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Transforming tropical rivers: an environmental perspective on hydropower development in Costa Rica

ELIZABETH P. ANDERSON[a,*], CATHERINE M. PRINGLE[a] and MANRIQUE ROJAS[b]

[a] *Institute of Ecology, University of Georgia, Athens, Georgia, USA*

[b] *Edificadora Beta SA, Ciudad Quesada, Costa Rica*

ABSTRACT

1. Tropical rivers are increasingly being altered by hydropower dams. In Costa Rica, more than 30 hydropower plants were built during the 1990s and more dams are being proposed. Hydropower dams currently provide more than 80% of electricity consumed by the country's 4 million residents, yet most of Costa Rica's hydropower potential remains untapped.

2. Ecological consequences of dams in Costa Rica stem primarily from river fragmentation, stream de-watering, and downstream hydrological alterations. Dams affect distribution and abundance of aquatic biota, especially migratory species. Cumulative effects of multiple dams on individual river basins, especially in the northern part of the country, are also of concern but have not been adequately documented.

3. In light of recent hydropower development, we recommend conservation strategies that protect remaining free-flowing rivers, call for assessment of ecological impacts of dams on a broader scale, encourage research on aquatic systems and sustainable hydropower technologies, and promote the development of methods for estimating environmental flows for Costa Rican rivers.

KEY WORDS: dams; hydropower; tropical streams; Central America

INTRODUCTION

The number of dams is increasing on many tropical rivers (Pringle *et al*., 2000; WCD, 2000; McCully, 2001). In the neotropics, dam construction is primarily motivated by growing demands for electricity, and many new dams are for hydropower production (Fearnside, 1995; Pringle *et al*., 2000). Growth in per capita electricity consumption in tropical, developing countries is expected to double over the period 2005–2025, as emerging economies expand, human populations grow, and access to electricity improves (Goldemberg, 2000; EIA, 2005). Furthermore, many dam builders and proponents of hydropower consider tropical regions as frontiers for new dam construction, given that most suitable sites for dams in temperate

*Correspondence to: Elizabeth Anderson, Department of Environmental Studies, ECS 347, Florida International University, Miami, FL 33199, USA. E-mail: elizabeth.anderson@fiu.edu

regions have been developed and much of the world's remaining hydropower potential is found in tropical countries (McCully, 2001). The ecological integrity of tropical freshwater ecosystems may therefore be a casualty of increasing hydropower development, as dams transform previously intact tropical rivers into fragmented systems.

There is little known about the ecological consequences of dams in the tropics compared with dams on temperate river systems (Collier *et al*., 1996; March *et al*., 2003; Pringle *et al*., 2000; WCD, 2000; Greathouse *et al*., 2006). This is partly based on the fact that tropical rivers have been substantially less altered by dams than highly dammed temperate systems. In addition, the necessary financial, logistical and scientific resources are often not readily available for applied ecological research in the tropics (Vaux and Goldman, 1990). Whereas broad-scale studies have quantified the extensive fragmentation of temperate landscapes by dams (Benke, 1990; Dynesius and Nilsson, 1994; Graf, 1999), similar comprehensive assessments are rare or non-existent in most tropical regions. Only recently has information about the degree of alteration of large tropical river systems by dams begun to be synthesized (Fearnside, 1995; Pringle *et al*., 2000; Nilsson *et al*., 2005). To date, most research on tropical dams has focused on large, individual dam projects, although a considerable proportion of the hydropower potential in the tropics is being exploited by small projects with a different suite of environmental impacts than large dams (Vaux and Goldman, 1990; Majot, 1997; Benstead *et al*., 1999).

Since the early 1980s, rivers in tropical Central America have been increasingly subject to hydropower development. This is especially true in Costa Rica, where hydropower is the most important source of electricity for the country's 4 million residents. New dams are viewed as a primary means for meeting demands for electricity, which is estimated to be growing by more than 5% annually (ICE, 2004; CEPAL, 2005). To this end, more than 30 new dams were built during the 1990s and at least double that number have been proposed (Braga *et al*., 2000; ICE, 2004). As the number of dams rises, free-flowing tropical rivers are quickly vanishing from Costa Rica's landscape.

This paper has two main objectives: to discuss recent hydropower development in Costa Rica and to identify conservation strategies for Costa Rican rivers in light of this development. It is our hope that a better understanding of hydropower development trends and implications for tropical freshwater ecosystems will lead to more informed decisions about location, size and operational characteristics of future dams. Information on hydropower dams in Costa Rica and other parts of Central America, especially proposed projects, is difficult to find. The material presented here was gathered from primary literature, electricity sector planning and summary documents, and interviews. Although the main focus is on Costa Rica, when applicable we broaden the scope of our arguments by providing information on hydropower development across the Central American region.

CONTEXT OF HYDROPOWER DEVELOPMENT

Topography and climate have created a considerable hydroelectric potential for Costa Rica and other Central American countries. The longitudinal orientation of mountain chains down parts of the isthmus, coupled with large amounts of precipitation (> 5 m annually in some areas), has resulted in hundreds of short, high-gradient streams. Hydropower plants can take advantage of abrupt changes in elevation in mountainous areas and precipitation-driven discharges to generate electricity. At present, the vast majority of Central America's hydropower potential remains untapped. Costa Rica provides an example: current installed capacity of hydropower dams (at approximately 1300 megawatts (MW)) is well below the country's theoretical hydroelectric potential, estimated at 25 500 MW (CFIA, 2005), and practical hydropower potential, estimated at 10 000 MW (FAO, 2005). In contrast to temperate regions, where multiple large dams often traverse the mainstems of principal rivers (e.g. Colorado, Mississippi, and

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Columbia-Snake Rivers in the USA), several large tropical rivers in Central America are still free-flowing, such as the San Juan River, which forms the border between Costa Rica and Nicaragua.

At a regional level, hydropower generates approximately 50% of electricity in Central America (EIA, 2004). This trend is largely driven by Costa Rica, where hydropower plants represent just under 70% of installed generation capacity and account for >80% of electricity produced (EIA, 2004; CEPAL, 2005; Table 1; Figure 1). Dams in Central America did not become widespread until the 1980s, much later than the era of large dam development in temperate regions of North America (e.g. the USA and Canada, north of 30°), which began in the 1930s and peaked in the 1960s (WCD, 2000). According to Gleick (2002), Central America has at least 37 large dams, with one-half of these projects located in Costa Rica and Honduras. The list of large dams in the region includes El Cajon (Honduras), Chixoy (Guatemala), Bayano (Panama), Cerron Grande (El Salvador), Arenal (Costa Rica) and Angostura (Costa Rica), among others. The Central American landscape is also marked with an unknown but larger number of small and medium-sized dams.

Construction of dams in Central America is expected to escalate in the next two decades in response to expanding human populations, increased rural electrification, and growing demands for electricity (Scatena, 2004). As of 2006, many new dams are either being studied or under construction throughout the region, by both private and public companies. A compilation of proposed hydropower projects in Central America prepared by the Conservation Strategy Fund, which documents projects in various stages from

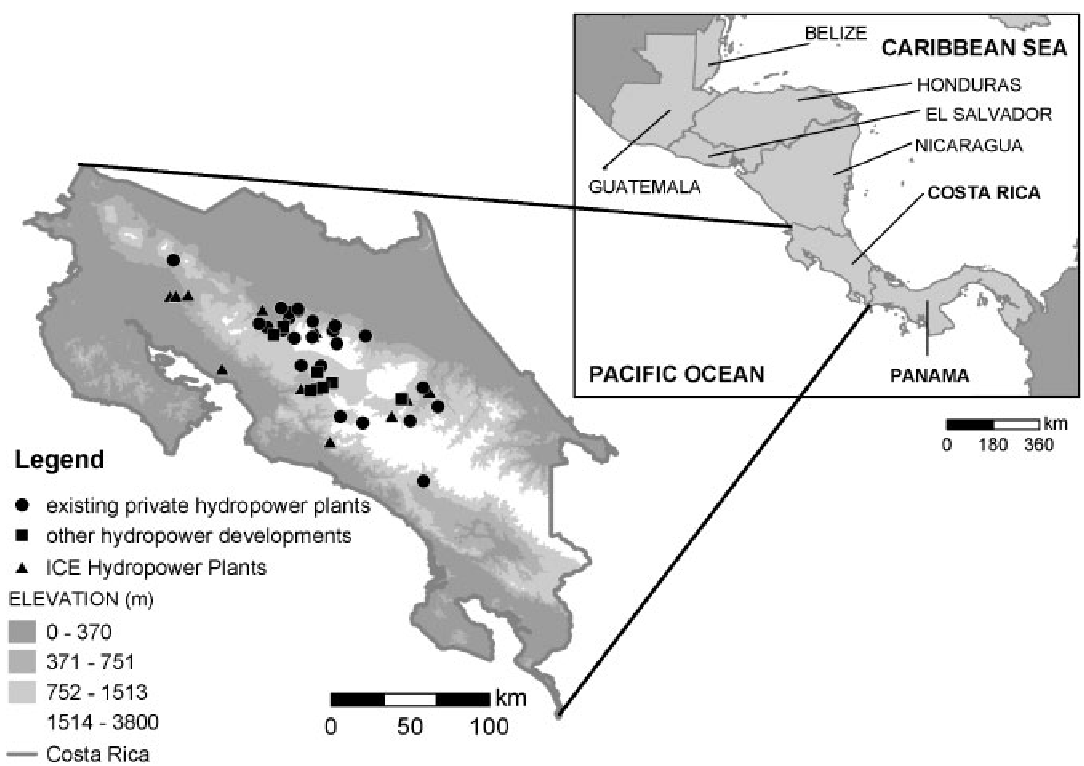

Figure 1. Costa Rica is the regional leader in Central America in hydropower development. In the past few decades, large and small dams have altered rivers throughout the country. This map indicates the location of existing hydropower developments that are owned by the Costa Rican Institute of Electricity (ICE), its subsidiaries (marked as other hydropower developments on the map), and private companies. Most dams are concentrated on gradient breaks in mountainous areas of the country. Source of information: Ortiz-Malavasi (2004).

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Table 1. Demographic and electricity sector statistics for Central American countries, as of 2004 (2003 for Belize). Sources: Information Please Almanac (2005) for demographic information; CEPAL (2005) for electricity sector information; Government of Belize (2002), Central Statistical Office of Belize (2004) and Launchpad Consulting (2003) for Belize's electricity sector information

	Region	Belize	Costa Rica	El Salvador	Guatemala	Honduras	Nicaragua	Panama
Estimated size (km^2)	523 780	22 966	51 100	21 040	108 890	112 090	129 494	78 200
Population (millions)	41.28	0.280	4.1	6.7	14.7	7.0	5.5	3.0
Electrification index (% of pop.)	78.9 (average)	87.4	97.9	81.4	83.0	65.9	52.1	84.8
Increasing demand (%); year 2003–04	5.6	9	4.7	3.1	6.0	7.5	5.4	4.8
Total installed capacity (MW)	8 924.2	~54	1 961.2	1 197.9	1 999.1	1 386.9	742.2	1 582.9
Hydropower	3 822.3	25	1 303.6	442.0	639.7	474.9	104.4	832.7
(%) hydro	42.8	46	66.4	36.9	32.0	34.2	14.1	52.6
Net generation (GWh)	33 333.8	361	7 968.4	4 689.1	6 999.0	4 907.9	2 647.4	5 761.0
Hydropower	16 152.2	90	6 497.1	1 433.4	2 655.9	1 401.3	311.4	3 763.1
(%) hydro	48.6	25	81.5	30.6	37.9	28.6	11.8	65.3

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'investment opportunity' to feasibility, counts approximately 400 potential new hydropower projects for the region that amount to ~16 000 MW of installed capacity (Burgues Arrea, 2005).

In Costa Rica, the Costa Rican Institute of Electricity (ICE) has plans to almost double the country's installed hydropower generation capacity by 2016 through nine new projects, seven of which are scheduled to begin operation by 2010 (ICE, 2005). The Boruca-Veraguas hydropower project in the Grande de Terraba River basin is the largest proposed project with a potential installed capacity of 622 MW. If constructed as planned, the Boruca-Veraguas project would become the largest dam in Central America (ICE, 2005). Several small dams are also being proposed by private companies and rural cooperatives (Braga *et al*., 2000), including the Pocosol Dam on the Peñas Blancas River, located in northern Costa Rica near the famed Monteverde Cloud Forest Reserve.

Expansion plans for the electricity sector in other Central American countries reflect a similar trend with respect to new hydropower development. In Belize, construction of the Chalillo Dam was recently completed following several years of debate between the dam's proponents and environmentalists. The private Chalillo Dam has an installed capacity of less than 10 MW, but flooded the country's Macal River Valley, a rainforest environment of high biological diversity. In El Salvador, new projects are being proposed for the already dammed Lempa River watershed, the largest basin draining the Pacific slope of Central America. In Guatemala, it has been estimated that an additional 900 MW of generation capacity will be needed to meet domestic electricity demands in 2010; the government hopes that a substantial part of this electricity will be supplied by several new hydropower projects (Taylor, 2005). The governments of Honduras and Nicaragua are encouraging private investment in renewable electricity sources, especially small hydropower plants. In Nicaragua, recently proposed legislation that provides incentives for private companies could result in construction of small hydropower dams throughout the country (Jochem, 2005).

Electricity privatization and hydropower

Recent hydropower development in Central America has been influenced by electricity privatization, a trend that has been affecting developing countries worldwide, especially during the 1990s (ECLAC, 1996; Izaguirre, 2000; Raphals, 2001; EIA, 2004). Until the 1990s, government-owned utilities were primarily responsible for the construction and operation of power plants in Central America. Financing of these facilities usually involved large loans from multilateral lending institutions (Vaux and Goldman, 1990). However, legislation passed in all seven Central American countries during the past 15 years has partially or totally privatized electricity generation (ECLAC, 1996; EIA, 2004). These reforms were designed to decrease pressures on governments to meet rising electricity demands and to attract foreign capital (ECLAC, 1996).

In Costa Rica, the participation of the private sector in power production has been directly linked to increased hydropower development, and has favoured the construction of small dams. Since its creation in 1948, the government-owned Costa Rican Institute of Electricity (ICE) has been primarily responsible for the country's electricity generation. The passage of a law in 1990 partially opened Costa Rica's electricity sector by granting private companies the right to generate electricity. This law was designed to decrease pressures on ICE to meet rising electricity demands and encourage investment in renewable energy projects, such as hydropower plants (Braga *et al*., 2000). The law limited the size of private power plants to 20 MW and restricted the collective contribution of private companies to 15% of the country's installed capacity to produce electricity. A subsequent reform passed in 1995 increased this percentage by 15% and expanded the allowable size of private power plants to 50 MW (Braga *et al*., 2000). Effects of these laws are visible today on rivers throughout Costa Rica: between 1990 and 2000, nearly 30 private hydropower plants began operation and as many private hydropower projects were proposed or are currently under study (Alvarez, 2005; Duran, 2005; Figure 1). In 2004, private generators provided ~10% of Costa Rica's electricity, and

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much of private hydropower development had been concentrated on the San Carlos and Sarapiquí watersheds in north-eastern Costa Rica.

In other parts of Central America, electricity privatization has thus far favoured thermoelectric generation over hydropower in terms of added installed generation capacity (CEPAL, 2005; Taylor, 2005). Thermoelectric projects may be more appealing to international companies than hydropower since they require a lower upfront investment, have shorter lifetimes and are therefore less risky from an economic standpoint. However, the upwards trend in the international price of oil and its derivatives, evidenced during 2005, has raised the cost of electricity produced with thermal power plants. With little to no oil reserves and low per capita income, it is uncertain how much Central America will be able to depend on thermoelectric generation over the long term and what impact this will have on new dam development. Considering that most of the region's hydropower potential is untapped and new legislation is now in place, the opportunity exists for private companies to build dams. In fact, several new private dams have been constructed in other Central American countries as a result of electricity privatization. For example, the Pasabien and Rio Hondo II hydropower projects were recently constructed by Hydrowest International in the Zacapa region of Guatemala (Stone and Manrique, 2002). In Panama, AES Corporation recently developed the Esti hydroelectric facility and upgraded the existing Bayano power plant.

BENEFITS OF HYDROPOWER FOR COSTA RICA

With Costa Rica's wealth of freshwater resources, hydropower provides a reliable source of domestically produced electricity that imparts several benefits. An estimated 98% of Costa Rica's residents have access to electricity, > 80% of which is generated by hydropower (CEPAL, 2005). In rural areas, construction of hydropower plants has facilitated the improvement of roads. Some dams in Costa Rica also function as multi-purpose facilities. For example, the reservoir for the Arenal Dam in north-western Costa Rica is a popular destination for national and international tourists, and after being used to generate electricity, water from the reservoir is used for irrigation of croplands. From an environmental standpoint, Costa Rica's dependence on hydropower generation (over thermoelectric generation) translates into a decrease in the burning of fossil fuels for electricity generation, reducing potential emissions of gases and particulates into the atmosphere. In 2004, for example, hydropower produced in Costa Rica avoided the emission of 6.4 billion tons of CO_2 equivalent into the atmosphere and reduced oil imports by 5 million barrels (CEPAL, 2005). An advantage of hydropower over wind and solar generation plants is that hydropower plants are frequently constructed with water storage capacity, and can thus store energy to produce electricity when it is most needed. In Costa Rica, many small, private hydropower plants play an instrumental role in providing electricity during peak hours of demand by operating with off-channel reservoirs (Alvarado, 2005).

Forest protection in catchments upstream from dams has emerged as an indirect beneficiary of hydropower development in Costa Rica. Several hydropower companies, including Global Energy of Costa Rica and Hidroeléctrica Platanar, which operate plants in the Sarapiquí and San Carlos catchments, have engaged in voluntary payment for environmental services (PES) programmes through the Costa Rican government's National Forestry Fund (FONAFIFO). Payments made by these hydropower producers to FONAFIFO have been used to provide economic incentives to landowners for forest protection in upstream catchments (Rojas and Aylward, 2003). Similarly, the La Esperanza Hydropower Project in north-western Costa Rica established a private PES contract with the Monteverde Conservation League, a non-profit organization which owns the land in the catchment upstream from the project (Rojas and Aylward, 2002). These PES agreements involving hydropower producers are based on the assumption that natural forest provides the environmental services of capturing and retaining water, and preventing excessive soil erosion in areas with steep slopes. There is still much uncertainty in these assumptions,

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however, as the links between land use and hydrology in Costa Rica have not been thoroughly investigated by quantitative research. Nevertheless, for a hydropower producer, investing in a PES scheme to maintain natural forest cover is still a good way to reduce the risk of changes in hydrology or sediment load that could result from human modifications to the landscape and reduce a hydropower plant's generation capacity (Rojas and Aylward, 2002).

ECOLOGICAL CONSEQUENCES OF HYDROPOWER DEVELOPMENT IN COSTA RICA

Hydropower dams in Costa Rica vary in terms of size, type or mode of operation, and location, and their ecological consequences usually relate to these characteristics. To examine the effects of dams on Costa Rican streams, it is useful to distinguish between two general kinds of common hydropower dams: large, storage dams and small, run-of-river plants. Large, storage dams can be defined as having a height of $\geqslant 15$ m; dams with spillway heights between 5 and 15 m can also be classified as large if they have a reservoir capacity of 3×10^3 m^3 or more (ICOLD, 1998; WCD, 2000). Small, run-of-river dams use the river's natural flow to generate electricity, or operate as water diversion projects that divert water from the main channel. Operational characteristics of many small, run-of-river dams in Costa Rica can be generally described as follows. Water is: diverted from the river at the dam site into an artificial canal, tunnel or pipeline; transported to an off-channel reservoir; stored until hours of peak electricity demand; sent via pipeline to a powerhouse; used to generate electricity; and then discharged into the river downstream. The magnitude of dam-related impacts in Costa Rica, for both large and small dams, is generally expected to be greater on the main stem of large rivers located <900 m above sea level, where most freshwater biodiversity is found (W. Bussing, Universidad de Costa Rica, pers. comm.).

Large dams in Costa Rica can alter the abundance and distribution of aquatic biota by blocking movement between upstream and downstream reaches. Isolation of upstream ecosystems by dams and the resulting lack of genetic exchange between populations in river fragments can imperil the viability of tropical freshwater biota, especially fish (Pringle *et al*., 2000). Migratory fauna that inhabit Costa Rican rivers may be particularly affected by the barriers presented by large dams. Of the 135 species of fish reported for Costa Rica, many are known or suspected to be diadromous (i.e. require a migration between fresh and salt water) or potomadromous (i.e. migrate long distances within fresh water) (Bussing, 1998). This list includes species such as *Joturus pichardi*, *Agonostomus monticola*, *Brycon guatemalensis* and *Sicydium altum*, which inhabit main-stem rivers where large dams are often located. For example, *J. pichardi* (Mugilidae) is thought to be a catadromous species (i.e. migrates to breed in salt water but does most feeding and growth in fresh water) that lives in cool, rapid waters of main-stem rivers (Cruz, 1987; Bussing, 1998). As one of the larger freshwater fish in Costa Rica, it is prized for sport fishing and valued as a food resource for local human populations in rural areas. The distribution and abundance of this species in Costa Rica is being altered by large dams: anecdotal evidence from the Reventazon River upstream of the large Angostura Dam (completed in 2002) suggests that *J. pichardi* may still be present in this area but only as small numbers of very large individuals (W. McLearney, pers. comm.). In addition to fish, migratory freshwater shrimps in the genus *Macrobrachium* are also an important component of Costa Rica's freshwater ecosystems (Pringle and Hamazaki, 1998; Pringle and Ramirez, 1998; Rosemond *et al*., 1998) that are probably adversely affected by large dams. Studies from Puerto Rico have shown that migratory shrimps have been extirpated above large dams without spillway discharge (Holmquist *et al*., 1998; Greathouse *et al*., 2006); this is likely to be the case for Costa Rica as well. Loss of migratory fish and shrimps from river reaches upstream from large dams in Costa Rica could substantially affect community structure and biotic interactions, as well as ecosystem functional processes such as organic matter decomposition in which these animals play an important role.

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The reservoirs of large, storage dams in Costa Rica often flood extensive terrestrial areas and river reaches upstream from dams. The Arenal Dam provides a case in point: its reservoir covers an area of approximately 88 km^2, with an estimated water volume of $2.416 \times 10^9 \, m^3$ (see ICE's website: www.grupoice.co.cr). Creation of the Arenal reservoir flooded a town and transformed at least four rivers (Arenal, Aguas Gatas, Chiquito and Caño Negro) into lentic systems. Many of the ecological consequences of large, storage dams such as Arenal for aquatic biota may be reservoir-mediated and stem from the dramatic conversion of riverine systems to lentic habitats. Because there are relatively few lakes in Costa Rica, many native freshwater species may not be well-adapted to lentic systems; reservoirs also present an additional impediment to the migration of catadromous and potomadromous fauna. Furthermore, water releases from reservoirs of large dams have been shown to have negative impacts on downstream aquatic ecosystems in Costa Rica. For example, releases of sediment-laden water from the Peñas Blancas Dam (an ICE hydropower plant) in October 2003 were linked to a massive fish mortality event on the Peñas Blancas and San Carlos rivers (*La Nación*, 14 November 2003).

Small, run-of-river hydropower plants have become substantially more numerous in the Costa Rican landscape than large, storage dams, mostly as a result of the legal framework that opened participation in power generation to private companies in the 1990s. While large dams usually have more complex, permanent, or wide-ranging environmental effects than small dams, the impacts of small dams may be greater when considered on a 'per unit electricity generated basis' (e.g. kilometres of fragmented river per MW electricity produced; Gleick, 1992). Moreover, the collective impact of multiple small dams may be greater than that of a single large dam.

Similar to large dams, small dams fragment streams and hinder longitudinal movement of aquatic biota. Previous studies from Caribbean streams have indicated that even small, low-head dams interfere with upstream migration of tropical biota, and that water withdrawals associated with these dams can cause significant mortality of downstream migrating shrimp (Benstead *et al*., 1999; March *et al*., 2003). Results from a study during 2001–02 at a small dam on the upper Puerto Viejo River in north-eastern Costa Rica also suggest that small, run-of-river dams affect the persistence of diadromous and potomadromous fauna. During this study, no individuals of *J. pichardi* or *B. guatemalensis* (a species suspected to be potomadromous) were captured or observed near the dam; however, local people reported that both species of fish had been abundant in previous years in the upper Puerto Viejo River (Anderson *et al*., 2006). The increasing rarity of these species, especially *J. pichardi*, is attributed to a combination of factors including overfishing and the presence of the dam. Furthermore, no shrimp were captured or observed upstream of the dam, but $\sim$90 individuals (*Macrobrachium* sp.) were captured in a single day from nearby downstream areas (E. Anderson, unpublished data).

While small, run-of-river dams in Costa Rica located on low-order, high-gradient streams probably do not significantly affect peak flows, their presence may alter ecosystem processes such as downstream transport of sediment and organic matter and nutrient cycling, based on what we know from other studies of dams and the ecology of headwater streams (Ward and Stanford, 1983; Waters, 1995; Meyer and Wallace, 2001; Peterson *et al*., 2001). For example, at the aforementioned dam on the Puerto Viejo River, we observed that after 5 years of operation, the dam had trapped a substantial amount of sediment, especially coarse materials such as cobbles and boulders. These increases in upstream sediment deposition were accompanied by an increase in the amount of exposed bedrock immediately downstream from the dam (E. Anderson, pers. obs., 1999 and 2004). Various other small, run-of-river projects built during the 1990s have similarly accumulated substantial amounts of sediments (M. Rojas, pers. obs.). Downstream transport of organic matter is also affected by dams: many projects have a special apparatus for trapping and removing suspended organic matter (e.g. leaves, woody debris) as water is being diverted at the dam (E. Anderson, pers. obs.). Depending on how the organic matter is treated after it is removed (e.g. whether or not it is returned to the channel downstream), shelter and food resource availability for aquatic biota downstream could be negatively altered.

Stream de-watering is one of the more serious ecological consequences of small, run-of-river dams that stems from their operations. In Costa Rica, operation of most run-of-river hydropower plants results in substantial flow reductions (in the order of 90–95% of average annual flow) between the diversion site and the powerhouse. This segment of stream is often referred to as the de-watered reach and can be several kilometres long. The physical environment of a de-watered reach is dissimilar to that of upstream and downstream areas, and characterized by slower water velocities and shallower depths in riffles and pools (Anderson *et al.*, 2006). These physical changes decrease the quality and quantity of habitat for native aquatic biota in the de-watered reach, creating conditions akin to those of a prolonged drought. Studies on other neotropical streams have shown that drought-like conditions cause crowding of aquatic biota into reduced areas and decreased resource availability (Covich *et al.*, 2003). Furthermore, de-watering may favour more opportunistic-type (see Winemiller, 1995), colonizing fish species (e.g. *Poecilia gillii*) that can adapt to altered flow and habitat over equilibrium-type species (e.g. cichlids) whose reproductive success depends on certain hydrological conditions (Coleman, 1999; Anderson *et al.*, 2006). Stream de-watering may also affect the subterranean water flows characteristic of volcanic regions of Costa Rica; alteration of recharge patterns in de-watered reaches at high or middle elevations could alter delivery of water to springs at lower elevations (Pringle and Triska, 2000).

Hydrological alterations downstream from power plants are an additional serious ecological consequence of small, run-of-river dams. Small hydropower plants in Costa Rica frequently operate on peaking power regimes, only generating electricity at full capacity during hours of peak demand. In Costa Rica, these hours occur between 10:00 and 12:30 and between 17:30 and 20:00 on weekdays. Peaking power generation causes significant fluctuations in flow and water temperature downstream from hydropower plants. For example, on the Puerto Viejo River, peak periods of electricity generation at the hydropower plant are linked to changes in river stage height of 35 cm or more downstream from the powerhouse; these changes occur over time intervals of 15 minutes or less. Increases in stage height during peak generation result in subsequent decreases in temperature of 3–4°C (Anderson *et al.*, 2006). Where in other systems reduced hydrological variability has been cited as a negative ecological consequence of dams, in this case the increased hydrological variability and frequency of physical disturbance (e.g. changes multiple times daily) downstream from peaking power dams can create an environment inhospitable to many species of fish and other aquatic biota. In Costa Rica, although no published studies have examined the ways that peak flows downstream from hydropower plants might affect aquatic biota, it is likely that unnatural fluctuations in flow and water temperature compromise the long-term persistence of species such as cichlids which benefit from periods of stable flow during reproduction and parental care of juveniles (Coleman, 1999; R. Coleman, pers. comm.). More research is needed downstream from hydropower plants in Costa Rica to examine this hypothesis.

Consideration of the cumulative effects of multiple hydropower plants on a river basin is equally important to the assessment of the ecological impacts of individual dams. Chains of dams in a catchment divide a river network up into many fragments, and the simultaneous operation of several dams on peaking power regimes results in an uneven hydrograph in downstream areas. In Costa Rica, much of recent hydropower development has been concentrated in the San Carlos and Sarapiquí River catchments, sub-basins of the San Juan River catchment which drain the country's northern Atlantic slope. In the San Carlos catchment, 16 private and three public hydropower plants were in operation from 2005 and an additional eight hydropower projects were under study. In the Sarapiquí catchment, eight hydropower plants were constructed between 1990 and 1999; six of these belong to private companies and two were built by the ICE (Toro I and Toro II). From 2005, two additional projects, the General and Cariblanco Hydropower Projects, were under construction in the Sarapiquí. These projects are expected to begin operation in 2006–07 (ICE, 2004). To date, very little effort has been made to examine the cumulative effects of multiple hydropower plants on either the San Carlos or the Sarapiquí catchment. Our own attempt to quantify fragmentation and losses in riverine connectivity resulting from existing hydropower

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development (not including Cariblanco and General projects) in the Sarapiquí River network concluded that dams had substantially reduced flows in more than 30 km of stream, corresponding to roughly 1% of the stream network. In addition, more than 300 km of stream, corresponding roughly to 10% of the network, are now located upstream from dams and discontinuous with downstream areas. Thus, dams have caused extensive fragmentation of the Sarapiquí network, and isolated ecosystems above dams in many headwater and low-order streams.

This discussion of the ecological effects of hydropower development in Costa Rica merits consideration of some of the trade-offs of three possible dam-building scenarios: (1) construction of one small dam on multiple rivers; (2) construction of multiple small dams on a few individual rivers; and (3) construction of single large dams on main-stem rivers. For example, with respect to the persistence of native aquatic biota, especially fish, multiple small dams on tributary streams at elevations above 900 m a.s.l. in Costa Rica might be a better development alternative to the construction of a large dam on a main-stem river at a lower elevation where fish diversity is higher. Large or small hydropower developments on tributary streams, rather than single large dams on main-stem rivers, could help maintain some degree of connectivity between freshwater and coastal systems. Concentration of multiple small dams on an individual tributary stream would help to ensure that not all important connections between headwaters and downstream areas were disrupted by hydropower development. While it is difficult to identify an ideal hydropower development scenario, these considerations suggest that from an ecological standpoint the placement of hydropower plants in a river network, and relative to one another, may be more important than the size or total number of dams.

RECOMMENDATIONS

This paper has provided a review of recent hydropower trends in Costa Rica and highlighted some of the ecological consequences of dams on neotropical rivers. Over the past two decades, dams have become a pervasive feature of the Costa Rican landscape. As the country strives to develop its economy, it is inevitable that new dams will continue to be built in the near future, altering tropical rivers in the process. In light of recent and ongoing hydropower development, we present four specific recommendations to minimize the impact of dams and protect the wellbeing of freshwater ecosystems in Costa Rica. These strategies may be applicable in other parts of Central America where hydropower development is also occurring.

Safeguard some rivers from hydropower development

In the early 1970s Costa Rica made a historic decision to set aside a significant portion of its forests for conservation. Today the country is reaping the economic benefits of that investment, as approximately 1.5 million foreign tourists per year visit Costa Rica, largely attracted by the system of protected areas. The tourism industry has become the main source of foreign currency in the country (Programa Estado de la Nación, 2005). It is time for Costa Rica to make a similar conservation choice with regards to its aquatic ecosystems, by safeguarding some rivers from hydropower development.

Development of a designation system for rivers that is similar to the USA's concept of Wild and Scenic Rivers could be a means for ensuring the persistence of free-flowing rivers in a landscape that is being altered rapidly by hydropower dams and other water projects. Given that all water resources in Costa Rica are publicly owned, the government is entitled to impose a set of restrictions for development projects in river ecosystems. A set of such restrictions already exists, such as the prohibition of riparian forest clearing. Similarly, a set of restrictions could also be incorporated into land-use planning to minimize detrimental land-use practices in a river's watershed.

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A series of 'protection' categories could be developed for rivers as already exist for terrestrial protected areas. The first step in this process might be to set priorities for individual rivers in terms of their biological and socio-economic value. Those rivers with high biological diversity and low economic value should be designated as rivers of national importance and not eligible for development projects. Rivers that have significant sections already within protected areas and therefore off limits to development could serve as a starting point, by imposing restrictions on the sections outside the protected areas.

Rivers of both biological and socio-economic importance could fall into a different category, with some uses permissible and others restricted. The Pacuare River in eastern Costa Rica provides a good example: known for its scenic beauty and encanyoned rapids, the Pacuare draws thousands of national and international tourists annually for river-related tourism (rafting). It is also one of the few remaining large rivers of biological importance on the Atlantic slope that is still well-preserved. A large hydropower project on the Pacuare River, which fuelled the debate over hydropower development in Costa Rica for more than a decade, was recently shelved by ICE on the grounds that it was against national interest. Designation of the Pacuare as a river of national importance, where whitewater rafting is allowed but infrastructure projects such as dams are prohibited, would help protect this natural resource and the local economies of surrounding communities that depend on its free-flowing state.

Should rivers that already have dams automatically be excluded from possible designation as rivers of national importance? This question must be considered, as several rivers of high biological, cultural and socio-economic value have dams in operation or currently under construction. The Sarapiquí River provides a good example here: the river drains one of the country's most biodiverse regions and harbours nearly one-third of freshwater fish species found in Costa Rica (Bussing, 1993, 1998). However, multiple dams are in operation or under construction in its catchment, including one small dam on the headwaters and the Cariblanco hydropower project on the mid-reaches of the main-stem Sarapiquí River. In response to hydropower development, local communities have expressed interest in declaring the Sarapiqui River a 'natural, historic monument' as a means for halting further dam construction (Aguilar, 2001). Perhaps in the case of the Sarapiquí and other already-dammed rivers, a certain segment downstream from existing dams could be eligible for protected status while the upper reaches could still be used for hydropower production.

Assess cumulative impacts of multiple projects in a river basin

Under the present system of environmental impact assessment (EIA) in Costa Rica, hydropower projects are mainly evaluated on an individual basis prior to construction. To our knowledge, there are few published studies on the environmental impacts of dams in Costa Rica during their operational phases. Furthermore, little to no consideration is given to the potential additive or interactive ecological effects that occur when more than one hydropower plant is built in a river basin. This is a problem for the San Carlos and Sarapiquí basins; there is still much uncertainty about the actual ecological impacts of existing dams and how these impacts multiply or interact in these systems.

Cumulative effects assessment (CEA) in tropical countries such as Costa Rica is hindered by the paucity of baseline data (e.g. biological, hydrological, water quality) needed for a meaningful assessment. With respect to freshwater biota, there is a need in Costa Rica for rapid species inventories, particularly of fish and shrimps, conducted at basin levels or similar broad scales appropriate for CEA. These inventories could be completed relatively easily through visual assessments or simple capture surveys; collection of historical and anecdotal information through interviews with riparian residents and fishermen could complement and enrich the biological data. In addition, follow-up studies (post-audits) of existing individual hydropower plants would help create information that could be used in initial CEAs. Furthermore, in the absence of comprehensive data sets, methods that use available information can be a first step towards beginning to think about basin-level effects of multiple dams. For example, Geographic

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Information Systems (GIS) data are now available for most river basins in Costa Rica; this information can be used to quantify lengths of de-watered reaches and isolated stream reaches upstream from dams in a river network. While this type of analysis would not be a substitute for a comprehensive CEA, it represents an initial attempt to consider river network-level fragmentation by dams, and could be used to facilitate better planning of future dams to minimize further losses in riverine connectivity.

Provide incentives to promote research on the ecological consequences of dams and on sustainable hydropower technologies

A major constraint for designing hydropower projects in Costa Rica, with lower ecological impacts, is the lack of basic scientific data. Many dam companies in Costa Rica have voluntarily participated in environmental conservation and research activities (see Rojas and Aylward, 2002; Anderson *et al.*, 2006). Similarly, several private hydropower plants are in the process of being certified under ISO 14001. However, these conservation efforts and the certification process have little to do with minimizing the environmental impact of dams or restoring ecological functions of aquatic ecosystems. This is not necessarily a result of a lack of interest in such activities by dam developers, but instead may be due to a lack of information on how to improve current practices. For example, if a hydropower company wants to design a dam operation regime less harmful to downstream ecosystems, it would first have to know the ecosystem's requirements in terms of water quantity and quality, and how these requirements change seasonally. Such information is scarce (only a few rivers in Costa Rica have gauges) and not readily available in terms that can be easily incorporated into dam design by engineers.

Incentives for research on aquatic ecosystems are critically important, as are incentives for research on new technologies such as low- and no-head hydropower. Several research institutions in Costa Rica and abroad could become involved in related projects, and government funding, as well as resources from international donors, could be focused towards such research. These incentives could also aid in facilitating increased opportunities for collaboration between hydropower developers, conservationists and scientists.

Develop methods for estimating environmental flows for Costa Rican streams and create legislation to protect environmental flows

There is a lack of regionally based methodology for determining environmental flows in river reaches downstream from dams and other water withdrawals in Central America (Scatena, 2004). In Costa Rica, no formal methodology or legislation related to environmental flows exists at present, but general guidelines recommend that 10% of average annual discharge be left in river channels downstream from water withdrawals such as dams. More information is needed to determine the flow needs of aquatic biota and develop adequate environmental flow standards tailored to rivers in Costa Rica. Toward this end, international conservation organizations (e.g. IUCN, Organization for Tropical Studies) and the ICE have organized a series of workshops and activities to stimulate dialogue and identify research needs related to environmental flows. These workshops involve a variety of stakeholders including conservationists, the ICE, private hydropower developers, the government, scientists, and national and international universities. In addition, ecological research on the flow requirements of possible indicator species and initial determination of environmental flows for individual rivers has been commissioned as part of the effort (Jimenez *et al.*, 2005). These are positive steps towards more applicable conservation measures for mitigating the effects of stream de-watering downstream from hydropower developments.

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CONCLUSIONS

Conservation of Costa Rica's freshwater resources, amid rapid hydropower development, will depend on careful consideration of the benefits of new dams compared with their environmental costs. Costa Rica should examine all of its options for meeting future electricity needs. This not only includes feasibility studies and environmental assessments of the different types of power generation centres, including large and small dam projects, and wind, solar and biomass projects, but also could include application of demand-side management programmes to reduce unnecessary electricity consumption. There may be room for necessary, well-planned hydropower development in Costa Rica as a means for meeting future needs. Carefully designed conservation strategies and a catchment-centred approach to planning will be essential in guiding future decisions about dams.

What role should aquatic ecologists play with respect to hydropower development in Costa Rica and other parts of the tropics? As tropical rivers in Costa Rica and other parts of Central America are increasingly transformed by dams, aquatic ecologists can assist in guiding development in three major ways. First, they can work to fill in gaps in current knowledge through the collection of long-term and baseline data on hydrological conditions and biological communities. Second, they can develop applied scientific research programmes that address management issues related to dams. Finally, aquatic ecologists can provide support in efforts to develop conservation strategies and promote a more integrated approach to use and management of water resources for hydropower.

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REFERENCES

Aguilar A. 2001. El conflicto por el desarrollo hidroelectrico de la cuenca del Río Sarapiquí, Costa Rica. CEDARENA. San Jose, Costa Rica. http://www.cedarena.org/hidrico/docs/Sarapiqui.doc [December 2005].

Alvarado M. 2005. Generación eléctrica privada y concesiones de fuerza hidráulica. *Ambientico* **137**: 4–7.

Alvarez M. 2005. Privatización de la generación eléctrica: el asalto del siglo. *Ambientico* **137**: 8–10.

Anderson EP, Freeman MC, Pringle CM. 2006. Ecological consequences of hydropower development in Central America: impacts of small dams and water diversion on neotropical stream fish assemblages. *River Research and Applications* **22**: 397–411.

Benke AC. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthological Society* **9**: 77–88.

Benstead JP, March JG, Pringle CM, Scatena FN. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications* **9**: 656–668.

Braga MJI, Tiffer-Sotomayor R, Jaubert-Vincenzi MA. 2000. Análisis de impacto ambiental del sector energético de Costa Rica. Informe final para el Proyecto Facilidad de Recursos para la Energía Renovable (FRER), San Jose, Costa Rica.

Burgues Arrea I. 2005. Inventario de Proyectos de Infraestructura en Mesoamérica. Conservation Strategy Fund, Proyecto: Integración de la Infraestructura y la Conservación de la Biodiversidad en Mesoamérica. Special Publication of the Fondo de Alianzas para los Ecosistemas Críticos, The Nature Conservancy. http://www.conservation-strategy.org/projects/index.htm [27 June 2006].

Bussing WA. 1993. Fish communities and environmental characteristics of a tropical rain forest river in Costa Rica. *Revista de Biología Tropical* **41**: 791–809.
Bussing WA. 1998. *Peces de las Aguas Continentales de Costa Rica*. Editorial de la Universidad de Costa Rica: San Jose.
Central Statistical Office of Belize. 2004. *Environmental Statistics at a Glance*. Ministry of National Development: Belmopan, Belize.
CEPAL (Comisión Económica para América Latina y el Caribe). 2005. Istmo Centroaméricano: Estadísticas del Subsector Eléctrico. Special Publication of CEPAL, Mexico. http://www.cepal.org/publications [November 2005].
CFIA 2005. Panorama Nacional y Regional de la Industria Eléctrica. Colegio Federado de Ingenieros y Arquitectos de Costa Rica (CFIA). www.cfia.or.cr/informesespeciales.htm [December 2005].
Coleman R. 1999. Cichlid fishes of the Puerto Viejo River, Costa Rica. *Cichlid News* **8**: 6–12.
Collier MR, Webb RH, Schmidt JC. 1996. Dams and rivers: a primer on the downstream effects of dams. Circular 1126, U.S. Geological Survey, Menlo Park, CA.
Covich AP, Crowl TA, Scatena FN. 2003. Effects of extreme low flows on freshwater shrimps in a perennial stream. *Freshwater Biology* **48**: 1199–1206.
Cruz GA. 1987. Reproductive biology and feeding habitats of cuyamel, *Joturus pichardi*, and tepemechin, *Agonostomus monticola* (Pisces: Mugilidae) from Rio Platano, Mosquitia, Honduras. *Bulletin of Marine Science* **40**: 63–72.
Duran O. 2005. La estafa legal de la energía privada. *Ambientico* **137**: 11–14.
Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**: 753–762.
ECLAC (Economic Commission for Latin America and the Caribbean). 1996. Progress in the privatization of water-related public services: a country by country review for Mexico, Central America, and the Caribbean. ECLAC: Environment and Development Division. http://www.eclac.cl [June 2006].
EIA (Energy Information Administration). 2004. Regional Indicators: Central America. www.eia.doe.gov/emeu/cabs/centamenv.htm [May 2005].
EIA (Energy Information Administration). 2005. International Energy Outlook 2005. Energy Information Administration, Office of Integrated Analysis and Forecasting, U.S. Department of Energy: Washington, DC.
FAO (Food and Agriculture Organization). 2005. Dirección de Fomento de Tierras y Aguas. AQUASTAT, Costa Rica. http://www.fao.org/ag/agl/aglw/aquastat/countries/costa_rica/indexesp.stm [10 December 2005].
Fearnside PM. 1995. Hydroelectric dams in the Brazilian Amazon as sources of 'greenhouse' gases. *Environmental Conservation* **22**: 7–19.
Gleick P. 1992. Environmental consequences of hydroelectric development: the role of facility size and type. *Energy* **17**: 735–747.
Gleick P. 2002. *The World's Water*: *Biennial Report on Freshwater Resources 2002–2003*. Island Press: Washington, DC.
Goldemberg J (ed.). 2000. *World Energy Assessment*: *Energy and the Challenge of Sustainability*. United Nations Development Programme, United Nations Department of Economic and Social Affairs and World Energy Council: New York.
Government of Belize. 2002. Poverty Assessment Report. National Human Development Advisory Committee.
Graf WL. 1999. Dam nation: a geographic census of large American dams and their hydrologic impacts. *Water Resources Research* **35**: 1305–1311.
Greathouse EA, Pringle CM, Holmquist JG. 2006. Conservation and management of migratory fauna: dams in tropical streams in Puerto Rico. *Aquatic Conservation*: *Marine and Freshwater Systems* **16**: 695–712.
Holmquist JG, Schmidt-Gengenbach JM, Buchanan Yoshioka B. 1998. High dams and marine-freshwater linkages: effects of native and introduced fauna in the Caribbean. *Conservation Biology* **12**: 621–630.
ICE (Instituto Costarricense de Electricidad). 2004. *Plan de la Expansión de la Generación Eléctrica*. ICE: San Jose, Costa Rica.
ICE (Instituto Costarricense de Electricidad). 2005. *Solicitud de Aumento Tarifario ante ARESEP*. ICE: San Jose, Costa Rica.
ICOLD (International Commission on Large Dams). 1998. *World Register of Dams*. ICOLD: Paris.
Information Please Almanac. 2005. http://www.infoplease.com/almanacs.html [10 December 2005].
Izaguirre AK. 2000. Private participation in energy. Public policy for the private sector. Note no. 208, The World Bank Group: Washington, DC.
Jiménez JA, Calvo J, Pizarro F, Gonzalez E. 2005. Conceptualización de caudal ambiental en Costa Rica: determinación inicial para el Rio Tempisque. UICN-Mesoamerica, San Jose, Costa Rica.
Jochem F. 2005. El Mercado de Energías Renovables en Nicaragua. Programa MASRENACE. http://www.blueenergy.org/NewFiles/Downloads/nica_RE.pdf [10 December 2005].
La Nación, 14 November 2003. ICE acepta responsibilidad para la muerte de peces.

Launchpad Consulting. 2003. Energy for sustainable development: toward a national energy strategy for Belize — energy sector diagnostic. Prepared for formulation of a national energy plan (Sector Diagnostic and Policy Recommendations) Project. http://www.puc.bz/nep.ose [1 March 2006].

Majot J (ed.). 1997. *Beyond Big Dams*: *A New Approach to Energy Sector and Watershed Planning*. International Rivers Network: Berkeley, CA.

March JG, Benstead JP, Pringle CM, Scatena FN. 2003. Damming tropical island streams: problems, solutions and alternatives. *BioScience* **53**: 1069–1078.

McCully P. 2001. *Silenced Rivers*: *The Ecology and Politics of Large Dams*. Zed Books: London.

Meyer JL, Wallace JB. 2001. Lost linkages and lotic ecology: rediscovering small streams. In *Ecology*: *Achievement and Challenge*, Press MC, Huntly N, Levin S (eds). Blackwell Science: Oxford, UK; 295–317.

Nilsson C, Berggren K. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience* **50**: 783–792.

Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.

Ortiz-Malavasi E. 2004. Atlas Costa Rica. Instituto Tecnológico de Costa Rica, Cartago, Costa Rica.

Peterson BJ, Wollheim WM, Mulholland PJ, Webster JR, Meyer JL, Tank JL, Marti E, Bowden WB, Valett HM, Hershey AE *et al*. 2001. Stream processes alter the amount and form of nitrogen exported from small watersheds. *Science* **292**: 86–90.

Pringle CM, Hamazaki T. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology* **79**: 269–280.

Pringle CM, Ramirez A. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshwater Biology* **39**: 359–373.

Pringle CM, Triska FJ. 2000. Emergent biological patterns and surface–subsurface interactions at landscape scales. In *Streams and Ground Waters*, Jones JB, Mulholland PJ (eds). Academic Press: New York; 167–193.

Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical–temperate comparisons. *BioScience* **50**: 807–823.

Programa Estado de la Nacion en Desarrollo Humano Sostenible. 2005. Undecimo Informe Estado e la Nacion en Desarrollo Humano Sostenible. San Jose.

Raphals P. 2001. *Restructured Rivers*: *Hydropower in the Era of Competitive Markets*. International Rivers Network: Berkeley, CA.

Rojas M, Aylward B. 2002. Cooperation between a small private hydropower producer and a conservation NGO for forest protection: the case of La Esperanza, Costa Rica. Food and Agriculture Organization, Land-water Linkages in Rural Watersheds Case Study Series, FAO, Rome.

Rojas M, Aylward B. 2003. What are we learning from experiences with markets for environmental services in Costa Rica? Markets for Environmental Services no. 2, International Institute for Environment and Development, London.

Rosemond AD, Pringle CM, Ramirez A. 1998. Macroconsumer effects on detrital processing in a tropical stream food web. *Freshwater Biology* **39**: 515–524.

Scatena FN. 2004. A survey of methods for setting the minimum instream flow standards in the Caribbean basin. *River Research and Applications* **20**: 127–135.

Stone D, Manrique J. 2002. US collaboration promotes integrated social development in Guatemala. *Hydropower and Dams* 2002: 102–104.

Taylor MJ. 2005. Electrifying rural Guatemala: central policy and local reality. *Environment and Planning C* **23**: 173–189.

Vaux PD, Goldman CR. 1990. Dams and development in the tropics: the role of applied ecology. In *Race to Save the Tropics*, Goodland R (ed.). Island Press: Washington, DC; 101–122.

Waters TF. 1995. *Sediment in Streams*; *Sources*, *Biological Effects*, *and Control*. American Fisheries Society: Bethesda, MD.

Ward JV, Stanford JA. 1983. The serial discontinuity concept of lotic ecosystems. In *Dynamics of Lotic Ecosystems*, Fontaine TD, Bartell SM (eds). Ann Arbor Science: Ann Arbor, MI; 101–123.

WCD (World Commission on Dams). 2000. Dams and development: a framework for decision-making. www.damsreport.org [10 December 2005].

Winemiller KO. 1995. Aspects structurels et functionnels de la biodiversite des peuplements de poissons. *Bulletin Francais du Peche et Pisciculture* **339**: 23–45.

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