996).

Eight species of omnivorous freshwater shrimps in three families (Palaemonidae, Atyidae, Xiphocarididae) occur in the Sonadora (Covich & McDowell, 1996). *Macrobrachium carcinus* (L) and *M. crenulatum* Holthius are the dominant palaemonids; *M. heterochirus* (Wiegmann) and *M. faustinum* (De Saussure) also occur. Atyid shrimps include *Atya lanipes* Holthius, *A. scabra* (Leach), and *A. innocous* (Herbst) (Villamil & Clements, 1976; Covich, 1988). *Xiphocaris elongata* (Guérin-Méneville) is the sole species representing the Xiphocarididae. Experiments in the study watershed have demonstrated that omnivorous feeding by freshwater shrimps affects algal biomass and species composition, quantity and quality of benthic organic matter, leaf breakdown rates, and abundance and biomass of benthic insects (Pringle *et al.*, 1993, 1999; Crowl *et al.*, 2001; March *et al.*, 2001, 2002). *Sicydium plumieri* (Bloch), the algivorous green stream goby, is the only fish species occurring at our study site. A closely related species has been found to affect algal biomass, quantity and quality of benthic organic matter, and abundance of benthic insects in Costa Rica (Barbee, 2002). All native freshwater shrimps and fishes in the Sonadora are amphidromous with adult females releasing larvae that passively drift downstream to the estuary before migrating back upstream as juveniles (Chace & Hobbs, 1969; Covich & McDowell, 1996; March *et al.*, 1998; Benstead, March & Pringle, 2000). Other fauna of the Sonadora include aquatic insects dominated by baetid and leptophlebiid mayflies and chironomids, and other invertebrates such as oligochaetes, copepods, and the crab *Epilobocera sinuatifrons* (A. Milne-Edwards) (Covich & McDowell, 1996).

Methods

We assessed the potential for ecosystem recovery using the recovery index developed by Cairns (1990) for determining a system's 'elasticity' or its ability to return to its approximate original condition. This index qualitatively categorises six ecological and sociological factors in a rating system of 1 (poor), 2 (moderate) or 3 (good), calculates a total score by multiplying the ratings of all of the factors, and categorises the chances for rapid recovery as excellent, fair to good, or poor.

From 15 June to 28 July 1999, we assessed actual recovery of shrimps, fishes, invertebrates in leaf packs, shrimp size distributions, algal colonisation, accrual of fine particulate inorganic and organic matter, and leaf breakdown rates in pool habitats of the upper 315 m of the 500-m reach affected by the March 1999 poisoning. We used a 250-m reach upstream of the poisoning as a reference for comparison with the poisoned reach. Five reference pools and 10 formerly poisoned pools were chosen for study.

In each pool, we haphazardly placed six unglazed ceramic tiles (7 × 15 cm) and six leaf packs, each tethered to cobble from the channel with cable ties and metal binder clips. Leaf packs were made from air-dried leaves of *Cecropia schreberiana* Miq. cut into smaller pieces (c. 100 cm² each), weighed to approximately 5 g, and held together with a binder clip. *Cecropia schreberiana* is a common tree species in the riparian zone of tabonuco forest (Brokaw, 1998) and has been used in previous leaf breakdown experiments in the Sonadora (Crowl *et al.*, 2001; March *et al.*, 2001). In the two study pools furthest upstream in the formerly poisoned reach, tiles and leaf packs were disturbed by swimmers (i.e. picked up and tossed). Tiles and leaf packs in the third study pool of the formerly poisoned reach suffered high washout during a storm 2 days after placement. Consequently, we excluded from all analyses any tile and leaf pack data collected in these three pools. The seven remaining study pools in the poisoned reach were below the Road 186 bridge crossing of the Sonadora and were similar to the pools of the reference reach in physical parameters (Table 1).

Table 1 Physical parameters of the studied stream reaches: mean depth at tiles and leaf packs, mean flow at tiles and leaf packs (Marsh–McBirney digital flow meter), per cent canopy cover (spherical densiometer), pool surface area

	Upstream reference reach	Formerly poisoned reach	F	d.f.	P-value
Depth (m)	0.40 ± 0.03	0.34 ± 0.02	2.39	1, 10	0.15
Flow (m s ⁻¹)	0.08 ± 0.02	0.05 ± 0.02	0.78	1, 10	0.40
% Canopy cover	55.88 ± 6.65	58.76 ± 6.92	0.08	1, 10	0.78
Pool surface area (m ²)	24.72 ± 6.13	27.48 ± 7.19	0.08	1, 10	0.79

Data are mean values ± 1 SE.

From each study pool, we randomly sampled one tile on days 11, 16, 20, 25, and 34 and one leaf pack on days 6, 11, 14, 16 and 20. We also sampled 25 leaf packs on day 0 to obtain an air-dried to oven-dried ratio to convert the original air-dried weight of each leaf pack to an oven-dried weight. We sampled tiles and leaf packs by cutting cable ties and raising the tile or leaf pack out of the water within a 363-µm hand net. The tile or leaf pack and hand net contents were placed into a ziplock bag and transported to the laboratory in a cooler.

Laboratory processing of tiles consisted of scraping the top surface of the tile with a razor blade and scrubbing the entire tile with a toothbrush. After removing insects from the resulting homogenate, two subsamples of known volumes were filtered onto combusted and preweighed glass fibre filters (Whatman GF/F, 0.7 µm). Mass of organic (AFDM) and inorganic matter was determined for one filter, dried at 50 °C for 24 h, weighed to the nearest 0.001 g, burned at 500 °C for 3 h, and re-weighed. The second filter was frozen until analysed for chlorophyll *a* using a fluorometer (model 10AU; Turner Designs Inc., Sunnyvale, CA, U.S.A.) and standard methods [American Public Health Association (APHA), 1985].

Laboratory processing of leaves consisted of rinsing off insects and sediments, oven-drying at 50 °C for 24 h, weighing to the nearest 0.001 g, burning at 500 °C for 3 h, and re-weighing. Leaf breakdown rates (*k*) were calculated for each pool by regressing ln (% AFDM remaining) against elapsed days. The slope of the regression is represented by *k* (Benfield, 1996). Insects and small benthic invertebrates were separated from sediments while alive, preserved in 70% ethanol, and identified to the lowest practicable level (generally family or order). We analysed the abundances of the four most common invertebrate taxa (Ephemeroptera, Chironomidae, Oligochaeta and Copepoda).

Shrimp abundance in each study pool was assessed by trapping and by systematic observation. Minnow traps, each baited with c. 200 mL of dry cat food, were set overnight at an approximate density of 1 trap m⁻² of pool surface area. On the following morning, trapped shrimps were identified to family, measured for carapace length (post-orbital, ± 1 mm), and released. Daytime observations were conducted at each tile and leaf pack on days 8, 13, 20, 25 and 33. These followed a standard protocol within an observation

date, but observation methods were not the same between observation dates. On all dates, we recorded the number of shrimps in each family. Day 8 observations were conducted for 1 min and recorded shrimps occurring on the tile or leaf pack. On days 13, 20, and 25, observations were 'spot checks', recording shrimps on the tile or leaf pack and in an estimated 5-in radius around the tile or leaf pack. On day 33, observations were conducted for 10 min, again recording shrimps on the tile or leaf pack and in a 5-in radius. One reference-reach pool was excluded from analyses of observation data reported here because 10-min observations were not done on day 33. Analyses including this pool did not alter results. On day 42, density of the green stream goby (*S. plumieri*) in each pool was determined by snorkeling the entire pool and counting all individuals observed. Visibility was similar across pools.

To assess differences between the reference reach and the formerly poisoned reach, we used one-way analysis of variance (ANOVA) for trapping data, physical parameters, leaf breakdown rates (k), and goby density. We used one-way repeated measures ANOVAs for shrimp observation data, chlorophyll a , organic and inorganic matter on tiles, and invertebrates in leaf packs. Trapping data, shrimp observation data, goby density and physical parameters were analysed with two-tailed tests. Based on results for relative shrimp abundances from trapping and observation data, one-tailed or two-tailed tests were chosen to analyse ecosystem and community properties previously shown to be influenced by shrimps (Table 2). We also used simple linear regression to assess whether recovery in ecosystem and community

properties changed with distance downstream from the location where the chlorine was added.

All statistical analyses used *pools* as the experimental unit and were performed using JMP 3.2.6 (SAS Institute Inc., 1999). We used a significance level of 0.05. The Shapiro–Wilk test was used to test data for normality. When appropriate, $\log_{10}(X)$ and $\log_{10}(X + 1)$ transformations were conducted to improve normality.

Results

We scored the Sonadora as having excellent potential for rapid recovery (score = 729 of 729). The following factors of the recovery index (Cairns, 1990) contributed to the high rating: nearby sources of organisms to reinvade the impaired reach; high mobility and transportability of organisms; habitat in excellent condition and not fundamentally damaged by the poisoning; no residual toxicants present or persisting after the poisoning event; normal chemical–physical environment with few lingering effects from the chlorine; and location within a national forest such that management agencies have high potential to conduct remediation efforts.

Shrimp abundances per trap were not significantly different between the reference reach and the poisoned reach (Xiphocarididae: $F_{1,13} = 0.08$, $P = 0.78$; Atyidae: $F_{1,13} = 0.42$, $P = 0.53$; Palaemonidae: $F_{1,13} = 0.59$, $P = 0.46$, Fig. 2). There were no significant differences in carapace lengths of shrimps trapped in the reference reach compared with the poisoned reach (Xiphocarididae: $F_{1,12} = 0.14$, $P = 0.71$; Atyidae: $F_{1,12} = 0.87$, $P = 0.37$; Palaemonidae: $F_{1,12} = 1.81$,

Table 2 Hypotheses and statistical analyses (one-tailed versus two-tailed tests) for patterns in the formerly poisoned reach compared with the upstream reference reach, and references on which hypotheses are based

Parameter	Hypothesis	Statistical test	References
<i>From tiles</i> (based on results for abundance for <i>Atya</i> spp.)			
Chlorophyll a	Increase	One-tailed	March <i>et al.</i> , 2002
Organic matter	Increase	One-tailed	Pringle <i>et al.</i> , 1999; March <i>et al.</i> , 2002
Inorganic matter	Increase	One-tailed	Pringle <i>et al.</i> , 1999; March <i>et al.</i> , 2002
<i>From leaf packs</i> (based on results for abundance of <i>X. elongata</i>)			
Leaf breakdown rate	No difference	Two-tailed	March <i>et al.</i> , 2001
Ephemeroptera biomass	No difference	Two-tailed	March <i>et al.</i> , 2001
Chironomidae biomass	No difference	Two-tailed	March <i>et al.</i> , 2001

Hypotheses are based on shrimp abundances in the formerly poisoned reach versus the upstream reference reach (i.e. lowered abundance of *Atya* in the formerly poisoned reach and no difference in abundance of *X. elongata* – see *Results* section).

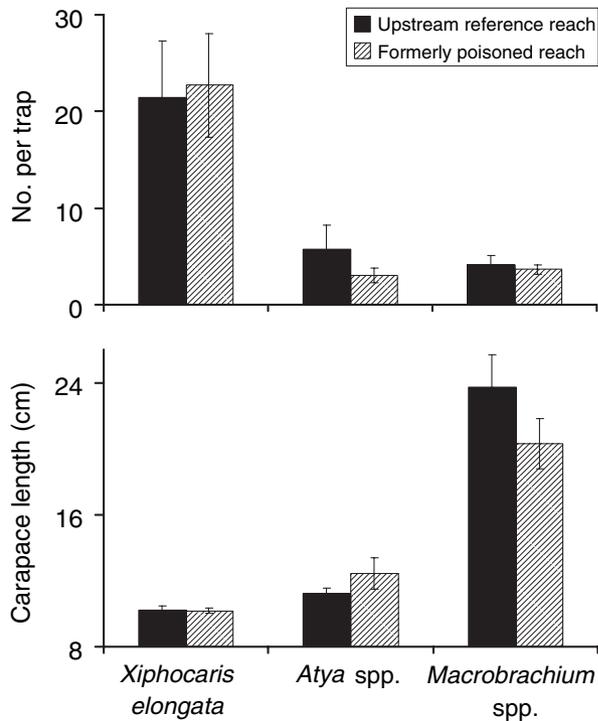


Fig. 2 Mean shrimp abundances and carapace lengths (± 1 SE) in minnow traps.

$P = 0.20$, Fig. 2). On 5 July, 185 m downstream from the poisoning, we observed one very large *Macrobrachium carcinus* with a carapace length of approximately 60 mm. Number of individuals observed near leaf packs and tiles were not significantly different for Xiphocarididae ($F_{1,9} = 0.55$, $P = 0.48$, Fig. 3) or

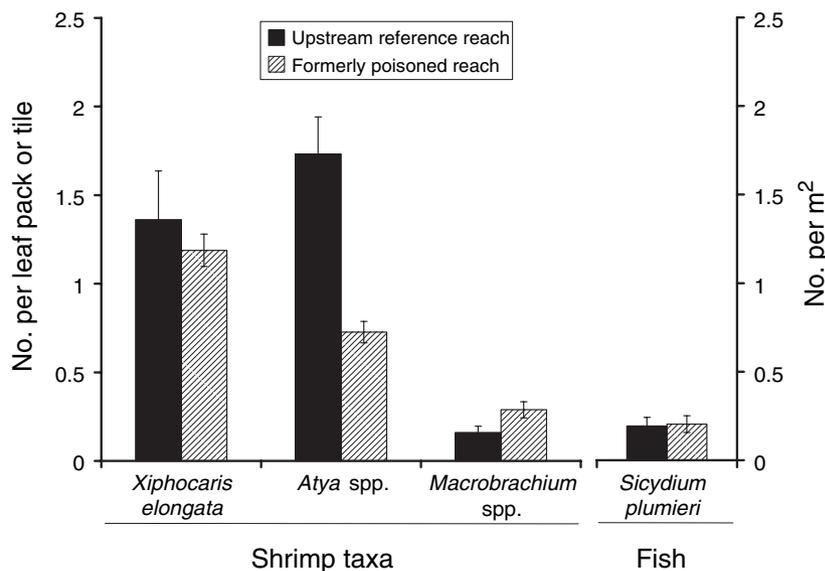


Fig. 3 Mean shrimp abundances during observations of leaf packs and tiles and mean fish densities obtained from snorkelling study pools. Error bars are 1 SE.

Palaemonidae ($F_{1,9} = 3.73$, $P = 0.085$, Fig. 3). Atyidae were significantly less abundant near leaf packs and tiles in the poisoned reach ($F_{1,9} = 35.43$, $P = 0.0002$, Fig. 3). Fish density also did not differ between the two reaches ($F_{1,13} < 0.01$, $P = 0.98$, Fig. 3).

Chlorophyll *a* and inorganic dry mass on tiles were significantly higher in the poisoned reach compared with the upstream reference reach (chlorophyll *a*: $F_{1,10} = 5.31$, $P = 0.022$; inorganic dry mass: $F_{1,10} = 4.43$, $P = 0.031$, Fig. 4). Organic matter (AFDM) on tiles was not significantly different between the two reaches ($F_{1,10} = 0.25$, $P = 0.31$). Lack of significance in AFDM, however, was because of a single tile on a single date indicated by Dixon's test (Sokal & Rohlf, 1995) to be an outlier. Exclusion of this tile resulted in significantly higher AFDM in the poisoned reach compared with the reference reach ($F_{1,10} = 5.61$, $P = 0.019$, Fig. 4). Leaf breakdown rates did not differ between the poisoned reach and the reference reach ($F_{1,10} = 0.01$, $P = 0.91$, Fig. 5). We found no significant differences in abundances of Ephemeroptera ($F_{1,10} = 0.40$, $P = 0.54$, Fig. 5) and Oligochaeta ($F_{1,10} = 0.42$, $P = 0.53$, Fig. 5) occurring on leaf packs. However, Chironomidae and Copepoda were significantly more abundant in leaf packs in the poisoned reach compared with the upstream reference reach (Chironomidae: $F_{1,10} = 6.65$, $P = 0.027$; Copepoda: $F_{1,10} = 11.46$, $P = 0.007$, Fig. 5). No regressions of ecosystem and community properties against distance downstream from the poisoning were statistically significant (Table 3).

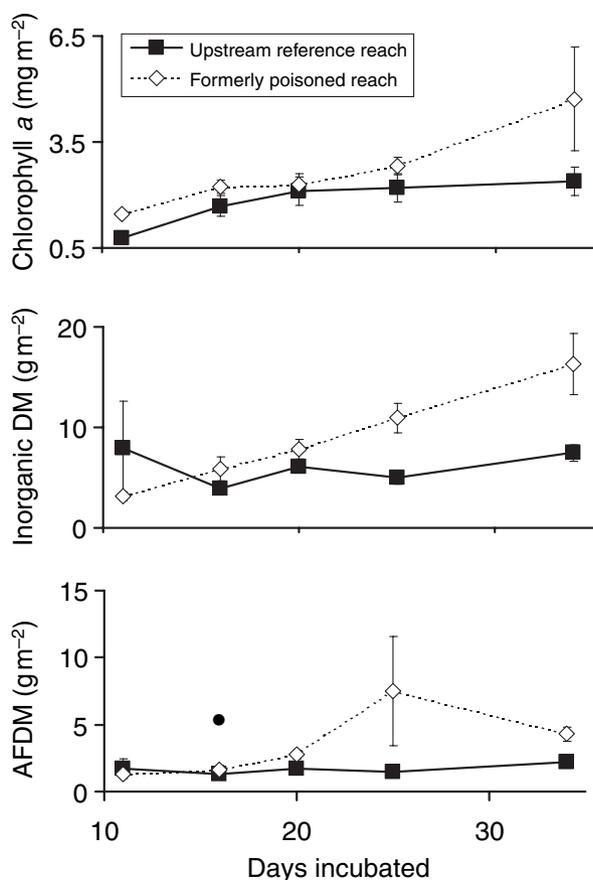


Fig. 4 Mean algal abundance (chlorophyll *a*), fine inorganic matter, and organic matter (AFDM) accruing on tiles over time. Error bars are 1 SE. The solid black circle indicates the average AFDM for the upstream reference reach on day 16 if the outlier is included (see text for explanation).

Discussion

Our findings indicate that the system showed significant recovery 3 months after the poisoning. Prior to the poisoning, conditions appeared visually similar between the poisoned reach and upstream reference reach for shrimp abundances, algae, organic, and inorganic matter (E.A. Greathouse *et al.*, unpublished data). Based on these visual observations and the physical similarity of the two reaches, we assume that prepoisoning conditions were similar between the two reaches. This indicates that recovery occurred in less than 3 months for abundance of *Xiphocaris* and palaemonid shrimps, size distributions of shrimps, leaf breakdown, and abundances of oligochaetes and mayflies on leaves. In contrast, atyid shrimps, fine inorganic and organic matter, algal abundance, and

abundances of chironomids and copepods had lingering differences 3 months after the poisoning. However, these differences were generally small and converging towards complete recovery, as evidenced by an analysis of differences between the reference reach and the poisoned reach in this study compared with those observed by E.A. Greathouse *et al.* (unpublished data) approximately 2 weeks after the poisoning (Fig. 6). Two weeks after the poisoning, ecosystem and community properties in the poisoned reach were substantially different than in the reference reach. Abundances of all three shrimp families in the poisoned reach were lower than abundances in the upstream reference reach, while values for chlorophyll *a*, inorganic and organic matter in the poisoned reach were at least 400% of those in the upstream reference reach (Fig. 6). Three months later, percentages converged towards 100% for all parameters measured in both studies: shrimp abundances increased towards 100%, and organic matter, inorganic matter and chlorophyll *a* decreased towards 100% (Fig. 6).

Conclusions on atyid recovery are complicated because trapping data indicated complete recovery, whereas data from systematic observations indicated lower abundances in the formerly poisoned reach. This may be because the two methods involved sampling different habitats and times of day. Baited traps attract shrimps from a large area, possibly including riffles surrounding the pool in which traps are set. Traps were also set at night when atyid shrimps are more active in areas of lower flow and at a variety of depths (Johnson & Covich, 2000). In contrast, our timed observations were conducted during the day on small areas at leaf packs and tiles within a pool. If atyid shrimps follow an approximate ideal free distribution with respect to food resources, baiting traps with a standard amount of a high quality food resource, like cat food, may attract the same number of shrimps over a range of shrimp densities. Thus, in estimating relative shrimp abundances, conducting systematic observations may be a more sensitive method compared with using baited traps.

Conclusions regarding recovery of *Cecropia* breakdown rates are complicated because breakdown was not measured immediately after poisoning. However, breakdown rates were probably slowed in the poisoned reach prior to recovery of *Xiphocaris* shrimps, whose shredding activities have been found

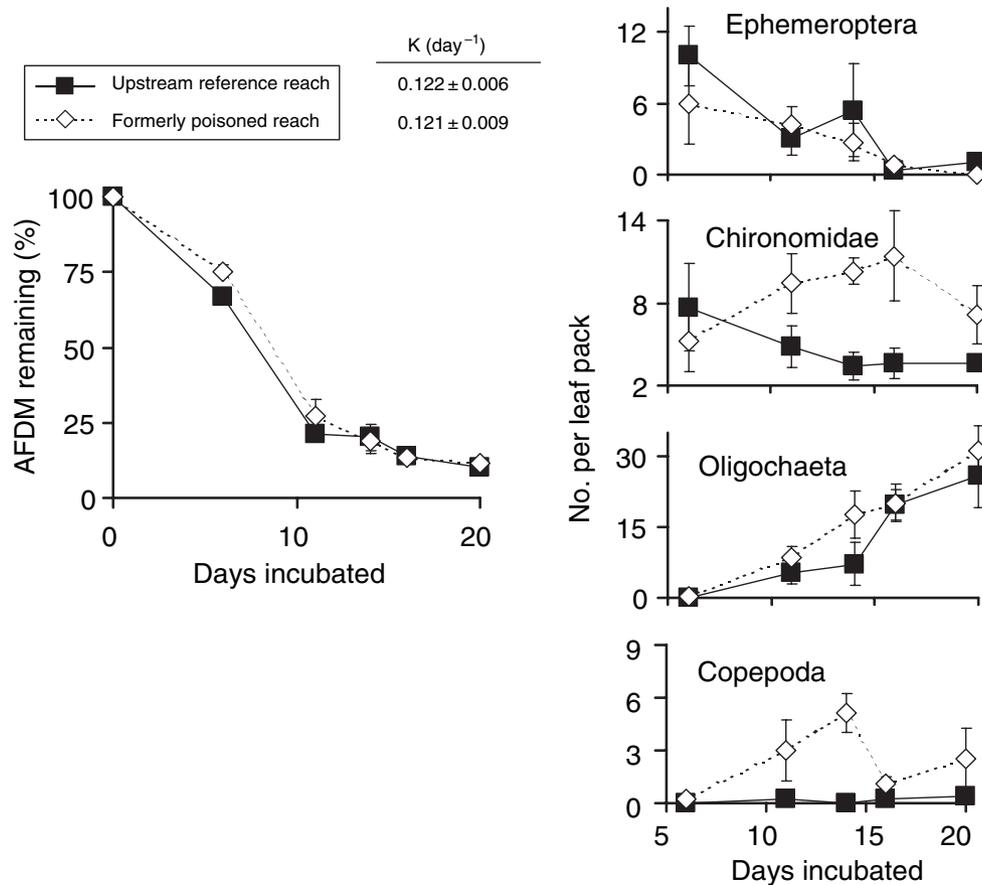


Fig. 5 Percent leaf ash-free dry mass (AFDM) remaining and abundances of the most common benthic invertebrates over time. Leaf breakdown rates (k) are also given for the upstream reference and formerly poisoned reaches. Error bars are 1 SE.

to have significant positive effects on *Cecropia* breakdown (March *et al.*, 2001; Crowl *et al.*, 2001). Thus, we hypothesise that our findings of *Xiphocaris* recovery and no difference in *Cecropia* breakdown rates between the poisoned and reference reaches reflect recovery of *Xiphocaris* shredding activity.

We also hypothesise that patterns in chlorophyll *a*, fine organic and inorganic matter, copepods and larval chironomids reflect interactions with atyid shrimps which have been previously found to reduce chlorophyll *a*, epilithic fine sediments, organic matter, and larval chironomids in the Sonadora (Pringle & Blake, 1994; Pringle *et al.*, 1999; March *et al.*, 2001, 2002). These findings are consistent with recovery studies examining biotic interactions in temperate streams. For example, recovery trajectories after chemical pulse disturbances often exhibit temporary increases in early-colonising dipterans such as chironomids followed by declines when dominant

competitors and predators return to the system (e.g. Niemi *et al.*, 1990; Yount & Niemi, 1990; Mackay, 1992). The few studies documenting recovery of herbivore–algae (Ide, 1967; Yasuno *et al.*, 1982; Lamberti *et al.*, 1991) and detritivore–organic matter (Newman *et al.*, 1987; Whiles, Wallace & Chung, 1993) interactions similarly show recovery of low standing stocks of basal resources following poisonings of grazers, shredders and collector–gatherers that cause temporary algal blooms and build-up of organic matter. Poisoned shrimp carcasses acting as a nutrient subsidy as they decayed immediately after the poisoning may also explain or contribute to the higher levels of algae, fine organic matter, and macroinvertebrates occurring in the poisoned reach.

Shrimp size distributions in the formerly poisoned reach indicate that recovery likely occurred as a result of adults, not juveniles, moving into the reach. Due to natural longitudinal distributions of adult and juven-

Table 3 Results of regression of mean values for ecosystem and community properties against distance downstream from the poisoning. Regression statistics test whether slopes of the regression lines are different from zero for data below the poisoning only.

	<i>F</i>	d.f.	<i>P</i> -value
<i>Xiphocaris elongata</i>			
Numbers per trap	0.14	1, 8	0.72
Carapace length	<0.01	1, 7	0.95
Number per leaf pack or tile	<0.01	1, 5	0.99
<i>Atya</i> spp.			
Number per trap	0.31	1, 8	0.59
Carapace length	0.80	1, 6	0.40
Number per leaf pack or tile	3.12	1, 5	0.14
<i>Macrobrachium</i> spp.			
Number per trap	0.58	1, 8	0.47
Carapace length	3.05	1, 7	0.12
Number per leaf pack or tile	0.74	1, 5	0.43
Goby density	0.01	1, 8	0.91
Chlorophyll <i>a</i> (per m ² of tile)	0.98	1, 5	0.37
Ash-free dry mass (per m ² of tile)	0.19	1, 5	0.68
Inorganic dry mass (per m ² of tile)	0.06	1, 5	0.81
Leaf breakdown rate (<i>k</i>)	0.20	1, 5	0.67
Macroinvertebrate abundance per leaf pack			
Ephemeroptera	0.05	1, 5	0.82
Chironomidae	0.17	1, 5	0.70
Oligochaeta	1.67	1, 5	0.25
Copepoda	0.20	1, 5	0.67

ile shrimps, which are related to their migratory life cycle (Villamil & Clements, 1976; Benstead *et al.*, 2000), potential sources of adult colonists occurred upstream and downstream from the poisoned reach but potential sources of juvenile colonists occurred only downstream. Shrimp recolonisation by upstream migration of juveniles would be expected to be dominated by shrimps smaller than those we observed in the poisoned reach. Thus, recovery by re-distribution of adult shrimps may represent a source-sink dynamic (i.e. the poisoned reach/sink depletes shrimp populations in surrounding undisturbed habitats). Because the population density of shrimps over a large length of stream may be slightly reduced and because processes of migration and growth of larval and juvenile shrimps are poorly understood (March *et al.*, 1998; Benstead *et al.*, 2000), true recovery may require longer than 3 months. Stream ecosystem response to repeated chlorine poisoning will remain unknown without intensive study of upstream recruitment by juveniles.

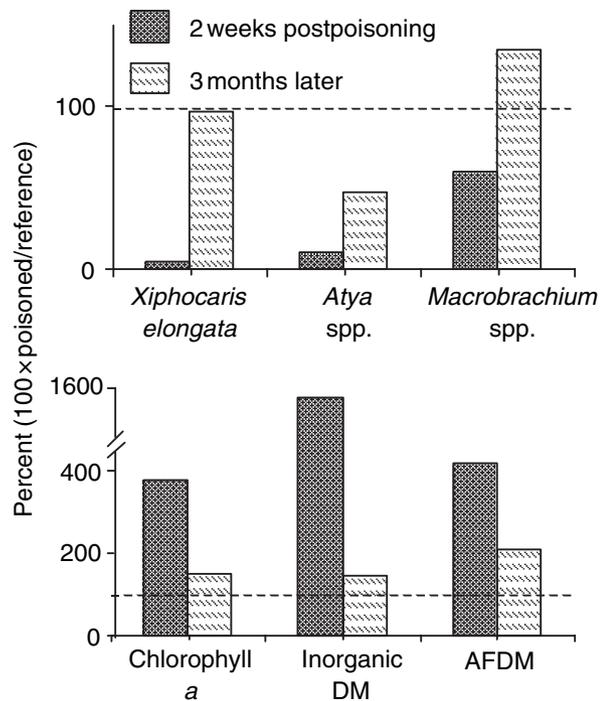


Fig. 6 Shrimp abundances and standing stocks of organic matter, fine inorganic matter and chlorophyll *a* in the formerly poisoned reach expressed as a per cent of values in the upstream reference reach. '2 weeks postpoisoning' calculations are from measurements taken by E.A. Greathouse *et al.* (unpublished data) approximately 2 weeks after the poisoning was discovered in March. '3 months later' calculations are from measurements taken in this study in June and July. Percents of shrimp abundances were calculated from averages for the two methods used in each study [trapping and electroshocking in E.A. Greathouse *et al.* (unpublished data) and trapping and observations in this study]. We did not compare absolute values between the two studies because of differences in season, river discharge, and methods.

Reduced abundances of atyids in the poisoned reach may be due to atyids having lower rates of movement compared with *Xiphocaris* and *Macrobrachium* (Fievet, 1999; T. Crowl, Utah State University, personal communication). Insect recovery likely occurred from drift, ovipositing adults and reproduction of survivors after the poisoning. Whereas the hyporheic zone is an important source of macroinvertebrates during recovery in other streams (Sedell *et al.*, 1990; Yount & Niemi, 1990), high-gradient boulder/bedrock-lined mountain streams of Puerto Rico, such as the Sonadora, lack substantial hyporheic zones (Ahmad, Scatena & Gupta, 1993).

The rapid recovery of the Sonadora is consistent with its calculated index of recovery potential (Cairns, 1990).

However, this finding has limited value as a test of the index because our study represents only a single case of comparison. The rapid recovery of the Sonadora is also consistent with results from other field studies on pulse chlorine disturbances and harvest-related fish poisonings. Recovery of a temperate lotic community after a chlorine spill in Germany occurred in 4 months (Heckman, 1983). Likewise, macroinvertebrate recovery from a harvest-related fish poisoning in a large depositional pool connected to the main channel of the Ikpoba River in Nigeria was substantial after 3 months (Victor & Ogbeibu, 1986). In contrast to our findings on a pulse disturbance in the field, laboratory streams exposed to chronic chlorine disturbance generally had not recovered after more than 3 months (Steinman *et al.*, 1992).

Recovery of stream macroinvertebrate densities, following pulse disturbances, generally ranges from 0.02 to 3 years (Niemi *et al.*, 1990; Wallace, 1990). The relatively rapid (≤ 3 months) recovery of the Sonadora community can be attributed to: (1) the relatively small scale of the Sonadora poisoning that left intact colonisation sources upstream and downstream, and (2) the rapid volatilisation, transformation and flushing of chlorine (Heckman, 1983; Pratt *et al.*, 1988; Stewart *et al.*, 1996). In contrast, recovery from other types of chemical disturbances is slower when the affected area is large and involves persistent chemicals such as DDT (Yount & Niemi, 1990).

Other factors likely contributed to the Sonadora's rapid recovery. First, freshwater shrimps are capable of moving over relatively large distances quickly (Covich *et al.*, 1991; Buzby, 1998; Fievet, 1999). Second, the non-shrimp macroinvertebrate fauna of the Sonadora is dominated by Diptera, Ephemeroptera and Oligochaeta which recover more quickly than other aquatic macroinvertebrates because of high drift rates, high frequency of polyvoltine life cycles, ability to exploit early recovering food resources, and/or high tolerance to pollution (Resh *et al.*, 1988; Steinman & McIntire, 1990; Mackay, 1992). Third, three high discharge events in the Sonadora during the 3-month recovery period (data from U.S. Geological Survey, gauge no. 50063440) likely distributed organisms and organic matter downstream. The flashy discharge regime of the Sonadora may also adapt the community to be resilient to disturbances, generally, whether natural or human-induced (Resh *et al.*, 1988; Poff & Ward, 1990; Covich *et al.*, 1991; Matthaei *et al.*, 1996). Fourth, seasonal restrictions which affect repro-

duction and activity, thus limiting colonisation and recovery in temperate streams, are not prevalent in tropical streams (Corbet, 1958; Jackson & Sweeney, 1995). Finally, some biota also displayed resistance to chlorine. For example, the green stream goby did not appear to be killed by the chlorine poisoning (E.A. Greathouse *et al.*, unpublished data).

The rapid recovery we observed was likely because of the location of the poisoning (in the *lower* Sonadora) and the relatively undisturbed nature of the drainage. If these factors are important to rapid recovery, recovery may be slower after poisonings in other Puerto Rican streams. Human impacts, such as water withdrawals and dams, shrimp trapping, deforestation and agriculture, could cause slow recovery from poisonings by degrading or isolating refugia that act as sources of colonists (Sedell *et al.*, 1990; Lonzarich, Warren & Lonzarich, 1998). A higher elevation stream poisoning in the LEF (at 540 m a.s.l. compared with 300 m a.s.l. in this study) showed that atyid recovery required several years compared with the 3 months suggested by our study (E. García, U.S. Forest Service and N. Hemphill, U.S. National Park Service, personal communication). This is consistent with other studies in which headwater streams had long recovery times due to a lack of upstream colonists, lower flushing rates and lower drift rates (Wallace, 1990).

Increased distance from upstream sources of colonists may also result in slower recovery rates (Gore & Milner, 1990). However, no pattern of differential recovery with distance downstream was observed in this study, as was observed by Gore (1982) for sites at 50 versus 250 versus 450 m downstream from recolonisation sources. The lack of downstream distance patterns suggests that recovery of atyid shrimps was not occurring as a wave of shrimps moving downstream – 315 m may be a distance over which shrimps move relatively easily, and atyids may have colonised not only from the upstream reference reach but also from downstream and/or from a small unaffected tributary entering the formerly poisoned reach at c. 180 m downstream.

In conclusion, our study indicates that the Sonadora study reach recovered rapidly from chlorine poisoning which caused massive mortality of shrimps and dramatically altered biotic interactions. Within 3 months, shrimp abundances had either matched those of the reference reach or were substantially increased, and ecosystem function appeared largely

restored in terms of shrimp effects on algal and macroinvertebrate abundance, accrual of fine inorganic and organic matter and *Cecropia* breakdown. However, with the potential for repeated poisonings to deplete sources of shrimp colonists, it is unknown whether such quick recovery is sustainable. Our findings are of direct concern to humans given the importance of commercial fisheries for gobies in Puerto Rico (Erdman, 1961) and the importance of shrimps and gobies for freshwater recreation (e.g. freshwater snorkelling, trapping and other harvest of shrimps; S. Kartchner and T. Crawl, Utah State University, personal communication) and ecosystem services (e.g. shrimps process organic matter and control algal biomass and standing stocks of sediments and FPOM; Pringle *et al.*, 1999; March *et al.*, 2001, 2002). Our observations of rapid recovery of structure, function and biotic interactions in a neotropical stream contribute to our understanding of stream recovery, which has generally been limited to studies of ecosystem structure in temperate streams (Fisher, 1990; Gore, Kelly & Yount, 1990).

Acknowledgments

We are indebted to Dr Nina Hemphill and Dr Ernesto García for discovering the poisoning event and providing critical information allowing us to conduct this study. We thank Honghua Ruan for assistance in the field, the staff of the El Verde Field Station for logistical support, and Dr Mary Freeman, the Pringle laboratory group, and two anonymous reviewers for helpful comments on manuscripts. Support was provided by the U.S. Forest Service (Department of Agriculture, grant to CMP, no. 10-21-RR551-112) and the National Science Foundation Graduate Fellowship program (fellowship to EAG). This research was also supported by grants BSR-8811902, DEB 9411973, and DEB 0218039 from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and to the International Institute of Tropical Forestry USDA, as part of the Long-Term Ecological Research Program in the LEF. The University of Puerto Rico gave additional support.

References

Ahmad R., Scatena F.N. & Gupta A. (1993) Morphology and sedimentation in Caribbean montane streams:

examples from Jamaica and Puerto Rico. *Sedimentary Geology*, **85**, 157–169.

American Public Health Association (APHA). (1985) *Standard Methods for the Examination of Water and Wastewater*, 16th edition. American Public Health Association, Washington, DC.

Baksh M.G. (1984) *Cultural Ecology and Change of the Machiguenga Indians of the Peruvian Amazon*. PhD Dissertation, Anthropology, University of California, Los Angeles, CA, 138pp.

Barbee N.C. (2002) *Grazer–Algae Interactions in a Tropical Lowland Stream (Costa Rica)*. PhD Dissertation, Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA, 166pp.

Benfield E.F. (1996) Leaf decay in stream ecosystems. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 579–590. Academic Press, San Diego, CA.

Benstead J.P., March J.G. & Pringle C.M. (2000) Estuarine larval development and upstream post-larval migration of freshwater shrimps in two tropical rivers of Puerto Rico. *Biotropica*, **32**, 545–548.

Brokaw N.V.L. (1998) *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *Botanical Review*, **64**, 91–120.

Buzby K. (1998) *The Effect of Disturbance on the Ecological Efficiency of a Small Tropical Stream*. PhD Dissertation, College of Environmental Science and Forestry, State University of New York, Syracuse, NY, 130pp.

Cairns J. (1990) Lack of theoretical basis for predicting rate and pathways of recovery. *Environmental Management*, **14**, 517–526.

Carlisle D.M. (2000) Bioenergetic food webs as a means of linking toxicological effects across scales of ecological organization. *Journal of Aquatic Ecosystem Stress and Recovery*, **7**, 155–165.

Chace F.A.J. & Hobbs H.H.J. (1969) The freshwater and terrestrial crustaceans of the West Indies with special reference to Dominica. *U.S. National Museum Bulletin*, **292**, 1–258.

Corbet P.S. (1958) Some effects of DDT on the fauna of the Victoria Nile. *Review Zoology Botany Africa*, **57**, 73–95.

Covich A.P. (1988) Atyid shrimp in the headwaters of the Luquillo Mountains, Puerto Rico: filter feeding in natural and artificial streams. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **23**, 2108–2113.

Covich A.P. & McDowell W.H. (1996) The stream community. In: *The Food Web of a Tropical Rain Forest* (Eds D.P. Reagan & R.B. Waide), pp. 433–460. University of Chicago Press, Chicago, IL.

Covich A.P., Crawl T.A., Johnson S.L., Varza D. & Certain D.L. (1991) Post-hurricane Hugo increases in

- atyid shrimp abundances in a Puerto Rican montane stream. *Biotropica*, **23**, 448–454.
- Crowl T.A., McDowell W.H., Covich A.P. & Johnson S.L. (2001) Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology*, **82**, 775–783.
- Erdman D.S. (1961) Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. *Bulletin of Marine Science of the Gulf and Caribbean*, **11**, 448–456.
- Fievet E. (1999) Daylight migration of freshwater shrimp (Decapoda, Caridea) over a weir during water release from the impoundment. *Crustaceana*, **72**, 351–356.
- Fisher S.G. (1990) Recovery processes in lotic ecosystems – limits of successional theory. *Environmental Management*, **14**, 725–736.
- Gawne B. & Lake P.S. (1996) The effects of disturbance on a herbivore-epilithon interaction in an upland stream. *Hydrobiologia*, **331**, 153–160.
- Gore J.A. (1982) Benthic invertebrate colonization: source distance effects on community composition. *Hydrobiologia*, **94**, 183–193.
- Gore J.A. & Milner A.M. (1990) Island biogeographical theory – can it be used to predict lotic recovery rates? *Environmental Management*, **14**, 737–753.
- Gore J.A., Kelly J.R. & Yount J.D. (1990) Application of ecological theory to determining recovery potential of disturbed lotic ecosystems – research needs and priorities. *Environmental Management*, **14**, 755–762.
- Heckman C.W. (1983) The recovery of the biotic community in a lotic freshwater habitat after extensive destruction by chlorine. *Internationale Revue Der Gesamten Hydrobiologie*, **68**, 207–226.
- Ide F.P. (1967) Effects of forest spraying with DDT on aquatic insects of salmon streams in New Brunswick. *Journal of the Fisheries Research Board of Canada*, **24**, 769–805.
- Jackson J.K. & Sweeney B.W. (1995) Egg and larval development times for 35 species of tropical stream insects from Costa Rica. *Journal of the North American Benthological Society*, **14**, 115–130.
- Johnson S.L. & Covich A.P. (2000) The importance of night-time observation for determining habitat preferences of stream biota. *Regulated Rivers: Research and Management*, **16**, 91–99.
- Kelly J.R. & Harwell M.A. (1990) Indicators of ecosystem recovery. *Environmental Management*, **14**, 527–545.
- Lamberti G.A., Gregory S.V., Ashkenas L.R., Wildman R.C. & Moore K.M.S. (1991) Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 196–208.
- Lonzarich D.G., Warren M.L. & Lonzarich M.R.E. (1998) Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2141–2149.
- Mackay R.J. (1992) Colonization by lotic macroinvertebrates – a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 617–628.
- March J.G., Benstead J.P., Pringle C.M. & Ruebel M.W. (2001) Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 470–478.
- March J.G., Benstead J.P., Pringle C.M. & Scatena F.N. (1998) Migratory drift of larval freshwater shrimps in two tropical streams, Puerto Rico. *Freshwater Biology*, **40**, 1–14.
- March J.G., Pringle C.M., Townsend M.J. & Wilson A.I. (2002) Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. *Freshwater Biology*, **47**, 377–390.
- Matthaei C.D., Uehlinger U., Meyer E.I. & Frutiger A. (1996) Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **35**, 233–248.
- Newman R.M., Perry J.A., Tam E. & Crawford R.L. (1987) Effects of chronic chlorine exposure on litter processing in outdoor experimental streams. *Freshwater Biology*, **18**, 415–428.
- Niemi G.J., Detenbeck N.E. & Perry J.A. (1993) Comparative-analysis of variables to measure recovery rates in streams. *Environmental Toxicology and Chemistry*, **12**, 1541–1547.
- Niemi G.J., DeVore P., Detenbeck N., Taylor D., Lima A., Pastor J., Yount J.D. & Naiman R.J. (1990) Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management*, **14**, 571–587.
- Poff N.L. & Ward J.V. (1990) Physical habitat template of lotic systems – recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management*, **14**, 629–645.
- Pratt J.R., Bowers N.J., Niederlehner B.R. & Cairns J.J. (1988) Effects of chlorine on microbial communities in naturally derived microcosms. *Environmental Toxicology and Chemistry*, **7**, 679–687.
- Pringle C.M. & Blake G.A. (1994) Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1443–1450.
- Pringle C.M., Blake G.A., Covich A.P., Buzby K.M. & Finley A. (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.

- Pringle C.M., Hemphill N., McDowell W.H., Bednarek A. & March J.G. (1999) Linking species and ecosystems: different biotic assemblages cause interstream differences in organic matter. *Ecology*, **80**, 1860–1872.
- Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.
- SAS Institute Inc. (1999) *JMP Start Statistics: A Guide to Statistics and Data Analysis Using JMP and JMPIN® Software*. Duxbury Press, Belmont, CA.
- Schindler D.W. (1987) Detecting ecosystem responses to anthropogenic stress. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 6–25.
- Sedell J.R., Reeves G.H., Hauer F.R., Stanford J.A. & Hawkins C.P. (1990) Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management*, **14**, 711–724.
- Sokal R.R. & Rohlf F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman and Company, New York.
- Steinman A.D. & McIntire C.D. (1990) Recovery of lotic periphyton communities after disturbance. *Environmental Management*, **14**, 589–604.
- Steinman A.D., Mulholland P.J., Palumbo A.V., Deangelis D.L. & Flum T.E. (1992) Lotic ecosystem response to a chlorine disturbance. *Ecological Applications*, **2**, 341–355.
- Stewart A.J., Hill W.R., Ham K.D., Christensen S.W. & Beauchamp J.J. (1996) Chlorine dynamics and ambient toxicity in receiving streams. *Ecological Applications*, **6**, 458–471.
- Victor R. & Ogbeibu A.E. (1986) Recolonisation of macrobenthic invertebrates in a Nigerian stream after pesticide treatment and associated disruption. *Environmental Pollution (Series A)*, **41**, 125–137.
- Villamil J. & Clements R.G. (1976) *Some aspects of the ecology of the fresh water shrimps in the upper Espíritu Santo River at El Verde, Puerto Rico*. PRNC-206. Puerto Rico Nuclear Center, University of Puerto Rico, Rio Piedras.
- Wallace J.B. (1990) Recovery of lotic macroinvertebrate communities from disturbance. *Environmental Management*, **14**, 605–620.
- Whiles M.R., Wallace J.B. & Chung K. (1993) The influence of *Lepidostoma* (Trichoptera, Lepidostomatidae) on recovery of leaf-litter processing in disturbed headwater streams. *American Midland Naturalist*, **130**, 356–363.
- Yasuno M., Fukushima S., Hasegawa J., Shioyama F. & Hatakeyama S. (1982) Changes in the benthic fauna and flora after application of temephos to a stream on Mt. Tsukuba. *Hydrobiologia*, **89**, 205–214.
- Yount J.D. & Niemi G.J. (1990) Recovery of lotic communities and ecosystems from disturbance – a narrative review of case-studies. *Environmental Management*, **14**, 547–569.

(Manuscript accepted 12 January 2005)