INDIRECT UPSTREAM EFFECTS OF DAMS: CONSEQUENCES OF MIGRATORY CONSUMER EXTIRPATION IN PUERTO RICO

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Abstract. Large dams degrade the integrity of a wide variety of ecosystems, yet direct downstream effects of dams have received the most attention from ecosystem managers and researchers. We investigated indirect upstream effects of dams resulting from decimation of migratory freshwater shrimp and fish populations in Puerto Rico, USA, in both high- and low-gradient streams. In high-gradient streams above large dams, native shrimps and fishes were extremely rare, whereas similar sites without large dams had high abundances of native consumers. Losses of native fauna above dams dramatically altered their basal food resources and assemblages of invertebrate competitors and prey. Compared to pools in high-gradient streams with no large dams, pool epilithon above dams had nine times more algal biomass, 20 times more fine benthic organic matter (FBOM), 65 times more fine benthic inorganic matter (FBIM), 28 times more carbon, 19 times more nitrogen, and four times more non-decapod invertebrate biomass. High-gradient riffles upstream from large dams had five times more FBIM than did undammed riffles but showed no difference in algal abundance, FBOM, or non-decapod invertebrate biomass. For epilithon of low-gradient streams, differences in basal resources between pools above large dams vs. without large dams were considerably smaller in magnitude than those observed for pools in high-gradient sites. These results match previous stream experiments in which the strength of native shrimp and fish effects increased with stream gradient. Our results demonstrate that dams can indirectly affect upstream free-flowing reaches by eliminating strong top-down effects of consumers. Migratory omnivorous shrimps and fishes occur throughout the tropics, and the consequences of their declines upstream from many tropical dams are likely to be similar to those in Puerto Rico. Thus, ecological effects of migratory fauna loss upstream from dams encompass a wider variety of species interactions and biomes than the bottom-up effects (i.e., elimination of salmonid nutrient subsidies) recognized for northern temperate systems.

Key words: amphidromy; benthic invertebrates; Decapoda; fishes; freshwater shrimps; migratory fauna; natural experiment; omnivorous macrobiota; primary consumer; tropical stream.

INTRODUCTION

Dam building is one of the primary means by which humans alter ecosystems (Rosenberg et al. 1997, World Commission on Dams 2000, McCully 2001). Effects include inundation of terrestrial systems (Nilsson and Berggren 2000), decreased export of water, sediments, and nutrients to marine systems (Postel et al. 1998, Ittekkot et al. 2000), displacement of human communities (Wu et al. 2004), contributions to greenhouse gas emissions (St Louis et al. 2000), increased outbreaks of parasites/diseases (Bonetto et al. 1987), facilitation of irrigated agriculture and urbanization (Postel and Carpenter 1997, Fitzhugh and Richter 2004), and dramatic changes in the physical, chemical, and biological structure and function of rivers and streams (Ward and Stanford 1983, Allan 1995). Most ecological research on impounded river systems examines the direct down-

stream effects of reservoirs (e.g., Petts 1984, Collier et al. 2000). However, ecological changes also occur upstream (Pringle 1997). Upstream effects include the transformation of lotic and floodplain habitat into lentic and reservoir-associated riparian or wetland habitat (Baxter 1977, Dynesius et al. 2004, Rains et al. 2004) and upstream invasion by exotic species introduced to the reservoir (Gido et al. 2002, Light 2003). Likewise, dams can block movements of aquatic organisms, causing upstream population isolation (Peter 1998) and extirpation of migratory fauna (Pringle et al. 2000).

Dams are causing population declines of migratory as well as nonmigratory species throughout the world (Rosenberg et al. 1997). Yet, except for the consequences of decreased nutrient subsidies due to Pacific salmon declines, ecological effects of these losses are poorly known, whether downstream (Power et al. 1996) or upstream (Freeman et al. 2003) from dams. In the tropics, streams often contain abundant and/or diverse fishes, shrimps, and snails that require a long-distance migration in order to complete their life cycles (e.g.,

Lowe-McConnell 1987, Barthem and Goulding 1997, Smith et al. 2003). These taxa exhibit large upstream declines when human alterations, such as dams, block their migrations (e.g., tropical fishes [Duque et al. 1998, Brasher 2003], shrimps [Miya and Hamano 1988, Bowles et al. 2000, Fièvet et al. 2001], snails [Resh et al. 1990]). Several taxa also play key roles as large-bodied omnivores with strong effects on primary producers, detritus, nutrients, and macroinvertebrates (e.g., Flecker 1992, 1996, Pringle and Hamazaki 1998). However, it is unknown whether dam-related declines of migratory strong interactors result in alterations in standing stocks of food resources and competitors upstream from dams.

In this study, we examine indirect effects of dams (e.g., dam A affects taxon B which affects taxon C) in neotropical streams of Puerto Rico, USA. Dams in Puerto Rico are already known to cause direct effects such as mortality of larval shrimps (e.g., Benstead et al. 1999). An island-wide survey of fishes and shrimps by Holmquist et al. (1998) found that large dams (height >15 m) without regular free crest spillway discharge cause upstream extirpation of all native fishes and shrimps because these taxa are diadromous (i.e., require a migration between fresh and salt water). In streams without large dams, in situ experiments indicate that such population declines in turn have additional ecological effects. Manipulations of shrimp abundances in stream pools show that grazing and detritivorous feeding by shrimps decrease standing stocks of epilithic chlorophyll *a,* organic and inorganic matter, carbon (C), nitrogen (N), carbon:nitrogen ratio (C:N), and chironomid biomass (Pringle et al. 1993, Pringle et al. 1999), and increase leaf decay rates (Crowl et al. 2001). In situ experiments and observational data also suggest that Puerto Rican shrimps alter macroinvertebrate communities through competition, bioturbation, and/or predation (Pringle et al. 1993, Covich and McDowell 1996, Buzby 1998). However, effects of experiments vary with stream gradient due to changes in shrimp and fish assemblages (March et al. 2001, 2002).

In this paper, our objective is to document ecosystem differences in benthic resources and macroinvertebrates associated with loss of native shrimps and fishes upstream from large reservoirs. We examined effects of dams on both high- and low-gradient streams (streams with slopes >4% and <4%, respectively). We predicted that standing stocks of epilithic algae, organic matter, inorganic matter, C, N, C:N ratio, and chironomid biomass would be higher in streams upstream from large dams that have no or few native shrimps and fishes. In streams with no large dams, and thus high and relatively natural abundances of native fauna, we predicted lower values for these benthic parameters.

METHODS

Study area

We studied streams in mountainous regions of Puerto Rico, USA, that are characterized by only slight sea-sonal variation in temperature and rainfall (Larsen 2000). Flash floods (discharge increases up to 10-fold in <1 h) occur throughout the year and wash out most accumulations of large woody debris. Land cover is mixed, with substantial recovery of tropical forest associated with declines in agriculture (e.g., pasture, coffee) and increases in low-density residential development over the past 30–60 years (Grau et al. 2003).

Puerto Rican streams are dominated by migratory shrimps and fishes. Except for the catadromous American eel (*Anguilla rostrata*), all native freshwater shrimps and fishes are thought to be amphidromous, with adult females releasing larvae that passively drift downstream to the estuary before migrating back upstream as juveniles (Chace and Hobbs 1969, March et al. 1998, Nieves 1998). Three families of omnivorous migratory shrimps occur: Xiphocarididae (*Xiphocaris elongata*), Atyidae (e.g., *Atya* spp.), and Palaemonidae (*Macrobrachium* spp.; Covich and McDowell 1996). Native fishes are the algivorous green stream goby (*Sicydium plumieri*) and five predatory fishes (*Agonostomus monticola*, *Gobiomorus dormitor*, *Eleotris pisonis*, *Awaous tajasica*, *Anguilla rostrata*) that feed primarily on shrimps and other invertebrates (Nieves 1998). Waterfalls block upstream migration of these predatory fishes. Shrimps and *Sicydium* are able to scale any gradient over which water flows, and they reach high abundances upstream from waterfalls (Covich 1988). Thus, shrimp and fish assemblages vary longitudinally in streams without large dams. Native predatory fishes are absent and shrimps and *Sicydium* are abundant in high-elevation, high-gradient streams without large dams; and native predatory fishes are present and shrimps are at low abundances in low-elevation, low-gradient streams without large dams (Covich and McDowell 1996).

Studies using electricity as a mechanism for experimental exclusion have allowed incorporation of the natural hydrologic regime in examinations of effects of Puerto Rican macroconsumers in pools (e.g., Pringle et al. 1999, March et al. 2001, 2002). Strong effects of experimental exclusion on benthic resources and invertebrates are primarily due to grazing and detritivory by shrimps during base flow. Effects of shrimps on their epilithic food resources are stronger and more persistent than are effects on these resources of typical flash floods, which occur about once every one or two months and last for about one or two days. Deposition of organic and inorganic materials during floods is common, but shrimps remove these materials in less than a day after return to base flow. At sites where shrimps are low in abundance (and thus standing stocks of their benthic food resources and invertebrate competitors/prey are high), scouring of benthic resources to low levels is only rarely evident after return to base flow (Pringle et al. 1999). When strong effects of scouring do persist, the benthic environment returns to nor-

mal preflood conditions in 11–19 days (E. Greathouse, *unpublished data*).

Although experimental research has primarily documented ecological effects of feeding by shrimps, grazing by *Sicydium plumieri* likely has similar effects. In Costa Rica, effects of algivorous *Sicydium* on algal biomass, quantity and quality of benthic organic matter, and abundance of benthic insects are similar to findings for shrimps in Puerto Rico (Barbee 2002). Nonmigratory aquatic fauna of our study systems include aquatic insects (e.g., gyrinid beetles, chironomids, dragonflies), other benthic invertebrates (e.g., limpets, oligochaetes, the crab *Epilobocera sinuatifrons*), tadpoles of *Leptodactylus albilabris*, and exotic fishes (predominantly poeciliids, such as *Poecilia reticulata*, *Xiphophorus maculates*) that primarily feed on small invertebrates (Erdman 1984, Covich and McDowell 1996, Mirando-Castro et al. 2000). Holmquist et al. (1998) reported higher abundances of exotic fishes in streams above large dams.

High-gradient stream survey

Study design and sampling.—Our main data set compares dammed and undammed streams that are high gradient (i.e., above waterfalls that block migration of predatory fishes). We used a natural experiment approach (sensu, Diamond 1986), sampling macroconsumers, benthic resources, and non-decapod invertebrates in seven stream reaches upstream from large dams and 10 undammed reaches (Fig. 1a). We refer to sites above large dams as ''dammed'' and sites with no large dams as ''undammed''; however, low-head dams (height <15 m) may occur upstream or downstream from any of our sites. The 10 undammed sites were dominated by shrimp and *Sicydium* with no predatory fishes. Physical conditions of the seven dammed sites are characteristic of streams that are dominated by shrimps and *Sicydium* (Table 1); it is highly likely that they were dominated by shrimp and *Sicydium* prior to dam construction. High-gradient dammed sites were above large dams without regular ''free crest'' spillway discharge (i.e., water flowing over the sloping face of a dam; hereafter referred to as spillway discharge). A lack of regular spillway discharge was previously found to cause upstream extirpation of shrimps and native fishes (Holmquist et al. 1998). Thus, our high-gradient stream survey was designed to compare sites where native shrimps and *Sicydium* were extirpated (dammed) and sites with relatively natural shrimp and *Sicydium* assemblages (undammed).

We chose sites so that physical and chemical parameters would not confound our comparison of dammed vs. undammed rivers. Table 1 includes the most ecologically relevant parameters measured; the Appendix lists measured parameters not included in Table 1 (number of headwater streams drained, 1977–1978 catchment land cover, aspect, gradient measured in the field, wetted width) and other physical habitat selection criteria assessed visually (forested riparian buffer, channel sinuosity, bank slope). Sites were sampled once between June 2001 and June 2003, in haphazard order, at base flow over a reach at least 10 times the channel width.

To sample epilithic chlorophyll *a*, fine (<1 mm) benthic inorganic matter (FBIM), fine benthic organic matter (FBOM), coarse (>1 mm) benthic organic matter (CBOM), and non-decapod invertebrates, we obtained randomly located samples from boulders/bedrock in each of the two major habitat types (pools and riffles that, on average, represented 44% and 54% of stream habitat, respectively). We also analyzed FBOM samples from pools for total C, N, and C:N (molar ratio). Chlorophyll *a*, FBIM, and FBOM were sampled using a suction device modified from Loeb (1981). Loeb samples were composited by habitat type (12 over three pools and 12 over three riffles) and brought back to the laboratory on ice for subsampling. A chlorophyll *a* subsample was filtered onto a precombusted glass fiber filter (Whatman GF/F, 0.7 μm), frozen, and analyzed fluorometrically according to standard methods (APHA 1985). A FBIM/FBOM subsample was filtered onto a precombusted, preweighed GF/F filter and dried at 50°C for at least 24 h. FBIM/FBOM filters from riffles were weighed to the nearest 0.001 g, ashed at 500°C for 3 h, and reweighed to determine inorganic and ash-free dry mass (AFDM) per unit area. For FBIM/FBOM filters from pools, we cut the dried filter into two roughly equal sections and weighed each section to the nearest 0.001 g. One filter section was analyzed for C and N using a PerkinElmer CHN analyzer (PerkinElmer, Wellesley, Massachusetts, USA). The other section was analyzed for inorganic mass and AFDM, as described for FBIM/FBOM filters from riffles.

Three riffles were sampled for CBOM and non-decapod benthic invertebrates by scrub brushing invertebrates and benthic matter from a known area into a 210-μm hand net. In three pools, we used the ''benthic block net'' described by Greathouse and Pringle (2005) to sample CBOM quantitatively (i.e., mass per unit area) and non-decapod invertebrates semiquantitatively (i.e., biomass per unit effort). Invertebrate/CBOM samples were preserved with ethanol and processed following methods modified from Lugthart and Wallace (1992). We sieved samples in nested 1-mm and 250-μm sieves prior to sorting for macroinvertebrates and performing AFDM analyses on CBOM using methods described for FBIM/FBOM filters. Invertebrates were identified to the lowest practicable level (generally family for insects and class or order for other non-decapod invertebrates), and length–mass regressions were used to determine biomass.

All sites except U9 were electroshocked for macroconsumers (fishes, adult shrimps, crabs, tadpoles) by using a catch-per-unit-effort method (point abundance sampling) modified from Fièvet et al. (1996). Two dip

EFFIE A. GREATHOUSE ET AL.

A) High-gradient sites

Arecibo/Tanamá   Manatí   La Plata   Mameyes

Añasco

Guanajibo

Yauco/Duey   Toa Vaca   Inabón
Guayanilla   Tallaboa

LEF

Sites with no large dam	
Site	Drainage
U1	Manatí
U2	Guanajibo
U3	Guayanilla
U4	Inabón
U5	Duey
U6	Añasco
U7	Tanamá
U8	Manatí
U9	Mameyes
U10	Tallaboa

Sites above large dams			Distance
Site	Drainage	Downstream reservoir	upstream (km)
D1	La Plata	Carite	0.7
D2	Arecibo	Garzas	0.9
D3	Manatí	Matrullas	2.0
D4	Yauco	Luchetti, Naranjo arm	2.9
D5	Yauco	Luchetti, Grande arm	4.0
D6	Toa Vaca	Toa Vaca	13.0
D7	Arecibo	Caonillas	20.0

N   30 km

B) Low-gradient sites

Guajataca

Loco

Sites with no large dam	
Site	Drainage
U11	Duey
U12	Inabón
U13	Guanajibo
U14	Guayanilla
U15	Tallaboa
U16	Tanamá

Sites above large dam			Distance
Site	Drainage	Downstream reservoir	upstream (km)
D8	Guajataca	Guajataca	2.5
D9	Toa Vaca	Jacaguas	7.6
D10	La Plata	Comerio	4.9
D11	Arecibo	Dos Bocas	5.7
D12	Loco	Loco	4.7
D13	Manatí	Matrullas	1.4
D14	Toa Vaca	Toa Vaca	2.9
D15	Yauco	Luchetti, Grande arm	0.3

■ above large dam *without* spillway Q
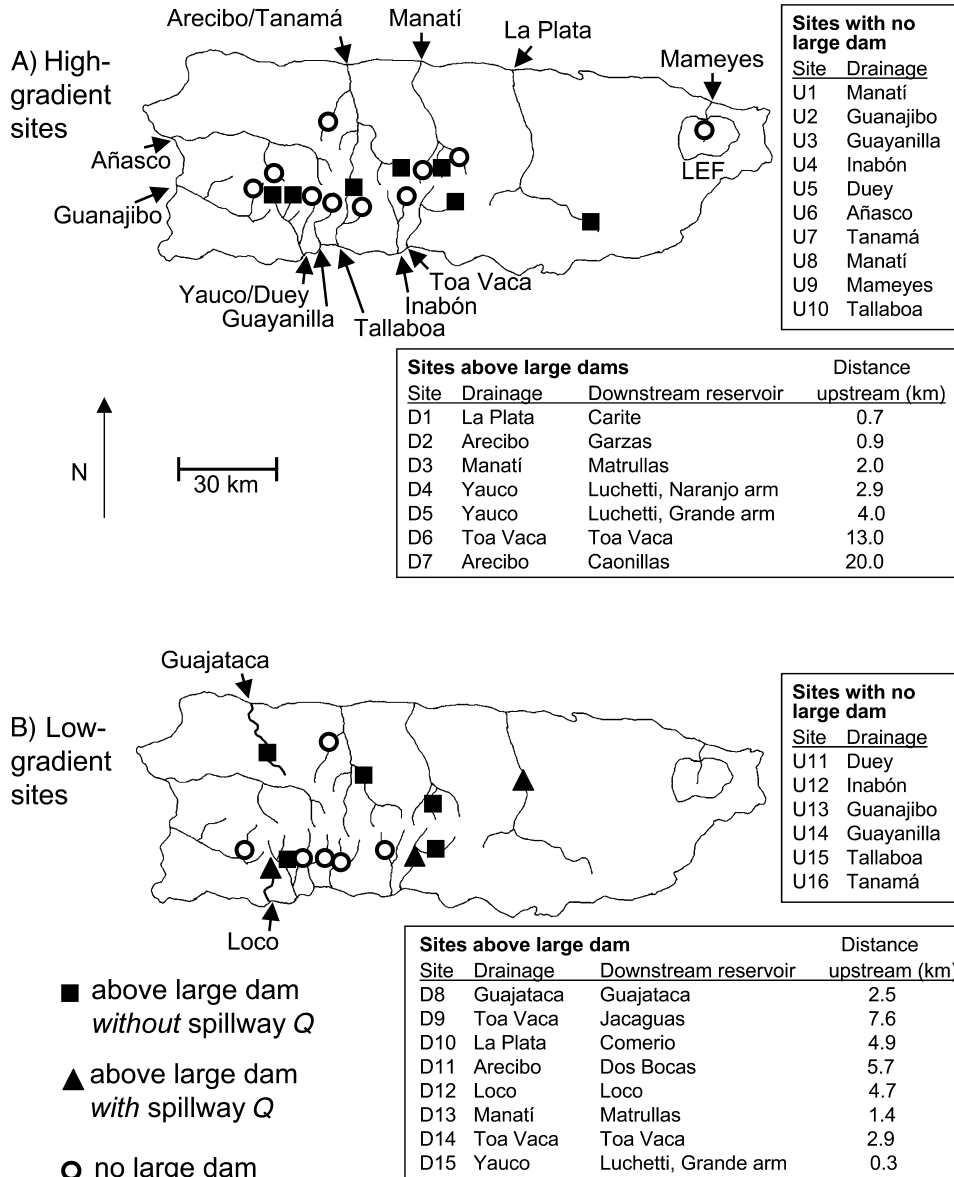
▲ above large dam *with* spillway Q

○ no large dam

FIG. 1. Maps of (A) high-gradient and (B) low-gradient study sites upstream from large dams with (solid triangles) and without (solid squares) regular spillway discharge (Q) and study sites on streams without large dams (open circles) in Puerto Rico, USA. The area outlined at the eastern end of the island is the Luquillo Experimental Forest (LEF), the site of the National Science Foundation's Long-Term Ecological Research (LTER) site in Puerto Rico. Tables list dammed and undammed sites, their site codes and drainages, the names of the large dam/reservoir occurring downstream from dammed sites, and the distance between the dammed site and the most upstream occurrence of inundation by reservoir water (i.e., distance upstream).

netters captured macroconsumers at 5–6 electroshocking points in pools. For riffles, point samples were collected by electroshocking over lengths of ~0.5–1 m into nets placed downstream (at four points per site, dip nets completely blocked flows of ~0.2–0.4 m wide; at two points per site, a 1-m seine net was placed in flows that were ~1–2 m wide). At site U9, electroshocking data from removal sampling in one riffle and one pool was normalized by shocking time and number of dip netters in order to obtain an estimate with effort

similar to point sampling. In pools of a few dammed sites, we also observed rare occurrences of native shrimps and fishes that were not captured during electroshocking.

Statistical analyses.—To compare data between dammed and undammed sites, we used multivariate and univariate ANOVAs. For physical and chemical parameters reported in Table 1, two separate one-way MANOVAs were conducted. We did not include agriculture and urban/barren land cover in the physical habitat

TABLE 1. Selected physical and chemical parameters at high-gradient sites.

Parameters	Sites above large dam				Sites without large dam			
	Mean	SE	Minimum	Maximum	Mean	SE	Minimum	Maximum
Physical parameters (MANOVA: $F_{11,5} = 0.55$, $P = 0.81$)								
Stream order	1.4	0.2	1	2	1.6	0.2	1	3
Gradient (m/m)	0.116	0.014	0.050	0.170	0.114	0.013	0.046	0.180
Elevation (m a.s.l.)	613	78	310	850	506	60	135	810
Catchment area (ha)	192	42	70	352	222	54	64	560
Catchment land cover, 1991–1992 (%)								
Forest	75.9	4.4	58.7	87.4	78.8	4.4	55.3	97.9
Agriculture	25.0	3.9	13.0	40.9	19.9	4.2	0.5	44.4
Urban/barren	0.7	0.2	0.2	1.7	1.3	0.5	0.0	5.1
Bankfull width (m)†	7.1	1.1	3.4	12.0	7.3	0.6	3.0	9.6
Canopy cover (%)	81.1	2.2	72.6	90.5	76.1	4.7	43.3	89.8
Water velocity (m/s)	0.27	0.05	0.16	0.55	0.31	0.02	0.21	0.42
Depth (m)	0.21	0.02	0.16	0.30	0.21	0.02	0.16	0.39
Substrate coarseness‡	4.86	0.13	4.15	5.16	4.84	0.17	3.97	5.82
Temperature (°C)	21.6	0.8	19.0	25.0	21.7	0.6	18.9	26.0
Chemical parameters (MANOVA: $F_{11,5} = 1.46$, $P = 0.29$)								
Conductivity (µS/cm)	231	42	74	390	211	27	107	380
TDN (µg N/L)	710	258	127	2118	585	117	208	1480
NO_3^- (µg N/L)	654	269	92	2114	508	120	175	1473
NH_4^+ (µg N/L)	3.6	0.7	0.5	5.3	10.3	4.6	0.3	48
DON (µg N/L)	52	22	0	171	67	31	0	327
SRP (µg P/L)	40	12	11	110	30	8	8	91
DOC (µg C/L)	721	144	350	1470	993	286	323	1404

Notes: See the Appendix for details on methods for determining physical and chemical parameters. MANOVAs test for significant differences between dammed and undammed sites. Univariate ANOVAs for individual parameters listed in the table were not significant ($P > 0.24$). The physical habitat MANOVA does not include percentage of agricultural land cover or percentage of urban/barren land cover, but excluding these response variables did not alter significance. Chemical parameter abbreviations: TDN, total dissolved nitrogen; DON, dissolved organic nitrogen; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon.

† Bankfull width is the width of the channel from one bank to the other.

‡ Values are the mean of substrate coarseness codes from random measurements: 1, silt; 2, sand; 3, fine gravel; 4, coarse gravel; 5, cobble; 6, boulder; 7, bedrock. See Bain et al. (1985) for details of coarseness calculation.

MANOVA because increasing forested land cover correlates with decreasing human-dominated land cover, but excluding the human-dominated land uses did not alter the significance of the MANOVA. Univariate ANOVAs were also performed for each physical and chemical parameter in Table 1 and the Appendix. Macroconsumer sampling was intended to confirm that previous findings of Holmquist et al. (i.e., extirpation of migratory fauna above dams) also operated at our specific sites (Holmquist et al. 1998). Thus we simplified analysis of macroconsumer data by categorizing captured fauna as migratory or nonmigratory and conducted separate one-way ANOVAs on each category. For benthic resources measured in both pools and riffles (chlorophyll *a,* CBOM, FBOM, FBIM), we conducted univariate split-plot ANOVAs, in which the whole-plot factor was dam status (i.e., above vs. without large dam), the within-plot factor was habitat (i.e., riffles vs. pools), and the plot was site nested within dam status. To facilitate interpretation of significant interactions in the split-plot ANOVAs, we conducted subsequent one-way ANOVAs that tested dam status separately in each habitat type. For benthic resources measured in pools only (C, N, C:N), we conducted one-way ANOVAs. Non-decapod invertebrates from pools and riffles were

analyzed with separate statistical tests because sampling methods in each habitat yielded different units (catch per unit effort in pools, per unit area in riffles). One-way ANOVAs were performed on total abundances and total biomasses. One-way MANOVAs were also conducted on biomasses of common taxa with subsequent univariate ANOVAs if the MANOVA was significant. For all analyses, we used site as the experimental unit, arcsine-transformed percentages, and performed $\log_{10}(x + 1)$ transformations on nonpercentage data when a Shapiro-Wilk test indicated lack of normality.

Low-gradient stream survey

Study design and sampling.—In July–August 2000, we resurveyed 14 of 15 streams (Fig. 1b) that Holmquist et al. (1998) surveyed for fishes and shrimps. We measured epilithic chlorophyll *a,* FBIM, FBOM, C, N, and C:N occurring on boulders and bedrock in pools. Methods generally followed those described for the high-gradient survey except that Loeb samples were haphazardly, not randomly, located. In our analysis, we excluded two problematic sites (D12, D15) out of the 14 resurveyed. Site D12 was a sandy-bottomed stream, whereas substrates at other sites were heterogeneous

TABLE 2. Physical and chemical parameters measured at low-gradient sites.

Parameters	Sites above large dam				Sites without large dam			
	Mean	SE	Minimum	Maximim	Mean	SE	Minimum	Maximum
Physical parameters (MANOVA: $F_{6,5}$ = 2.45, P = 0.17)								
Stream order	3.0	0.4	2	5	3.5	0.2	3	4
Gradient (m/m)	0.016	0.005	0.004	0.035	0.027	0.005	0.007	0.039
Elevation (m a.s.l.)	273	101	95	770	208	37	90	320
Wetted width (m)†	12.4	3.9	4.8	31.0	10.1	2.4	6.0	21.5
Canopy cover (%)	34.0	11.8	0.0	72.0	27.8	8.1	6.0	48.0
Depth (m)	0.26	0.05	0.11	0.43	0.30	0.03	0.22	0.40
Substrate coarseness	1.11	0.08	0.88	1.46	0.87	0.06	0.58	1.05
Chemical parameters (MANOVA: $F_{6,5}$ = 2.40, P = 0.18)								
TDN (µg N/L)	612	312	120	2170	862	147	410	1490
NO_3^- (µg N/L)	456	299	4	1930	732	146	230	1330
NH_4^+ (µg N/L)	14.7	2.3	8.0	24.7	17.1	5.2	5.3	41.0
DON (µg N/L)	142	30	80	240	113	14	80	160
SRP (µg P/L)	14	2	7	23	12	2	6	20
DOC (µg C/L)	1341	260	820	2350	947	194	420	1700

Notes: See the Appendix for details on methods for determining physical and chemical parameters. Parameters listed in Table 1 but not in Table 2 were not measured in the pilot project on low-gradient streams. MANOVAs test for significant differences between dammed and undammed sites. Univariate ANOVAs for individual parameters indicate a significant difference for substrate coarseness (P = 0.05); all other univariate ANOVAs were not significant (P > 0.12). See Table 1 for definitions of substrate coarseness and chemical parameters.

† Wetted width is the width of the wetted part of the stream at the time of measuring the stream width.

mixtures of boulder, cobble, gravel, and sand. Site D15 was sampled one day after a large storm event, and in subsequent visits to this site in 2002 and 2003, the stream was intermittent with a few isolated pools in a dry channel. In addition, the location of site D15 in the Yauco basin was not on the same tributary as the Yauco basin sites sampled by Holmquist et al. (1998). Excluding sites D12 and D15 left six undammed and six dammed sites. Because these 12 sites were low gradient (Table 2), most of the undammed sites contained predatory fishes and low abundances of shrimps, and it is highly likely that most of the dammed sites contained predatory fishes and low shrimp abundances prior to damming. Physical and chemical parameters measured at the six dammed and six undammed sites were comparable (Table 2).

Two sites (D9, D10) were above large dams with regular spillway discharge, allowing low numbers of shrimps and *Sicydium* to scale the sloping face of the dam and recruit into upstream habitats. Although shrimps and *Sicydium* are present above these two semipermeable dams, their abundances are greatly reduced (Holmquist et al. 1998). Thus we expected our low-gradient stream survey to compare dammed streams, in which native shrimps and fishes were either extirpated or reduced, to undammed streams with relatively natural shrimp and fish assemblages.

Statistical analyses.—Dammed and undammed low-gradient sites were compared with one-way multivariate and univariate ANOVAs. Physical and chemical parameters were analyzed with separate MANOVAs and univariate ANOVAs (Table 2). Benthic resources were analyzed with ANOVAs. Site was the experimental unit, and data transformations followed those described for analyses of high-gradient sites.

RESULTS

High-gradient stream survey

Macroconsumers.—Macroconsumer assemblages in sites above large dams were dramatically different than those in sites without large dams (Fig. 2). Abundance of migratory fauna was significantly higher in undammed sites (number per point sample = 12.3 ± 2.2 [mean ± SE]) compared to dammed sites (number per point sample = 0.04 ± 0.04; ANOVA: $F_{1,15}$ = 110.7, P < 0.0001). In contrast, abundance of nonmigratory fauna was lower in undammed sites (number per point sample = 1.7 ± 0.8) vs. dammed sites (number per point sample = 3.5 ± 1.3; $F_{1,15}$ = 4.7, P = 0.047). The dominant migratory fauna at undammed sites were *Xiphocaris* and atyid shrimps. Abundances of migratory *Macrobrachium* and *Sicydium* were comparatively low.

We collected three *Xiphocaris* from a single pool during electroshocking at site D1 (Fig. 2). No other native fishes or shrimps were captured during electroshocking at dammed sites. However, over the course of our field work and study site selection, we observed rare occurrences of additional native fishes and shrimps at sites above dams with no regular spillway discharge (D1, *Gobiomorus dormitor*; D6, *Xiphocaris*; D15, *Xiphocaris* and atyid shrimps).

Benthic resources.—Differences between dammed and undammed sites for epilithic chlorophyll *a*, FBOM, and FBIM varied by habitat (Fig. 3, Table 3). Pools above large dams had dramatically higher chlorophyll *a*, FBOM, and FBIM relative to pools at undammed sites. In riffles, there were no significant differences between dammed and undammed sites for chlorophyll *a* and FBOM, and though FBIM was significantly higher in dammed compared to undammed riffles, the dif-

FIG. 2. Number of migratory and nonmigratory macroconsumers captured per point sample (mean and SE; $n = 7$ dammed and 10 undammed sites) at high-gradient sites without large dams or upstream from large dams. Migratory fauna are native adult shrimps (*Xiphocaris elongata*, atyids, *Macrobrachium* spp.) and the native green stream goby, *Sicydium plumieri*. Nonmigratory fauna are the native crab, *Epilobocera sinuatifrons*, nonnative poeciliid fishes, and the native tadpole, *Leptodactylus albilabris*.
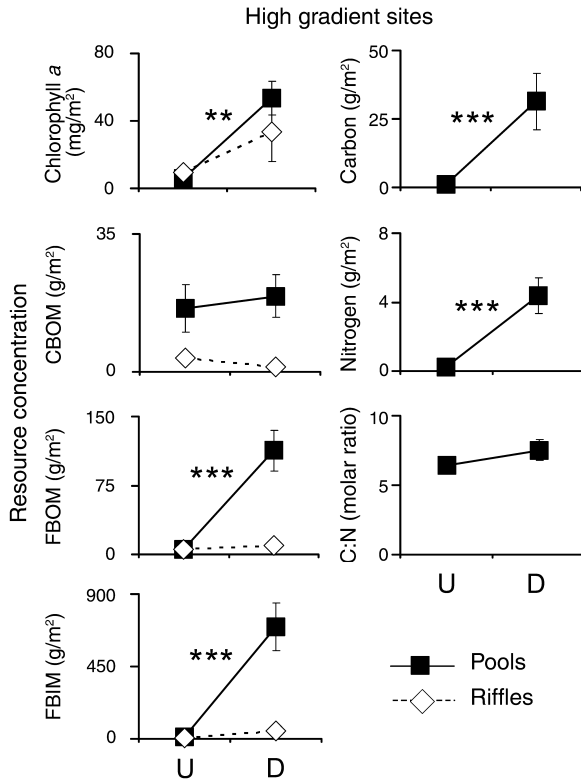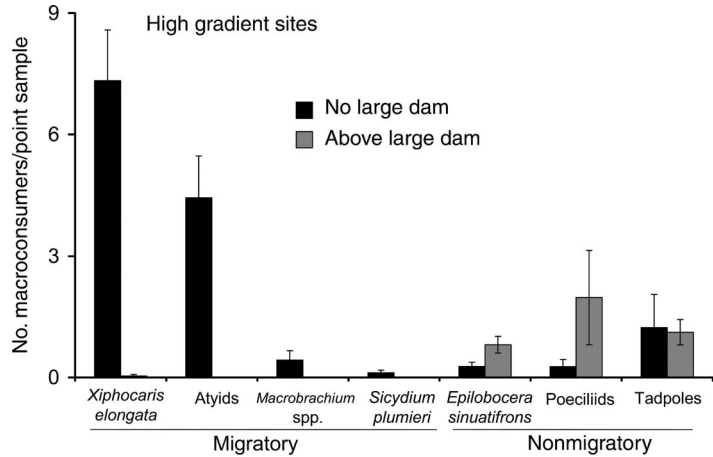

FIG. 3. Resources (mean and SE; $n = 7$ dammed and 10 undammed sites) by habitat (pools, riffles) for epilithic chlorophyll *a,* coarse benthic organic matter (CBOM), fine benthic organic matter (FBOM), fine benthic inorganic matter (FBIM), carbon, nitrogen, and C:N ratio in high-gradient sites above (D) vs. without (U) large dams. Molar ratio for C:N was calculated as mol/L of C vs. mol/L of N. Lines connecting means are only intended to ease visualization of interactions (between dams and habitat) and maintain consistency of symbols across figures. Connecting lines are not intended to suggest a continuous relationship. Asterisks indicate parameters showing significant differences due to dams.
$**P < 0.01$; $***P < 0.001$.

ference was small compared to that observed in pools. CBOM did not differ between dammed and undammed sites for either habitat, but pools had significantly higher standing stocks of CBOM than did riffles (Fig. 3, Table 3). Epilithic standing stocks of C and N in pools were significantly higher in dammed compared to undammed sites (ANOVAs: C, $F_{1,15} = 77.67$, $P < 0.0001$; N, $F_{1,15} = 67.63$, $P < 0.0001$; Fig. 3), but epilithic C:N showed no significant difference ($F_{1,15} = 1.78$, $P = 0.2$; Fig. 3).

Non-decapod invertebrates.—Compared to pools in sites without large dams, pools above large dams contained significantly higher total biomass of non-decapod benthic invertebrates (ANOVA: $F_{1,15} = 11.88$, $P = 0.004$; Table 4). Total abundance in pool samples was also significantly higher above dams ($F_{1,15} = 25.94$, $P = 0.0001$; Table 4). In riffles, differences between dammed and undammed sites in total biomass and abundance per unit area were not significant ($F_{1,15} = 0.31$, $P = 0.59$) and marginally significant ($F_{1,15} = 4.13$, $P = 0.060$), respectively (Table 4). Nine of 11 common non-decapod invertebrate taxa in pools showed significant, or marginally significant, differences in biomass between dammed and undammed sites (Table 4). Higher biomass in dammed sites was significant or marginally significant for eight taxa, including several predators (Gyrinidae, Odonata, Ceratopogonidae) and grazers/collector–gatherers (Chironomidae, Hydroptilidae, Caenidae, Ancylidae, Oligochaeta). Baetid biomass was marginally higher in undammed sites. In riffles, biomass of common taxa was not significantly different between dammed and undammed sites (Table 4).

Low-gradient stream survey

Benthic resources.—Pools above large dams had higher epilithic chlorophyll *a,* C, and N (ANOVAs: chlorophyll *a,* $F_{1,10} = 6.92$, $P = 0.02$; C, $F_{1,10} = 12.62$, $P = 0.005$; N, $F_{1,10} = 13.25$, $P = 0.004$; Fig. 4). There were marginally significant trends of higher FBOM and epilithic C:N in dammed sites (FBOM, $F_{1,10} = 4.62$, $P = 0.06$; C:N, $F_{1,10} = 4.34$, $P = 0.06$; Fig. 4). FBIM

TABLE 3. ANOVAs on chlorophyll *a*, coarse and fine benthic organic matter, and fine benthic inorganic matter at high-gradient sites.

| | | Variable | | | | | | | |
| | | Chlorophyll *a* | | CBOM | | FBOM | | FBIM | |
Source of variation	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Whole model (split-plot ANOVAs)									
Dam	1, 15	15.3	**<0.0014**	<0.1	0.8411	48.7	**<0.0001**	64.1	**<0.0001**
Habitat	1, 15	2.9	0.1069	36.4	**<0.0001**	30.3	**<0.0001**	38.0	**<0.0001**
Dam × habitat	1, 15	11.0	**0.0048**	3.1	0.1009	36.1	**<0.0001**	23.1	**0.0002**
Above vs. without large dam, by habitat type (one-way ANOVAs)									
Riffles	1, 15	1.8	0.1941	2.0	0.1801	1.6	0.2293	7.3	**0.0165**
Pools	1, 15	48.2	**<0.0001**	<0.1	0.8041	86.9	**<0.0001**	149.6	**<0.0001**

Notes: Effects listed are from split-plot ANOVAs (whole model). "Dam" is the whole-plot factor with levels "above dam" and "without dam." "Habitat" is the within-plot factor with levels "riffles" and "pools." Plots are sites nested within dams. Results from one-way ANOVAs that test dam status separately in riffles and in pools are also listed. Significant *P* values are shown in bold. Fig. 3 presents means and standard errors. Key to abbreviations: CBOM, coarse benthic organic matter; FBOM, fine benthic organic matter; FBIM, fine benthic inorganic matter.

was not significantly different ($F_{1,10} = 2.20$, $P = 0.17$; Fig. 4). Mean standing stocks of chlorophyll *a,* FBOM, FBIM, C, and N above dams reached higher values in high-gradient sites than they did in low-gradient sites, whereas the reverse was true for sites with no large dams. Ratio of C:N was similar between the low-and high-gradient surveys.

DISCUSSION

Our study has two main findings. First, large dams dramatically reduce upstream abundances of migratory shrimps and fishes in high-gradient systems. Second, migratory shrimp and fish losses alter benthic resources and assemblages of non-decapod invertebrates. However, alterations vary by mesohabitat (riffles vs. pools) and by stream gradient. We discuss these findings in detail below.

Upstream effects of dams on migratory fauna, benthic resources, and non-decapod invertebrates

High-gradient streams.—We found that large dams decimate upstream populations of migratory shrimps and fishes in high-gradient systems, supporting the findings of Holmquist et al. (1998) in low-gradient streams. Our observations of rare migratory fauna in three dammed sites are attributable to landlocked reproduction by the migratory fish *Gobiomorus dormitor* (Bacheler et al. 2004) and occasional upstream recruitment by shrimps during infrequent high discharge events over reservoir spillways (Holmquist et al. 1998, Greathouse 2005).

The benthic environment in high-gradient sites was dramatically and visibly different between sites above vs. without large dams. Epilithon in pools of dammed streams had nine times more chlorophyll *a,* 20 times more fine benthic organic matter (FBOM), 65 times more fine benthic inorganic matter (FBIM), 28 times more C, 19 times more N, 14 times more non-decapod invertebrate abundance, and four times more non-deca-

pod invertebrate biomass. We attribute these differences to decimation of shrimp and *Sicydium* populations based on several lines of evidence. First, electroshocking data demonstrate that we are comparing streams with high abundance vs. dramatic losses of shrimps and *Sicydium*. Second, experimental manipulations in pools at four of our sites show that macroconsumer exclusion at undammed sites and shrimp addition to dammed sites cause the same differences observed here, whereas experimental exclusion of non-migratory macroconsumers (exotic fishes, native crabs, native tadpoles) at dammed sites does not affect benthic resources and non-decapod invertebrates (Greathouse 2005). Third, numerous other field experiments have found similar effects of shrimps and *Sicydium* in pools of other high-gradient sites (Pringle et al. 1993, 1999, Pringle and Blake 1994, Pringle 1996, March et al. 2001, 2002). Fourth, other comparative research has illustrated similar differences among stream pools that vary naturally in shrimp abundances (Pringle 1996, Buzby 1998, Pringle et al. 1999). Fifth, the feeding mechanisms by which shrimps and *Sicydium* "clean" pool rocks are well documented (atyids use cheliped fans to brush rock surfaces clean; *Xiphocaris* uses small cheliped pincers to scrape, collect, and shred organic matter from surfaces; and *Sicydium* cleans rock surfaces with a ventral scraping mouth; Fryer 1977, Covich and McDowell 1996, Pringle et al. 1999, March et al. 2001). Finally, dammed vs. undammed sites showed no significant differences for a wide variety of physical and chemical parameters (i.e., differences observed were not a result of physico-chemical differences, Table 1). Moreover, differences in response variables between the two stream types were strong despite wide ranges in agricultural land cover (0.5–44%), gradient (0.05–0.18 m/m), and nitrate concentrations (92–2114 µg N/L) within each stream type (Table 1).

Most benthic resources in pools were higher in dammed streams, consistent with our hypotheses. How-
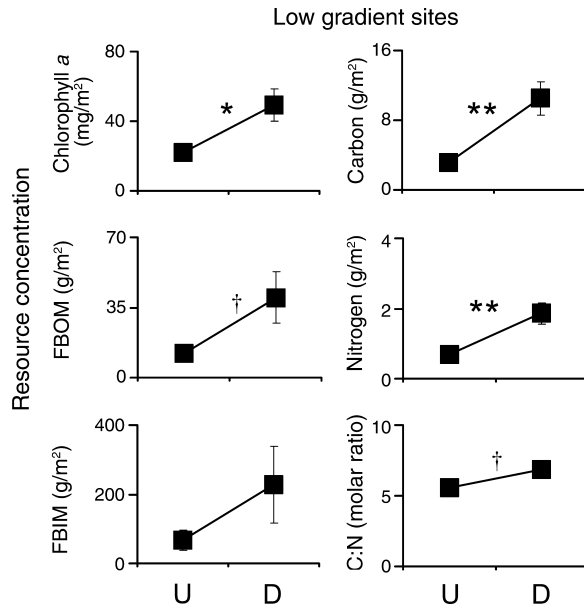
Low gradient sites

FIG. 4. Resources (mean and SE; $n = 6$ dammed and 6 undammed sites) for epilithic chlorophyll *a*, fine benthic organic matter (FBOM), fine benthic inorganic matter (FBIM), carbon, nitrogen, and C:N ratio in pools of low-gradient sites above (D) vs. without (U) large dams. Lines connecting means are only intended to maintain consistency of symbols across figures, not to suggest a continuous relationship. Asterisks (*) indicate parameters showing significant differences and daggers (†) indicate marginally significant differences ($P < 0.1$) due to dams.
   *$P < 0.05$; **$P < 0.01$.

ever, results for epilithic C:N and coarse benthic organic matter (CBOM) were unexpected. The lack of a pattern for C:N in dammed vs. undammed pools contrasts with previous findings at a high-gradient site where shrimp exclusion increased epilithic C:N ratios (Pringle et al. 1999). Based on previous studies, we also did not anticipate the lack of pattern in CBOM between dammed and undammed sites, which indicates that native shrimps and fishes do not alter overall standing stocks of leaves, small woody debris, and fruits. *Xiphocaris* shrimps are known to be effective shredders, increasing decay rates of *Cecropia* leaves (Crowl et al. 2001, March et al. 2001); thus, we expected increased CBOM upstream from large dams. However, because shrimp effects on decay rates are much lower on leaves that are less palatable than *Cecropia* (E. Greathouse, C. Pringle, M. Hunter, D. Coleman, *unpublished data*), effects of large dams on upstream standing stocks of palatable leaves and CBOM dynamics may be obscured by the coarse resolution of our measurement of overall CBOM standing stocks, which may be more influenced by abiotic factors (e.g., frequent flash floods).

Most benthic resources in riffles showed no effect of dams, contrary to our expectation that riffles might show dramatic responses to loss of migratory fauna as

did pool habitats. However, this expectation was based on little prior knowledge of conditions in riffles. Previous studies of shrimp effects in high-gradient Puerto Rican streams (e.g., Pringle et al. 1999, Crowl et al. 2001) have generally focused on pools and ignored riffles where biotic interactions may be different from those in pools, due to differences in abiotic conditions and assemblage composition (Fryer 1977, Moulton et al. 2004). Our finding of only one significant difference between dammed and undammed riffles (dammed riffles had five times more fine benthic inorganic matter) indicates that bioturbation by native shrimps and fishes has weaker effects where water flow continuously removes and transports sediment and organic matter.

Increased abundance and biomass of non-decapod invertebrates in boulder/bedrock pool habitat above dams reflects increased standing stocks of their probable food resources (e.g., algae, fine organic matter, invertebrate prey) and indicates a release from competition with shrimps and *Sicydium*. In addition, due to their relative immobility and lack of protective structures (e.g., shells, hard stone cases), several taxa (Chironomidae, Hydroptilidae, Ceratopogonidae, Oligochaeta) may be vulnerable to direct bioturbation or predation during omnivorous feeding by shrimps and *Sicydium*. Vulnerability of small instars to direct bioturbation or predation is also likely to explain why total abundance increased 14-fold while total biomass only increased four-fold. The different patterns in abundance vs. biomass were largely driven by increased numbers of small Chironomidae and Caenidae above dams, which resulted in a more dramatic change in overall abundance and a less marked change in biomass (E. Greathouse, *unpublished data*). Shrimp and *Sicydium* bioturbation may also negatively affect some taxa by reducing their habitat resources (e.g., fine inorganic matter used in chironomid cases). For riffles, our results indicate that, in contrast to pools, competition, predation, and bioturbation by shrimps and *Sicydium* do not affect epilithic non-decapod invertebrates.

Our results corroborate past experiments, which showed that shrimps in pools have large and highly significant effects on sessile collector-gatherer chironomids and no effects on case-making calamoceratid caddisfly larvae (Pringle et al. 1993, March et al. 2001, 2002). The marginal increase in baetid biomass in undammed sites is also consistent with these studies, which found increased mayfly biomass with shrimps present. High mobility appears to allow baetid mayflies to avoid being ingested by shrimps and *Sicydium* (Buzby 1998, March et al. 2002). Baetids also may benefit from sediment removal by shrimps and *Sicydium*, which may expose epilithic algal food resources (Pringle et al. 1993). A lack of significant differences in leptophlebiid mayflies, and an opposite pattern in caenids, between dammed and undammed pools, does not match the previously observed pattern for mobile mayflies. These results suggest that positive shrimp/*Sicy-*

TABLE 4. Mean abundance and biomass (as ash-free dry mass) of non-decapod invertebrates in high-gradient sites above dams vs. without large dams ($n = 7$ dammed and 10 undammed sites).

| | Pools | | | | |
| | Above dam | | No dam | | |
Variable	Mean	SE	Mean	SE	P
Total N (no./sample)	1735	576	127	38	**0.004**
Total biomass (mg/sample)	30.9	8.7	7.1	2.3	**0.0001**
Biomass (mg/sample) of common taxa: (MANOVA: $F_{12,4} = 29.53$, $P = 0.0025$)					
Gyrinidae (C)	7.81	4.45	1.17	1.17	0.089†
Chironomidae (D)‡	6.46	2.45	0.14	0.04	**<0.0001**
Odonata	4.66	1.66	0.56	0.46	**0.0049**
Baetidae (E)	0.76	0.36	3.13	1.17	0.096†
Hydroptilidae (T)	2.64	1.62	0.11	0.05	**0.016**
Calamoceratidae (T)	1.70	1.43	0.26	0.25	0.248
Caenidae (E)	1.69	1.38	0.06	0.04	0.079†
Ceratopogonidae (D)	1.64	1.30	<0.01	<0.01	0.051†
Leptophlebiidae (E)	0.38	0.13	0.51	0.22	0.806
Ancylidae (limpets)	0.84	0.61	<0.01	<0.01	0.064†
Oligochaeta	0.55	0.35	<0.01	<0.01	**0.036**
Other	1.74	0.26	1.10	0.50	0.090†

Notes: Boldface type indicates significant differences ($P < 0.05$) between dammed and undammed sites. Riffles and pools were analyzed with separate statistical tests because they were sampled with different methods, yielding densities and relative abundances, respectively. Because the MANOVA on common pool invertebrates was significant, P values from univariate ANOVAs are given. Uppercase letters indicate insect orders: C, Coleoptera; D, Diptera; E, Ephemeroptera; L, Lepidoptera; T, Trichoptera.

† Marginally significant differences ($P < 0.1$) between dammed and undammed sites.

‡ Does not include Tanypodinae or leaf-mining Chironomidae.

dium effects on mayflies can be outweighed by negative effects due to competition for food resources associated with depositional sediments (cf., Solomon et al. 2004).

Results for many other non-decapod invertebrate taxa in pools also do not match results from previous small-scale experiments manipulating presence/absence of shrimps and fishes (e.g., Pringle et al. 1993, March et al. 2001, 2002). We found significant differences between dammed and undammed sites for many taxa that, in previous studies, were rare or absent and showed no differences. These previous studies differed from our survey of dammed vs. undammed sites in terms of the scale of exclusion (experimental exclusion replicates were ~0.25 m² and ran for ~30–40 d, whereas large dams eliminated or severely reduced shrimps and fishes from whole watersheds for decades) as well as non-decapod invertebrate sampling methods and catchment conditions (e.g., agricultural land use ranges from 0.5% to 44% in this study, but previous study sites had 100% forested land cover). Conducting small-scale experiments at four of the high-gradient survey sites showed results for non-decapod invertebrates that match those observed here (Greathouse 2005). Treatments in these sets of experiments differed from the survey in terms of experimental scale but not in terms of sampling methods or overall catchment conditions. Thus, the differences between this study and previous experiments are likely due to the more effective invertebrate sampling method used in this study (Greathouse and Pringle 2005) and/or differences in catchment conditions such as land use. An important question for future applied research is whether abundance

of migratory shrimps and fishes interacts with land use to affect non-decapod invertebrates.

Low-gradient streams.—Results from low-gradient streams suggest that effects of migratory fauna losses above large dams depend on stream gradient. Differences in benthic resources between dammed and undammed streams were less pronounced in low-gradient than in high-gradient sites. For low-gradient sites, pool epilithon in dammed streams had only twice as much chlorophyll *a,* three times more FBOM, three times more C, and three times more N compared to pools in undammed sites, and FBIM showed no significant difference. Although we did not collect concurrent data on macroconsumer abundance, data from the low-gradient sites 6–7 yr prior to our study show that dams caused upstream declines in native shrimps and fishes (Holmquist et al. 1998). Our undammed low-gradient sites also had low abundances of native shrimps and fishes in comparison to the high abundances we observed at high-gradient sites (E. Greathouse, *personal observation*). Thus, these findings support those of March et al. (2001, 2002): effects of macroconsumers are stronger in high-gradient, shrimp-dominated rivers than they are in low-gradient rivers where predators limit shrimp abundances and activity.

Significance, implications, and recommendations

We demonstrated strong ecological effects of dams on free-flowing streams above reservoirs. Effects were observed for all major food web components: primary producers (chlorophyll *a*), detritus (FBOM), and nutrients (C, N); grazers, detritivores, and predators (*Si-*

TABLE 4. Extended.

	Riffles				
	Above dam		No dam		
Variable	Mean	SE	Mean	SE	P
Total N (no./m^2)	16 142	4496	7576	2044	0.06†
Total biomass (mg/m^2)	1006	367	647	171	0.59
Biomass (mg AFDM/m^2) of common taxa: (MANOVA: $F_{12,4} = 0.65$, $P = 0.75$)					
Hydroptilidae (T)	573.4	285.2	262.4	134.2	
Simuliidae (D)	186.2	88.3	177.8	119.0	
Chironomidae (D)	87.9	24.9	45.4	21.5	
Blephariceridae (D)	46.7	41.0	79.0	30.0	
Crambidae (L)	74.9	55.4	16.1	12.1	
Hydropsychidae (T)	3.37	1.74	45.3	22.6	
Baetidae (E)	15.8	14.8	1.70	1.23	
Odonata	3.33	3.13	6.57	6.57	
Psychodidae (D)	3.42	1.55	2.38	1.20	
Empididae (D)	4.89	3.61	0.43	0.17	
Ceratopogonidae (D)	1.09	0.81	2.99	1.97	
Other	0.67	0.11	0.74	0.13	

cydium and non-decapod invertebrates); and omnivores (shrimps). Because similar assemblages of migratory shrimps and fishes occur in coastal and insular streams throughout the Caribbean, Latin America, the Pacific islands, and Asia (e.g., Dudgeon 1999, Moulton et al. 2004), similar upstream effects of dams likely occur in many regions throughout the world.

Our findings have important management implications for tropical insular and coastal streams. Water resource demands on these ecosystems are often extreme because of dense human populations and limited land areas (Smith et al. 2003). In Puerto Rico, human population growth, unplanned development, and an outdated water supply system have led to severe water rationing during droughts (Pringle and Scatena 1999). At the same time, public interest in protecting stream biota and ecosystem services is high (González-Cabán and Loomis 1997). There is also a growing recognition among biologists and managers that biodiversity conservation should include protection of strongly interactive species at densities that maintain key species interactions (Soulé et al. 2005). Thus, managers and the public face difficult decisions about dam management. Our results provide useful information for weighing the costs and benefits of building, operating, and decommissioning dams.

Our findings also have implications for development of stream health indices in the tropics. For example, researchers at the U.S. Environmental Protection Agency have been unable to find correlations between water quality and benthic insects in a data set from Puerto Rican streams, which included sites above and without large dams (J. Kurtenbach, *personal communication*). The lack of correlations may be partly due to interstream variation in shrimp and fish populations causing high variation in benthic insect assemblages. We recommend that tropical stream managers include shrimps and their effects on other taxa in macroinvertebrate-based indicators of stream pollution. Managers should consider whether dams obscure macroinvertebrate responses to water quality.

There are also implications from our findings for general research on ecological effects of dams. For both terrestrial (Diamond 2001, Terborgh et al. 2001) and aquatic (Patten et al. 2001, Hart et al. 2002) ecosystems, dams provide unique opportunities to examine consequences of ecological alterations that are difficult to impossible to examine in controlled and replicated manipulations. Although we examined response variables that can be measured in small-scale experiments, our approach (i.e., comparing replicated, well-matched streams above vs. without large dams) would be ideal to use in determining effects of migratory fauna on large-scale ecosystem processes. Processes such as nutrient spiraling, whole-stream metabolism, and seston dynamics require study at large spatial and temporal scales. Large dams eliminate migratory fauna over such scales (i.e., whole catchments, decades). Studies using our approach would be especially useful if combined with long-term, whole-stream experimental exclusion of migratory organisms. Costs generally limit large-scale manipulation to a single site (Diamond 1986), but as we have shown, sampling matched dammed and undammed sites can be easily replicated. Together, the two approaches may provide the strongest inference possible for ecosystem-scale research on effects of migratory fauna.

We also suggest that studies using reaches upstream from a dam as ''control'' sites in evaluating downstream dam effects (e.g., Stanford and Ward 2001) should be analyzed carefully. Upstream effects of dams may confound comparisons between downstream sites and upstream reference reaches, even if the upstream reaches are never under reservoir water. Some studies

have found these upstream effects of dams on fish assemblages to be small, due to apparent dominance by nonmigratory fauna (Cumming 2004) and due to large basin size and consequent long distances between study sites and the downstream reservoir (Gido et al. 2002). Our study indicates that in tropical streams dominated by migratory fauna, upstream effects of dams are large and extend beyond changes in fish assemblages, even at great distances (0.7–20 km, Fig. 1) from a given reservoir. Thus, the best study design to examine comprehensive effects of dams would include sites located downstream from dams, upstream from dams, and in undammed drainages.

In summary, we have quantified strong indirect effects of dams on free-flowing reaches upstream from neotropical reservoirs in Puerto Rico. Ecologists working in both aquatic (Vinson 2001, Gregory et al. 2002, Freeman et al. 2003) and terrestrial (Elderd 2003) systems are becoming increasingly interested in indirect ecological effects of dams, particularly because sound ecosystem management will depend on understanding these effects (Power et al. 1996). However, published studies on this topic are focused on sites downstream from dams or within reservoirs and have rarely been quantitative. Our results demonstrate that dams can indirectly affect upstream free-flowing reaches by eliminating strong top-down effects of migratory consumers. Whereas researchers have recognized that dams strongly alter bottom-up effects in northern temperate systems (i.e., they eliminate salmon nutrient subsidies from upstream ecosystems; reviewed by Freeman et al. 2003), our study indicates that the consequences of migratory fauna loss upstream from dams encompass a wide variety of species interactions and extend to tropical biomes.

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APPENDIX

A description of methods used to determine physical and chemical parameters at high- and low-gradient survey sites and a table showing additional physical parameters at high-gradient sites (*Ecological Archives* A016-016-A1).