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High dams and marine-freshwater linkages in the Caribbean: effects on native and introduced fauna

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Abstract: Caribbean streams are dominated by a shrimp and fish assemblage for which amphidromy (eggs or larvae carried to the ocean followed by migration of juveniles upriver) is suspected. Effects of dams on this assemblage are likely to demonstrate complex interactions as a function of reproductive strategy and type of dam structure. Our goals were to determine 1) whether high dams reduce or eliminate stream corridor permeability with respect to migration, 2) the extent to which permeability is a function of spillway discharge, 3) the relative roles of native fauna and disturbance suppression (river regulation) as predictors of success of exotic fishes, and 4) the uniformity and extent of obligate amphidromy in this assemblage. We sampled adult and juvenile shrimps and fishes in Puerto Rican streams via electrofishing and sampled shrimp larvae with drift nets. Replicate streams and stream reaches were assigned to the following five categories: undammed, and either above or below dams, with or without water released over the spillways of the dams. Dams without spillway discharge were impermeable barriers that eliminated all native fish and shrimp fauna from upstream reaches. Dams with spillway discharge, although more permeable, had smaller populations of native species above these structures than below the dams or on undammed streams. Our data on adult and larval distributions, combined with the absence of first stage shrimp larvae, indicate that amphidromy is obligate for most of the native fauna. Disturbance regime appeared to be a poor predictor of successful invasion of exotics, whereas exotic abundance was consistently inversely related to abundance and species richness of native fauna across all sampling categories. The prevalent amphidromy in these streams provides a tight marine-upland linkage that is disrupted by dams in several ways. We recommend adding passages for shrimps and fishes to dams on these tropical streams.

Resumen: Los ríos del Caribe están dominados por un complejo de camarones y peces los cuales se sospecha que la gran mayoría son anfidromos (los huevos o larvas regresan al mar ántes de que los juveniles migren río arriba). Es probable que los efectos de las represas de agua se expresen como interacciones complicadas entre el diseño de las estructuras y las estrategias reproductivas de estos animales. Nuestras metas fueron las de determinar: 1) si las represas elevadas reducen o eliminan la permeabilidad del río con respecto a la migración de este complejo de animales, 2) hasta donde el tipo de permeabilidad es una función de la descarga por el derramadero, 3) la uniformidad y extensión de la anfidromía obligada en este complejo de organismos, y 4) los roles relativos de la fauna acuática nativa y la supresión por perturbación como pronosticadores del éxito de las especies de peces exóticas. Se colectaron muestras en algúnos ríos en Puerto Rico usando técnicas de equipo de electropesca y redes de plancton. Replicar se tomaron en ríos smilares o ramales de ríos que fueron asignados a las siguientes categorias: sin represa u obstrucción, y río arriba y río abajo de las represas con o sin descarga por encima de la represa. Represas sin descarga por encima constituyen obstáculos impermeables que eliminaron los peces y camarones nativos río arriba de las presas. Las represas con descarga encima, aunque eran más permeable en ese respecto, reduteron significativamente las poblaciones de camarones y peces río arriba de las estructuras. Los datos de distribuciones de adultos y larvas, considerando particularmente que solamente encontramos larvas de camarones de la primera etapa, indican que la vida anfidroma es obligada para los peces y camarones nativos. Parece que el régimen de perturbación no es un buen pronosticador de la habilidad de invasión de los peces exóticos, considerando que su abundancia era inversamente proporcional a la abundancia de especies nativas en todas las categorias de ríos muestreadar. La prevalencia de anfidromos en estos ríos indica un enlace fuerte entre el mar y los sitios río arriba que puede ser perturbada por la construcción de represas a varias escalas de consideración. Nosotros recomendamos la siembra de peces y camarones en las represas construidar en los estos ríos tropicales.

Introduction

Unregulated rivers provide highly permeable (*sensu* Wiens et al. 1985; Wiens 1992) corridors for aquatic fauna, but high (tall) dams can reduce or eliminate this permeability. In a system dominated by animals requiring both fresh and salt water for life cycle completion, such impermeability can lead to major shifts in assemblage structure. Little is known about migratory patterns of tropical stream fauna (Clay 1995), and barriers posed by dams in the tropics are likely to differ from effects of dams on the well-known salmonid migrations in temperate regions (e.g., Stuart 1962; Mills 1989; Linløkken 1993); extrapolation to other systems is not necessarily warranted (McDowall 1993). Like McDowall's (1993) New Zealand fishes, many shrimps and fishes of Caribbean streams attempt to overcome obstacles by climbing (via walking legs, pelvic-fin suction discs, or wriggling) rather than jumping (Covich & McDowell 1996). Dams differ in many ways and effects of these structures vary as well (Petts 1984; Clay 1995). For instance, Ibrahim

(1962) and Lee and Fielder (1979) found that some shrimps (in India and Australia, respectively) could climb structures but only in conjunction with flowing water. This paper examines effects of river regulation in a tropical stream system.

Problems associated with exotic fishes are manifold and often exacerbated by river regulation (e.g., Courtenay & Stauffer 1990; Allan 1995; Courtenay & Moyle 1996; Vitousek et al. 1996). Much emphasis has been placed on biotic resistance to invasions (e.g., Elton 1958; Li & Moyle 1981; Case 1991; Vermeij 1991; Lodge 1993). However, Moyle and Light (1996a, b) contend that biotic resistance to exotic fishes, though important, is often secondary to abiotic control. Regulated rivers and streams are viewed as being particularly susceptible to invasion because of suppression of natural disturbance regimes (e.g., Walker 1985; Moyle & Light 1996a, b; Vitousek et al. 1996; see also Meffe 1984).

The stream macrofauna of the Caribbean is dominated by an assemblage of decapod crustaceans (e.g., Abele & Blum 1977; Hunte 1978; Crowl & Covich 1990; Covich & McDowell 1996); fishes are present (e.g., Erdman 1972; Penczak & Lasso 1991; Covich & McDowell 1996) but generally less abundant. Salt water may be essential for life cycle completion for many of these fauna. Although the eel *Anguilla rostrata* is catadromous, and the freshwater crab *Epilobocera sinuatifrons* has direct development (Erdman 1972), there is evidence that at least some of these species may be washed to the sea as larvae or eggs and return to the streams as juveniles ("amphidromy;" McDowall 1992, 1993). Support for this assumption has been provided by observations of larvae of the fish *Sicydium plumieri* (a goby) being carried down streams to the ocean

(Bell & Brown 1995) and upstream migrations of shrimps and fishes (Erdman 1972, 1986; Felgenhauer & Abele 1983; Covich & McDowell 1996) as well as shrimp rearing experiments (e.g., Choudhury 1971; Hunte 1977, 1979, 1980). It is unclear, however, if this suspected amphidromy is obligate or uniform across all species. For example, Soltero (1991) successfully raised shrimp in freshwater, and some related species in other systems are known to complete their life cycles in freshwater (e.g., Hughes et al. 1995). McKaye et al. (1979) and Erdman et al. (1984) report successful reproduction in freshwater for some fishes (Eleotridae or "sleepers"), and there are reports of native shrimps and fishes in Puerto Rican reservoirs (I. Corujo, pers. comm.).

Our first two goals were to determine whether high dams reduce or eliminate stream corridor permeability in tropical drainages and to ascertain the extent to which permeability is a function of "free crest" spillway discharge (i.e., water released over the sloping face of a dam; Clay 1995). A third aspect of our study was an examination of the relative roles of native fauna and disturbance suppression (reduction of flow variability) as predictors of success by exotic fishes. Our final goal was to use a system of regulated rivers to provide a field test of the degree of obligate amphidromy in this tropical shrimp and fish assemblage.

We pursued our objectives by sampling shrimps, shrimp larvae, and fishes in Puerto Rico in accord with the following three contrasts: 1) undammed streams versus streams above dams with free crest spillway discharge (referred to hereafter as "spillway discharge") versus streams above dams without spillway discharge; 2) streams below, versus streams above, dams with spillway discharge; and 3) streams below, versus streams above, dams without spillway discharge. If access to salt water is not requisite for native fauna, then adult populations and shrimp larvae should be found in all stream categories, including reaches above long-established dams without spillway discharge. Alternatively, if access to the ocean is necessary for development, we should not find these fauna above dams lacking discharge. In addition, if shrimp larvae do not have a requisite marine phase, then we should find advanced larval stages in the streams, but if such a phase is necessary, we should find only first stage larvae. Complete blockage of faunal migration would clearly eliminate stream corridor permeability for the dominant macrobiota of these tropical streams. We also hypothesized that dams *with* spillway discharge might only reduce, rather than eliminate, such permeability. Finding native fauna present, but with reduced abundances or species richness, above such dams would be consistent with this hypothesis.

If native taxa are absent above dams without spillway discharge, the relative importance of biotic resistance and intact disturbance regimes in limiting invasion can be compared. There would be native fauna and disturbance suppression below-dam, and no native fauna and an intact disturbance regime above-dam. In such a scenario, presence of many exotic species and individuals below-dam but few above-dam would support the importance of intact disturbance regimes relative to biotic resistance in this system, whereas the opposite pattern would be consistent with greater importance of biotic resistance than intact disturbance regimes.

Methods

We established replicate streams or stream reaches for the following five categories (Fig. 1): undammed (n= 6: Duey, Guayanilla, Inabón, Tallaboa, Guanajibo, and Tanamá Rivers); above (n= 3) or below (n= 3) dams (Table 1) with spillway discharge (on the Loco, Jacaguas, and Plata Rivers); and above (n= 6) or below (n= 6) dams without spillway discharge (on the Bayamón, Matrullas, Arecibo, Guajataca, Yauco, and Toa Vaca Rivers). Each replicate stream or stream reach was subsampled three times over 2 years, each at a different location. Sample locations for replicates for the four dammed categories were chosen randomly within 5 river km of the dams so as not to confound elevation or reach with effects of dams. We randomly selected replicates for controls from mid-river reaches within the elevation range of the dams. Because we only had three replicate streams with dams allowing spillway discharge, there was a greater possibility for Type II error, and results of contrasts using these streams should be considered conservative.

We sampled shrimp larvae with a 45 cm wide x 30 cm high Wildco drift net (0.363 mm mesh) with a General Oceanics rotary flowmeter (with high-speed rotor) mounted in the aperture. Samples were taken during daylight hours. Although release of larvae peaks soon after sunset, some larvae are still present in the water column throughout the day in mid-elevation reaches (J.G. Holmquist, unpublished data). Prior to other sampling at a station, the drift net was positioned at least 25 m upcurrent of the portion of the stream to be used for electrofishing, because physical disturbance and electrofishing can increase drift, at least for insects (Elliott & Bagenal 1972; Mesick & Tash 1980). The top of the net was emergent so that animals floating near the surface would be sampled. The entire water column was usually sampled in this way. Samples were preserved in the field. All larvae were counted by hand in the laboratory for determination of drift density (number of drift organisms per 100 m^3).

Adult and juvenile shrimps and fishes were sampled with a Smith-Root Model 12 backpack electrofisher with a circular anode. At each sampling the field team progressed upstream and used burst pulses of 300V DC to stun animals in all non-pool habitats; stunned individuals were carried by the stream current into a stationary dipnet held just downstream of the anode. This method is somewhat similar to the point abundance sampling of Fièvet et al. (1996). We did not sample pools, because our pilot work indicated that estimates from low-flow pool habitats were unreliable. Species accumulation curves became asymptotic at 50 to 70 seconds, and we used catch per unit effort (100 seconds of actual shocking time) as our standard measure. Samples were kept on ice and later identified to species.

The outlined contrasts were examined with one-tailed t-tests for differences in faunal abundances and species richness. Three-way, independent comparisons were preceded by significant ANOVAs. Tests were followed by correction to family-wise error rate via the sequential Bonferroni inequality (Holm 1979; Rice 1989). We calculated power ($1-\beta$) for contrasts not significant at $p = 0.05$ (family-wise).

Results

We collected 14 species of decapods and 12 species of fishes via electrofishing. The shrimps *Macrobrachium faustinum, Micratya poeyi,* and *Atya lanipes* were the most common decapods collected across all stream categories (Table 2). The fish fauna was dominated by the introduced livebearers *Poecilia reticulata* and *Xiphophorus maculatus* and the native goby *Sicydium plumieri* (Table 2).

The assemblage of fauna above dams with no spillway discharge was different from that of undammed streams and streams above dams with spillway discharge (Fig. 2). We collected a mean of 175 and 120 shrimps per 100 seconds on undammed streams and above dams with spillway discharge, respectively (Fig. 2a). The mean of 0.17 shrimp above dams lacking spillway discharge was a result of three *Macrobrachium faustinum* collected above the dam on the Yauco stream during the first sampling series. There was an average of 5.7 native fishes per sample on undammed streams versus only 0.33 above dams with spillway discharge (Fig. 2b); the latter group was represented only by *Sicydium*. Not a single native fish was collected above dams without spillway discharge. The opposite pattern was apparent for exotic fishes: few on undammed streams, an intermediate number above dams with spillway discharge, and the most above dams without spillway discharge (Fig. 2c). Species richness of decapods and fishes above dams lacking discharge was significantly lower than in the other two categories with or without the inclusion of several exotic fishes (Fig. 2d). The only native species collected above this type of dam was the crab *Epilobocera sinuatifrons*. The proportion of overall species richness represented by exotic fishes paralleled the trend for abundance of exotic species (Fig. 2d).

The two below-above contrasts showed similar results (Fig. 3). There was significantly lower shrimp abundance above than below dams with spillway discharge. Again, there were virtually no shrimps above dams without discharge (Fig. 3a). The below-above comparisons for fishes were equally striking. Native fish abundance was much higher below than above dams with spillway discharge (Fig. 3b). Although no native fish were collected above dams lacking spillway discharge, native fishes were collected downstream of such dams. There was a higher mean abundance of exotic fishes above than below both types of dams, but this difference was significant only for dams without spillway discharge (Fig. 3c). Species richness was relatively high both above and below dams with spillway discharge but was significantly lower above dams lacking spillway discharge than below these structures, whereas the proportion of exotic species showed the opposite pattern (Fig. 3d).

The shrimp larval data echoed the patterns observed for adults (Figs. 4 and 5). Large numbers of larvae were collected on undammed streams, an intermediate number were found below dams, few were collected above dams with spillway discharge, and not one larva was collected above dams without discharge. There were also fewer larvae below dams without spillway discharge than below dams with spillway discharge. Furthermore, we did not collect a single larva that was past first stage.

Discussion

Our results demonstrate that dams without spillway discharge were impermeable barriers that eliminate the entire native fish and shrimp fauna from upstream reaches. Aside from the crab *Epilobocera sinuatifrons*, with direct development, the only other native fauna found above these dams were the three *Macrobrachium faustinum* collected above the Yauco dam during the first sampling series. Notably, this dam had a brief spillway release 4 months before we began the study, and a few shrimps were apparently able to scale the dam during this short period.

Dams with spillway discharge, though more permeable to migrating fauna, still greatly reduced the populations of shrimps and fishes above these structures. Most shrimp species found below these dams were also found above the reservoirs but in reduced numbers. Some individuals apparently scale the wet surfaces of these dams, successfully navigate the associated reservoirs, and survive to reach the upper reaches of these watersheds. Only a single native fish, the goby *Sicydium* with its ventral suction disc, was able to negotiate these obstructions, albeit in reduced numbers (eels are likely to breach such structures as well). Although high dams generally cannot be passed by this tropical fauna (Erdman 1961; 1972; 1986), spillway discharge can allow passage for a fraction of the species capable of climbing.

Demonstrating absence of fauna is of course problematic, and it is possible that we simply failed to collect less-common native fauna in our above-dam samples. However, the data on adult and larval distributions, together with the fact that only first stage larvae were collected, indicate that ocean access (generally amphidromy, although the eel *Anguilla* is known to be catadromous) is obligate for the native fauna. The occasional reports of adult native fauna in reservoirs lacking spillway discharge are probably better explained by the input of juveniles into the reservoirs by fishermen (pers. obs.) than by larval survival in freshwater. Sleepers do apparently reproduce in lakes in at least some systems (McKaye et al. 1979), but such life cycle completion must be rare in Puerto Rico, or the animals must not enter rivers from the reservoirs, despite occurrence in undammed rivers at similar elevations.

The removal of this suite of fauna from above-dam reaches is likely to cause major shifts in assemblage structure as well as lesser effects on the physical environment. Absence or removal of atyid shrimps has been shown to increase sedimentation, shift algal assemblage composition, and depress populations of some chironomids (Pringle et al. 1993; Pringle & Blake 1994; Pringle 1996). Removal of the most abundant native fish, *Sicydium*, a grazer (Erdman et al. 1984), is also likely to influence algal assemblages and other herbivores. Further, the larger *Macrobrachium* (e.g., Crowl & Covich 1994), mountain mullet (*Agonostomus*), and sleepers (Erdman et al. 1984) are top predators in these streams, and their elimination above dams lacking spillway discharge is likely to cause complex changes in community structure and dynamics. Cascading effects should be expected above dams with spillway discharge as well. Although *Sicydium* and shrimps can reach streams above dams with spillway discharge, these populations were small, and mountain mullet and sleepers were absent. Such effects of stream regulation should be anticipated in other systems in which amphidromy is important (e.g., Ibrahim 1962; Lee & Fielder 1979; Radtke & Kinzie 1996).

Barrier creation in these Antillean streams is also likely to cause effects on a larger spatial scale. Ecologists are increasingly emphasizing the openness of natural systems (e.g., Stamps et al. 1987; Wiens 1992); this connectivity also extends across large-scale marine-terrestrial interfaces. Transport of materials, nutrients, and organisms can either be seaward (Aleem 1972; Mann & Lazier 1991; Valiela et al. 1992) or landward (Mathisen et al. 1988; Polis & Hurd 1995; 1996), and forested islands in particular are tightly linked to the ocean (Ingram 1992). Undisrupted streams can be seen as a marine-terrestrial ecotone or as a corridor for longitudinal exchange between the two ecosystems, and this coupling is strong in Antillean streams. Larvae of shrimps, eggs of fishes, and metamorphosed juveniles provide an allochthonous input to estuarine and coastal waters that may be an important food resource for marine organisms (Gilbert & Kelso 1971), particularly planktivorous fishes. In turn, juveniles migrating into the streams from the estuary will have garnered almost all of their biomass from the marine environment. Further, movement upstream occurs throughout the lives of many of these fauna, so biomass gained in the lower reaches is also transported upstream; fishes migrating upstream have been shown to be important in such biomass transfer in other systems (e.g., Hall 1972). Instream discontinuities such as dams can be expected to disrupt all of these linkages.

Our system provides a test for Moyle and Light's (1996a) general contention that invasibility is better predicted by the integrity of the natural disturbance regime than by presence of a native assemblage. Above dams on these tropical streams, native fishes were excluded, but there was an intact disturbance regime (natural flow variability). Below these dams, native fishes were present, but the disturbance regime has been modified by river regulation (discharge generally reduced and peaks suppressed). These latter conditions result in slow, shallow reaches below dams that should be conducive to exotics in general (Forman 1995; Moyle & Light 1996a, b; Vitousek et al. 1996) and to tilapia and poeciliids in particular (e.g., Dudley 1974; Meffe & Snelson 1989). Based on Moyle and Light's (1996a) argument, we should therefore expect to find few exotics above dams but many below dams. However, the opposite trend was apparent in our tropical streams. Disturbance regime appears to be a poor predictor of invasibility in this system, whereas exotic abundance consistently had an inverse relationship to abundance of native species across all sampling categories (Table 3).

Moyle and Light (1996a; b) also suggest that native species richness is a poor predictor of resistance to exotic fishes in stream systems. In contrast, our results show an inverse relationship between number of exotics and native species richness (Fig. 2c, d; Fig. 3c, d) and are consistent with a positive relationship between invasion resistance and diversity (e.g., Elton 1958; Case 1991; Ross 1991; Vermeij 1991; Lodge 1993). Predators often prevent establishment of exotics (Lodge 1993), and Courtenay and Stauffer (1990) note that predatory fishes are usually absent in the uncommon cases in which the introduced poeciliids *Poecilia* and *Xiphophorus* have established permanent populations. This condition was evident above dams in our tropical streams. Competition by native fishes or shrimps may be a factor as well. Thus Caribbean streams, like many other lotic systems (e.g., Minckley & Deacon 1968; Holden 1979; Vitousek et al. 1996; Moyle & Light 1996a) are made more vulnerable to invasion by regulation. However, the most vulnerable reaches were above, rather than below, dams because of apparently strong biotic resistance combined with obligate amphidromy of native fauna. On a positive note, these results suggest that the native fauna, if restored to the above-dam reaches via shrimp/fishways, could limit the populations of exotic species.

In this system of dammed Antillean streams, a hierarchy of effects is present. Preeminent among these effects is elimination or reduction of river corridor permeability for native fauna. An indirect effect of this loss of permeability appears to be enhanced vulnerability to invasion by exotic species. Although, in Puerto Rican streams, disturbance was not as important as biotic resistance in structuring assemblages of exotics, disturbance is undeniably a powerful influence in both temperate (Moyle & Light 1996a, b; Wootton et al. 1996) and tropical streams (references in Covich 1988; Ahmad et al. 1993; Covich & McDowell 1996). Above dams with spillway discharge, reservoir-associated obstacles are likely to take their toll on the native shrimps and fishes that do manage to scale the spillways, further reducing the permeability of these regulated streams. Such obstacles include 1) a gauntlet of predatory fishes introduced for sport fishing (Erdman et al. 1984), 2) inappropriate habitat, 3) low dissolved oxygen (Goldman 1976; Hunter & Arbona 1995), and 4) the lack of a flow stimulus from distant tributary streams (see also Barthem et al. 1991). Nevertheless, both disturbance and reservoir-associated mortality should be viewed as subsidiary influences above dams; if few or no native fauna can migrate past structures, other potential influences have little relevance.

Managerial Recommendations

Because dams on these tropical streams alter habitat and assemblage structure, sever links with the marine ecosystem, and encourage invasion by exotic species, our primary recommendation is to avoid creation of new dams. Water conservation, distribution efficiency, and tapping of groundwater resources would provide sound alternatives to building additional structures in some cases (see Goodland 1993; Goodland et al.1993; Morris 1994; Hunter & Arbona 1995, González-Cabán & Loomis 1997).

We also recommend retrofitting fishways to existing tropical dams. Because both dams and reservoirs are impediments to migration, we advocate construction of side channels that, if possible, circumvent the entire dam and reservoir complex. Providing spillway discharge at run-of-river flow is a partial solution to restoring above-dam populations. Still, all native fishes except *Sicydium* and *Anguilla* would be eliminated, and these fishes and all shrimps would be greatly reduced in number above the structure. This option does have the added benefit of enhancing below-dam habitat via restoration of the natural disturbance regime. Short-term, pulsed releases are an additional possibility. These recommendations are not specific to the Caribbean, but rather should be applicable in other amphidromy-dominated systems.

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Table 1. Characteristics of structures and associated reservoirs on dammed rivers sampled in study.[a]

River	Free crest spillway discharge[b]	Age (years)	Reservoir volume (m^3)	Elevation (m)	Dam height (m)
Loco	present	46	1.3×10^6	70	18
Jacaguas	present	84	5.9×10^6	104	75
Plata[c]	present	23, 84, 90	2.0×10^7	47, 163, 173	40, 10, 10
Arecibo[d]	absent	55	2.4×10^7	90	57
Matrullas	absent	63	2.8×10^6	736	37
Yauco	very rare	45	1.4×10^7	174	54
Toa Vaca	absent	25	6.2×10^7	165	61
Guajataca	absent	69	3.7×10^7	197	37
Bayamón	very rare	51	6.5×10^6	403	24

[a] Sources: Díaz et al. (1995); J. R. Bas-García (pers. comm.), U.S. Geological Survey topographic quadrangles, and personal observation; see also Hunter and Arbona (1995).

[b] Discharge was usually less than run-of-river (i.e., less discharge from dam into downstream reach than from upstream reach into reservoir) for both types of dams. Dams without spillway discharge release hypolimnetic water from pipes at the bases of the dams.

[c] Three-dam complex.

[d] The Dos Bocas structure; this dam alone directly incorporates hydropower turbines.

Table 2. Mean number and SE of decapods and fishes collected per 100 seconds electroshocking time in Puerto Rican streams.

Decapods			Fishes		
Macrobrachium faustinum	71	(9.7)	*Poecilia reticulata*[a]	5.4	(1.7)
Micratya poeyi	50	(1.4)	*Xiphophorus maculatus*[a]	4.7	(1.4)
Atya lanipes	28	(6.0)	*Sicydium plumieri*[b]	3.2	(0.63)
Atya scabra	20	(5.3)	*Tilapia/Oreochromis* spp.[a,c]	0.78	(0.26)
Xiphocaris elongata	8.9	(2.0)	*Agonostomus monticola*	0.40	(0.23)
Atya spp.[d]	4.2	(1.6)	*Puntias conchonius*[a]	0.26	(0.18)
Macrobrachium heterochirus	1.8	(0.41)	*Gobiomorus dormitor*	0.16	(0.060)
Potimirim mexicana	1.8	(0.96)	*Xiphophorus helleri*[a]	0.14	(0.13)
Atya innocous	0.52	(0.41)	*Awaos taiasica*	0.078	(0.036)
Potimirim americana	0.30	(0.22)	*Eleotris pisonis*	0.078	(0.042)
Epilobocera sinuatifrons[e]	0.16	(0.050)	*Erotelis smaragdus*	0.022	(0.022)
Macrobrachium acanthurus	0.16	(0.11)	*Anguilla rostrata*	< 0.01	
Macrobrachium carcinus	0.067	(0.050)			

Potimirim glabra	0.022	(0.020)

Footnotes for Table 2.

[a] Exotic species but not actively stocked (C. Lilyestrom, pers. comm.).

[b] We treat all *Sicydium* in Puerto Rico as *S. plumieri* as per Erdman (1986) and Hildebrand (1935).

[c] Mostly *O. mossambicus.*

[d] Unidentifiable juveniles.

[e] Freshwater crab.

Figure Legends

Figure 1. Sampled drainages in Puerto Rico including undammed streams and dammed streams with and without spillway discharge. Sample locations for dammed rivers were within 5 river km of the symbols (dam locations). Sampling stations for controls were from mid-river reaches within the elevation range of the dams, and were centered around the indicated locations.

Figure 2. Mean values (SE) per 100-second shocking sample for shrimp abundance (a), native fish abundance (b), exotic fish abundance (c), and combined decapod and fish species richness (d) on undammed streams and reaches above dams with and without spillway discharge. Bars for species richness are divided into native (below break) and exotic (above break) species. Horizontal lines above two bars indicate that the pair of means was not significantly different at $p = 0.05$ for multiple one-tailed t-tests followed by correction to family-wise error rate via the sequential Bonferroni inequality. Italicized numbers below horizontal lines are power values for non-significant comparisons. An asterisk denotes a comparison not significant after Bonferroni correction but with a per contrast error rate of 0.033. T-tests followed significant ANOVAs.

Figure 3. Mean values (SE) per 100-second shocking sample for shrimp abundance (a), native fish abundance (b), exotic fish abundance (c), and combined decapod and fish species richness (d) below (B) and above (A)

dams with and without spillway discharge. Bars for species richness are divided into native (below break) and exotic (above break) species. Probability values (non-italicized numbers) represent results of one-tailed independent t-tests. Asterisks highlight results at $p < 0.05$. Italicized numbers are power values for non-significant comparisons.

Figure 4. Mean values (SE) for shrimp larvae per 100 m^3 on undammed streams and reaches above dams with and without spillway discharge. Horizontal bar indicates that this pair of means was not significantly different at $p = 0.05$ for a one-tailed multiple t-test. Italicized number below horizontal line is the power value for this comparison. The tests followed a significant ANOVA.

Figure 5. Mean values (SE) for shrimp larvae per 100 m^3 below and above dams with and without spillway discharge. The probability value (non-italicized number) represents result of one-tailed independent t-test. Italicized number is the power value for this comparison.

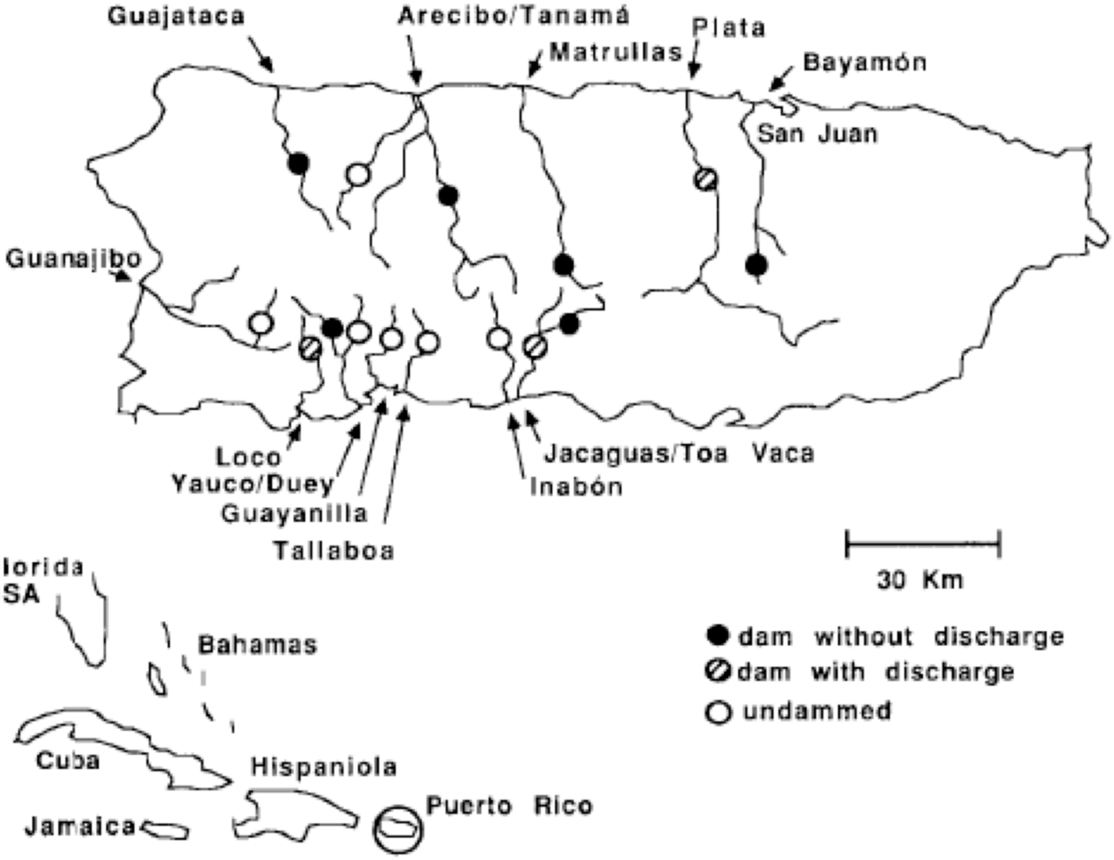
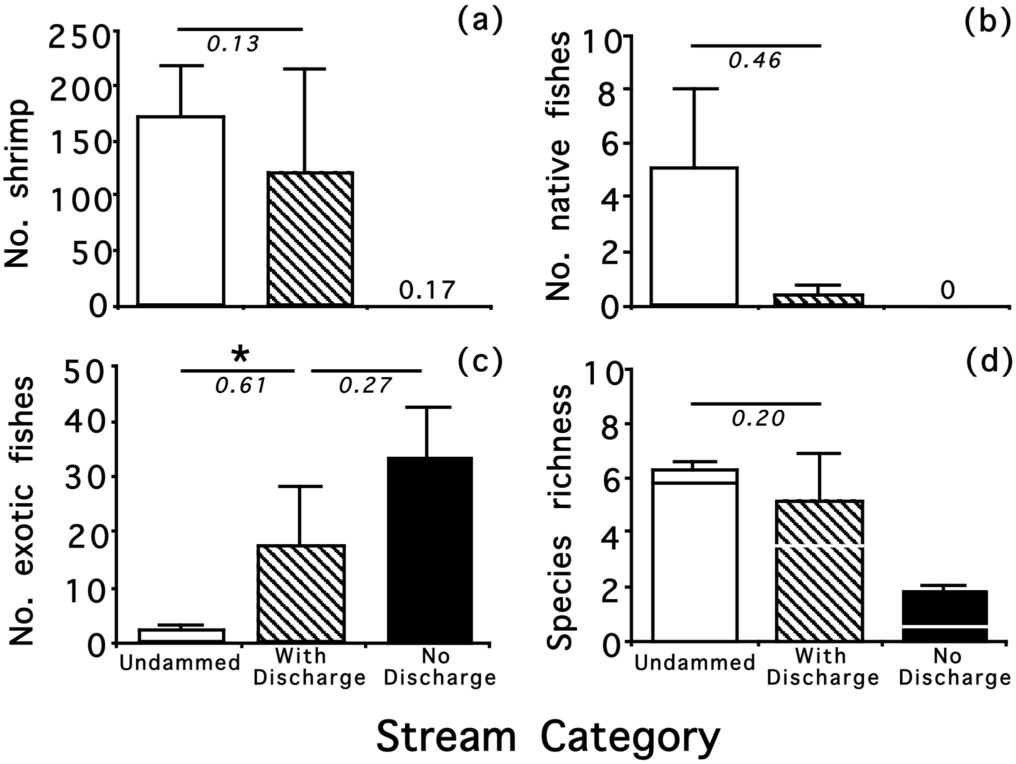

Guajataca
Arecibo/Tanamá
Plata
Matrullas
Bayamón
San Juan
Guanajibo
Loco
Yauco/Duey
Guayanilla
Tallaboa
Jacaguas/Toa Vaca
Inabón
30 Km
● dam without discharge
⊘ dam with discharge
○ undammed
Florida USA
Bahamas
Cuba
Hispaniola
Jamaica
Puerto Rico

Fig. 1



(a)
No. shrimp
250
200
150
100
50
0
0.13
0.17
(b)
No. native fishes
10
8
6
4
2
0
0.46
0
(c)
No. exotic fishes
50
40
30
20
10
0
*
0.61
0.27
(d)
Species richness
10
8
6
4
2
0
0.20
Undammed
With Discharge
No Discharge
Undammed
With Discharge
No Discharge
Stream Category

Fig.2

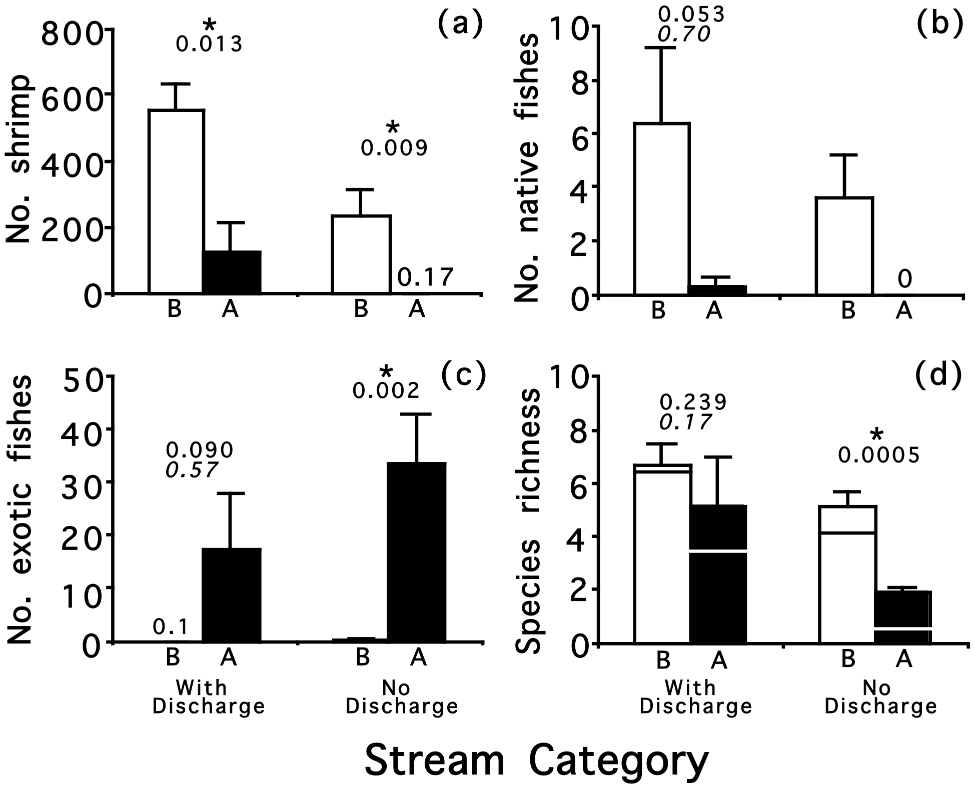

(a)
No. shrimp
800
600
400
200
0
*
0.013
*
0.009
0.17
B
A
B
A
(b)
No. native fishes
10
8
6
4
2
0
0.053
0.70
0
B
A
B
A
(c)
No. exotic fishes
50
40
30
20
10
0
0.090
0.57
0.1
*
0.002
B
A
B
A
With Discharge
No Discharge
(d)
Species richness
10
8
6
4
2
0
0.239
0.17
*
0.0005
B
A
B
A
With Discharge
No Discharge
Stream Category

Fig. 3

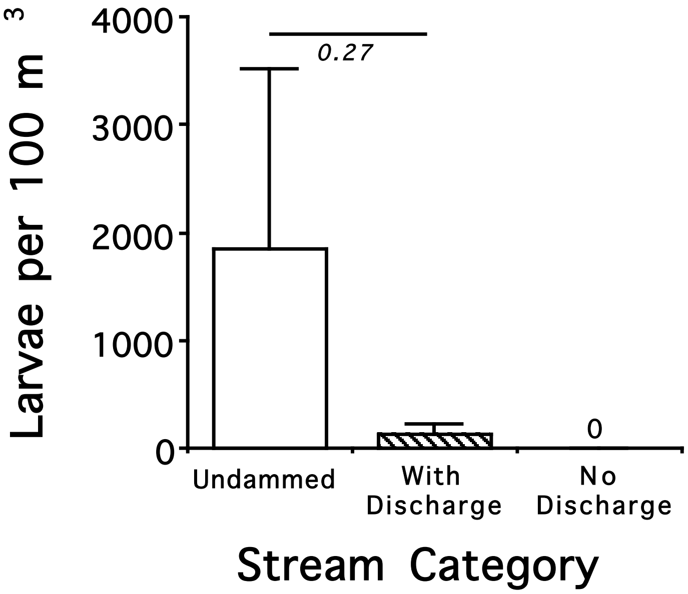

Larvae per 100 m ^{3}
4000
3000
2000
1000
0
0.27
0
Undammed
With Discharge
No Discharge
Stream Category

Fig. 4

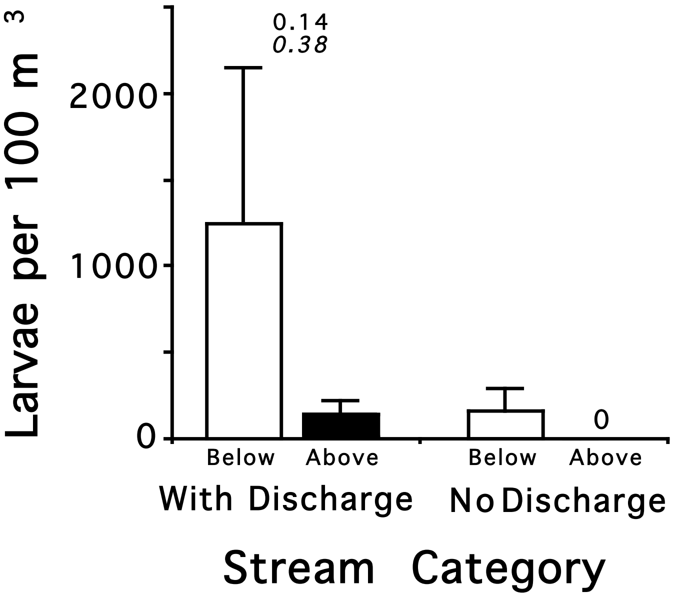

Larvae per 100 m 3
2000
1000
0
0.14
0.38
0
Below
Above
Below
Above
With Discharge
No Discharge
Stream Category

Fig. 5