

RESEARCH ARTICLE

Long-term (37 years) impacts of low-head dams on freshwater shrimp habitat connectivity in northeastern Puerto Rico

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Abstract

Freshwater migratory shrimp in Puerto Rico depend on watershed connectivity, from stream headwaters to the ocean, to complete their life cycle. Moreover, shrimp populations in different watersheds are known to be connected in an island-wide metapopulation. However, low-head dams paired with water intakes on streams draining the El Yunque National Forest (EYNF) reduce streamflow. Here, we examine the cumulative effects of low-head dams on shrimp habitat connectivity over 37 years across seven EYNF watersheds. We calculate total and refugia habitat connectivity (where refugia habitat is defined as predator-free upstream reaches above waterfalls >5 m in height) at a monthly time step using a habitat-weighted index of longitudinal riverine connectivity, which incorporates location and operation of water intakes and streamflow variability. Findings indicate total and refugia habitat connectivity declined over 37 years (by 27% and 16%, respectively) as additional water intakes have been placed in lower reaches of watersheds. On a monthly time step, the proportion of streamflow withdrawn has the largest effect on habitat connectivity, with the result that connectivity is ~17% lower during drought years than in nondrought years and ~7% lower in dry compared with wet seasons. Our analysis of this long-term dataset highlights how cumulative effects of low-head dams paired with water intakes have reduced shrimp habitat connectivity. These results underscore the importance of reducing existing withdrawal rates in EYNF, and locating intakes where effects on connectivity are minimal, if conserving shrimp habitat is a management objective.

KEYWORDS

connectivity index, freshwater shrimp, long term, low-head dams, metapopulation, partial barriers

1 | INTRODUCTION

Nearly all large river ecosystems are experiencing decreased connectivity across multiple dimensions due to a variety of factors (Nilsson, Reidy, Dynesius, & Revenga, 2005). For example, longitudinal connectivity (along the stream network) is significantly altered by dams, water withdrawals, and road networks (Kondolf et al., 2006; Pringle, Freeman, & Freeman, 2000; Ward & Stanford, 1995), and temporal connectivity (flow continuity) is influenced by natural or anthropogenic variables affecting stream discharge (Fullerton et al., 2010; Ward,

1989). Loss of connectivity threatens migratory stream populations dependent on movement through stream networks to persist (Freeman, Pringle, Greathouse, & Freeman, 2003; Morita & Yamamoto, 2002; Pringle, 2003). In many cases, these migratory organisms provide ecosystem services such as water filtration, nutrient cycling, and provisioning of basal food resources (Pringle, Hemphill, McDowell, Bednarek, & March, 1999; Willson & Halupka, 1995).

Longitudinal connectivity may be quantified through a variety of indices, which estimate both upstream and downstream passage probabilities for migratory or resident organisms (Bourne, Kehler, Wiersma,

& Cote, 2011; Cote, Kehler, Bourne, & Wiersma, 2009; Diebel, Fedora, Cogswell, & O'Hanley, 2014). Some connectivity indices combine passage probabilities with habitat quality, quantity, or both, allowing stream habitat to be weighted by the impact on the organism of interest (Diebel et al., 2014; McKay, Schramski, Conyngham, & Fischenich, 2013). Although many analyses assess connectivity as a time-averaged index, connectivity indices can be applied at smaller time steps to allow for the detection of seasonal patterns, long-term trends, or periodic connectivity losses (Bourne et al., 2011; Jaeger, Olden, & Pelland, 2014).

Changes in longitudinal riverine connectivity are relevant to migratory organisms, including amphidromous freshwater shrimps. In Puerto Rico, for example, island-wide metapopulations of at least seven amphidromous shrimp species are maintained by connectivity from stream headwaters to the ocean in multiple basins lacking large dams (Cook, Bernays, Pringle, & Hughes, 2009). In this study, we examine temporal trends in shrimp habitat connectivity across seven watersheds in northeastern Puerto Rico by applying a habitat weighted index of longitudinal connectivity at a monthly time step. These watersheds drain El Yunque National Forest (EYNF) and lack large dams; however, low-head dams and associated water intakes can limit habitat connectivity and lead to direct mortality of shrimp larvae through entrainment (Benstead, March, Pringle, & Frederick, 1999).

Conversely, natural barriers over 5 m tall (i.e., waterfalls) block upstream movement of shrimp predators, which include mountain mullet (*Agonostomus monticola*) and American eel (*Anguilla rostrata*; Cooney & Kwak, 2013), creating refugia habitat and leading to higher shrimp densities in predator-free reaches (Covich, Crawl, Hein, Townsend, & McDowell, 2009). Given the abundance of refugia habitat and lack of large dams in northeastern Puerto Rico (Cooney & Kwak, 2013; Snyder, Anderson, & Pringle, 2011), the EYNF may serve as an important larval shrimp source for the island-wide metapopulation. In 2015, Puerto Rico experienced a severe drought, which led to water supply shortages and accompanying proposals for expanded water intake infrastructure. This paper employs a suite of methods to assess cumulative impacts of existing municipal water intakes at low-head dams on migratory shrimp populations.

Our first of three objectives was to (a) examine the magnitude of regional decline in total and refugia habitat connectivity along streams draining EYNF over the last 37 years and (b) quantify the effects of water withdrawal, dry season, and drought on both total and refugia habitat connectivity. We define total habitat connectivity as the proportion of EYNF stream habitat connected to the island-wide metapopulation (i.e., the ocean). We define refugia habitat connectivity as the proportion of EYNF refugia habitat (i.e., upstream from waterfalls >5 m in height) connected to the island-wide metapopulation. We expected a temporal decline in both total and refugia habitat connectivity as a result of increased municipal population and associated water withdrawal over the same period, particularly during dry season and drought conditions.

Our second objective was to determine the effects of water intake location on connectivity by examining temporal and spatial patterns of water intake development within individual watersheds. We examined

whether more recent water intakes were installed in downstream locations outside of EYNF, resulting in the disconnection of larger proportions of upstream habitat. We predicted that more recent intakes would reduce total habitat connectivity but have a minimal effect on refugia habitat connectivity, given the location of waterfalls in the upper portions of watersheds. Our final objective was to explore the implications of regional reductions in total and refugia habitat connectivity and consequent reductions in export of larvae on shrimp metapopulation dynamics across the island.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study is based in EYNF, also known as the Luquillo Experimental Forest, which is managed by the U.S. Department of Agriculture Forest Service. The EYNF spans over 110 km² of tropical rainforest (Weaver, 2012) and includes the Luquillo Mountains, which rise from sea level to a maximum elevation of 1,074 m in less than 20 km (Figure 1). The EYNF receives an average rainfall of 3,860 mm/year (García-Martín, Warner, Scatena, & Civco, 1996), with higher precipitation typically from May through November (Larsen, 2000). Eleven major rivers have headwaters originating from within EYNF boundaries, with numerous waterfalls greater than 5 m in height, and much of the island's northeastern population depends on these rivers for potable water and other uses (Crook, Scatena, & Pringle, 2007). Additionally, the rivers contain a diverse community of migratory organisms, including fishes (Kwak, Cooney, & Brown, 2007), snails (Blanco & Scatena, 2006), and shrimps (Covich & McDowell, 1996). Eleven shrimp species from three families (Decapoda: Atyidae, Xiphocarididae, and Palaemonidae) provide a variety of ecosystem services, such as nutrient cycling (Crawl, McDowell, Covich, & Johnson, 2001; Pringle et al., 1999) and regulating algal growth and community composition (Pringle, 1996). The most prevalent shrimp genera are *Atya*, *Xiphocaris*, and *Macrobrachium* (Scatena & Johnson, 2001).

We focused on seven rivers draining EYNF: Blanco, Canovanas, Espiritu Santo, Fajardo, Gurabo, Mameyes, and Sabana (Figure 1 and Table 1). We included only watersheds with known intakes, withdrawal amounts, and publicly available stream gage data. Our analysis is temporally limited to 1980 through 2016 (37 years), as this represents the most complete data set encompassing all seven watersheds. However, we excluded 17 months from our analysis when no discharge data were available at one or more gages: September 1990, October 2011 to September 2012, January 2016, and October–December 2016. We assumed shrimp presence in all focal watersheds based on long-term monitoring by the U.S. Forest Service (Felipe Cano, U.S. Forest Service, unpublished data).

2.2 | Calculating total habitat connectivity

We applied a modified index of longitudinal riverine connectivity for shrimp (ILRC; Crook et al., 2009) to each intake within our focal

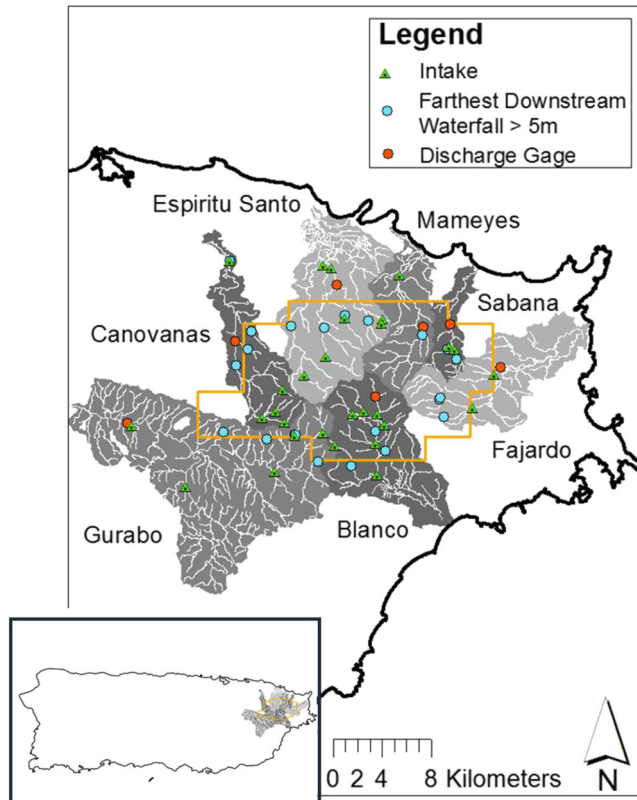


FIGURE 1 The seven study watersheds of El Yunque National Forest. Each watershed is labelled, and the drainage area is coloured in distinct shades of grey. The orange line represents the boundaries of El Yunque National Forest. The white lines indicate the stream flowlines. The red points are the U.S. Geological Survey discharge gages, and the green triangles represent intakes. The blue circles indicate the farthest downstream waterfall over 5 m in height, which were identified using elevation differences between adjacent digital elevation model raster cells in ArcGIS. Inset: Puerto Rico and the seven study watersheds

watersheds, using stream discharge and water withdrawals from intakes averaged for each month, 1980–2016. We delineated each watershed using National Hydrography Dataset Plus (EPA (Environmental Protection Agency), USGS (United States Geological Survey), Horizon Systems Corporation, 2012) flowlines in ArcGIS (Figure 1). Delineations for two watersheds (Canovanas and Gurabo) do not extend to the ocean as we could not identify all intakes and associated withdrawal amounts in the lower portion of the basins. We selected one USGS gage per watershed to estimate daily discharge at each intake, scaling discharge by drainage area at the intake in proportion to drainage area at the gage (Figure 1). We use this technique to estimate discharge based on the minor role of groundwater in these watersheds (Crook et al., 2007), as well as the central location of gages within each watershed in comparison to intake placement (Figure 1 and Table 1). We estimated each intake's daily total withdrawal amount based on data compiled from various agencies, including the Puerto Rican Aqueduct and Sewage Authority, the Department of Natural and Environmental Resources, and the U.S. Forest Service. From these data, we identified 29 intakes with associated withdrawal amounts for our analysis.

The ILRC evaluates the probability a shrimp can move downstream to the ocean (as a larva) and return upstream to the same headwater location (as a juvenile). This index is appropriate as it is specific to migratory freshwater shrimp and aligns with findings by Malvadkar, Scatena, and Leon (2015), which suggest that an index based on flow is the most appropriate for examining the impact of intakes on downstream larval migration. The ILRC incorporates upstream and downstream passage rates at the barrier (i.e., intake) of interest and the cumulative effects of barriers downstream. We calculate the downstream passage rate at a given intake as the proportion of discharge remaining downstream of the barrier, as did Crook et al. (2009). Upstream passage is treated as binary, as juvenile shrimp can migrate over the face of barriers if water is flowing over the surface (Benstead et al., 1999; Holmquist, Schmidt-Gengenbach, & Yoshioka, 1998).

TABLE 1 Characteristics of the seven EYNF watersheds studied

Watershed	Total drainage area (km ²)	USGS gage number	Gage drainage area (km ²)	Maximum number of intakes	Maximum monthly water withdrawn (cms)	Maximum habitat affected (%)	Earliest intake online
Blanco	74.1	5007500	3.3	5	1.1	55.3	1928
Canovanas	46.4	50061800	25.5	5	0.2	93.7	1968
Espiritu Santo	91.4	50063800	22.3	7	0.8	91.3	1980
Fajardo	68.3	50071000	38.6	1	0.5	49.8	1966
Gurabo	179.0	50055750	57.8	5	0.7	84.4	1939
Mameyes	40.3	50065500	17.8	1	0.1	71.7	1998
Sabana	18.5	50067000	10.3	2	0.1	41	1956

Note. Gage drainage area indicates the drainage area of the gage as reported by USGS (km²). Maximum number of intakes represents the highest number of intakes withdrawing water in a month. Maximum monthly water withdrawn represents the largest amount of water withdrawn in a month. Maximum habitat affected is the maximum proportion of habitat upstream of at least one intake over the study period. Earliest intake online is the first year a watershed has a known intake withdrawing water.

Abbreviations: EYNF: El Yunque National Forest; USGS: U.S. Geological Survey.

Thus, upstream passage only affects connectivity at a given barrier when water withdrawal equals or exceeds stream discharge, in which case both downstream and upstream passage probabilities are zero. As such, connectivity at a given time and barrier simplifies to the downstream passage probability.

We estimated cumulative connectivity for each barrier as the product of passage probabilities at that barrier and all (known) downstream intakes as in Crook et al. (2009). However, whereas Crook et al. (2009) estimated connectivity based on median annual flows and constant withdrawal amounts, we estimated cumulative connectivity on a daily time step using stream gage records and accounting for changing withdrawal amounts through time. From daily cumulative connectivity, we estimated a mean monthly ILRC value for each month, 1980–2016, for each of the 29 barriers in our study area. We consider shrimp migrations to be continuous through time, as previous studies do not indicate seasonal trends (Benstead et al., 1999; Crook et al., 2009). The ILRC is calculated as:

$$\text{ILRC} = \text{PrDC}_k * \text{PrUC}_k$$

where PrDC_k is the probability of larvae reaching the ocean originating from upstream of intake k (i.e., cumulative downstream passage rate) and PrUC_k is the probability of juveniles migrating above intake k from the ocean (i.e., cumulative upstream passage rate).

To evaluate the proportion of available shrimp habitat in the study area connected to the island-wide metapopulation (i.e., to the ocean), we weighted monthly ILRC values by habitat quantity, which was calculated using NHDPlus (EPA (Environmental Protection Agency), USGS (United States Geological Survey), Horizon Systems Corporation, 2012) flowlines. We estimated stream length upstream of each intake (extending to the next upstream intake or to the top of the watershed, as appropriate) and then multiplied by the intake's ILRC to estimate habitat connectivity upstream of the intake on a monthly time step. We summed connected habitat across all intakes to determine the shrimp habitat connectivity across the seven EYNF watersheds. We then divided this sum by total stream length across all seven study watersheds to estimate the proportion of total habitat connected:

$$H_c = \frac{\sum_{k=1}^m \text{ILRC}_k * H_k}{H_t},$$

where k represents the intake of interest, ILRC_k is the index of connectivity for intake k , H_k is the stream length upstream of intake k , m is the number of intakes, and H_t is the total stream length across the study area. This provides the proportion of total habitat connected for the entire study area (H_c) to the shrimp metapopulation.

Similar to total habitat calculations, we used NHDPlus flowlines to determine refugia habitat. Waterfalls over 5 m in height were identified using the digital elevation model of Puerto Rico at 10-m \times 10-m resolution and pin-pointing where the difference in elevation between two adjacent raster cells was larger than 5 m along a stream in ArcGIS. We then marked the waterfall farthest downstream in each stream channel (Figure 1) and considered all upstream length to be refugia

habitat. The calculations to determine the proportion of refugia habitat connected were the same as for the proportion of total habitat connected but using refugia stream length.

2.3 | Statistical analysis

We used linear regression to test our predictions that total habitat connectivity and refugia habitat connectivity declined through time, and with droughts and dry seasons. Prior to analyses, we applied a logit transformation ($\log[H_c/(1 - H_c)]$) to the monthly values for proportion habitat connected to better meet the assumptions for linear regression, particularly that the dependent variable is unbounded (Warton & Hui, 2011). We modelled these transformed monthly values ($n = 427$ months per watershed) of habitat connectivity in relation to alternative predictor variables that represented our hypotheses. We represented time in the models with chronological month (i.e., 1–444, for 1980–2016), as we expected the response variable (habitat connectivity) to change through time. Because we also expected the proportion of water withdrawn in relation to total discharge to affect habitat connectivity, this variable (calculated for all intakes combined) along with month was included in all candidate models.

Additional binary variables indicated whether the month fell within a drought year or a dry season. The dry season in Puerto Rico is December to April, and the drought years were 1993, 1994, 1995, and 2015. As droughts can be difficult to identify (Larsen, 2000), drought years were classified based on previous studies (Jennings, Douglas, Treasure, & Gonzalez, 2014; Weaver, 2012) and percent of normal precipitation as defined by National Oceanic and Atmospheric Administration. We did not include the number of intakes withdrawing water in a given month because this also increased through time (correlation with month = 0.84). Finally, we evaluated whether the effects of drought and dry season on habitat connectivity have changed over time by including interactions between each of these variables and chronological month. We standardized the two nonbinary predictors (proportion water withdrawn and month) by subtracting the mean and dividing by the standard error for each.

We fit a total of seven models for each response variable (total and refugia habitat connectivity) using lm in R (v. 3.3.2, R Core Team, 2013; code is available on request from the authors). We used Akaike's information criterion (AIC) to assess relative support among our candidate models (Burnham & Anderson, 2002). The best-supported model was identified as having the lowest AIC value, and the difference in AIC values between the best fit and alternative models indicated relative model support.

2.4 | Watershed analysis

To examine a potential spatial pattern in water intake development, we examined how the proportion of total and refugia habitat upstream of intakes changed through time. We evaluated a correlation between the average annual proportion of habitat upstream of intakes (i.e.,

habitat affected) and habitat connectivity (i.e., H_c). We also evaluated the timing and location of additional intakes, and their impact on the proportion of total and refugia habitat affected within the individual watersheds.

3 | RESULTS

The proportion of total habitat connected, averaged by month, ranged from 0.26 to 0.96, and the proportion of refugia habitat connected ranged from 0.18 to 0.90 over the study period (Figure 2). The lowest monthly values for habitat connectivity occurred near the end of the study period (2015) during wet and drought months (Figure 2). Fewer months were classified as dry ($n = 178$) than wet ($n = 249$), and fewer months were classified as drought ($n = 48$) than nondrought ($n = 379$), with only two recognized droughts occurring between 1980 and 2016. Overall, monthly habitat connectivity declined over time more for total (slope logit transformed = -0.0015 , standard error = 0.0002 ; Figure 2) than for refugia habitat (slope logit transformed = -0.0008 , standard error = 0.0002 ; Figure 2), and refugia habitat connectivity averaged lower than total habitat connectivity at the beginning of the study period (0.64 and 0.86, respectively).

The best-supported model for total habitat connectivity included the proportion of water withdrawn, month, drought, and dry season (Table 2; adjusted $R^2 = 0.63$). The next best-supported model also included an interactive effect of dry season and drought ($\Delta \text{AIC} = 1.22$; Table 2). The best-supported model for refugia habitat connectivity only contained the proportion of water withdrawn and month (Table 2; adjusted $R^2 = 0.66$), and the second best-supported model included either dry season ($\Delta \text{AIC} = 1.88$) or drought ($\Delta \text{AIC} = 1.9$),

TABLE 2 Linear regression models for predicting total habitat connectivity and refugia habitat connectivity

Model	Total habitat Δ		Refugia habitat Δ AIC
	K	AIC	
(1) Proportion withdrawn, month	4	7.8	0
(2) Proportion withdrawn, month, dry	5	5.9	1.9
(3) Proportion withdrawn, month, drought	5	2.8	1.9
(4) Proportion withdrawn, month, dry, month * dry	6	7.4	2.9
(5) Proportion withdrawn, month, drought, month * drought	6	4.8	3.9
(6) Proportion withdrawn, month, drought, dry	6	0	3.8
(7) Proportion withdrawn, month, drought, dry, dry * drought	7	1.2	5.5

Note. Models are listed based on increasing parameter number (K), along with AIC values relative to the best-supported model (ΔAIC).

Abbreviation: AIC: Akaike's information criterion.

but the parameter estimates for both variables included 0 (no effect; Table 3). Both total and refugia habitat connectivity averaged higher in months classified as wet and nondrought (0.78 and 0.61, respectively, for total and refugia habitat) than in months classified as dry and drought (0.63 and 0.47, respectively).

The proportion of water withdrawn (i.e., relative to total discharge; Figure 3) had the largest modelled effect (Tables 3 and 4) for both total and refugia habitat connectivity and varied from 0.02

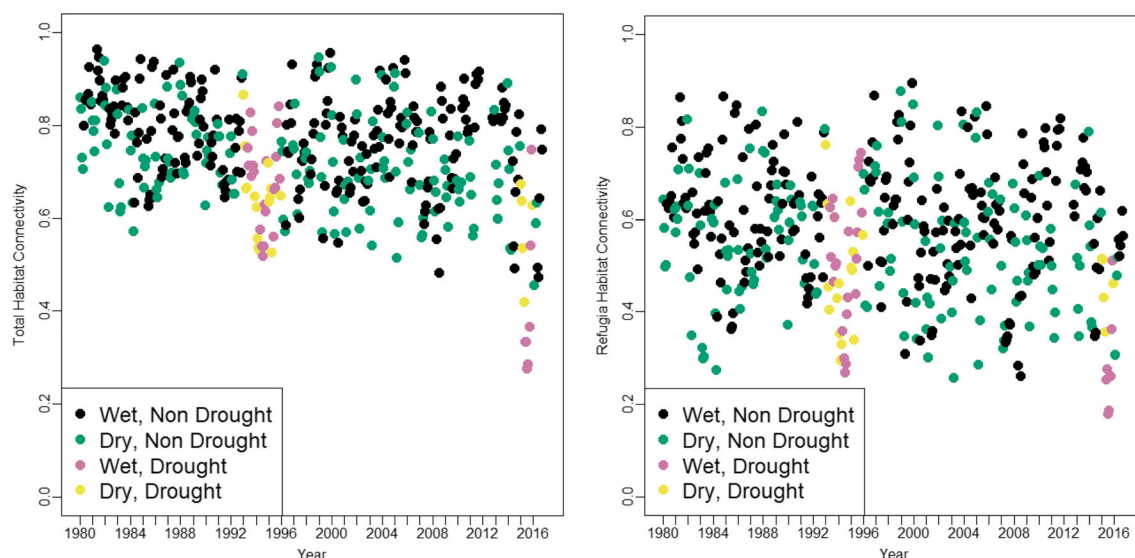


FIGURE 2 (left) Proportion of total habitat connected to shrimp metapopulation throughout El Yunque National Forest (across the seven focal watersheds). (right) Proportion of refugia habitat connected across El Yunque National Forest from 1980 to 2016. Seasons and drought years were classified based on previously accepted values. Habitat connectivity was calculated as the accessible habitat divided by the total stream length across all watersheds

TABLE 3 Refugia habitat connectivity parameter estimates (and standard errors) for predictor variables included in linear regression models

Model	Intercept	Proportion withdrawn	Month	Drought	Dry	Drought * month	Dry * month	Dry * drought
1	0.306 (0.018)	-0.503 (0.018)	-0.073 (0.018)					
2	0.306 (0.018)	-0.502 (0.018)	-0.073 (0.018)		-0.006 (0.018)			
3	0.306 (0.018)	-0.502 (0.002)	-0.073 (0.018)	-0.006 (0.018)				
4	0.306 (0.018)	-0.503 (0.018)	-0.073 (0.018)		-0.007 (0.018)		-0.018 (0.018)	
5	0.306 (0.018)	-0.503 (0.018)	-0.073 (0.018)	-0.007 (0.018)		-0.018 (0.018)		
6	0.306 (0.018)	-0.504 (0.019)	-0.074 (0.018)	0.006 (0.019)	-0.006 (0.018)			
7	0.306 (0.018)	-0.503 (0.019)	-0.074 (0.018)	0.005 (0.019)	-0.006 (0.018)			0.009 (0.018)

Note. Models are listed based on increasing parameter size, as in Table 2. Model 1 (in bold) was the best-supported model.

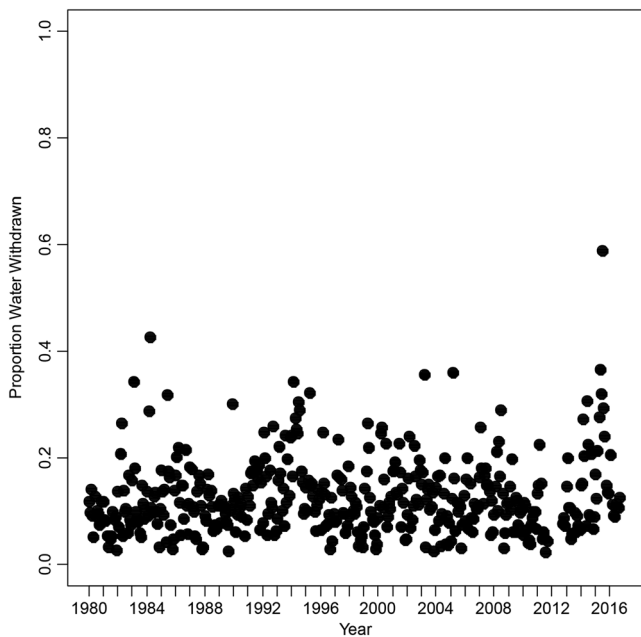


FIGURE 3 The relationship between the proportion of water withdrawn from within El Yunque National Forest and month was not significant (adjusted $R^2 = 0.003$). We calculated the proportion of water withdrawn by dividing the total water withdrawn from all intakes by the total water amount reaching the ocean from the study area

to 0.59 across all months (mean = 0.13, $SD = 0.07$). Increasing the proportion of water withdrawn by 0.07 (i.e., 1 SD) was associated with approximately the same decrease in habitat connectivity expected to occur over 369 months (i.e., ratio of parameter estimates = $-0.46/-0.16$, multiplied by 128, 1 SD of month; Table 4). The relative effect of the proportion of water withdrawn to month on refugia habitat connectivity was even larger (Table 3; ratio of parameter estimates = 7.1). Although total water withdrawal amount and total number of intakes increased through time (Figure SS1 in the Supporting Information), the proportion of water withdrawn did not (adjusted $R^2 = 0.003$; Figure 3).

The proportion of total habitat upstream from one or more intakes in the study area (i.e., habitat affected) increased from <0.3 in 1980 to >0.6 in 2015 (Figure SS2). This reflected the addition of intakes lower in the watersheds. In comparison, refugia habitat affected already exceeded 0.6 in 1980 and increased to 0.8 in 2016 (Figure 4). Total habitat affected reached a maximum of 0.73, indicating over 70% of shrimp habitat in northeastern Puerto Rico was upstream of an intake, and the maximum refugia habitat affected was 98% (Figure 4). Increased amounts of habitat upstream of intakes were associated with lower monthly habitat connectivity ($r^2 = -0.42$; Figure SS2).

Two watersheds, Fajardo and Gurabo, had intakes added in the lower portions of the stream network during the study period. In the remaining watersheds, however, intakes were either removed (Blanco

TABLE 4 Total habitat connectivity parameter estimates (and standard errors) for predictor variables included in linear regression models

Model	Intercept	Proportion withdrawn	Month	Drought	Dry	Drought * month	Dry * month	Dry * drought
1	1.12 (0.020)	-0.492 (0.020)	-0.162 (0.020)					
2	1.134 (0.020)	-0.483 (0.020)	-0.163 (0.020)		-0.040 (0.020)			
3	1.135 (0.020)	-0.474 (0.021)	-0.160 (0.020)	-0.056 (0.021)				
4	1.134 (0.020)	-0.484 (0.020)	-0.163 (0.020)		-0.041 (0.020)		-0.015 (0.020)	
5	1.135 (0.0120)	-0.474 (0.021)	-0.160 (0.020)	-0.056 (0.021)		0.002 (0.023)		
6	1.135 (0.020)	-0.463 (0.021)	-0.161 (0.020)	-0.059 (0.021)	-0.044 (0.020)			
7	1.135 (0.020)	-0.461 (0.022)	-0.162 (0.020)	-0.060 (0.021)	-0.045 (0.020)			0.017 (0.020)

Note. Models are listed based on increasing parameter number, as in Table 2. Model 6 (in bold) was the best-supported model.

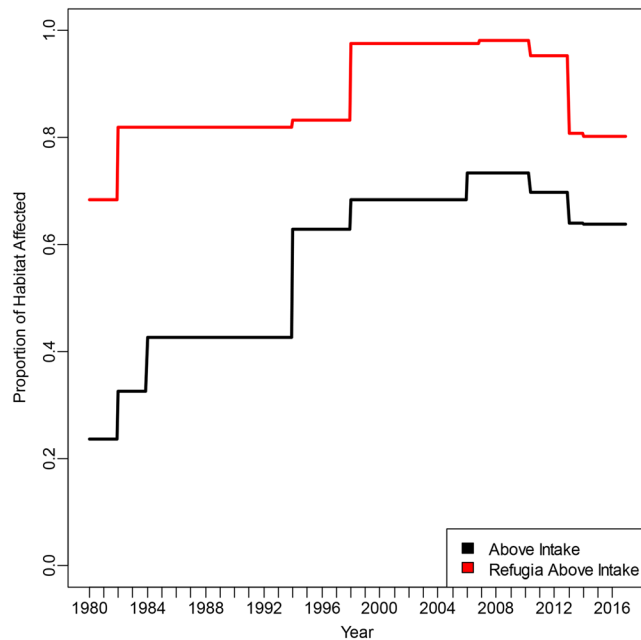


FIGURE 4 The proportion of habitat affected (i.e., habitat upstream of an intake) across the study area. We calculated the proportion of habitat affected by adding all stream habitat upstream of intakes across watersheds and dividing by the total stream habitat. Stream habitat was determined using NHDPlus flowlines

and Mameyes), installed upstream of existing intakes (Canovas and Espiritu Santo), or unchanged (Sabana; Tables SS1 and SS2). Although additional intakes in Fajardo and Gurabo increased the proportion of total habitat affected, the impact on affected refugia habitat was minimal. In Fajardo, the proportion of total habitat affected increased by 34%, and in Gurabo the affected total habitat increased by 72% over the study period. Conversely, refugia habitat impacted increased by 12% in Gurabo and did not change in Fajardo, as all refugia habitat was already upstream of an intake in 1980 (Table SS1 in the Supporting Information).

4 | DISCUSSION

Riverine connectivity within EYNF has decreased over 37 years as a result of increased water withdrawals associated with low-head dams, with total and refugia habitat connectivity declining by 27% and 16%, respectively. This temporal decline in connectivity resulted from the placement of new water intakes at locations farther downstream in the watersheds that could disconnect additional upstream habitat when withdrawal rates were high relative to streamflow. Refugia habitat, located in the headwaters of these systems, could be disconnected by a single intake placed relatively high in a watershed.

On a monthly time step, the strongest driver of shrimp habitat connectivity in EYNF is the proportion of water withdrawn from the study area, with the result that habitat connectivity declines during the dry

season and droughts. For both total and refugia habitat, the lowest connectivity values were observed during low-flow periods, such as the annual dry season (December–April) and extreme droughts (1993–1995 and 2015). During droughts, withdrawals at multiple intakes within EYNF reduced flow directly downstream to zero over several consecutive days (personal observation), severing connectivity to habitat upstream of the intake. Although periods of naturally occurring low flow can result in low habitat connectivity, water withdrawals from intakes paired with low-head dams further reduced habitat access during such periods. Other connectivity studies evaluating cumulative effects arising from multiple barriers have identified an increasing number of barriers as the main driver of connectivity (Diebel et al., 2014; Grill, Ouellet Dallaire, Fluet Chouinard, Sindorf, & Lehner, 2014). However, these studies focus on fish and assume barriers completely block upstream and downstream passage or that passage rates are constant. In contrast, our study assumes that downstream passage rates of shrimp larvae past water intakes vary with the proportion of flow remaining in the stream (Benstead et al., 1999). Thus, proportion of water withdrawn across the system can have an effect independent of the total number of intakes and associated low-head dams.

Despite the large effect of withdrawal on habitat connectivity, it appears that placement of new intakes rather than increasing proportional water withdrawal is responsible for the observed multidecadal decline in connectivity. Intakes installed at downstream locations in the watershed increased the proportion of habitat affected by 60% over 37 years, reinforcing the importance of barrier placement as noted elsewhere (Cote et al., 2009; McKay et al., 2013; Ziv, Baran, Nam, Rodríguez-Iturbe, & a Levin, 2012). Specifically, new intakes installed at downstream locations in two watersheds (Fajardo and Gurabo) have resulted in this temporal trend of reduced total habitat connected and available to support shrimp metapopulations.

Refugia habitat connectivity demonstrated a more gradual temporal decline as refugia connectivity was initially lower. Initial barriers within a watershed are known to have the largest impact on connectivity (Cote et al., 2009), and this effect in our study is explained by the geomorphology of Puerto Rico; waterfalls draining the high gradient terrain of the Luquillo Mountains create refugia habitat in the headwaters. Refugia habitat is important because it is relatively predator-free and supports a high abundance of shrimps that can potentially contribute large numbers of larvae to the island-wide metapopulation. For example, in refugia habitat within the Espiritu Santo watershed, *Atya lanipes* and *Xiphocaris elongate*, the two dominant shrimp species, reach densities of 24 and 13 individuals/m², respectively (Covich et al., 2009). In contrast, below waterfalls in the Mameyes watershed, where the shrimp predator mountain mullet occurs, *Atya* and *Xiphocaris* densities are smaller by an order of magnitude (0.94 and 0.61 individuals/m²; Covich et al., 2009). Accordingly, previous research suggests that the Rio Espiritu Santo has a mean daily larval drift rate that is 15% higher than Rio Mameyes (3.731 million larvae/day and 3.171 million larvae/day, respectively; March, Benstead, Pringle, & Scatena,

1998), as the Espiritu Santo has 12% more refugia habitat above waterfalls. Periodic losses of refugia habitat connectivity could potentially result in large declines of larvae supplied to the island-wide metapopulation given the significant amount contributed by refugia habitat.

Our study emphasizes the importance of examining cumulative effects of partial barriers in the context of long-term flow records. Although other studies have looked at partial barriers (Diebel et al., 2014; King & O'Hanley, 2014) and long-term (20 years) studies have treated passage rates as dynamic (Bourne et al., 2011), here we also calculate connectivity on a monthly time step to examine intra-annual connectivity patterns. We recognize that there may be some barriers with associated intakes that were not included in this study, especially within the Canovanas and Gurabo watersheds, but adding additional barriers would lower habitat connectivity, indicating that our connectivity values represent the best-case scenario. Our results illustrate that even partial barriers can decrease connectivity over decades, a trend which may have been obscured at shorter time scales.

As a result of climate change, the Caribbean is predicted to receive less precipitation, resulting in drier wet seasons, drier dry seasons, and extended droughts (Jennings et al., 2014). As connectivity is highly correlated with streamflow, lower discharge will likely lead to a decline in habitat connectivity if withdrawal amounts are maintained or increased. In the western United States, which is also predicted to have reduced streamflow from the effects of climate change, models indicate that longitudinal riverine connectivity could decrease by up to 14% during the dry season (Jaeger et al., 2014). Although droughts are difficult to predict, EYNF managers could implement strategies, which mitigate effects of these extreme climatic events on connectivity, such as maintaining a minimum flow. This management step could potentially reduce the magnification of "natural" low connectivity (i.e., caused by reduced precipitation during droughts) by anthropogenic factors (i.e., human water withdrawals) and maintain a minimum connectivity threshold.

Additionally, strategies that mitigate the effects of water withdrawals via intakes could be considered. Our results suggest that the impacts of water withdrawals on total habitat connectivity can be minimized if future intakes are installed upstream of existing intakes or if the proportion of water withdrawn in relation to streamflow is decreased. However, in terms of refugia habitat, any barrier within the stream network will likely lower connectivity. Cote et al. (2009) and King and O'Hanley (2014) note that barriers placed high in watersheds without existing dams will have a smaller impact on migratory species, but this may not be true for shrimp taxa where predator-free refugia habitat is located in the headwaters. Management plans that limit intakes in watersheds with ample refugia habitat could be considered for the purpose of maintaining shrimp larval supply to island-wide metapopulations.

In summary, here we provide a baseline of how longitudinal riverine connectivity in the EYNF of northeastern Puerto Rico has been reduced by low-head dams and associated intakes. Establishing a long-term baseline of shrimp habitat connectivity provides critical

context for natural resource managers conserving freshwater ecosystems. Just as managers of potable water supplies are proactively considering how climate change may affect freshwater supply, ecological management can proactively consider impacts to freshwater shrimp resulting from a combination of naturally occurring low flow periods and human water withdrawals.

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DATA AVAILABILITY STATEMENT

All discharge data are available from the US Geological Survey (gage numbers provided in the manuscript). Water withdrawal volumes were provided by the Puerto Rico Aqueduct and Sewer Authority, and average withdrawal amounts are available in Table S2.

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SUPPORTING INFORMATION

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