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Cover: A natural waterfall, such as this one on Río Lajas in the Grande de Añasco river basin in Puerto Rico, may limit diadromous fishes’ dispersal and access to habitat. Dams and other artificial obstacles may do likewise, and in the article that begins on page 176, Thomas J. Kwak and Patrick B. Cooney describe their study of the critical influence of both natural and artificial barriers in structuring the fish assemblages of streams in Puerto Rico. Photograph: Patrick B. Cooney.
Spatial Extent and Dynamics of Dam Impacts on Tropical Island Freshwater Fish Assemblages

Patrick B. Cooney and Thomas J. Kwak

Habitat connectivity is vital to the persistence of migratory fishes. Native tropical island stream fish assemblages composed of diadromous species require intact corridors between ocean and riverine habitats. High dams block fish migration, but low-head artificial barriers are more widespread and are rarely assessed for impacts. Among all 46 drainages in Puerto Rico, we identified and surveyed 335 artificial barriers that hinder fish migration to 74.5% of the upstream habitat. We also surveyed occupancy of native diadromous fishes (Anguillidae, Eleotridae, Gobiidae, and Mugilidae) in 118 river reaches. Occupancy models demonstrated that barriers 2 meters (m) high restricted nongoby fish migration and extirpated those fish upstream of 4-m barriers. Gobies are adapted to climbing and are restricted by 12-m barriers and extirpated upstream of 32-m barriers. Our findings quantitatively illustrate the extensive impact of low-head structures on island stream fauna and provide guidance for natural resource management, habitat restoration, and water development strategies.

Keywords: Caribbean, diadromy, fish passage, restoration, road crossings

Habitat quantity, quality, and connectivity are among the most critical influences on community dynamics and the conservation of biodiversity, but anthropogenic activities have resulted in habitat loss, degradation, and fragmentation. In aquatic riverine environments, dams are constructed and operated to support services for humans (e.g., hydropower, flood control, municipal and agricultural water supplies, and recreation), but dam effects on the aquatic community are widespread and severe, including hydrologic and habitat alterations in the upstream and downstream directions (March et al. 2003, Johnson et al. 2008). Dams also fragment the river network continuum, and that habitat fragmentation is especially problematic for diadromous fauna that require connectivity between marine and freshwater habitats (figure 1; Holmquist et al. 1998, Neal et al. 2009). The effects of large, high dams in temperate regions have been characterized in the published literature, but small- or medium-size dams are much more prevalent, and there have been few studies of them in tropical environments (Pringle et al. 2000, Heinz Center 2002).

To better understand the effects of artificial barriers (e.g., dams, flood-control structures, road crossings) on fish migration and occurrence, we conducted extensive surveys to locate and characterize artificial barriers of all sizes to native fish migration in the tropical rivers of Puerto Rico. We then integrated fish survey data among all 46 island river drainages (Kwak et al. 2007) with the artificial barrier inventory and identified the characteristics of barriers that block native fish migration and limit fish distribution. This analysis allowed us to quantify the limitations to native fish distributions caused by artificial in-stream barriers of all sizes, especially the more widespread low-head structures. We hypothesized that including in-stream barriers of all sizes in our assessment would reveal a substantial impact on native fishes, but we could not predict a priori the extent or dynamics of those effects islandwide.

Diadromous fish habitat requirements and limitations Diadromous fish use both freshwater and marine habitats to complete their life cycle, exposing them to in-stream, estuarine, and oceanic environmental impacts and greater risks than nonmigratory species (Kinzie 1988, Jonsson et al. 1999). Diadromous fish face human exploitation, dense human populations, habitat degradation, spread of alien species, and exclusion from critical habitats by dams and impoundments (McDowall 1999, Brashier 2003). Of the approximately 250 known diadromous species worldwide, 18% are of conservation concern (McDowall 1999), which indicates a conservation need to identify and minimize anthropogenic effects on migratory species.
Figure 1. Dams and other in-stream barriers to diadromous fish migration come in many sizes and forms, including (a) large, high dams with regulated flow; (b) large, high dams with run-of-the-river flow; (c) large, flood-control structures; (d) road crossings with various bridge and culvert designs; (e) small, low-head dams; and (f) natural waterfalls. Among these barrier types, those represented by panel (a) block the migration of all native diadromous fish species; those depicted in panels (b), (c), and (f) block the migration of all species but gobies; those depicted in panels (d) and (e) restrict but do not block the migration of all species but gobies; and all in-stream barriers reduce fish migration and river habitat connectivity. Photographs: Patrick B. Cooney.
Habitat connectivity is a primary factor in shaping stream communities (Vannote et al. 1980, Cote et al. 2009), and interruptions in the river continuum can hinder fish passage (Neal et al. 2009, McDowall 2010). At the transition from saltwater to freshwater environments, upstream migration distances and distributions of diadromous fish depend on stream and habitat connectivity (Kwak et al. 2007, Hall et al. 2011). Therefore, diadromous fish are reduced in abundance and diversity and frequently extirpated from affected river reaches (Reyes-Gavilán et al. 1996, Holmquist et al. 1998, Greathouse et al. 2006).

Most diadromous species are widely distributed because of their larval marine dispersal (McDowall 2010), but local populations typically occupy restricted areas or isolated regions and may carry unique genetic signatures (Jonsson et al. 1999). Further extirpation and reduction in the abundance of diadromous fish through anthropogenic actions may cause the loss of important yet highly vulnerable populations (McDowall 2010). Society is growing aware of the benefits of preserving the integrity of the remaining aquatic ecosystems and the need to restore those that are damaged (González-Cabán and Loomis 1997); therefore, current losses may be reversed or mitigated through conservation, but identifying, evaluating, and minimizing relevant factors will first be necessary (Cote et al. 2009).

Stream barriers play an important role in fish distribution and abundance and cause limitations to fish movement, depending on the ability of each species to ascend or descend the obstruction. Numerous diadromous species worldwide have evolved traits that enable passage of formidable natural stream barriers (McDowall 2010). Anadromous salmonids have strong jumping abilities (Kondratieff and Myrick 2006), whereas numerous amphidromous goby species have fused pelvic fins that form a suction disc, which allows them to ascend steep, wetted gradients and waterfalls (Schoenfuss et al. 2011). This allows them access to critical spawning habitat and release from predators that lack similar climbing capabilities (Tate 1997). Conversely, those diadromous fish species that lack strong jumping or climbing abilities are restricted to lower-elevation river reaches, below major migration impediments (Holmquist et al. 1998).

Beyond natural barriers, a loss of stream connectivity occurs with diversion, damming, and channelization of rivers and with modification of habitat through impoundment and bed alteration (Benbow et al. 2002). Similar to natural waterfalls, artificial barriers block passage of some upstream-migrating fish, especially high dams that lack wetted sloped spillways and create large lentic reservoirs that are unsuitable for stream fish (Holmquist et al. 1998). Similarly, small dams reduce stream corridor connectivity. Consequently, both high dams and smaller artificial barriers, including low-head dams and road crossings (figure 1), may extirpate fish from upstream environments and critically reduce habitat availability (Trombulak and Frissell 2000, March et al. 2003). Furthermore, high densities of migratory fish in a bottleneck below migration barriers could lead to greater predation and competition (Benstead et al. 1999).

Diadromous fish have been extirpated from riverine habitats throughout the world by dams and other anthropogenic effects, critically endangering numerous species and metapopulations (Jelks et al. 2008). Ecoregions with a high incidence of diadromous and endemic fishes are most vulnerable to dam effects (Reidy Liermann et al. 2012). Nonnative fish are often introduced through deliberate and accidental actions affecting reservoirs and upstream fluvial habitat (Neal et al. 2009). Sport fish are stocked to provide consumption and recreational opportunities, and aquarium and aquaculture fish are introduced without concern for or understanding of native food webs and ecosystem processes. Because of the decline or lack of native fish species in impounded environments, introduced fish species often thrive and subsequently spread to downstream habitats, where interactions with native fauna and the spread of foreign parasites may further affect distributions and abundances, possibly leading to extirpation (Quinn and Kwak 2003, Fitzsimons et al. 2007).

**Tropical island native diadromous fish**

Globally, native fish assemblages of tropical and subtropical islands of volcanic origin are often composed entirely of diadromous species (Keith 2003, March et al. 2003). These insular populations require connectivity between riverine and marine environments—and perhaps among islands—for stream fauna to complete their life cycle (McDowall 1999, 2010). Permeable stream corridors are vital for migration, and interruptions caused by barriers are dominating factors in determining local stream macrofauna diversity (Kwak et al. 2007). High-elevation mountains dominate volcanically formed island landscapes, forming high-gradient rivers with waterfalls and cascades that may restrict fish distribution (Brasher 2003, McRae 2007).

One such island is Puerto Rico, the fourth largest of the Antilles Islands. Puerto Rico represents the densest human population in the Caribbean and ranks among the densest populations in the world (Hunter and Arbona 1995). Although urbanization affects water quality within a watershed, the presence and abundance of native amphidromous species (Anguillidae, Eleotridae, Gobiidae, and Mugilidae) in tropical urban streams is best explained by longitudinal habitat connectivity rather than by the degree of urban impact (Kwak et al. 2007, Ramírez et al. 2012). Over the past century, an expanding human population, accompanied by agricultural and industrial needs, led to higher demand for water and the subsequent damming of almost all of the 46 major rivers in Puerto Rico (Hunter and Arbona 1995, Cooney and Kwak 2010). As dam construction expanded in the first half of the twentieth century, the consequences for migratory stream fish in Puerto Rico were not considered, because the fish assemblages and their life-cycle needs were not fully understood, which led to the fishes’ extirpation from upstream habitats (Holmquist et al. 1998). Compared
with other tropical regions, the density of large dams in Puerto Rico is high, and the dams and road crossings have been in place for an extended period of time (Greathouse and Pringle 2006). These conditions render Puerto Rico a model system for evaluating the effects of dams on aquatic environments and for the exploration of conservation management options.

Up to 10 native freshwater fish species inhabit Puerto Rico, including gobies (Gobiidae, up to five species), sleepers (Eleotridae, three species), mullet (Mugilidae, one species), and an eel (Anguillidae) (Neal et al. 2009). All of these native species are diadromous; the American eel (Anguilla rostrata) is catadromous, and the others are amphidromous. Amphidromous fish are represented by about 60 species worldwide (McDowall 1999) and have a unique life history in which adults live and spawn in streams, larvae hatch and drift downstream to the sea, pelagic larvae develop in estuaries or the ocean, and postlarvae recruit to rivers and migrate upstream (Keith et al. 2008). All of these species require a connection between rivers and the ocean to complete their life cycle (McDowall 1999, 2010).

Similar to other diadromous species, amphidromous species function ecologically to import marine-derived nutrients and biomass into rivers during their migrations (Bell 1999). Disruption of this cycle not only carries consequences for stream flora and fauna but may also influence in-stream basal food sources and terrestrial–aquatic nutrient and energy exchanges (Nakano and Murakami 2001, Greathouse et al. 2006). In addition to their ecological value, amphidromous species support historically important subsistence fisheries and provide cultural, recreational, and food values to humans (Bell 1999, Cooney and Kwak 2010). Throughout the tropics, amphidromous goby larvae and adult mullets are harvested in large quantities to supply vital protein to island communities depauperate of large native terrestrial animals (Phillip 1993, Bell 1999). Declining populations of upstream migrating fish could therefore limit the available nutrients and biomass for stream flora, fauna, and human populations.

Of the amphidromous fishes in the Caribbean region, the sirajo goby (formerly Sicydium plumieri, recently recognized as four distinct species; Watson 2000) and the river goby (Awaous banana) are commonly found at all elevations in free-flowing rivers because of modified pelvic fins that allow them to climb waterfalls (Ford and Kinzie 1982, Benstead et al. 1999), whereas the smallscaled spinycheek sleeper (Eleotris perniger), the bigmouth sleeper (Gobionorus dormitor), and the mountain mullet (Agonostomus monticola) are found only upstream of barriers over which they can jump (Kwak et al. 2007). Native amphidromous shrimp species are occasionally found upstream of high dams and large reservoirs in Puerto Rico (Kwak et al. 2007), and one bigmouth sleeper population is found in a high mountain reservoir (Bacherler et al. 2004), which indicates exceptional spillway flow events that would have enabled upstream migration or populations that are uniquely adapted to strictly freshwater life cycles. However, because of artificial migration barriers, much of the island currently lacks native diadromous fish species, but the magnitude of this habitat loss is unknown (Kwak et al. 2007).

A critical knowledge gap

Existing databases, such as the US National Inventory of Dams, document the locations of high dams. Accordingly, the impacts of such large in-stream structures on stream ecosystems and faunal composition have been examined by the scientific community. In contrast, smaller in-stream barriers are rarely mapped, their effects on faunal composition and ecology are poorly known, and their potential impact on tropical islands is especially high.

As the optimal locations for high dams in the tropics were exhausted over time, a shift to smaller-scale projects ensued (Vaux and Goldman 1990). Therefore, in addition to high dams and reservoirs, low-head dams span streams and rivers, posing additional migration barriers to native amphidromous species (figure 1; Benstead et al. 1999, March et al. 2003). Low-head dams not only fragment river landscapes but also degrade habitat and water quality (Santucci et al. 2005). Because islands are restricted in area, many island species exist as small networks of a few populations, and habitat loss is a more pronounced problem in these regions (Murphy and Cowan 2007). Therefore, mismanagement of the freshwater resource could potentially decimate these populations.

No comprehensive database of dams and artificial migration barriers exists for Puerto Rico, which prohibits the assessment of the limitations that these dams pose to stream fauna migration. The 2010 US National Inventory of Dams lists only 32 dams, all of which exceed 7.5 meters (m) in height, and a majority are more than 30 m high (http://nid.usace.army.mil). There is a clear need to document artificial barriers of all sizes to quantify and understand aquatic habitat loss in order to guide the decisions associated with the barriers’ impact on migratory fishes and the increasing demand for water, because dams and road crossings continue to be constructed across the Caribbean and tropics (Hunter and Arbona 1995, Benstead et al. 1999). This integrated research is also urgently needed to assist resource agencies in identifying dams that may be unsafe, dysfunctional, or otherwise candidates for removal, as well as dams that might be candidates for the installment of fish passage devices to mitigate upstream habitat loss.

Islandwide fish and dam surveys

We surveyed fish assemblages from 118 river reaches in all 46 of the major river drainages of Puerto Rico (figure 2). The reaches ranged from 100 to 150 m; incorporated riffle, run, and pool habitats; and were blocked at each terminus with block nets. Triple-pass-depletion methods were conducted with either a barge or two backpack electrofishers, proceeding in an upstream direction, which allowed a high rate of detection (Kwak et al. 2007). All fish were weighed, measured, and identified to the species level.
We identified 335 dams and other in-stream barriers along the 9187 river kilometers (rkm) in Puerto Rico using aerial photographs, maps, observations while hiking and driving along river corridors, and personal communication (figure 2). The locations of 29 large reservoirs used for hydropower, irrigation, and public supply, mostly built in the 1930s and 1940s, were previously known (Hunter and Arbona 1995); however, we identified, located, and surveyed all other artificial barriers in the rivers of Puerto Rico for this research. Each barrier was visited, and its location, physical, and descriptive characteristics were recorded. The location characteristics included the river basin, the river name, the municipality in which it was situated, the distance to nearest town, the nearest highway, and global positioning system coordinates. The physical characteristics of each barrier included the presence or absence of a fish ladder, the distance to river mouth, elevation, the barrier’s height above the substrate, its height above the water surface at stream base flow on the downstream margin, its width, wetted width, length, construction material, and primary purpose. Photographs were taken of each barrier for future reference.

Integrating fish and dam surveys to understand barrier effects

We observed fish ascending in-stream barriers by climbing or jumping, and we sampled native fish species in reaches upstream of some artificial barriers. To determine those barriers restricting or eliminating fish migration, we integrated our barrier inventory and fish sample data to determine the highest downstream barrier of each sample site. The height above the water surface for each artificial barrier was measured from the surface of the water at stream base flow on the downstream side of the barrier up to the lowest point on each barrier. We then used the highest downstream dam from each fish sample site to represent the limiting height to model migration blockage. Additional artificial barriers of lower height and natural barriers of varying height were present, but we did not account for combined effects, which may further restrict fish migration.

We examined six native fish species individually, as well as the same species stratified into two groups that were based on their abilities to ascend barriers, for artificial barrier heights that block migration. One group included the gobies (sirajo goby and river goby), which have modified pelvic fins that allow them to climb wetted surfaces; the other was the nongoby group (bightmouth sleeper, smallscaled spinycheek sleeper, mountain mullet, and American eel), which more commonly jump out of the water to ascend dams. Although American eels may be associated with climbing wetted surfaces as juveniles, their distribution patterns in Puerto Rico and the dominant presence of vertical artificial barriers yielded American eel distribution patterns similar to those of nongoby species. Furthermore, American eels elsewhere in the Caribbean were blocked from migration by a single barrier that also blocked mountain mullet migration but allowed goby passage (Fièvet et al. 2001).

To determine the dam height at which fish would be expected to be completely blocked from upstream migration, we fit logistic regression models in the program R. The logistic regression model for nominal response is

\[
P(\gamma) = \frac{1}{1 + e^{-\beta_0 - \beta_1 x}}
\]
where \( P(y) \) is the probability of blocking fish passage, \( B_0 \) is the intercept, and \( B_1 \) is the regression coefficient of dam height \( x \). We also estimated the standard error using the delta method to calculate 95% prediction intervals (PI). Approximate 95% PI values were obtained using a normal approximation back-transformed to the probability scale.

To classify the ability of fish species or groups to migrate upstream to a particular river reach, we used inverse prediction to estimate dam heights at two migration-blocking probabilities. A 50% blocking probability indicates that half of the artificial barriers at the given height would be expected to allow fish of the species or group upstream, reflecting 50% expected occupancy. We also estimated a 95% blocking probability that is expected to allow fish upstream of 1 in 20 artificial barriers at the dam height, or 5% expected occupancy. Given that only one individual need be present to indicate occupancy, the 50% blocking height is interpreted as highly restrictive of fish migration, and the 95% height signifies extirpation of fish from upstream habitat. Therefore, to estimate habitat loss, we considered a river reach accessible if there were no downstream artificial barriers greater than or equal to the 50% blocking height, restricted if it was above the 50% blocking height value but below the 95% value, and extirpated if it was above the 95% blocking value.

We then analyzed the barrier heights that restrict or extirpate fish from migration in a geospatial context (ESRI ArcGIS v.10.0) to determine the total amount and spatial distribution of restricted and inaccessible habitat. We estimated the total length of upstream riverine habitat affected by any artificial barrier (higher than 0.1 m), including those lower than the 50% blocking height, and the restricted and extirpated total reach lengths. US National Hydrography Dataset flowlines were obtained from the Puerto Rico Gap Analysis Program (Gould et al. 2007) and were georeferenced using the Geographic Coordinate System North America 1983 and projected using the North American Datum 1983 State Plane Puerto Rico Virgin Islands FIPS 5200 coordinate systems.

**Widespread barrier effects vary among fish taxa**

The native diadromous fish species were sampled with varying abundances and distributions among 118 sample sites (table 1, figure 2). Native fish were completely lacking from 20 sites, and at 22 other sites, only goby species were found, primarily at high elevations with downstream artificial barriers. Gobies were present at 86 sites, whereas the 4 nongoby species were found at 76 sites, predominantly in middle- and lower-elevation river reaches.

We identified and surveyed 335 artificial barriers, including 203 dams, 115 road crossings, 14 pipe crossings, and 3 aqueduct crossings (table 2, figure 2). This amounted to an average dam density of 0.036 dams per rkm or 0.038 dams per square kilometer over the island, with a frequency of one dam every 27.4 rkm. More than 300 were constructed from cement, which was the most frequent construction material, followed by earthen, stone, and brick structures. Water withdrawal (44%) and road crossings (34%) were the predominant primary purposes of the barriers, whereas flood control (10%) and hydroelectric (4%) dams were less common. The height above the water surface of all barriers ranged from 0.1 to 98.0 m, and those for road crossings ranged from 0.1 to 12.0 m (table 2, figure 3). A vast majority of the artificial barriers were small dams less than 5 m high (283 dams, 84.5%), and only 27 (8.1%) exceeded 20 m in height (figure 3). Despite their low occurrence, hydroelectric dams played a significant role in altering native fish distributions because of their height, which averaged 30.6 m, compared with a mean of 4.2 m for all other artificial barriers.

Many more roads cross Puerto Rico streams than those we surveyed, but our account represented those crossings with artificial structures spanning the entire riverbed. We did not include crossings with free-spanning bridges that were passable by fish. The road crossings that most frequently blocked fish migration were smaller roads, predominantly in rural areas and with culvert crossings that were presumably designed to exit at grade along the downstream edge. However, high flows passing through restricted culverts had

<table>
<thead>
<tr>
<th>Table 1. Native diadromous fish species and number of sites (among 118 total) where each was sampled in Puerto Rico rivers.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Common name</strong></td>
</tr>
<tr>
<td>Nongoby species</td>
</tr>
<tr>
<td>Mountain mullet</td>
</tr>
<tr>
<td>Bigmouth sleeper</td>
</tr>
<tr>
<td>American eel</td>
</tr>
<tr>
<td>Smallscaled spinycheek sleeper</td>
</tr>
<tr>
<td>River goby</td>
</tr>
</tbody>
</table>

**Note**: The American eel is catadromous, and all of the other species are amphidromous. The sirajo goby, formerly *Sicydium plumieri*, was recently recognized as four distinct species (Watson 2000).

<table>
<thead>
<tr>
<th>Table 2. Characteristics of 335 artificial in-stream barriers surveyed in Puerto Rico rivers.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dam attribute</strong></td>
</tr>
<tr>
<td>Distance to river mouth (in kilometers)</td>
</tr>
<tr>
<td>Elevation (in meters)</td>
</tr>
<tr>
<td>Height above water (in meters)</td>
</tr>
<tr>
<td>Width (in meters)</td>
</tr>
<tr>
<td>Downstream wetted width (in meters)</td>
</tr>
</tbody>
</table>
scoured and downcut the downstream bed material at these sites, creating perched drops.

We encountered only 15 fish-passage structures among the 335 artificial barriers (4.5%). Only four (1.2%) appeared specifically designed to allow fish passage, and just one, on Rio Culebrinas, was functional, and the remaining three were dilapidated beyond repair. The other 11 fish-passage devices were notches incorporated into the barrier to allow the removal of sediment from the upstream pool; 4 of those were actively passing water in river reaches where native fish were present. However, the lack of design for fish passage of these notches may render them a hazard to fish that ascend artificial barriers using that route. Almost all of the notches were positioned adjacent to water intake screens within the upstream pool, which would pose a risk of impingement or entrainment to the fish. In addition, the notches were often decommissioned by a metal plate that blocked water flow, except when personnel manually removed the plate to flush accumulated upstream sediment.

The logistic regression for the nongoby fishes (bignose sleeper, smallscale spinycheek sleeper, mountain mullet, American eel) yielded a 50% blocking dam height of 1.9 m, with a 95% PI of 1.4–2.4 m (table 3). This indicated that we would expect to detect at least one nongoby fish upstream of any dam 1.9 m in height 50% of the time. The 95% blocking height of this group was 4.1 m, with a 95% PI of 2.8–5.4 m. Therefore, it is highly unlikely to find a native nongoby fish upstream of a 4.1-m barrier. Empirically, we found nongoby individuals upstream of several barriers 2.4 m high but never upstream of any barrier 2.5 m or higher. Among the 335 dams that we surveyed, 130 (38.8%) were higher than the nongoby 50% blocking height (1.9 m), and 59 (17.6%) were higher than the 95% blocking height (4.1 m).

For the goby species group, the 50% blocking dam height was 12.1 m (95% PI = 5.1–19.1 m), about 6.5 times greater than that for the nongoby species (table 3). The height at which gobies were extirpated from upstream habitat (i.e., the 95% blocking height) was 31.9 m (95% PI = 13.0–50.7 m), which reflects the climbing ability of these fishes. Among our sample sites, we empirically found river goby upstream of a single artificial barrier that was 10 m high and sirajo goby upstream of several artificial 10-m barriers but no native fish upstream of any 17-m barrier. We surveyed 29 dams (8.7%) that were higher than the goby 50% blocking height (12.1 m) and 19 (5.7%) were higher than their 95% blocking height (31.9 m).

The individual-fish-species effects of artificial barriers were similar to those of the within-groups (i.e., gobies and nongobies) comparison, with overlapping 95% PIs (table 3). Of the four nongoby species, the mountain mullet had the greatest ability to ascend artificial barriers, followed by the bigmouth sleeper, the American eel, and the smallscale spinycheek sleeper. Low dams and road crossings played a dominant role in limiting the distribution of these four species. Most low dams did not function as migration barriers for gobies; high dams were the prevailing migration barriers for that taxon. The sirajo goby demonstrated greater climbing abilities than the river goby, with higher barriers required to restrict the sirajo goby’s migration.

### Table 3. Dam height (in meters) that blocks migration of amphidromous fish species and species groups at 50% and 95% of dam occurrences, with 95% prediction intervals (PI).

<table>
<thead>
<tr>
<th>Species</th>
<th>50% blocking</th>
<th>95% blocking</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nongoby</td>
<td>Dam height</td>
<td>95% PI</td>
</tr>
<tr>
<td>Bigmouth sleeper</td>
<td>1.9</td>
<td>1.4–2.4</td>
</tr>
<tr>
<td>Mountain mullet</td>
<td>1.1</td>
<td>0.7–1.5</td>
</tr>
<tr>
<td>Smallscale spinycheek sleeper</td>
<td>1.6</td>
<td>1.1–2.0</td>
</tr>
<tr>
<td>American eel</td>
<td>0.4</td>
<td>0.1–0.7</td>
</tr>
<tr>
<td>Goby</td>
<td>12.1</td>
<td>5.1–19.1</td>
</tr>
<tr>
<td>Sirajo goby</td>
<td>7.0</td>
<td>1.5–12.5</td>
</tr>
<tr>
<td>River goby</td>
<td>5.4</td>
<td>1.0–9.8</td>
</tr>
</tbody>
</table>

### Extensive habitat loss

Of the 9187 rkm in Puerto Rico, native fishes were restricted in or extirpated from a majority of the habitat (table 4, figures 4 and 5). The length of river downstream of artificial barriers greater than or equal to 1.9 m in height totaled...
Articles

3917 rkm, or 43% (table 4), and nongobies were restricted in access or extirpated from 5270 rkm, or 57% of the island’s riverine habitat (figure 4b). Artificial barriers as high as or higher than 12.1 m restricted the two goby species in or extirpated them from 36% of the upstream habitat (table 4, figure 4a). Intermediate zones—between barriers 4.1 m and 31.9 m in height—that were available to only goby species among native fishes spanned 1586 rkm, or 17.3% of the total river length (figure 5b). However, only 280 of those 1586 rkm were below barriers 12.1 m high (50% blocking height; table 4). Finally, all artificial barriers of any height affected migration to 6846 rkm of the upstream habitat, potentially limiting fish abundance and distribution in 75% of all Puerto Rico riverine habitats.

A model for comprehensive dam impact assessment

Our comprehensive study approach and results provide a model that may be applied more broadly to assess the extent and elucidate the attributes of artificial in-stream barriers and the associated mechanisms that block fish passage. Our research is the first integration of complementary stream surveys on fish distributions of an entirely diadromous native assemblage and artificial migration barriers at a comprehensive spatial scale. This allowed the identification and quantitative description of impacts that would not be possible by either data set alone.

Previously, high dams that impound large reservoirs were known to prevent the upstream passage of migrating diadromous fish (Holmquist et al. 1998, Greathouse and Pringle 2006); however, the degree to which low-head dams and road crossings acted as migration barriers was unknown. Dams are the most critical influence on community structure in regions in which diadromy is prevalent (Joy and Death 2001), and therefore, documenting artificial barrier locations and their impact is imperative to lotic fauna conservation. Dams and road crossings that are constructed across natural gradient changes and that allow passage similar to that of the original natural barrier may function as a minimal barrier to migration beyond historical natural constraints. However, dams and barriers constructed in downstream coastal plains in locations free of natural barriers are most detrimental to the lotic community (Joy and Death 2001). Therefore, low-head dams and road crossings may play a larger role than high dams in limiting diadromous fish distribution in areas with coastal plains that prohibit high-dam construction. Throughout the tropics, modifications to stream ecosystems have been most ecologically destructive at lower elevations (Brasher 2003). Low-head dams and road crossings in Puerto Rico were found at lower elevations (at a mean of 153.3 m above sea level) and shorter distances from river mouths (a mean of 25.6 kilometers [km]) than were high dams (236.2 m and 35.7 km, respectively), which demonstrates the prevalence and significant ecological impacts of small dams and other low artificial in-stream barriers on diadromous fish migrations and distributions. Therefore, the spatial location of all artificial barriers is critical in guiding strategic planning for the construction, modification, operation, and removal of dams in the future.

Patterns and differences among taxa and regions

The effects of artificial in-stream barriers on fish migration and habitat availability vary among species, which results in changes in the fish assemblage within and among rivers. Diadromous fish species vary in swimming and climbing abilities and instinctive migratory drive, which causes differences in their upstream distribution (McDowall 1999) that we quantified for Puerto Rico streams. The two gobies show greater migratory capacity and occur farther inland and higher in elevation than the other four species. We found high occupancy of exotic species in upstream habitats in which native species had been extirpated (Kwak et al. 2007). Our findings describe a longitudinal continuum in the stream fish assemblage driven by in-stream migration barriers and habitat availability ranging from the complete native assemblage at lower elevations, upstream through zones of

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### Table 4. The length and accessibility of affected habitat (in river kilometers [rkm], out of 9187.02 total rkm) and cumulative affected habitat (in rkm) of Puerto Rico rivers with artificial barriers of varying height.

<table>
<thead>
<tr>
<th>Artificial barrier height (in meters)</th>
<th>Length of the river habitat affected by barriers of this height</th>
<th>Proportion of the total habitat affected by barriers of this height</th>
<th>Length of the river habitat affected by barriers of this or greater height</th>
<th>Proportion of the total habitat affected by barriers of this or greater height</th>
<th>Habitat status for nongoby species</th>
<th>Habitat status for goby species</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–0.1 (free flowing)</td>
<td>2340.92</td>
<td>0.255</td>
<td>9187.02</td>
<td>1.00</td>
<td>Accessible</td>
<td>Accessible</td>
</tr>
<tr>
<td>0.1–1.9</td>
<td>1575.93</td>
<td>0.171</td>
<td>6846.10</td>
<td>0.745</td>
<td>Accessible</td>
<td>Accessible</td>
</tr>
<tr>
<td>1.9–4.1</td>
<td>1695.24</td>
<td>0.185</td>
<td>5270.17</td>
<td>0.574</td>
<td>Restricted</td>
<td>Accessible</td>
</tr>
<tr>
<td>4.1–12.1</td>
<td>280.33</td>
<td>0.031</td>
<td>3574.93</td>
<td>0.389</td>
<td>Extirpated</td>
<td>Accessible</td>
</tr>
<tr>
<td>12.1–31.9</td>
<td>1306.42</td>
<td>0.142</td>
<td>3294.60</td>
<td>0.358</td>
<td>Extirpated</td>
<td>Restricted</td>
</tr>
<tr>
<td>31.9 and higher</td>
<td>1988.18</td>
<td>0.216</td>
<td>1988.18</td>
<td>0.216</td>
<td>Extirpated</td>
<td>Extirpated</td>
</tr>
</tbody>
</table>

Note: Accessible river lengths were available to all individuals of the fish assemblage component. Restricted lengths allowed access to the assemblage component at 50% of barrier occurrences. Extirpated lengths were unavailable to all individuals of the assemblage component. See the text for information on the species surveyed.
that many diadromous fish species in Japan were blocked by low-head dams, but several amphidromous gobies were unaffected by low-head dams several meters high because of their climbing abilities. Research from the Lesser Antilles suggested that the mountain mullet and the American eel variably reduced numbers of native species, to an entirely exotic fish assemblage at the highest elevations (figure 6).

Similar patterns, with a loss of native diadromous species as barriers are encountered, have been documented in other locations. Fukushima and colleagues (2007) found

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Figure 4. Accessible, restricted, and extirpated river reaches for (a) goby (sirajo goby and river goby) and (b) nongoby (bignose sleeper, mountain mullet, smallscale spinycheek sleeper, and American eel) native diadromous fishes, limited by artificial in-stream barriers in Puerto Rico rivers. Abbreviations: km, kilometers; m, meters.
Figure 5. Accessible, restricted, and extirpated river reaches for goby fishes (sirajo goby and river goby), nongoby fishes (bigmouth sleeper, mountain mullet, smallscaled spinycheek sleeper, and American eel), and the entire native diadromous fish assemblage, (a) 50% and (b) 95% blocked by artificial in-stream barriers in Puerto Rico rivers. Abbreviations: km, kilometers; m, meters.
were blocked from upstream migration by a 4-m diversion weir, whereas *Sicydium* gobies were not (Fièvet et al. 2001). Our findings confirm the general pattern that amphidromous fish distributions are anchored in lower river reaches and expand variably into upstream habitats.

Related research on Pacific island diadromous fishes suggests similar patterns to those we found. Hawaii is host to five amphidromous fish species, and most of Hawaii’s streams are diverted, dammed, or channelized (Benbow et al. 2002). Similarly, Japan has a diverse assemblage of diadromous fishes in affected stream systems (Katano et al. 2006). Upstream migration of Pacific amphidromous fish is species dependent and varies with the species’ climbing ability (Benbow et al. 2002, Fitzsimons et al. 2007). In Hawaii, a sleeper (*Eleotris sandwicensis*) and a goby (*Stenogobius hawaiiensis*) species are each limited by barriers a meter or more in height; two other species with modified pelvic fins for climbing, including an *Awaous* species, are limited by barriers approximately 10–20 m high (Fitzsimons et al. 2007); and one goby species is found above much higher barriers, including a waterfall over 300 m high (Englund and Filbert 1997). Similarly, nonclimbing species were unable to migrate over artificial barriers 1.5–3.9 m high in Japanese streams, whereas two goby species were able to ascend (Katano et al. 2006).

Comparatively, the nongobies in our study were limited by barriers 0.4–4.1 m high, the *Awaous* (river goby) by barriers 5.4–25.7 m high, and *Sicydium* by those 7.0–35.5 m high (table 3), which indicates common climbing abilities and barrier height restrictions for related taxa among regions. Furthermore, we collected the sirajo goby (*Sicydium*) upstream of waterfalls over 30 m high in Puerto Rico and upstream of an extensive subterranean river system in the Río Arecibo drainage (figure 2). McDowall (1999) claimed that given suitable conditions, there is virtually no barrier height that gobies with pelvic fins modified for climbing could not pass.

Despite the climbing abilities of goby species, their densities and biomass are commonly significantly reduced above artificial barriers (Joy and Death 2001, Katano et al. 2006, Kwak et al. 2007). Diadromous fishes expend energy jumping and scaling artificial barriers, which may lead to a loss of energy reserves and which may limit migration distance (Benbow et al. 2002, Blob et al. 2007). Furthermore, as body size increases, goby climbing abilities decline, which indicates that a maximum size may ultimately be reached that prevents upstream passage and suggests that a greater habitat fragmentation effect occurs for adults than for juveniles or that farther-inland barriers pose a greater climbing restriction to postlarvae that grow as they migrate upstream (Blob et al. 2007). In addition, amphidromous goby species demonstrate different climbing modes that allow for varying climbing durations (Schoenfuss et al. 2011). This is in accord with our finding that the sirajo goby, the smaller goby species with greater climbing duration abilities, was able to migrate above higher barriers than was the larger river goby (table 3). Conversely, species that jump rather than climb over barriers are able to jump higher as they grow (Kondratieff and

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**Figure 6. In-stream barriers block the upstream migration and limit the distribution of native diadromous fish species at varying heights, forming a continuum in the fish assemblage from native to exotic species proceeding upstream. Abbreviation: m, meters.**
Myrick 2006), which suggests greater migration challenges for juvenile mountain mullets, bighorn sleepers, and small-scaled spinycheek sleepers than for the adults.

American eels are catadromous and, therefore, face different migration constraints than do amphidromous fish, because they actively migrate downstream as adults and ascend rivers as juveniles. American eel populations have declined across the Atlantic basin, owing to multiple contributing factors, including migration barriers in freshwater environments (Haro et al. 2000). Dams and other artificial barriers are detrimental to American eels through adult eel mortality during downstream passage, blocked upstream migration of juveniles, skewed sex ratios, reduced growth rates, and altered population size structure (Haro et al. 2000).

**Indirect fish migration and ecological effects**

Although gobies have greater access to upstream habitat, they are highly affected by dam construction. Currently, only 3% of the river length in Puerto Rico is accessible to gobies where nongobies have been extirpated by artificial barriers (table 4). Previously, beyond the first major waterfall that acted as a barrier against predators, the schooling and escape behaviors of the gobies were replaced by agonistic interactions between individuals competing for space and food (Keith 2003), whereas with artificial barriers, they are forced to share downstream habitats with the entire community and to continuously avoid predation.

Beyond increasing predation on gobies, a reduction in migration to upstream habitat may eliminate the goby’s access to critical habitats at higher elevations. Amphidromous gobies are frequently found at higher abundances in inland stream habitats above natural barriers than below (Kwak et al. 2007, Kido 2008), and different species have been found to distribute into separate stony riverbeds above natural barriers for suitable spawning ground (Tamada 2011). When blocked by artificial barriers, gobies are forced to share habitat in downstream areas. Therefore, the prevention of migration to upstream habitats by artificial barriers may cause a worse reduction in critical habitat for some species than for others and may reduce reproductive isolation among similar species.

Most artificial structures constructed across streams not only block fish migration but also alter water flow patterns. Water flow regulation at artificial barriers affects downstream habitats in numerous ways, including sediment transport. Water quality and temperature alterations caused by artificial structures can reduce the productivity, survival, and growth of downstream fish populations and can restructure fish assemblages (Trombulak and Frissell 2000, Quinn and Kwak 2003), whereas complete extraction of flows, which occurs at multiple sites in Puerto Rico, can leave a dry riverbed. Low flows, dry reaches, and isolated pools diminish navigation for migratory species and prevent downstream larval dispersal and upstream postlarval recruitment (March et al. 2003). Dams exacerbate flow extremes, and pulsed high–low releases create unfavorable conditions and rapid fluctuations that may cause fish population declines (Fiévet et al. 2001).

River flow also plays a role in transporting larvae to estuaries and the ocean, where ocean currents can carry them to other rivers (Cook et al. 2009). Communities at sink locations or following catastrophic events (e.g., drought or flooding) rely on this supply of recruits from source populations through marine larval dispersal. Habitat loss in upstream reaches combined with altered flow conditions from dams may reduce larval outmigration, which may affect both local and distant distribution and dispersal patterns (Luton et al. 2005). Therefore, local declines in affected island rivers may have widespread implications.

Rivers in Puerto Rico generally conform to the river continuum concept. Upstream communities contribute energy and nutrients to downstream estuarine and marine communities (Vannote et al. 1980, Greathouse and Pringle 2006), and altered food webs in upstream reaches could affect downstream freshwater and marine environments that support subsistence and recreational fisheries. The elimination of diadromous populations upstream of high dams has cascading effects on benthic algae, organic and inorganic matter, nutrients, and invertebrates (Greathouse and Pringle 2006).

Amphidromous fish not only contribute energy and nutrients to downstream communities, but their upstream migration also transports marine-derived nutrients to inland environments. The loss of amphidromous fishes from inland stream habitats may reduce terrestrial–aquatic energy exchanges, which may, in turn, affect terrestrial productivity (Nakano and Murakami 2001). Therefore, the impacts of dams and artificial barriers in tropical island streams may be direct—the elimination of migratory fauna—or indirect—altered trophic or energy pathways—and may transmit in upstream, downstream, or lateral directions.

**Informed conservation and management strategies**

Dams have ecological costs, especially in terms of habitat loss for amphidromous fishes, but there is potential to mitigate or eliminate those impacts. Caribbean cultures place great value on island river ecosystems; two-thirds of the Puerto Rico households surveyed said that they would be willing to pay a monthly fee to restore and maintain in-stream flows and the associated environmental quality of local rivers (González-Cabán and Loomis 1997). Our findings can serve as a quantitative basis to prioritize and guide conservation measures associated with dams and artificial barriers, including dam construction, modification to enhance fish passage, operation to provide seasonal flows, and removal of suitable dams.

**Fish passage structures.** Fish passage structures were rare among the dams and road crossings that we surveyed in Puerto Rico. Those few structures for fish passage in river reaches with native species present were damaged or filled with debris, which rendered them impassable by fish. Furthermore, fish
passage devices are rarely designed to accommodate unique morphometric features of amphidromous fish and must incorporate such consideration to be effective (Fièvet 2000). Conversely, effective American eel passage devices have been developed and are among the most simple and cost-effective designs (Knights and White 1998), but their effectiveness with amphidromous fish remains unknown.

Fish passage over a dam that impounds water may appear a logical mitigation measure, but passage must be considered in an ecologically holistic context for it to be successful. Unlike waterfalls, where water velocities increase as the streamflow approaches the cascade, dams impound pools of standing water upstream that function as unsuitable habitat and an additional barrier to migrating diadromous fish. Navigation through reservoirs to upstream riverine habitat can be problematic for diadromous fish (Harris and Smith 1998). Unlike waterfalls, where water velocities increase as the streamflow approaches the cascade, dams impound pools of standing water upstream that function as unsuitable habitat and an additional barrier to migrating diadromous fish.

Navigation through reservoirs to upstream riverine habitat can be problematic for diadromous fish (Harris and Hightower 2011) because of the lack of flow that is critical for amphidromous larvae migration (Benstead et al. 1999) and because of a high abundance of introduced species in the impoundment that either prey on or compete for resources with the native fish (March et al. 2003, Neal et al. 2009). However, research on two Pacific amphidromous goby species demonstrated rapid acquisition of directional migration preferences that aided in upstream swimming over a 10-minute period in minimal flow conditions (Smith and Smith 1998), which suggests that amphidromous species may be able to navigate smaller impoundments.

Amphidromous fish that successfully ascend artificial barriers and navigate through reservoirs may be caught in an ecological trap when they spawn upstream of dams (Schlaepfer et al. 2002). Downstream-drifting embryos and larvae must access saltwater for survival, yet reservoirs can act as traps. Slack water can cause drifting larvae to prematurely settle out in unlivable conditions (March et al. 2003), can expose them to intense predation from invasive species in impounded water (Pelicice and Agostinho 2008), or can cause the larvae to exhaust their yolk sac, which may promote starvation before they reach the estuary (Bell and Brown 1995, Moriyama et al. 1998). Furthermore, water extraction can impinge or entrap downstream-drifting larvae or upstream-migrating juveniles, with mortality estimates ranging from 42% to 100% in one Puerto Rico river (Fièvet and Le Guennec 1998, Benstead et al. 1999, March et al. 2003). Additional research is warranted to improve understanding of amphidromous fish passage dynamics and their efficacy under varying conditions.

**Dam removal.** Numerous dams among the 335 that we surveyed in Puerto Rico are no longer performing their designed function, are unsafe, or are otherwise unnecessary and may be considered for removal. It may be impractical to consider removal of a high dam, but small dams are much more prevalent on the riverscape (nearly 85% are less than 5 m high in Puerto Rico; figure 3). We found numerous low-head dams at abandoned sugarcane and coffee plantations that serve as examples of dams that could be removed to enhance fish habitat without affecting human water needs. Dam removal is an appealing approach to enhance ecological function and allow fish migration in rivers, but removal is costly and complex, so this process warrants careful consideration of the physical and biotic outcomes, and prioritization among sites is critical.

Our integrated findings on the spatial occurrence and attributes of artificial in-stream barriers and associated fish assemblages provide the most basic information to elucidate respective dam impacts and to project the ecological gains from removal. For example, the most downstream-restricting dam on Río Bayamón (9.78 rkm from the river mouth) is 4 m above the water surface, and the only native fish that we collected among multiple fish samples upstream of this dam was a single river goby specimen. Effective fish passage or removal of this dam would restore 195 rkm of native fish habitat. Another example of potential habitat restoration is a pair of dams on Río Tamamá in the Arecibo basin. Removal of the upstream dam of the pair (10.5 rkm from the river mouth, 8 m high) would yield no additional fish habitat, and similarly, removal of the downstream dam (9.6 rkm from the river mouth, 10 m high) would restore less than 1 km of river, but removal of both dams would allow native fish access to an additional 99 rkm of habitat. Our findings may suggest other opportunities among existing barriers for fish habitat restoration.

**Conservation implications.** Our survey is the only known inventory in the Caribbean of dams and other artificial barriers that function to block or restrict amphidromous fish migration. With the widespread distribution of amphidromous species across the tropics and these particular species throughout the Caribbean basin, fish migration limitations for other areas can be inferred from our analyses and may serve as a model for similar assessments in the future. Other investigators have suggested that the approaches and techniques for ensuring the maintenance of amphidromous fish diversity are interchangeable among tropical Pacific islands (Ford and Kinzie 1982, Fitzsimons et al. 2002). Similarities in the scaling patterns of amphidromous gobies from the Pacific and Atlantic suggest that they face similar constraints on performance (Schoenfuss et al. 2011). Catadromous eels also exhibit similar constraints across the globe from artificial barriers to migration, and the construction of passage devices or the removal of dams is an important step toward enhancing stocks and the total breeding population. Amphidromous shrimp in the Caribbean and globally are affected by dams, the disruption of riverine connectivity, and the associated water impoundment and withdrawal (Crook et al. 2009) in a manner similar to that of amphidromous fishes. Considering commonalities in research findings, species composition, and life-history strategies between Pacific high island fish communities and those in the Atlantic basin, our findings here may be broadly but cautiously applicable to the understanding, conservation, and management of all tropical island streams.
The maintenance of viable populations of native diadromous stream fish will require effective and holistic freshwater management strategies. Our findings are directly applicable in Puerto Rico to identify, further assess, and prioritize for removal those dams that are in poor condition or that serve no current function; likewise, our findings may help identify dams that are required for human use but may be considered for fish-passage device retrofitting. Future in-stream construction beyond Puerto Rico and the Caribbean could be designed more ecologically according to the characteristics of those barriers with native fish upstream to minimize the impact of new dams or road crossings. We consider this a comprehensive first step in enhancing the understanding and management of tropical island stream ecosystems, and we look forward to future research on the flow effects of dams and the efficacy of fish-passage approaches to conserve and maintain these unique fish species and their habitats.

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Articles


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