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Conservation and management of migratory fauna: dams in tropical streams of Puerto Rico

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ABSTRACT

1. Compared with most other tropical regions, Puerto Rico appears to have dammed its running waters decades earlier and to a greater degree. The island has more large dams per unit area than many countries in both tropical and temperate regions (e.g. three times that of the USA), and the peak rate of large dam construction occurred two or three decades before reported peak rates in Latin America, Asia and Africa.
2. Puerto Rico is a potential window into the future of freshwater migratory fauna in tropical regions, given the island's extent and magnitude of dam development and the available scientific information on ecology and management of the island's migratory fauna.
3. The paper reviews the ecology, management and conservation of migratory fauna in relation to dams in Puerto Rico. It includes a synthesis of recent and unpublished observations on upstream effects of large dams on migratory fauna and an analysis of patterns in free crest spillway discharge across Puerto Rican reservoirs.
4. Analyses suggest that large dams with rare spillway discharge cause near, not complete, extirpation of upstream populations of migratory fauna. They also suggest several management and conservation issues in need of further research and consideration, including research on the costs, benefits and effectiveness of simple fish and shrimp passage designs involving simulating spillway discharge. The appropriateness of establishing predatory fish in reservoirs of historically fishless drainages also needs to be considered.

KEY WORDS: amphidromy; catadromy; dams; diadromy; migratory fauna; tropical stream

INTRODUCTION

Running waters in the temperate zone are heavily fragmented by dams (Dynesius and Nilsson, 1994), and the substantial amount of research on ecological effects of temperate dams (e.g. Collier *et al.*, 2000; Rosenberg *et al.*, 2000; Hart and Poff, 2002) reflects scientific and public concern about the problems

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caused by this high level of fragmentation. In the tropics, the prevalence of river fragmentation by dams is yet to be determined because many tropical systems are still free-flowing but are proposed for extensive dam development in the future (Pringle *et al.*, 2000b). Moreover, present understanding of the effects of dams on tropical ecosystems is severely limited (Pringle *et al.*, 2000a; March *et al.*, 2003).

Declining populations of migratory species (i.e. diadromous fauna which require a migration between fresh and salt water, and potomadromous fauna which migrate over long distances within fresh water) represent an important ecological impact of dams (Dudgeon, 2000; Pringle *et al.*, 2000a). Migratory species are most well-studied in temperate streams and rivers where they are predominantly represented by anadromous fish (i.e. fish that migrate to fresh water to breed but do most of their feeding and growth in the ocean (Gross *et al.*, 1988; McDowall, 1992)). Dams affect anadromous fish through a variety of mechanisms, but the most conspicuous is the physical barrier to migration with consequent declines of anadromous species in large areas upstream (e.g. Frissell, 1993). In contrast to migratory fauna in temperate systems, migratory fauna in tropical streams and rivers are poorly studied and are dominated by fish, freshwater shrimps and snails with non-anadromous patterns of migration. Tropical migratory fauna are predominantly catadromous (i.e. migrate to the ocean to breed but do most feeding and growth in fresh water), freshwater amphidromous (i.e. migrate to saltwater at a non-breeding life stage but breed and do most feeding and growth in fresh water), or potomadromous (Gross *et al.*, 1988; McDowall, 1992; Barthem and Goulding, 1997). As in temperate rivers, migration of tropical aquatic fauna is also thwarted by dams, but little is known about the extents, mechanisms, and appropriate management of these impacts (e.g. Pringle *et al.*, 2000a).

This review focuses on stream conservation and management on the tropical island of Puerto Rico. Running waters in Puerto Rico are dominated by a set of migratory fauna which are similar to migratory shrimp, fish and snail species in many other regions of the tropics (Barthem and Goulding, 1997; Smith *et al.*, 2003; Moulton *et al.*, 2004). Furthermore, patterns of development and dam building suggest that the island can offer insights into the potential future of diadromous fauna in other parts of the tropics.

DEVELOPMENT AND DAM BUILDING IN PUERTO RICO: COMPARISONS WITH OTHER REGIONS

Puerto Rico's history of development more closely parallels that of the temperate zone than that of most other tropical regions, owing to the island's commonwealth status with the USA. As a consequence, the island has already undergone socio-economic and ecological changes that are only now occurring in other tropical regions. For example, Grau *et al.* (2003) documented Puerto Rico's unique history of land-cover change. Prior to World War II, deforestation dominated in Puerto Rico. However, the island's increasing industrialization since that time has led to socio-economic trends and ecological patterns that are similar to those in deforested agricultural regions of the temperate zone, which have seen rapid rates of rural to urban migration and dramatic recovery of forests on abandoned agricultural land (Grau *et al.*, 2003). Elsewhere in the tropics, current land-cover change is typically deforestation accompanied by increases in agriculture. Rural to urban migration, industrialization and globalization (with the potential to lead to widespread tropical forest recovery on abandoned agricultural land) are only now occurring in most developing countries. Thus, Puerto Rico's unique post-agriculture status provides a model for understanding potential future ecological effects of land-cover change associated with industrialization and globalization in other tropical regions (Grau *et al.*, 2003).

Development of water resources in Puerto Rico similarly offers potential insight into the future of conservation and management in the tropics. Over the last century, 25 large dams (height >15 m) have been built, and one is currently under construction (Table 1; Figure 1). A large but unknown number of small dams (height <15 m) were also built. Although there is not an island-wide compilation of numbers of small dams, this information does exist for drainages of the Caribbean National Forest (CNF) (Figure 1):

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33 small dams are located in an area of approximately 250 km^2 (Crook, 2005). Temporal patterns of large-dam development in Puerto Rico resemble patterns in temperate regions more closely than those in most other tropical regions. Construction of large dams in Puerto Rico peaked in the 1950s (nine dams completed; Table 1). Large-dam construction over the whole of North America, which was largely driven by construction in temperate regions of the continent, peaked in the 1960s, as did construction in Europe (World Commission on Dams, 2000). Construction on continents dominated by developing and tropical countries peaked in later decades: Asia (excluding China) in the 1970s, South America in the 1970s, and Africa in the 1980s (World Commission on Dams, 2000).

Puerto Rico has also had a very high level of damming compared with other regions (Figure 2). Over the last century, the number of large dams built per unit land area has outpaced, by an average of 2 to 1, that in the state of California (USA), which is well-known for its extensive hydrologic engineering (Figure 2(A)). Likewise, the peak decade for dam construction in California (1960s) was a decade later than it was in Puerto Rico. In contrast, the Dominican Republic, on the neighbouring tropical island of Hispaniola, has had a much slower rate of large-dam construction, which only started to take off in the 1970s (Figure 2(A)). If 30 proposed large dams are built in the Dominican Republic by 2015, the Dominican trajectory of large-dam construction will start to resemble the Puerto Rican trajectory shifted 50 years later (Figure 2(A)). The level of damming in Puerto Rico is also much higher than in three haphazardly selected temperate countries and 10 other haphazardly selected tropical countries (Figure 2(B)).

Although future tropical dam construction may be limited by social, economic and environmental concerns (McCully, 2001), increasing demand for electricity, water and flood control is leading to continued tropical dam construction (e.g. Sanchez-Sierra, 1993; Pringle *et al*., 2000a; Anderson-Olivas, 2004), especially given that most suitable sites for dams in temperate regions have already been developed. Puerto Rico is therefore a potential window into the future of tropical dams and their ecology (cf. Benstead *et al*., 1999; Pringle and Scatena, 1999). Running waters here were dammed earlier and to a greater degree than in most other tropical regions, and there is a substantial programme of research and management focusing on Puerto Rican migratory fauna in relation to dams and water withdrawals (e.g. Pringle, 1997; Holmquist *et al*., 1998; Benstead *et al*., 1999, 2000; Scatena and Johnson, 2001; March *et al*., 2003). Puerto Rico offers potential insights on the future impacts of current tropical dams which tend to be younger than those in Puerto Rico, and on what may occur if rates of dam construction are maintained or increased, such that tropical regions with currently low levels of damming reach extensive levels of damming. For example, Puerto Rico is now facing a need to manage its antiquated system of dams, many of which have passed their designed lifespans of 50 years. Moreover, many of these reservoirs no longer serve their original purposes. Jobin (1998) argues that this is because most of the large dams were built during the height of the island's agricultural economy, to provide irrigation and power for sugarcane production, but now the society is dominated by growing urban populations in regions far from the locations of most dams. In addition, reservoirs across the island have lost much of their water storage capacity owing to high rates of sedimentation (e.g. Soler-López, 2001), and at least two of the oldest dams (Comerio and Coamo) are filled with sediment and no longer trap water (Jobin, 1998).

Puerto Rico has the potential to provide the first tropical example of dam decommissioning given: (1) its antiquated dams and rapidly infilling reservoirs; (2) the Puerto Rican public's level of interest in conservation of running waters and stream fauna (González-Cabán and Loomis, 1997); (3) the influence of US policy in Puerto Rico; and (4) the growing acceptance in the USA of dam removal when appropriate (e.g. Hart and Poff, 2002). On the other hand, Puerto Rico may also take tropical dam construction to a new level. Urban growth and poorly planned water infrastructure have led to intense water resource demands (reviewed in Pringle and Scatena, 1999). Plans to meet these demands include at least three additional large dams proposed by the Puerto Rico Aqueduct and Sewage Authority over the next 4–10 years (F. Quinones, Puerto Rico Office of the Water Plan, pers. comm.).

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Table 1. Large dams of Puerto Rico, in order of year constructed. Table lists: (1) each reservoir's primary purpose when originally built, the dam's structural height (ht.), and year when construction was completed (Year built), (2) whether the reservoir contains any inter-basin transfers (IBT) to basins without large dams or basins with dams of a different type of spillway discharge regime, and the dam's spillway type (U = uncontrolled/ungated, C = controlled/gated, F = free crest spillway over dam face, M = morning glory tunnel spillway, ? = unknown), (3) findings for a new analysis of free crest spillway discharge ('Dates analysed' = the years of the dates included in the analysis; 'Spillway Q %' = the percentage of daily lake elevations during the record that exceeded the spillway crest elevation; for additional information and explanation, see supplemental data set and appendix in the National Science Foundation's Luquillo LTER database at luq.lternet.edu), (4) free crest spillway discharge ('Spillway Q type') as categorized by Holmquist *et al.* (1998) based on USGS data from 1993 to 1994 and personal communications from dam operators, (5) observations over the last 15 years on occurrences of native migratory fish and shrimps in reservoirs and/or streams upstream from large dams (if an additional large dam occurs upstream, reported observations do not include stream sites above the second dam, e.g. observations for Comerio are for sites between Comerio and Carite and do not include taxa observed upstream from Carite; G = *Gobiomorus dormitor*, S = *Sicydium plumieri*, X = *Xiphocaris elongata*, A = Atyidae, M = *Macrobrachium*, 'no obs done' = no sites above the dam have been visited, blank spaces indicate that sites above the dam have been visited or sampled and no migratory taxa were observed, for additional information and explanation, see supplemental data set and appendix in the National Science Foundation's Luquillo LTER database at luq.lternet.edu), and (6) citations for tabled data

	(1)			(2)		(3)		(4)	(5)		(6)
									Observations		
Dam	Primary purpose	ht. (m)	Year built	IBT?	Spillway type	Dates analysed	Spillway Q%[a]	Spillway Q type	Fish	Shrimp	Citations[b]
Carite	Irrigation/ municipal supply	32	1913	Y	CF	1989–2003	<0.1	—	G	X	4, 6, 7
Comerio	Municipal supply	39	1913	N	UF	2004–2005	100	present		X, A	1, 2, 4, 6, 8
Guayabal	Irrigation	40	1913	Y	CF	1998–2000	100	present	S	A, M	4, 6, 7, 8
Coamo	Irrigation	20	1914	N	UF	2005	100	—	no obs done		1, 2, 4
Patillas	Irrigation	45	1914	N	CF[c]	1998–2000	100	—	G		4, 6, 7
Guajataca	Irrigation	37	1928	N	UF	1998–2000	0	absent	G		4, 6, 7, 8
El Guineo	Irrigation/power	38	1931	N	UM	—	—	—		X	4, 6
Matrullas	Irrigation/power	37	1934	N	UM	—	—	absent			1, 4, 6, 8
Dos Bocas	Power	57	1942	N	UF	1999–2003	1.3	absent		X, A, M	2, 4, 6, 7, 8, 9
Garzas	Irrigation/power	62	1943	Y	UM	—	—	—			2, 4, 6

Las Curias	Municipal supply	25	1946	N	UM	—	—	—	no obs done		4
Cidra	Municipal supply	24	1946	N	UF	1998–2000	20.2	very rare			4, 6, 7, 8
Caonillas	Power	72	1948	N	UF	1996-2003	6.5	—			4, 6, 7
Adjuntas	Power	24	1950	N	?F	2005	43.8	—			1, 2, 4, 6
Pellejas	Power	15	1950	N	?F	no gage	—	—	no obs done		1, 2, 4
Víví	Power	26	1950	N	??	2005	100	—	no obs done		1, 2, 4
Loco	Power/irrigation	22	1951	Y	UF	1998–2000	66.5	present	S	X, A, M	4, 6, 8
Luchetti	Power/irrigation	54	1952	Y	UF	1989–2003	2.0	very rare	G	X, A, M	4, 6, 7, 8
Loíza[d]	Power/municipal supply	29	1954	N	CF	1998–2000	100	—		X, A	1, 2, 4, 6, 7, 9
Prieto	Power/irrigation	30	1955	Y	UF	2005	0	—		A	1, 2, 3, 4, 6
Guayo	Power/irrigation	58	1956	Y	UF	1998–2000	15.2	—		X, A	4, 6, 7
Yahuecas	Power	27	1956	Y	UF	2005	0	—		A	1, 2, 3, 4, 6
Toa Vaca	Municipal supply/ irrigation	65	1972	N	CF	1997–2003	27.2	absent		X	1, 4, 6, 7, 8
La Plata	Municipal supply	40	1974	N	CF[c]	1998–2000	92.3	present		X, A	4, 6, 7, 8
Cerrillos	Flood/municipal supply	98	1992	N	UF	1998–2000	0	—	S	X, A	4, 5, 6, 7, 8
Portugués[e]	Flood/municipal supply	83	—	N?	UF	—	—	—	N/A		5

[a] Calculations for Guayabal, Patillas, Loíza, Toa Vaca and La Plata assumed that spillway gates were always open. As the main water supply for the capital city of San Juan, spillway discharge over Loíza may actually be limited to high runoff events (L. Soler-López, USGS, pers. comm.).

[b] Citations for physical data on dams are: (1) Jobin (1998), (2) Sheda and Legas (1968), (3) Soler-López (2001), Soler-López and Webb (1999), Soler-López *et al.* (1999) and references therein, (4) USGS (2000), (5) U.S. Army Corps of Engineers (1998). Citations for biological data are: (6) Greathouse (2005, pers. obs.), (7) Bacheler *et al.* (2004b), Neal *et al.* (1999, 2001b), (8) data on shrimp and fish distributions from Holmquist *et al.* (1998) and Holmquist (unpublished data), (9) Roghair *et al.* (2001), Miranda-Castro *et al.* (2000).

[c] Patillas' spillway is separated physically from the dam but is an open chute similar to free crest spillways over the faces of other dams. La Plata's spillway only became controlled in 1989.

[d] Lago Loíza is also known as Lago Carraizo.

[e] The Portugués is under construction, is designed to have rare spillway discharge, and data on fauna observed prior to and during construction can be found at luq.lternet.edu

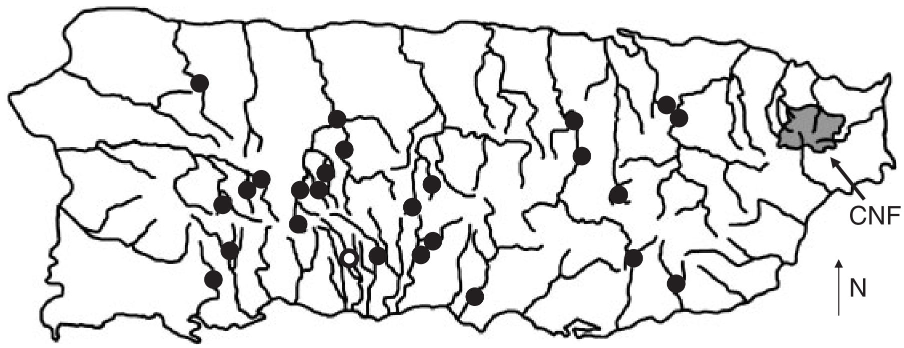

Figure 1. Map of Puerto Rico showing major stream drainages, locations of completed large dams (height >15 m, black dots), an additional large dam under construction on the Río Portugués (open dot), and the Caribbean National Forest (CNF).

LIMITATIONS TO EXTRAPOLATING PUERTO RICO LESSONS

There are several ecological and socio-economic limitations to extrapolating findings in Puerto Rico to other tropical regions. First, there are limitations based on differences between the ecology of Puerto Rico's island streams (e.g. short drainages, lack of native non-migratory fish and shrimps, comparatively low diversity of fauna due to distance from mainland streams, and the island's relatively small size) compared with that of many continental tropical drainages (which include large drainages and drainages with higher faunal diversity, including native non-migratory fish and shrimps). Second, while the unique political status of Puerto Rico in relation to the USA has fostered its potential to provide a window into the future of tropical dams, it may also limit extrapolation. Some forms of environmental degradation in much of the tropics may ultimately remain more severe than in Puerto Rico because other countries currently lack policies and agencies similar to US federal legislation and agencies (e.g. the Clean Water Act, the US Environmental Protection Agency, the US Forest Service and the US Fish and Wildlife Service) which have various levels of influence and jurisdiction in Puerto Rico. Although Puerto Rico has serious water-quality problems in relation to sewage treatment and toxic industrial pollution (Hunter and Arbona, 1995), the relationship with the USA will be more likely to lead to clean-up and investment in improved sewage treatment than in other tropical countries where economic conditions continue to limit even the most basic development of sewage treatment infrastructure (Pringle, 2000). Finally, although Puerto Rico contains numerous large dams, the sizes of reservoirs are smaller than those of well-publicized mega-projects developed in other tropical regions (e.g. World Commission on Dams, 2000). On the other hand, smaller projects may typify dams that are currently proliferating in the tropics (Benstead *et al.*, 1999) and are thought to be the most likely to be built in the future (McCully, 2001).

DAMS AND DIADROMOUS FAUNA IN PUERTO RICO: ECOLOGY AND MANAGEMENT

Ecological effects of temperate dams have repeatedly been found to depend on dam design and operation, as well as on variation among fauna in life history patterns (e.g. Collier *et al.*, 2000). As a consequence, the conservation of diadromous species requires detailed information on migratory life histories and how each life stage is affected by different types of dams. Research on species that occur in Puerto Rico has begun to reveal such insights, including how effects vary with dam design and operation as well as migratory strategies and distributions.

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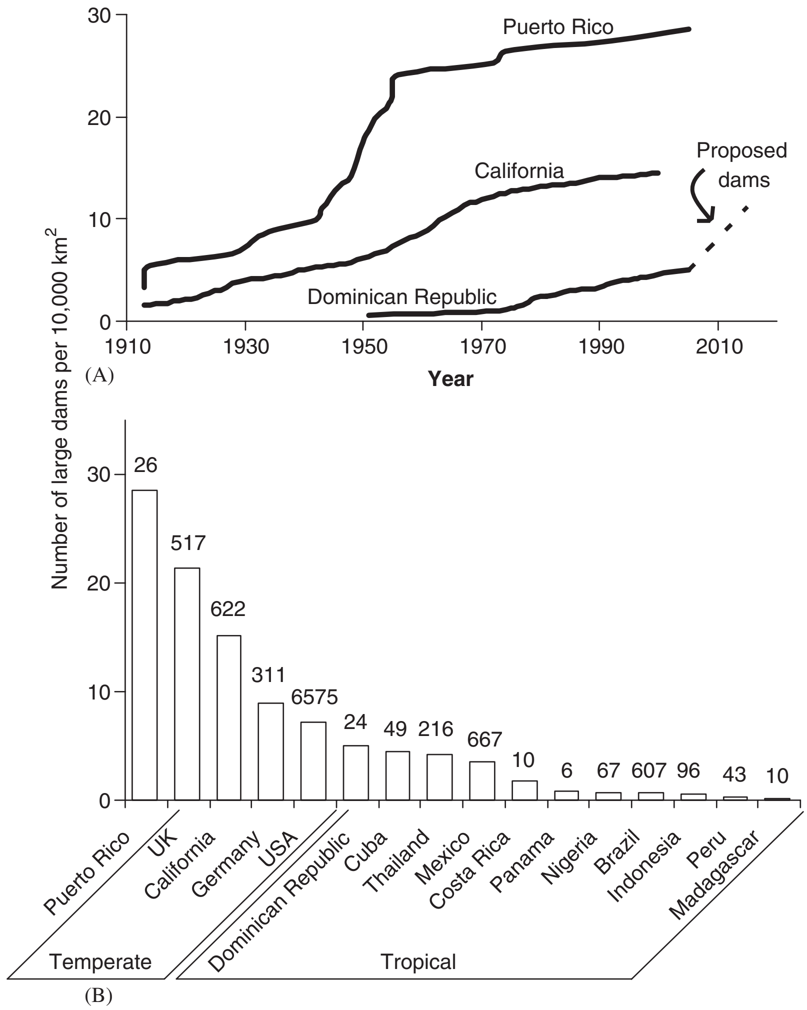

Figure 2. Numbers of large dams (height >15 m) per unit land area in Puerto Rico and selected regions of North America and the tropics. (A) Number per unit land area over time in Puerto Rico, California (USA), and the Dominican Republic. Solid lines represent dams completed and under construction. Dotted line represents potential future trajectory of damming if the 30 currently proposed large dams for the Dominican Republic are built by 2015. Note: years of construction for three large dams in the Dominican Republic are unknown, but were conservatively estimated as 1951, based on reports that the first dam (a small dam) in the country was built in 1950 (Instituto Nacional de Recursos Hidrálicos, 2005). (B) Estimates of current numbers (completed and under construction) in haphazardly selected regions: bars are numbers per unit land area; numbers above bars are total number of large dams. Data from World Commission on Dams (2000), International Commission on Large Dams (2003), U.S. Central Intelligence Agency (2004), Hammond World Atlas Coporation (2000), U.S. Army Corps of Engineers (2005), Food and Agriculture Organization of the United Nations (2005), Comisión Nacional del Agua (2004), Instituto Nacional de Recursos Hidrálicos (2005), and Anderson-Olivas (2004).

The diadromous fauna of Puerto Rico — life histories and longitudinal distributions

Insular and coastal streams and rivers in the tropics are generally dominated by assemblages of diadromous fish, freshwater shrimps, and snails (e.g. Smith *et al.*, 2003). In Puerto Rico, all native fish and shrimps (excluding cave/karst specialists) are reported to be diadromous and the native freshwater snail, *Neritina virginea*, is also diadromous (Covich and McDowell, 1996; Holmquist *et al.*, 1998; Blanco, 2005). Native fish include one species of algivorous goby (*Sicydium plumieri*) and six predatory fish: mountain mullet

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(*Agonostomus monticola*), American eel (*Anguilla rostrata*), three eleotrids (*Gobiomorus dormitor*, *Eleotris pisonis*, *Dormitator maculatus*), and one species of predatory goby (*Awaous tajasica*). Thirteen species of freshwater shrimps occur in three families (Atyidae, Xiphocarididae, Palaemonidae). Atyidae are represented by eight species in four genera (*Atya*, *Micratya*, *Potimirim*, *Jonga*), while four species of *Macrobrachium* comprise the palaemonid shrimps. *Xiphocaris elongata* is the sole species of Xiphocarididae.

Results of research on shrimps and *Neritina* are uniformly consistent with a freshwater amphidromous life-cycle in which adults breed in freshwater and larvae passively drift to the estuary before migrating back upstream as juveniles several months later (e.g. Hunte, 1977; March *et al*., 1998). However, for fish, detailed life-histories are only clear for some species. *Anguilla rostrata* and Gobiidae (*Sicydium plumieri* and *Awaous tajasica*) are known to be catadromous (Erdman, 1972) and freshwater amphidromous (Nieves, 1998; Keith, 2003), respectively. The life-cycles of other fish species are known to be either catadromous or amphidromous because adults primarily occur in fresh water and larvae have been sampled from saltwater (*Agonostomus monticola*; Anderson (1957), cited in Phillip (1993)) or migration of juveniles from estuarine to freshwater habitats has been observed (*Agonostomus monticola* (Cruz, 1987); *Eleotris pisonis* (Bell *et al*., 1995); Eleotridae (Winemiller and Ponwith, 1998)). However, the natural location of adult spawning, which would provide strong evidence for determining each species' type of life-cycle, has not been directly observed for *Agonostomus monticola*, *Eleotris pisonis*, *Gobiomorus dormitor* or *Dormitator maculatus* (Cruz, 1987; Bell and Brown, 1995). *G. dormitor* may also be capable of reproducing entirely within fresh water (Greenfield and Thomerson, 1997; Bacheler *et al*., 2004b).

Puerto Rican assemblages of diadromous fauna vary with stream gradient/elevation owing to waterfalls acting as natural but permeable barriers to upstream migration. Waterfalls block upstream migration of predatory fish, whereas shrimps and *Sicydium* are able to climb any gradient over which water flows, and they reach high abundances upstream from waterfalls (Covich, 1988). Thus, native predatory fish are naturally absent and shrimps and *Sicydium* are abundant in high-elevation, high-gradient streams; whereas native predatory fish are present and shrimps are at low abundances in low-elevation, low-gradient streams (Covich and McDowell, 1996). *Neritina* also occur at high densities in mid- and low-elevation sites but are not found at higher elevations (e.g. Pyron and Covich, 2003).

Upstream effects of large dams: loss of native migratory fauna and effects of spillway discharge

A major focus of conservation research on native Puerto Rican fish and shrimps is the loss of populations upstream from large dams (> 15 m in height). Large dams are barriers to fish and shrimp migration, but upstream loss of native migratory fauna varies with dam design and operation as well as with location along the stream continuum and with faunal adaptations. The first major Puerto Rican study of large dams and diadromous fauna focused on loss of native migratory fauna from low-gradient streams (Holmquist *et al*., 1998). Sampling for shrimps and fish above and below nine large dams compared with six drainages without large dams showed dramatic faunal changes in free-flowing sites upstream from reservoirs (Holmquist *et al*., 1998). However, effects depended on the dam's spillway discharge regime. Native fish and shrimps were abundant and diverse in sites without large dams and below large dams. In contrast, native predatory fish (eels, mullet, Eleotridae and *Awaous* gobies) were not found upstream from any large dam, regardless of spillway discharge regime. Likewise, Holmquist *et al*. (1998) concluded that shrimps and *Sicydium* gobies were extirpated from streams above large dams without spillway discharge (Cidra, Dos Bocas, Guajataca, Luchetti, Matrullas, Toa Vaca; Table 1, column 4); the only occurrence of native migratory fauna above any of these six dams were three *Macrobrachium faustinum* shrimps above the Luchetti Reservoir, which were captured four months after Luchetti had a spillway discharge event. However, abundances of shrimps and *Sicydium* upstream from large dams with regular spillway discharge were only partially reduced (Table 1; Holmquist *et al*., 1998). Holmquist *et al*. (1998) concluded that

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shrimps and *Sicydium*, which are capable of climbing waterfalls, can recruit past large dams when spillway discharge is regular enough to allow these animals to climb the face of the dam.

Our research has extended findings of Holmquist *et al.* (1998) to high-gradient streams where native predatory fish are naturally absent (i.e. above waterfalls) (Greathouse, 2005). Our goal was to compare sites above dams that fit Holmquist and colleagues' 'no regular spillway discharge' category to sites with no large dams. Electroshocking and standardized snorkelling showed that populations of migratory fauna differed dramatically between sites upstream from large dams compared with sites without large dams — numbers of migratory shrimps and *Sicydium* at undammed sites were >300 times higher than in dammed sites (Greathouse *et al.*, 2006). However, during field work at three streams above dams without regular spillway discharge, extremely rare occurrences of migratory shrimps and fish were visually observed that were undetectable by electroshocking and snorkelling methods. *Xiphocaris elongata* and *Gobiomorus dormitor* occurred above the Carite Reservoir, *Xiphocaris elongata* occurred above Toa Vaca, and atyid and *Xiphocaris* shrimps occurred above Luchetti, (Table 1; detailed descriptions of these observations are reported in the National Science Foundation's Luquillo Long-term Ecological Research Site's data information management system at luq.lternet.edu).

During the course of the study, low abundances of shrimps were also observed in streams above other reservoirs (El Guineo, Loíza, Guayo, Yahuecas, Prieto, Cerrillos; Table 1; detailed descriptions are also reported in the Luquillo database) that Holmquist *et al.* (1998) did not sample. In addition, other researchers have made limited observations of native shrimps and fish above large dams. Forest Service personnel have collected medium abundances of *Xiphocaris* and atyid shrimps while electroshocking a CNF stream above the Loíza reservoir (Roghair *et al.*, 2001). Within the Carite Reservoir, *G. dormitor* has a relatively large population (1800 and 3300 fish in 2000 and 2001, respectively; Bacheler *et al.*, 2004b). *Xiphocaris* was also observed within the reservoir (N. Bacheler, North Carolina State University, pers. comm.), but no shrimps were found during gut content analyses of Carite fish (Bacheler *et al.*, 2004a). *G. dormitor* are always at extremely low abundances in other reservoirs (generally one or two individuals collected) and are disappearing (Neal *et al.*, 1999). Historical observations of native fauna in reservoirs have also been reported. Erdman (1972) reported *G. dormitor* and shrimps occurring in the Loíza reservoir, *A. tajasica* and shrimps in the Loco reservoir, and shrimps in the Dos Bocas and Patillas reservoirs. Santiago (1979) sampled above and below Dos Bocas, Yauco and Loíza in 1977 and 1978 and found no shrimps above the dams but plentiful *Macrobrachium*, atyids and *Xiphocaris* below the dams. Finally, in 1996 and 1997, in experiments using a pump to discharge water over small portions of the spillways at Yauco, Dos Bocas and Loco, large numbers of *Macrobrachium*, atyids and *Xiphocaris* climbed to the tops of the dams (J. Holmquist, unpublished manuscript), and following Hurricane Hortense causing spillway discharge over Dos Bocas, sampling in the reservoir and associated tributaries yielded shrimps (J. Holmquist, unpublished data, see description in the Luquillo database).

Taken together, these observations of native shrimps and fish above dammed sites indicate that upstream effects of large dams on diadromous fauna are more complicated than initially indicated by the work of Holmquist *et al.* (1998): migratory shrimps and fish are not completely extirpated but instead are nearly extirpated from sites above large dams lacking regular spillway discharge, and rare occurrences of native shrimps and fish above these types of dams now extend to other taxa in addition to *M. faustinum* (Table 1). However, native fauna are exceedingly rare and often can only be documented by chance visual observation or targeted sampling after rare spillway discharge events. Regular sampling protocols (i.e. our standardized electroshocking and snorkelling methods from Greathouse, 2005) may fail to detect them.

Probable explanations for occurrences of migratory fauna at these sites vary for shrimps *vs.* fish. *Gobiomorus dormitor* is thought to have a landlocked population in the Carite Reservoir because no *G. dormitor* have been observed in the La Plata reservoir downstream from Carite, and movement by the species between the La Plata estuary and the Carite reservoir would necessitate a migration over the spillways of three large dams (Bacheler *et al.*, 2004b). Because *G. dormitor* is known to be incapable of

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migrating past waterfalls, spillway discharge over these dams does not explain its presence in Carite. In addition, size ranges of *G. dormitor* (total lengths: 25–399 mm) suggest that recruitment of juveniles into the population occurs regularly. Samples also included reproductive individuals, but no larval sampling was conducted (Bacheler, 2002, Bacheler *et al*., 2004b). The presence of *G. dormitor* in Carite is especially surprising because it is unable to climb waterfalls and therefore is not normally present at high elevation sites. It is thus unlikely that *G. dormitor* colonized Carite and associated tributaries naturally. A potential alternative explanation for *G. dormitor* in Carite is diadromous migration via an inter-basin transfer between the upstream end of the reservoir and an undammed Guamaní drainage (Table 1). Juveniles may recruit into the system by upstream migration from the Guamaní estuary, especially given that no individuals smaller than 25 mm have been captured within the reservoir. Moreover, co-occurrence with *Xiphocaris* shrimps (for which there is no evidence suggesting an ability to form landlocked populations) strongly suggests a migratory pathway between the watershed and saltwater. Methods to determine whether the Carite *G. dormitor* population is landlocked rather than migratory could include larval sampling and subsequent testing for survival in fresh water or examination of Sr/Ca ratios from otoliths (K.N.I. Bell, Memorial University, Canada, pers. comm.). The rarity of *G. dormitor* in other reservoirs also suggests that it is not capable of forming landlocked populations. Alternatively, this rarity may be due to factors such as fluctuating water levels, absence of aquatic macrophytes or competition with exotic fish (Neal *et al*., 1999).

For shrimps above large dams, we hypothesize that these individuals scaled the dams during spillway discharge events. In order to evaluate this hypothesis, a more thorough analysis of free crest spillway discharge was conducted than in previous analyses by Holmquist *et al*. (1998) and Greathouse (unpublished data). The results are generally consistent with our hypothesis: spillway discharge occurred sometime during the 5 years prior to our observations for all but four of the reservoirs where shrimps were observed (Table 1). Puerto Rican shrimp species are known to have lifespans greater than 5 years (A. Covich, University of Georgia, pers. comm.) so it would be reasonable to expect shrimps to be present from recruitment during spillway discharge 5 years prior to observations. The analysis also showed that five of the seven large dams downstream from the high-gradient sampling sites of Greathouse *et al*. (2006) had free crest spillway discharge events despite previous analyses indicating no spillway discharge (Table 1). For dams with recently installed gauges (Comerio, Coamo, Adjuntas, Víví, Prieto, Yahuecas), we consider the estimate obtained to be an unreliable indicator of spillway discharge regime. However, the analysis does indicate additional dams with frequent spillway discharge (e.g. Loíza, Coamo, Patillas) that were not included in this study or by Holmquist *et al*. (1998). These additional dams would be useful for conducting more detailed research on upstream effects of spillway discharge. Considering that Holmquist *et al*. (1998) only examined three drainages with such dams and that not all of them have been included in the present study, upstream effects of spillway discharge dams merit additional research.

Shrimps occurred above four dams (Prieto, Yahuecas, Cerrillos and El Guineo) which, according to the analysis, lack spillway discharge. However, for Prieto and Yahuecas, the USGS records are only 1 month long, which is too short to indicate reliably a lack of spillway discharge events. Yet because USGS records for Cerrillos and El Guineo are relatively long, alternative explanations for shrimps occurring upstream from large dams must be considered. One potential alternative is long-lived shrimps that have survived from the time before dams were built. Atyids and *Xiphocaris* have survived in aquaria for up to 12 and 4 years, respectively (*Atya lanipes*: 6 years; A. Covich, University of Georgia, pers. comm.; *Atya lanipes* and *Xiphocaris elongata*: 4 years; E. Greathouse and C. Pringle, pers. obs.; *Atya tenella*, a species from Central America: 12 years; Bruce Felgenhauer, University of Louisiana, Lafayette, pers. comm.). Furthermore, bioenergetic models suggest that *Xiphocaris* may have a lifespan of approximately 30 years (T. Crowl, Utah State University, pers. comm.). Thus, survival of long-lived shrimps is a probable explanation for shrimps above Cerrillos, which was built in 1992, only 11 years before the most recent observation of a shrimp in

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this system (E. Greathouse, pers. obs.). However, shrimp longevity seems an unlikely explanation for other systems where dams are several decades old.

Alternative access between the estuary/sea and watersheds above large dams (for example, by canals, inter-basin water transfers, outlets through the bases of the dams, direct heavy rainfall on spillways, and experimental spillway discharge) is likely and may explain the presence of migratory fauna above some dams, including El Guineo. A series of extensively engineered inter-basin water transfers involve many of the large dams across the island (Table 1) (Díaz *et al*., 1999). In the case of El Guineo, the dam does not have a free crest spillway; instead the overflow spillway is a 'morning glory tunnel' (i.e. a concrete structure within the reservoir leading to an outlet though the base of the dam). This morning glory spillway does have frequent discharge (E. Greathouse, unpublished data), and it is possible that discharge over the grassy face of the dam occurs during flows that exceed the capacity of the morning glory tunnel (B. Yoshioka, US Fish and Wildlife Service, pers. comm.). The system, like many other Puerto Rican reservoirs, also has outlets involving other tunnels through the base of the dam. Likewise, heavy rainfall directly onto spillways can produce large amounts of spillway runoff that are similar in magnitude to spillway discharge that induces shrimp migration. However, shrimps have not been observed to climb during such rainfall events (J. Holmquist, pers. obs.), suggesting that shrimps detect a difference in water chemistry between rainwater runoff and reservoir water flowing over the dam.

Other potential explanations for native shrimps occurring above El Guineo and other large dams include landlocked populations. However, landlocked populations of shrimps are unlikely because larvae of all Puerto Rican shrimp species have been shown to require high salinity for survival and metamorphosis (e.g. Hunte, 1977; Bjahan *et al*., 1980). Moreover, non-diadromous shrimp populations would be likely to reach high abundances upstream from large dams lacking regular spillway discharge, but shrimps above these dams are rare. Human addition of shrimps to watersheds above dams also occurs. Fishermen are reported to occasionally add small *Macrobrachium* shrimps to reservoirs in Puerto Rico because *Macrobrachium* grow to large sizes and are sought after for recreational and commercial harvest (Greathouse *et al*., 2005). *Xiphocaris* may be mistakenly added because *Xiphocaris* and small *Macrobrachium* have similar morphologies. In the Loco reservoir, live shrimps have also been used as bait in traps (J. Holmquist, pers. obs.).

Other effects of dams: downstream effects, effects of low-head dams, and effects on snails

Large dams can affect downstream populations of diadromous fauna as well (e.g. Freeman *et al*., 2003), but there has been little research on this in Puerto Rico. Data from Holmquist *et al*. (1998) indicate similar population abundances of native shrimps and fish in reaches downstream from large dams and in reaches without large dams, but this study was not explicitly designed to examine downstream impacts. Furthermore, downstream impacts of large dams could be complex. For example, dams may cause loss and degradation of downstream shrimp habitat. Shrimps that recruit to streams below dams may thus have less habitat to occupy, resulting in artificially high densities. At the bases of many large Puerto Rican dams, migrating shrimps moving upstream also 'stack up,' reaching high densities (J. Holmquist, pers. obs.).

Dams may also affect downstream diadromous populations by dampening high flows, which serve as migration or spawning triggers. Experiments on the effects of varying flows on shrimp spawning have shown no clear effect (J. Holmquist, unpublished data). However, postlarval/juvenile gobies in a variety of systems have been found to return to fresh water during high flows (Keith, 2003). Gobies may also be affected by dams that alter hydrological conditions within estuarine larval habitat and stream flows that transport larvae downstream. Approximately 50% of larvae of Dominican *Sicydium punctuatum* (which may be the same species as *S. plumieri*; taxonomy is unresolved) survive downstream migration to the sea and most of these surviving larvae reach the sea in less than a day after hatching (Bell and Brown, 1995). Based on laboratory experiments by Bell and Brown (1995), larvae have 2–4 days to reach salt water before

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their ability to swim actively upwards (to remain in the river drift) is exhausted. The point of swimming exhaustion occurred before exhaustion of the yolk sac, suggesting that larvae are simply unable to develop past an early stage in fresh water. Moreover, laboratory experiments indicated that proper development of larvae requires a halocline with a range of intermediate salinities. Dams which reduce freshwater flows may lengthen larval drift times and may alter the natural haloclines of estuaries to the point of limiting larval development and survival.

Research has also documented negative effects of low-head dams on shrimp migration in Puerto Rico (e.g. water withdrawals cause mortality of passively drifting shrimp larvae, Benstead *et al.*, 1999). Effects of low-head dams in Puerto Rico are reviewed elsewhere (e.g. Pringle and Scatena, 1999; March *et al.*, 2003). In contrast, effects of dams on native migratory snails are unknown (but see Blanco (2005)). No research has examined effects of dams on *Neritina*, and our data shed little light on the topic because *Neritina* are naturally absent from high elevations (Greathouse, 2005) and may also be naturally absent from elevations studied by Holmquist *et al.* (1998).

Management of dams and diadromous fauna in Puerto Rico

Current management of reservoirs and dams in Puerto Rico is highly influenced by perspectives that are prevalent in the USA. Thus, similar to the USA, Puerto Rico has a mix of management goals that sometimes favour conservation of native diadromous fauna but more often contribute to migratory faunal declines. Two examples of recent management decisions to protect migratory fauna include: (1) a decision to build an alternative, low-impact water intake structure instead of a small dam on the last drainage in the CNF with no dam on its mainstem (March *et al.*, 2003), and (2) a revised water withdrawal permit for a low-head dam requiring construction of a fish/shrimp-pass and cessation of withdrawals during peak hours of larval shrimp drift (B. Yoshioka, US Fish and Wildlife Service, pers. comm.).

In the CNF, interaction between researchers and managers has resulted in substantial science-based efforts to protect migratory fauna. However, outside the CNF, migratory fauna are often a low management priority compared with other critical societal concerns such as water supply (e.g. large numbers of urban households routinely go without running water), flood control, and minimizing dam construction costs. An example of this is the lack of provision of fish/shrimp passage devices for two dams constructed by the Army Corps of Engineers (ACOE), the Cerrillos (built in 1992) and Portugués (under construction). In its discussion of fish and wildlife in relation to reservoir management, the ACOE Water Control Manual for the Cerrillos dam mentions nothing about native fish or freshwater shrimps and erroneously describes the Cerrillos basin as lacking in native game and food fish populations (US Army Corps of Engineers Jacksonville District, 1997), despite the provision of funding to the US Fish and Wildlife Service for extensive studies on effects of dams on migratory native fauna (e.g. Holmquist *et al.*, 1998).

A second example involves the focus on exotic sport fish in reservoirs. Funding through the Federal Aid for Sport Fish Restoration programme to the Puerto Rico Department of Natural and Environmental Resources (DNER) is almost entirely focused on research and management of largemouth bass fisheries in reservoirs (Neal *et al.*, 2004). Because the programme's funds are federally mandated to be used for recreational finfish only, native taxa receive substantially less focus. For example, *Sicydium* are 'of lesser importance' (Neal *et al.*, 1999), and shrimps are excluded entirely. Activities at the Maricao Fish Hatchery are likewise focused on production of largemouth bass fingerlings for stocking in reservoirs (Neal *et al.*, 2004). Moreover, there is a wealth of studies about the life histories, diets, reproduction, genetics, human use and even protection of largemouth bass in reservoirs across the island (e.g. Neal *et al.*, 1997, 2001a; Neal and Lopez-Clayton, 2001; Neal and Noble, 2002). In comparison, published research on native shrimps and fish outside the CNF is virtually non-existent beyond limited studies conducted on *G. dormitor* in Carite and the study by Holmquist *et al.* (1998) on shrimps and fish. Research on native fisheries is so

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limited that even the most basic life history information is not known for most of the fish species (Greathouse *et al*., in preparation).

Important native fisheries include *Agonostomus monticola*, *Sicydium* postlarvae, and shrimp (Erdman, 1972, 1986; S. Kartchner and T. Crowl, Utah State University, pers. comm.). For example, *Macrobrachium* shrimp are prized for harvest (Greathouse *et al*., 2005), and mountain river shrimp festivals such as the 'Festival de Camarones' on the Río Bauta draw hundreds of recreationists whereas a typical largemouth bass reservoir tournament draws <30 anglers (Neal and Lopez-Clayton, 2001; E. Greathouse, pers. obs.). Larval and juvenile stages of native migratory fauna also appear to play important roles in the diets of commercially important marine/estuarine fish (Erdman, 1972, *Bairdiella* spp. and *Centropomus* spp., K. Smith and C. M. Pringle, unpublished data). Despite the cultural importance of Puerto Rico's native fisheries, information on fresh water, provided by Puerto Rico DNER's major public education programme (Programa de Educación en Recursos Aquatícos, 2005), largely focuses on promotion of recreational fishing for exotic sport fish in reservoirs, even though reservoirs may be more likely than rivers to be habitats for Puerto Rican populations of *Biomphalaria glabrata* (the snail host of the trematode that causes human schistosomiasis, a public health problem that has diminished but remains on the island (Hillyer and de Galanes, 1999)).

Research questions and recommendations for conservation and management

Upstream passage for anadromous fish (e.g. salmonids) in temperate regions typically involves complicated and expensive structures (Clay, 1995). However, there is potential for providing upstream passage for some native Puerto Rican fauna using comparatively inexpensive engineering solutions (cf. Fièvet, 2000). Specifically, the occurrence of *Sicydium* and shrimps upstream from spillway discharge dams indicates that they can successfully pass a dam during upstream migration if there is regular flow of small amounts of water over the dam. The results of simple and successful experiments on artificial spillway discharge further indicate potential for inexpensive upstream passage for *Sicydium* and shrimps. A small academic research group used an inexpensive pump to draw small amounts of water from three Puerto Rican reservoirs for release over only small parts of the spillways. These experiments resulted in large numbers of shrimps and *Sicydium* scaling the dams during experimental flows (J. Holmquist, unpublished manuscript). Potential benefits of such passage include restoration of native *Sicydium* and shrimp presence in free-flowing streams above dams as well as the ecosystem services they support. For example, shrimps support recreational and commercial harvest, and native fauna are charismatic (e.g. bright colours, territorial displays and a pelvic-fin suction disc make *Sicydium* fascinating to fish hobbyists (Erdman, 1986)). Furthermore, shrimps and *Sicydium* are key benthic algae grazers. In high-elevation stream pools where shrimps and *Sicydium* are functionally extirpated owing to large dams blocking their migration, algal biomass reaches levels that are nine times higher than those in undammed stream pools (Greathouse *et al*., 2006), and algal blooms above dams can include dense masses of filamentous forms (E. Greathouse, pers. obs.). Such effects of dams on algae and charismatic native fauna are relevant issues, given the importance of stream aesthetics to ecotourism and recreation in Puerto Rico and other tropical islands.

Alternatively, spillway discharge could have limited restoration potential for native fauna. Native migratory populations above large dams may be sink populations because high water-residence times, exotic predatory fish, and low oxygen conditions in Puerto Rican reservoirs are unlikely to allow passively drifting larvae to reach their estuarine habitat (cf. Pringle *et al*., 2000b). On the other hand, downstream passage of larvae past smaller reservoirs and dams may be viable; positively phototropic larvae may be most likely to be released during high flow events, and thus, larvae may be most abundant in, and remain at the surface of, flood waters passing over spillways (B. Yoshioka, U.S. Fish and Wildlife Service, pers. comm.). There is also a need for research on interactive effects of spillway discharge and flow regime. For example, without attempts to mimic the natural flow regime below dams, spillway-discharge-type passage

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may be unable to support migration of large shrimp and *Sicydium* populations. Policy decisions on dam construction and operation should also consider how changes in the flow regime alter the estuarine environment for tropical diadromous fauna.

Questions in need of study include the following. What are the economic and ecological costs and benefits of spillway-discharge-type passage? Which would be most beneficial/cost-effective: providing passage past low-head dams or large dams? Do shrimps and *Sicydium* above spillway discharge dams reach population sizes that are large enough to sustain the ecosystem services they provide in streams without large dams? Are these populations sink populations? If so, does this matter to island-wide populations (i.e. if adult habitat regulates shrimp and *Sicydium* populations, island-wide population viabilities may not be affected by 'extra' reproductive individuals migrating to sink habitat above existing dams)? What are the cumulative effects of damming on basin-, island-, and Caribbean-wide population abundances (e.g. large dams eliminate or reduce access of migratory biota to $\sim 2000\,km^2$ of the island's watershed area, or $\sim 22\%$ of the island's land area)? Is the true percentage of lost habitat higher than 22% for *Sicydium* and atyid populations, because they prefer high-elevation streams which are, in turn, more likely to be isolated by dams than are low-elevation streams? How do dams interact with other human impacts to limit shrimp and fish populations? Answering such questions would require a more complete understanding of population processes (e.g. birth, death, immigration, emigration) over different habitat conditions (e.g. elevations, etc.).

A final conservation issue needing more careful consideration is the current management focus that prioritizes population enhancement of non-native fish in reservoirs over conservation of native fauna. Such activities have resulted in the presence of predatory fish in high-elevation basins that were historically lacking in predatory fish and therefore would have supported abundant populations of native shrimps and *Sicydium*. The *G. dormitor* population in the Carite Reservoir, for example, may be viewed as a unique opportunity to promote a native fishery (e.g. Bacheler *et al*., 2004b). However, *G. dormitor* would not have historically occurred in the streams drained by Carite, and in low-elevation streams where this fish is native it may severely limit shrimp abundances. Thus, *G. dormitor* may also be viewed as an exotic shrimp predator that limits the potential for restoration of native Carite shrimp populations. Interestingly, the few *Xiphocaris* shrimp observed above Carite had long rostrums which are typical of younger shrimp occurring in low-elevation streams containing predatory fish (such as *G. dormitor*) (Villamil and Clements, 1976); long rostrums may be a morphological defence against predatory fish (J. March, Washington and Jefferson College, pers. comm.). Before managers attempt to establish *G. dormitor* populations in other reservoirs, there should be consideration of historical distributions of diadromous fauna and the potential for restoration of historical distributions. Establishing *G. dormitor* populations may be appropriate in some reservoirs but not in others. For example, it may be appropriate in reservoirs that: (1) are at an elevation below the historical upstream limit of native predatory fish, (2) have dam operations or importance to urban water supply that limit even the most minimal pumping of water over the spillway for shrimp passage, and/or (3) already contain a wide variety of exotic predatory fish which limit shrimp restoration potential, even in the absence of *G. dormitor*. In contrast, El Guineo may be a reservoir in which introduction of *G. dormitor* would conflict with conservation of native fauna because this high-elevation reservoir is probably above the natural limit of native predatory fish and native shrimps are present (Table 1).

Addressing these research questions is especially pressing in light of Puerto Rico's plans for continued large dam construction. The Puerto Rico Aqueduct and Sewage Authority (PRASA) has proposed to build on at least two systems that at present have no large dams (F. Quinones, Puerto Rico Office of the Water Plan, pers. comm.). The Casei Reservoir (proposed height: $> 30\,m$), near Añasco in the west of the island, is currently under preliminary study. PRASA is also proposing a new reservoir near the El Verde area of the CNF to provide municipal water supply at 10 million gallons per day. At least two more dams are proposed for sites upstream from the Loíza Reservoir (Valenciano Reservoir, near Juncos, $\sim 30\,m$ in height, and

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Beatriz Reservoir, near Caguas, 12–15 m in height, F. Quinones, pers. comm.), potentially affecting shrimp populations that migrate past Loíza due to its frequent spillway discharge.

In summary, Puerto Rico provides a potential window into the future of migratory fauna in tropical regions, given the extent of dam development on the island combined with the relatively large amount of scientific information available on migratory freshwater fauna that are affected by dams. It is our hope that the synthesis of information provided here will contribute to management and conservation of migratory fauna in tropical streams.

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