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ECOLOGICAL CONSEQUENCES OF HYDROPOWER DEVELOPMENT IN CENTRAL AMERICA: IMPACTS OF SMALL DAMS AND WATER DIVERSION ON NEOTROPICAL STREAM FISH ASSEMBLAGES

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ABSTRACT

Small dams for hydropower have caused widespread alteration of Central American rivers, yet much of recent development has gone undocumented by scientists and conservationists. We examined the ecological effects of a small hydropower plant (Doña Julia Hydroelectric Center) on two low-order streams (the Puerto Viejo River and Quebradon stream) draining a mountainous area of Costa Rica. Operation of the Doña Julia plant has dewatered these streams, reducing discharge to ~10% of average annual flow. This study compared fish assemblage composition and aquatic habitat upstream and downstream of diversion dams on two streams and along a ~4 km dewatered reach of the Puerto Viejo River in an attempt to evaluate current instream flow recommendations for regulated Costa Rican streams. Our results indicated that fish assemblages directly upstream and downstream of the dam on the third order Puerto Viejo River were dissimilar, suggesting that the small dam (<15 m high) hindered movement of fishes. Along the ~4 km dewatered reach of the Puerto Viejo River, species count increased with downstream distance from the dam. However, estimated species richness and overall fish abundance were not significantly correlated with downstream distance from the dam. Our results suggested that effects of stream dewatering may be most pronounced for a subset of species with more complex reproductive requirements, classified as equilibrium-type species based on their life-history. In the absence of changes to current operations, we expect that fish assemblages in the Puerto Viejo River will be increasingly dominated by opportunistic-type, colonizing fish species. Operations of many other small hydropower plants in Costa Rica and other parts of Central America mirror those of Doña Julia; the methods and results of this study may be applicable to some of those projects. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: small dams; tropical; Costa Rica; streams; fish; hydropower; Central America

INTRODUCTION

The rapid conversion of pristine, free-flowing tropical rivers into regulated systems is one of the most pressing concerns in global freshwater conservation (Allan and Flecker, 1993; Dudgeon, 2000; Pringle *et al*., 2000a, 2000b). Expanding urban populations and subsequent increases in demands for electricity have resulted in the construction of hundreds of dams on tropical rivers over the last two decades (Petts, 1990; Vaux and Goldman, 1990; WCD, 2000). Large dam projects in the tropics have often attracted attention from the international conservation community, on the basis of their widespread environmental and social impacts; examples of these impacts include flooding of tropical forests, greenhouse gas emissions from reservoirs, altered flow and sediment regimes, imperilment of aquatic biota, resettlement of human populations, and road construction in wilderness areas (Goodland *et al*., 1993; Fearnside, 1995; Rosenberg *et al*., 1995, 1997; WCD, 2000). However, much of the hydropower development currently occurring throughout the tropics involves small or medium sized projects that generate <50 megawatts (MW) of electricity and have dams that are <15 meters high (Vaux and Goldman,

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1990; Majot, 1997). The ecological impacts of these smaller developments are poorly understood and are not being adequately studied (Benstead *et al*., 1999; March *et al*., 2003).

Reductions in stream flow are a substantial ecological impact frequently associated with hydropower dams, regardless of their size. Flow reductions affect the physical characteristics of a stream (e.g. water velocity, sediment transport, water temperature) and alter the quantity and quality of aquatic habitat, with cascading impacts on stream biota. Toward this end, much research has examined the flow requirements of aquatic biota in dry, temperate areas of North America, Europe, South Africa, and Australia (King *et al*., 1999). Several methods now exist for determining instream flow standards for regulated rivers draining these regions (Jowett, 1997; Tharme, 2003). In contrast, there is little published research related to the impacts of flow reductions on neotropical stream biota. This paucity of information translates into a lack of methods for setting minimum instream flow standards in many Caribbean and Central American countries (Scatena, 2004).

In Central America, conservation of freshwater biodiversity is challenged not only by the regional lack of instream flow methods but also by rapid hydropower dam development. In the past decade, private companies have constructed dozens of small hydropower dam projects (< 20 MW generation capacity; <15 m high) on Central American rivers. The majority of these projects are located on low-order streams draining areas of high relief, such as Costa Rica's Central Volcanic Corridor. Costa Rica provides a case in point: nearly 30 small, private hydropower plants have been constructed in mountainous areas since 1990; additional hydropower projects are under construction or being proposed (Anderson, 2002). Much of recent hydropower development in Central America has gone undocumented by scientists and conservationists, with the exception of a few proposals for large dams, such as the Boruca Dam in Costa Rica or the Patuca River dam series in Honduras.

In Costa Rica, virtually all small hydropower plants operate as water diversion dams, where water is diverted from a river to generate electricity and then returned to the main channel downstream. These types of dam project result in substantial flow reductions (often for several kilometers) between the water diversion site and the downstream water return. Currently, no formal legislation for setting minimum instream flow standards exists in Costa Rica. However, the government recommends that small dam projects leave a compensation discharge that corresponds to ~10% of average annual flow in river reaches downstream from dams (R. Corrales, Doña Julia Hydroelectric Company, personal communication). This percentage is based on studies of temperate streams in North America and Europe and its applicability to Costa Rican streams has not yet been examined. Furthermore, although hydropower companies are required to complete an environmental impact statement during the planning phase of a dam, scientific studies of the actual ecological impacts of dam project operations are rare or non-existent in Costa Rica.

Since the late 1990s, the Doña Julia Hydroelectric Company has operated a small hydropower plant on the Puerto Viejo River in northeastern Costa Rica. The plant is located in a remote area that was inaccessible by road until it was chosen for hydropower development. Operation of Doña Julia has resulted in substantial flow reductions of the Puerto Viejo River and one of its tributaries, the Quebradon stream. The company leaves a compensation discharge that corresponds to ~10% of average annual flow in each river downstream from two small dams (<10 m tall) to ameliorate the effects of flow reductions. An additional noteworthy characteristic of the Doña Julia plant is that the compensation discharge is augmented during high flow events (e.g. flows more than twice the average annual discharge) when excess water is allowed to pass over dams.

The Doña Julia hydropower plant provides a model system for examining the ecological consequences of the many small hydropower plants that have recently proliferated on high-gradient streams draining the isthmus of Central America. The main objective of our study was to evaluate the current instream flow recommendations in Costa Rica by determining the ecological impact of the Doña Julia hydropower plant on neotropical stream fish assemblages. In addition, we aimed to form a basis for making initial management recommendations that may help maintain biotic integrity in dammed streams, in light of regional hydropower development trends. To the best of our knowledge, the present study is among the first in Central America to investigate the ecological impacts of a diversion dam during its operational phase. Data collection for our study began ~1 yr after the plant started full operation. We used a descriptive study design to examine (1) fish assemblage composition and aquatic habitat upstream and downstream of the plant and (2) progressive patterns in fish assemblages and aquatic habitat along a reach of river with significantly reduced flow.

STUDY SITE: THE PUERTO VIEJO RIVER AND THE DOÑA JULIA HYDROPOWER PLANT

The Puerto Viejo River, located on the northern Caribbean slope of Costa Rica, drains part of Braulio Carrillo National Park, a large tract of protected wet tropical forest in Central America that spans elevations from near sea level to 2900 m.a.s.l. Natural forest is the dominant land cover near the headwaters and mid-reaches of the Puerto Viejo drainage; pasture and croplands are the major land uses in the river's lower watershed. Abrupt changes in elevation (>100 m/km) characterize the upper Puerto Viejo River watershed, which receives in excess of 4 m annual precipitation. The watershed experiences wet (May to Dec) and dry (Jan to April) seasons, although rainfall here is more evenly distributed throughout the year than in other parts of Costa Rica (Sanford *et al*., 1994). A total of 44 freshwater fish species have been recorded from the Puerto Viejo River in the lowlands (Bussing, 1993; Anderson, unpublished data). Most of these fishes were collected in 1962–63 during a comprehensive study of a 1 km reach near the mouth of the river in the vicinity of La Selva Biological Station (Bussing, 1993). Collections of fishes in the Puerto Viejo River after the 1960s have been limited (Burcham, 1988; Coleman, 1999), and the watershed has since experienced a dramatic conversion of much forested land to pasture and other agricultural land uses (Butterfield, 1994; Vargas, 1995; Read, 1999).

High topographic relief and year-round rainy conditions have created a large hydropower potential for the upper watershed of the Puerto Viejo River. Since 1999, the Doña Julia Hydroelectric Company has operated an 18 MW hydropower plant on the river near the border of the national park (Figures 1 and 2). The project draws water from the Puerto Viejo River and the Quebradon stream; these rivers carry respective mean annual discharges of 8.5 m^3/s and 1 m^3/s at the dam site, respectively (CLC Ingenieros, 1994). The plant's main function is to

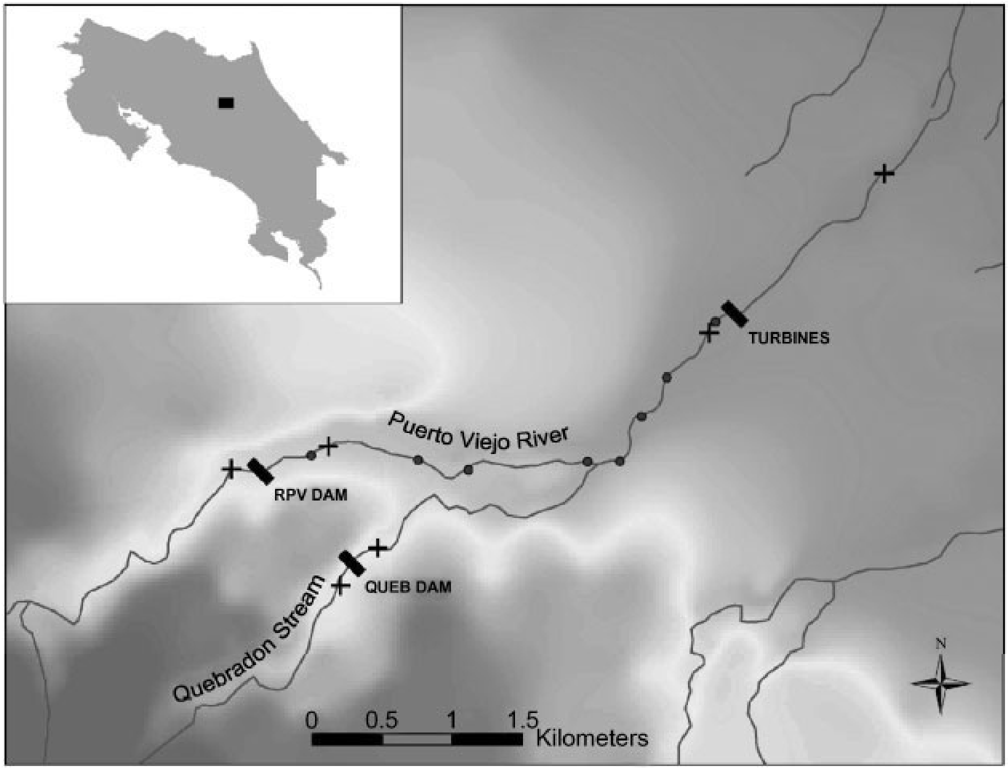

Figure 1. The upper Puerto Viejo River and the Quebradon stream are used for hydropower production by the Doña Julia hydropower plant. The location of the plant's two dams and turbine house are indicated on the map. Shading represents topographic variation; the lightly shaded ribbon represents a gradient break or an abrupt change in elevation. Our sampling sites are marked on the map with either a cross (for 2001 sites) or a circle (for 2002 sites). The inset shows the location of the drainage on the northern Caribbean slope of Costa Rica. (Figure prepared by A. Trabucco, Organization for Tropical Studies)

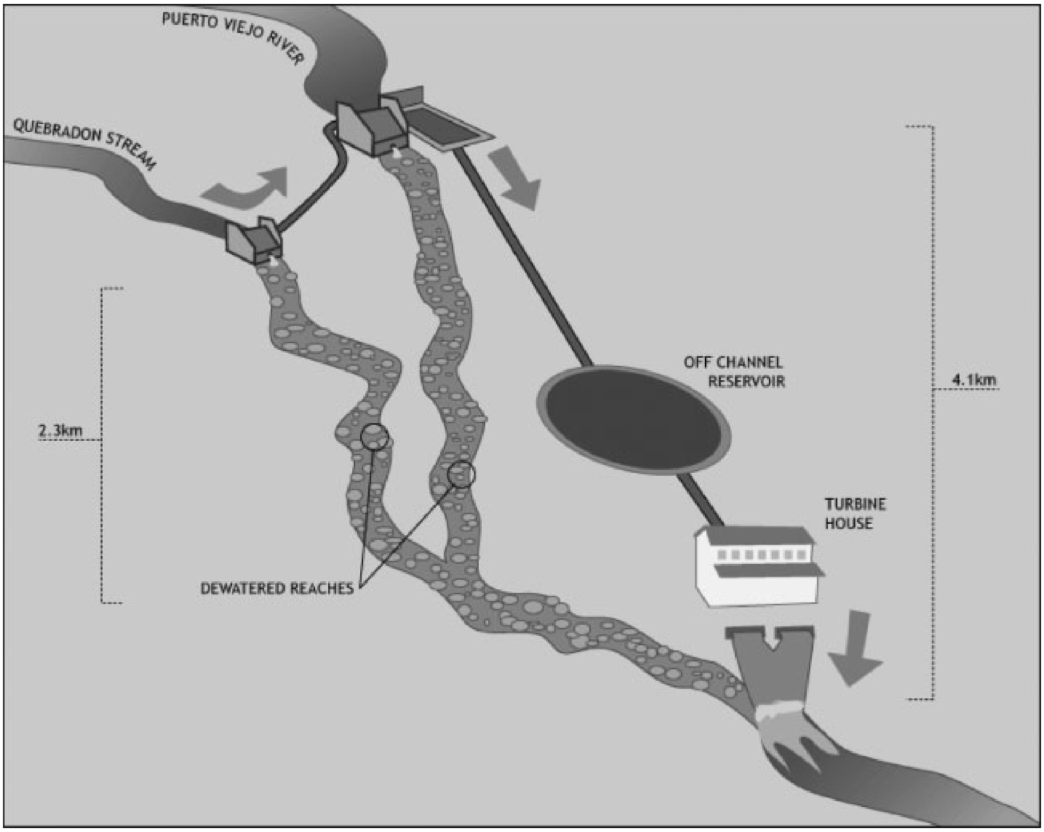

Figure 2. Schematic diagram of the Doña Julia Hydroelectric Center. A dam diverts water from the Quebradon stream and sends it via pipeline to the Puerto Viejo River. Water from the Quebradon stream is diverted along with water from the Puerto Viejo River at a dam site on that river. Suspended sediments fall out in a settling tank before water is sent via tunnel to an off-channel reservoir. Water is stored in the reservoir until peak hours of generation, when it is transported via pipeline down an elevation gradient of ~100 m to a turbine house. After being used to generate electricity, water is returned to the river. (Figure prepared by C. Lowe)

provide electricity to Costa Rican residents during peak hours of demand, which occur between approximately 10:00–12:30 and 17:30–20:00 daily.

Operation of the plant has created a 'de-watered' reach of stream on both rivers, where 90–95% of the average annual discharge is removed from the river and piped to an off-channel reservoir for storage until peak electricity generation times (Figure 2). On the Puerto Viejo River and Quebradon stream, the distance of the dewatered reach corresponds to ~4 km and ~2 km, respectively. During normal flow conditions, a constant compensation discharge is left in the stream at each diversion site. On the Puerto Viejo River, tributary inputs (e.g. from Quebradon stream and other smaller first order streams) and groundwater seeps incrementally increase the compensation discharge such that flow at the downstream end of the dewatered reach is roughly 10% of average annual discharge. During flood events or flows that surpass the capacity of the diversion canal (~16 m^3/s), the dewatered reach fills with the excess water that passes over the dam. Based on long-term discharge estimations, these high flow events are concentrated during months of heaviest rainfall, such as November, December, and July (CLC Ingenieros, 1994).

Operation of the dam has also created variable conditions in the reach downstream from the turbines where water is returned to the river. Generation periods result in marked increases in discharge over several kilometers, due to the large amount of water released from the turbines during a short time period. Discharge increases are accompanied by temperature decreases of up to 4 °C over time intervals of <15 minutes (Anderson, unpublished data).

METHODS

This study was conducted during January 2001–June 2002. To test for an effect of plant operations on fish assemblage composition, we sampled fish once during the ‘dry’ season (Feb–April 2001) and once during low flows in the ‘wet’ season (July–Nov 2001) at four sites on the Puerto Viejo River and two sites on the Quebradon stream (Figure 1). Sampling sites were selected based on their accessibility and location relative to the dam’s water diversion sites and turbine house. These sites consisted of stream reaches that were 20 times the mean width of the channel, or a maximum length of 300 m. To test for a progressive pattern in fish assemblage composition along the dewatered reach, we sampled fish during the dry season (Jan–April 2002) at eight study sites located along the Puerto Viejo River between the water diversion and water return (Figure 1). Sampling sites consisted of 100 m long reaches and were selected using a stratified random study design based on downstream distance from the dam. To supplement the study, pools >1 m deep along the dewatered reach (13 total) also were sampled for fishes.

Fish sampling

We used a Smith-Root backpack electrofisher for all fish collections. In 2001, all fishes captured during one pass of each study reach were measured for standard length, identified to species, and then returned to the river. A voucher collection was deposited at the Museum of Natural History at the Universidad de Costa Rica in San José, Costa Rica. In 2002, we used the removal method (White *et al*., 1982) to examine fish assemblages along the de-watered reach. Block nets were placed at the upstream and downstream ends of each 100 m study reach and three passes of the reach were made with the electrofisher, moving in an upstream direction. After completing a pass, fish were identified to species and measured for standard length. Fish then were released $\sim$100 m from the block net at the downstream end of the reach to prevent recapture in subsequent passes.

Visual assessments were conducted in pools >1 m deep and consisted of timed trials performed by two observers. Using a mask and snorkel, observers took turns slowly swimming a pre-determined route through the pool during a 10 min period, noting all fish species present in the pool. These 10 min trials were repeated three times by each observer, for a total sampling time of 60 min in each pool. In two pools where no fish were seen during the first three trials, the sampling period was stopped after 30 min. In cases where an observer was uncertain about species identification, both observers returned to the pool after the 60 min period to note specific characteristics about the fish and its behavior. Based on this information, fish were identified to species using the work of Bussing (1998).

Habitat descriptions

Physical variables related to aquatic habitat were measured at all sites in 2001 and 2002. These included temperature, water velocity, substrate, wetted channel width, and water depth. In 2001, Onset Stowaway Temperature Dataloggers recorded temperature at two sites on the Quebradon stream (QA; QB), three sites on the Puerto Viejo River (PVA; PVB; PVT), and at the water release from the turbine house (PVD) during Feb-April. Geomorphic channel units were mapped using 50 m measuring tapes to estimate the percentage of pools and rapids at each site and to measure channel width. Using a stratified random study design, we sampled water velocity (using a Marsh-McBirney FloMate meter), depth, and dominant substrate at 1 m intervals along 10 bank-to-bank channel cross-sections (five in pools and five in rapids) at each of the six sites. We also collected two water samples from each of the six study sites that were later analyzed for soluble reactive phosphorus, nitrate, and ammonium at the University of Georgia Institute of Ecology’s Analytical Laboratory.

In 2002, Onset Stowaway Temperature Dataloggers were placed at three points to record differences in temperature along the dewatered reach of the Puerto Viejo River: 100 m, 2000 m, and 4200 m downstream from the diversion dam. Water velocity and depth were sampled at 1 m intervals along 10 channel cross-sections, spaced equidistantly along each 100 m study reach. A pebble count (Wolman, 1954) was used to identify dominant bed sediment, and geomorphic channel units were mapped in each of the eight 100 m study reaches after fish and other habitat sampling was completed.

Data analysis

To test for an effect of dam operations on fish assemblage composition (2001 sample data), we used non-metric multidimensional scaling (NMS) to ordinate a species abundance by sample (site and season) matrix of 2001 data.

Our analysis was completed using PC-ORD software (MjM Software Design^{TM}, Glendale Beach, OR, USA; McCune and Mefford, 1999), using Sorenson similarity. Abundance data were root–root transformed (e.g. fourth root) prior to ordination. Species richness for each sample was estimated using the limiting form of the jackknife estimator described by Burnham and Overton (1979), and calculated using SPECRICH software provided by the Patuxent Wildlife Research Center (www.pwrc.usgs.gov). This estimator uses species count data to account for variability in capture probabilities among different species (see Burnham and Overton, 1979). To test for progressive patterns in fish assemblage composition along the de-watered reach (2002 sample data), we estimated species richness from pooled data from all three passes at each 100 m study reach. This analysis was accomplished using the jacknife richness estimator. Species richness estimates from 100 m reaches and species count data from visual assessments in pools were tested against downstream distance from the dam using bivariate correlation analysis. We also used bivariate correlation analysis to test for patterns in fish abundance and aquatic habitat variables with downstream distance from the dam. Analysis of variance (ANOVA) was used to test for differences in nutrient chemistry between sites.

RESULTS

Fishes: Distribution and abundance near the hydropower dam

A total of 2401 individuals were collected by electrofishing from the Puerto Viejo River and Quebradon stream: 1519 individuals from all sites in 2001, and 882 individuals from the de-watered reach of the Puerto Viejo in 2002. Captured fishes represented 14 species in six families (Table I). In 2001, the most common species captured was

Table I. List of families and species of fish captured in the upper Puerto Viejo River and the Quebradon stream, Costa Rica, during 2001–02 as a part of this study. Common names are listed in parentheses

Family and species
Family Characidae
Astyanax aeneus (sardina)
Bryconamericus scleroparius (sardina)
Family Pimelodidae
Rhamdia nicaraguensis (barbudo)
Rhamdia rogersi (barbudo)
Family Poeciliidae
Alfaro cultratus (olomina)
Poecilia gillii (olomina)
Priapichthys annectens (olomina)
Family Gobiosocidae
Gobiosox nudus (chupapiedra)
Family Cichlidae
Archocentrus septemfasciatus (mojarra)
Archocentrus nigrofasciatus (mojarra)
Astatheros alfari (mojarra)
Parachromis dovii (guapote)
Theraps underwoodi (vieja; moga)
Family Mugilidae
Agonostomus monticola (tepemechin)

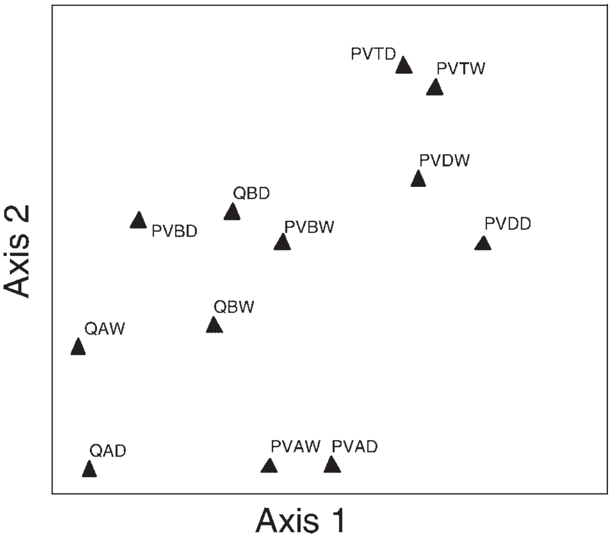

Figure 3. The NMS ordination of 2001 fish data, showing a separation of sites according to increasing abundances of most species from above the dams (QA, PVA), to below the dams (QB, PVB), to the downstream end of the dewatered reach (PVT) and downstream from the turbines (PVD). Wet (W) and dry (D) season samples generally clustered together

Poecilia gillii (Poecilidae), which accounted for 43.5% of all individuals. *Rhamdia rogersi* (Pimelodidae), which accounted for 23.5% of individuals, was the second most common species in 2001. *Poecilia gillii* was also the dominant species captured in 2002, accounting for 46.0% of all individuals captured along the dewatered reach. Despite few individuals (only 22 captured in total), the most species-rich family was Cichlidae, with five species. No additional species were recorded during visual assessments.

Ordination of 2001 data indicated that samples separated along two axes that described increasing abundances of most fishes (Figure 3). Together, axes 1 and 2 represented 92% of the variation in the original distance matrix. Transformed abundances for 12 of the 14 species had correlation values > 0.4 with one or both axes, and of these all except two of the poeciliid species increased along one or both axes (Table II). The ordination also indicated that fish assemblage composition was most affected by site location rather than season. Although slight seasonal differences in assemblages may exist, these differences were small in comparison with site differences. Samples

Table II. Correlations (r values) between transformed species abundances and site positions along NMS axes 1 and 2

Species	Axis 1	Axis 2
Alfaro cultratus	−0.44	−0.43
Poecilia gillii	0.96	0.39
Priapichthys annectens	0.95	−0.52
Gobiosox nudus	−0.16	0.21
Rhamdia nicaraguensis	0.65	0.79
Rhamdia rogersi	0.20	0.83
Astyanax aeneus	0.78	0.80
Bryconamericus scleroparius	0.40	0.54
Theraps underwoodi	0.70	0.63
Astatheros alfari	0.59	0.40
Archocentrus septemfasciatus	0.61	0.33
Archocentrus nigrofasciatus	0.46	0.07
Parachromis dovii	0.31	0.22
Agonostomus monticola	0.86	0.72

taken from the Puerto Viejo River at the downstream end of the dewatered reach (PVT) clustered with samples taken downstream from the water return (PVD) to form a group distinguished by the occurrence of cichlids and increased catches of most species (Table II; Figure 3). Samples taken upstream of the dam on the Puerto Viejo River (PVA) ordinated together, distinguished by low catches of all species except *P. gillii*. Samples taken upstream of the dam on the Quebradon stream (QA) had similarly low abundances across taxa, including *P. gillii*. Finally, samples from the upstream end of the Puerto Viejo dewatered reach (PVB) and in the dewatered reach of the Quebradon stream (QB) also lacked cichlids but had greater numbers of *Rhamdia spp*. than samples above the dams, placing these sites intermediately on axis 2 (Figure 3).

Estimated species richness varied by site and slightly by season at each location. Estimated species richness was highest (15 species) downstream from the turbines (PVDD) during the dry season and lowest (three species) upstream from the dam on the Quebradon stream during the wet season (QAW). At sites within the dewatered reach of the Puerto Viejo River (PVB; PVT), estimated species richness was higher during the wet season (PVB = 8 (wet) versus 4 (dry); PVT = 10 (wet) versus 9 (dry)), whereas at sites upstream from the dams (QA; PVA), estimated species richness was higher during the dry season (QA = 7 (dry) versus 3 (wet); PVA = 6 (dry) versus 4 (wet)).

Fishes: Progressive patterns along the dewatered reach

We found that the removal method (White *et al*., 1982) was unsuccessful at estimating fish populations along the dewatered reach of the Puerto Viejo River. As required by the method, at all study reaches we captured the largest number of individuals during the first pass with the electrofisher and then substantially fewer individuals during the second pass. However, during the third pass, we typically captured many more individuals than the second pass and often as many as during the first pass. This result clearly contradicted the assumption of the removal method that capture efficiencies are constant across passes. Therefore, we were never able to estimate population size from our data. In our study system, we believe that dominant bed sediments, such as boulder and cobble, may have created ample hiding spaces for fishes during the first and second passes, and then fish weakened by the electrofisher were caught during the third pass.

Analysis of 2002 fish data revealed several patterns in species richness along the dewatered reach of the Puerto Viejo River (Table III). Species count was highest at the downstream end of the dewatered reach (eight species) but bivariate correlation indicated no significant trend towards increasing fish species richness with downstream distance from the dam ($r = 0.25$, $p = 0.20$); richness changed by only two species from the upstream to the downstream end of the dewatered reach. Overall fish abundance in samples at each study site was not significantly

Table III. Species presence/absence along the dewatered reach of the Puerto Viejo River. Letters after a species name indicate life history strategies: P = periodic; O = opportunistic; E = equilibrium

Species	Downstream distance from dam (m)							
	208	1043	1484	2190	2493	2873	3250	4179
Agonostomus monticola (P)	x	x	x	x	x	x	x	x
Astyanax aeneus (O)				x	x		x	x
Gobiosox nudus (O)	x	x	x	x		x	x	x
Poecilia gillii (O)	x	x	x	x	x	x	x	x
Priapichthys annectens (O)			x					
Rhamdia nicaraguensis (O)	x	x	x	x	x	x	x	x
Rhamdia rogersi (O)	x	x	x	x	x	x	x	x
Archocentrus septemfasciatus (E)								x
Astatheros alfari (E)								x
Theraps underwoodi (E)						x	x	
Species Count:	5	5	6	6	5	6	7	8
Estimated species richness:	6	6	7	8	5	8	7	8

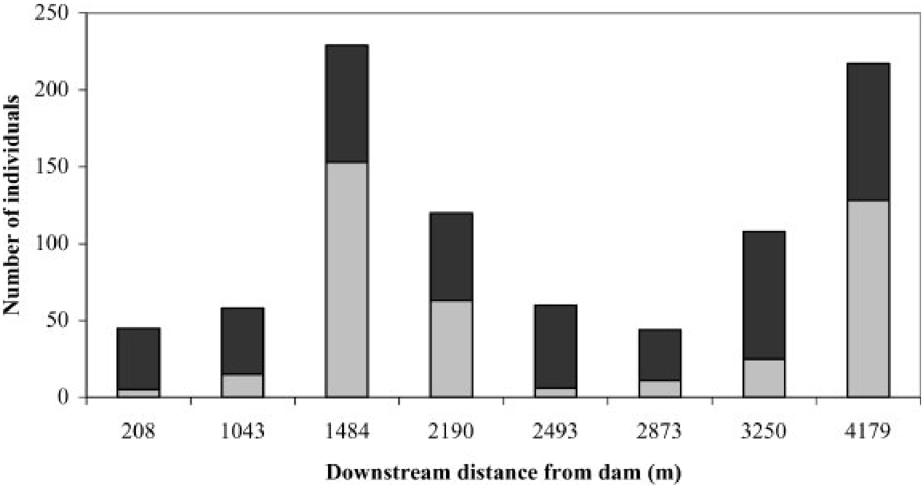

Figure 4. Number of individual fish versus downstream distance from the dam on the Puerto Viejo River. The lightly shaded part of the column represents the number of individuals of *Poecilia gillii* at each site

related to downstream distance from the diversion dam ($r = 0.14$, $p = 0.35$). Peaks in the number of individuals captured occurred at 1484 and 4179 m downstream from the dam; these peaks resulted from the dominance of *Poecilia gillii*, which accounted for more than half of the individuals at each of these two sites (Figure 4).

Data from visual assessments along the de-watered reach of the Puerto Viejo River revealed that fish species counts in pools were significantly related to downstream distance from the dam ($r = 0.73$, $p = 0.0002$; Figure 5). Cichlid fishes, found only in pools in the lower half of the dewatered reach (>2500 m downstream from the diversion dam), accounted for this increase in species count.

Habitat descriptions

Basic habitat characteristics of all sites are shown in Tables IV and V. Several trends are evident in the data. Rapids and riffle habitats tended to compose a larger percentage of the channel at sites upstream from the dam than at downstream sites within the dewatered reach, where pool or low water velocity habitats dominated. Water

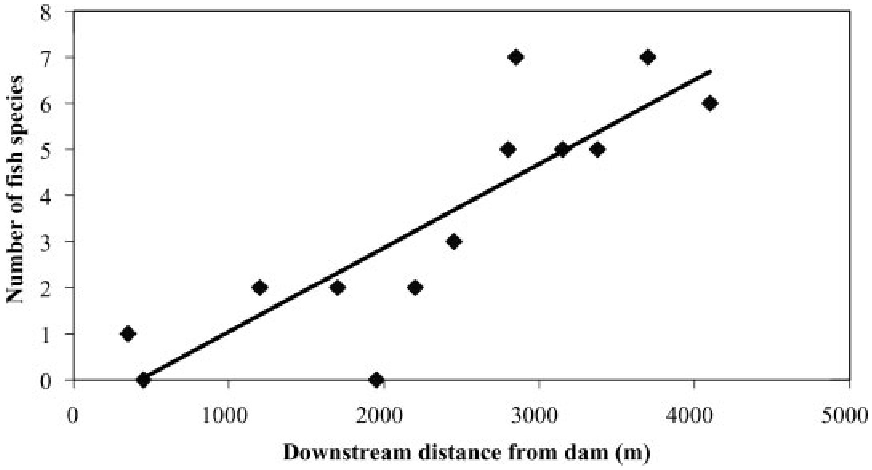

Figure 5. Number of fish species in pools versus downstream distance from the dam along the dewatered reach of the Puerto Viejo River. Data were collected by visual assessments in pools during Jan–Feb 2002

Table IV. Summary of selected habitat data from sites upstream and downstream from the dam (2001). Q = Quebradon stream; PV = Puerto Viejo River; A = above dam; B = below dam; T = upstream from turbine house; D = downstream from hydropower plant

	QA	QB	PVA	PVB	PVT	PVD
Approximate distance from dam	50 m upstream	50 m downstream	100 m upstream	100 m downstream	4000 m downstream	6000 m downstream
Reach length (m)	255	204	300	300	300	200
Pool habitat (%)	13.01	6.80	18.56	12.43	20.30	19.37
Rapid/rifle habitat (%)	24.93	58.92	4.55	56.77	50.65	56.15
Run habitat (%)	0	0	25.49	0	0	0
Temperature range (°C)	18.6–21.7	18.7–22.3	17.1–20.7	17.7–22.3	19.2–23.6	N/A
Pool depth (cm)	28.57	14.16	63.12	39.88	20.71	36.90
Riffle depth (cm)	24.11	9.54	34.09	14.07	18.89	35.83
Pool velocity (m/s)	0.276	0.032	0.544	0.129	0.112	0.319
Riffle velocity (m/s)	0.38	0.049	0.665	0.156	0.138	0.51
NO_3 μg/L	92.2	84.0	57.7	80.0	48.0	51.3
NH_4 μg/L	5.9	5.15	6.3	5.1	9.3	7.6
SRP μg/L	278.4	233.1	221.8	222.1	342.8	194.6

velocity in both pools and riffles was four to 10 times greater at sites upstream from the dams than in de-watered reaches. Water depths tended to be greater at upstream sites as well, with the exception of greater average riffle depth at one site within the dewatered reach (Table IV). However, there were no significant relations between distance downstream from the dam and average depth or velocity in pools ($r = 0.10$, $p = 0.44$ [depth]; $r = 0.0004$, $p = 0.96$ [velocity]) or riffles ($r = 0.019$, $p = 0.75$ [depth]; $r = 0.057$, $p = 0.57$ [velocity]), respectively (Table V). Boulder (250–4000 mm), followed by cobble (64–250 mm), was the dominant bed sediment at all sites. Minimum water temperatures tended to be lower at upstream sites, while maximum water temperatures were higher at downstream sites during Feb–April 2001 (Table IV). Dewatering appeared to increase water temperature: during Feb–April 2001, maximum water temperatures recorded from the Puerto Viejo River in the dewatered reach (PVB) were ~2°C higher than temperatures upstream (PVA; Table IV). Results were similar for the Quebradon stream; the maximum temperature of the dewatered reach was ~1°C higher than upstream water temperature. Across all sites, average concentrations of nutrients were 7 μg/L (±3) of ammonium (NH_4-N), 70 μg/L (±21) of nitrate (NO_3-N), and 249 μg/L (±94) of soluble reactive phosphorus (SRP), and there were no significant differences between sites for any of the nutrients (NO_3-N, $F_{(5,6)} = 3.06$, $p = 0.10$; NH_4-N, $F_{(5,6)} = 0.44$, $p = 0.81$; SRP, $F_{(5,6)} = 0.51$, $p = 0.76$). The naturally high concentrations of phosphorus indicate that the water chemistry of the Puerto Viejo River and Quebradon stream may be influenced by geothermal inputs from volcanic activity (see Pringle *et al*., 1993).

Table V. Summary of selected habitat data from sites along the dewatered reach of the Puerto Viejo River (2002)

Downstream distance from dam (m)	Average width (m)	Pool habitat (%)	Rapid/riffle habitat (%)	Temperature (C)		Average depth (cm)		Average velocity (m/s)	
				min	max	pool	rapid	pool	rapid
208	9.89	53.2	46.8	18.41	23.01	42.19	23.09	0.073	0.144
1043	10.42	76.3	23.7	—	—	29.68	33.46	0.086	0.224
1484	10.24	59.2	40.8	—	—	32.86	19.50	0.065	0.159
2190	17.57	65.3	34.7	—	—	14.56	21.20	0.04	0.114
2493	14.10	82.8	17.2	19.02	24.15	38.58	31.80	0.116	0.424
2873	11.67	69.5	30.5	—	—	42.62	37.45	0.109	0.227
3250	13.55	69.8	30.2	—	—	29.59	30.70	0.069	0.199
4179	23.68	53.4	46.6	19.36	25.20	24.13	22.05	0.059	0.203

DISCUSSION

This study was a descriptive examination of the impacts of flow reductions caused by a small hydropower plant on neotropical stream fish assemblages. It provided a unique opportunity to test whether current recommendations for compensation flows downstream from diversion dams in Costa Rica are sufficient for fishes. Our investigation is one of the only studies of its kind, despite the fact that small hydropower projects like Doña Julia are becoming increasingly common in wet areas of high topographic relief in Costa Rica and other Central American countries. Certain aspects of our study design were not ideal, especially the absence of a control stream with no impoundment. However, the variability of streams draining the Puerto Viejo River watershed, in terms of nutrient chemistry, pH, and conductivity due to geothermal influences (Pringle *et al*., 1993), made it difficult to identify control streams. Variations in slope (due to rugged topography), discharge (due to precipitation microclimates), and land use were additional factors that presented a challenge to finding control streams for this study. Although the results of our study may be applicable to other small hydropower projects at similar elevations along the Caribbean slope of Costa Rica, more research is needed in other dammed and unimpounded neotropical streams to test the generality of our conclusions.

Fish assemblages of the upper Puerto Viejo River

The present study marks the first comprehensive survey of the fishes of the upper Puerto Viejo River. An environmental impact statement completed as part of the planning process of Doña Julia plant claimed that multiple fish species inhabited the river in the area near the dam; these conclusions, however, were based on previous studies conducted at lower elevations and on interviews with area residents. No field collections of fishes were reported in the environmental impact statement (Flores and Soto, 1992). During the present study, we collected a total of 14 fish species from the upper Puerto Viejo River along a ~5 km reach. Of these, one species, *Agonostomus monticola* (Mugilidae), is highly mobile and suspected to be either amphidromous or catadromous (Cruz, 1987; Phillip, 1993; Aiken, 1998). An additional migratory fish, *Joturus pichardi* (Mugilidae), was reported by local fishermen to have been abundant in the area in the past and mentioned in the environmental impact statement, yet this fish was not collected or seen during the present study.

Our results suggest that there is a measurable effect of hydropower plant operations on fish assemblage composition; this effect is most pronounced on the Puerto Viejo River. The dissimilarity between fish assemblage composition at the site above the dam (PVA) and below the dam (PVB), as indicated by ordination of catch data, suggests a fragmentation effect on fishes. In the absence of the dam, we would expect these two assemblages to resemble one another, due to their close geographic proximity. However, our results indicate that the fish assemblage directly downstream from the dam (PVB) is more closely related to assemblages of the Quebradon stream (QA; QB). The physical barrier presented by the dam restricts fish movement between the two sites on the Puerto Viejo (PVA; PVB) and thus may influence the structure of the upstream assemblage. Whereas fish from upstream areas are capable of swimming downstream and passing over the dam during high flow conditions, the dam hinders upstream movement, making it only possible during very high flows, if at all. A potential consequence of this restricted movement is the isolation of fish populations upstream from the dam. This isolation could result in decreased intraspecific genetic diversity or local extirpation of highly mobile species (Winston *et al*., 1991; Pringle, 1997). Our data indicate that in the future at least one species, *Agonostomus monticola*, may face local extinction upstream of the dam: during the dry season we captured three large adults above the dam and observed four adults swimming at the base of the dam, yet during the wet season six months later we neither captured or observed any *Agonostomus monticola* upstream of the dam.

Similarity of certain aquatic habitat conditions may be the best explanation for the differences in fish assemblage composition as indicated by the ordination analysis. The resemblance between the fish assemblage directly downstream of the dam on the Puerto Viejo and the assemblage in the dewatered reach of the Quebradon stream may be explained by the fact that the sites are comparable in terms of stream width, temperature range, and substrate, and experience similar flow depletion. Extensive run habitat and occurrence of rapid water velocities, in addition to isolation caused by the dam, probably explain distinctiveness of the fish assemblage upstream of the dam on the Puerto Viejo River. Warmer water temperatures, lower elevation, and increased stream width may be reasons for the similarity between assemblages at the downstream end of the dewatered reach (PVT) and below the water return (PVD).

Progressive patterns of fish distribution along a dewatered reach

Our results indicate that there is a detectable change in fish assemblage composition downstream of the dam on the Puerto Viejo River. However, is this pattern actually the result of dam operations and consequent flow reductions and if so, to what degree? Alternatively, do observed patterns reflect a natural longitudinal gradient of species additions, as has been predicted for Central American streams without large dams (Welcomme, 1985)? The paucity of pre-impoundment data on natural fish distribution and the lack of comparable rivers in the region make it impossible to answer these questions with complete certainty. In addition, our inability to estimate capture efficiency and population sizes with removal sampling confounds interpretation of the results of this study. Nevertheless, some trends evident in our data can provide insights. Specifically, when we classify fishes by their life history strategies (according to Winemiller, 1995), our results indicate that species with more 'opportunistic' strategies dominated assemblages closer to the dam, whereas assemblages further downstream along the dewatered reach contained a mix of 'opportunistic' and 'equilibrium' species (Table VI). Equilibrium species, such as cichlids, generally have more complex reproductive requirements; in the case of Puerto Viejo drainage cichlid species, these requirements include parental care (Coleman, 1999). The distribution of 'equilibrium' species in this part of the Puerto Viejo River may be the result of incremental increases in discharge along the dewatered reach due to tributary and groundwater inputs, since they were only present downstream from the confluence of the Puerto Viejo River and the Quebradon stream. Increased discharge in the downstream half of the dewatered reach may have three consequences that relate to fishes: (1) more habitat during dry periods with little rainfall; (2) reduced disturbance during high or 'flashy' flows (e.g. when flows exceed the diversion canal capacity and spill into the dewatered

Table VI. Characteristics of life history strategies and classification of Puerto Viejo River fishes by strategy. Adapted from Winemiller (1995)

	Opportunistic	Periodic	Equilibrium
Demographic factors	Juvenile and adult survivorship low and variable; short generation times.	Low and variable juvenile survivorship; adult survivorship high with low variance; Large generation times.	Juvenile and adult survivorship high with low variance; variable generation times.
Physiological factors	Small adult body size; small neonate body size; short- lived.	Large adult body size; small neonate body size; intermediate–long lived.	Variable adult body size; large neonate body size; intermediate–long lived.
Behavioral factors	No–little parental care; long reproductive season; many reproductive bouts per season.	No–little parental care; short reproductive season; one or few reproductive bouts per season.	Parental care; variable length of reproductive season; one or few reproductive bouts per season.
Environmental factors	Harsh and unstable physical conditions; variable access to food resources; predation pressures common.	Patchy or cyclic physical conditions; food resources vary periodically; populations may be density dependent.	Stable or predictable physical conditions; relatively stable food resources; populations often density dependent.
	Puerto Viejo River fishes		
	Poecilia gillii *Rhamdia nicaraguensis* *Rhamdia rogersi* *Astyanax aeneus* *Bryconamericus scleroparius* *Gobiosox nudus* *Priapichthys annectens*	*Agonostomus monticola*	*Astatheros alfari* *Archocentrus septemfasciatus* *Archocentrus nigrofasciatus* *Parachromis dovii* *Theraps underwoodi*

reach); and (3) easier access to refugia near channel edges (e.g., during high flows). Furthermore, slightly lower minimum water temperatures at the upstream end of the dewatered reach may also explain why cichlids (equilibrium species) were restricted to downstream areas.

CONCLUSIONS AND RECOMMENDATIONS

The presence of dams and water diversions may impact long-term persistence of fish populations in the upper Puerto Viejo River drainage. Our study suggested that diversion dams, like Doña Julia, hinder upstream movement of mobile/migratory fishes. Our results also imply that compensation flows downstream from dams that equal $\sim 10\%$ of average annual discharge probably provide enough water for opportunistic-type fishes but may not be sufficient for species with more involved reproductive requirements. The increased likelihood of desiccation downstream of a diversion dam, particularly before the confluence of any major tributaries, may be a mechanism limiting the occurrence of equilibrium-type species like cichlids. Our results suggest that the presence of certain cichlids (e.g. *Theraps sp*., *Archocentros sp*.) may be a good indicator of whether or not compensation flows leave sufficient water for neotropical stream fishes.

Because we conducted this study soon after Doña Julia began operation, our dataset provides a valuable tool that can be used for tracking changes over time in fish assemblages near the Doña Julia hydropower plant. Changes could occur in response to temporal adjustments to present operating conditions or modifications in operation designed to minimize environmental impacts. If management goals at Doña Julia and other similar hydropower plants in Costa Rica include maintaining biotic integrity in dammed streams, alternatives to current operations should be considered. Providing fish passage at dams located at middle and low elevations and increasing flows in diverted streams during dry periods may help facilitate upstream persistence of periodic- and equilibrium-type fish species. At higher altitudes, fish assemblages are dominated by only a few small species adapted to colder water temperatures (Bussing, 1998). Because the Doña Julia dam and other private diversion dams in Costa Rica are usually <15 m in height, installation of a fish ladder or an artificial side channel may be practicable. Increasing flows in diverted streams could be accomplished in the context of adaptive management (Irwin and Freeman, 2002): a trial period of augmented flows accompanied by fish sampling would show whether or not more periodic- and equilibrium-type species move upstream when discharge is increased. In the absence of changes to current operations, we expect that fish assemblages in the upper Puerto Viejo River, and other streams used for hydropower, will be increasingly dominated by opportunistic-type fishes.

In summary, hydropower dam plants like Doña Julia are currently transforming river ecosystems throughout the tropics. The ecological impacts of these developments on tropical rivers will depend on the type of facility, degree of hydrologic alteration, local climate, and life histories of stream biota. More research is needed to provide insight into the ecological requirements of tropical stream biota and to predict their response to hydrologic alterations caused by dams. Establishment of monitoring programs and the use of adaptive management at operational dams can help guide future development in a way that maximizes the benefits of hydropower while minimizing its negative environmental consequences. In addition, studies like the one we present here can be useful in developing formal methods and legislation for setting minimum instream flow standards for rivers in Costa Rica and along the Caribbean slope of Central America.

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