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Advection exacerbates population decline from habitat loss: maintaining threatened taxa while restoring natural river flow regimes

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Abstract

Modification of flow regimes and habitat degradation are the strongest, most common, and often co-occurring human activities affecting riverine populations. Ongoing efforts to restore peak flow events found under pristine flow regimes could increase advection-driven dispersal for many species. In rivers with extensive habitat loss, increased advection could transport individuals from remnant populations into degraded downstream areas, causing restored flow regimes to decrease persistence of threatened species. To demonstrate such possible 'washout' effects across imperiled taxa, we evaluate population growth in spatial models of insect, fish, and mollusc taxa that experience advective dispersal and either long-term habitat loss or temporary drought disturbances. As a case study to quantify advective dispersal in threatened species, we use intensive mark-recapture methods in a Rio Grande population of the endangered mussel *Popenaias popeii* belonging to the Unionida order, the most threatened faunal taxa worldwide. Our mark-recapture models estimate high levels of annual downstream emigration (16–51%) and immigration from upstream habitats (32–48%) of adult *P. popeii*, a result consistent with hydrodynamic experiments. Across taxa where such advective dispersal occurs in specific life stages, our population model suggests that washout effects might strongly reduce population recovery under high levels of habitat loss, especially for sessile or shorter lived species. Averting this potential negative consequence of restoring hydrology requires simultaneously restoring or protecting long, contiguous stretches of suitable habitats. In heavily impacted systems, we suggest integrating hydrodynamic studies and field surveys to detect the presence of advective dispersal and prioritize areas for habitat restoration to enhance population persistence.

Keywords Spatial population dynamics · Dispersal · Catastrophic drift · Habitat loss · Unionidae · Environmental flows

Introduction

Steeply rising human impacts over the past century have made freshwaters among the most endangered ecosystems, with a nearly tenfold higher concentration of imperiled species compared to marine and terrestrial habitats (Strayer and Dudgeon 2010; Geist 2011). Decline and ultimate extirpation of native species within ecosystems characteristically occurs in response to multiple human-induced stressors (Dudgeon et al. 2006; Geist 2011). Emerging conservation approaches optimize dam discharges to mimic natural flow conditions ('environmental flows' hereafter, Tharme 2003; Yarnell et al. 2015), while others focus on restoring pristine habitats at smaller scales by altering riparian vegetation, riverbed substrates, or nutrient loading (Bernhardt et al. 2005). However, co-occurrence of multiple human impacts in degraded ecosystems might limit success of efforts focused on alleviating individual stressors (Ormerod et al. 2010).

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Flow modification is a ubiquitous anthropogenic impact on rivers world-wide. Dams regulate 77% of discharge in the largest rivers in North America, Europe, and the former Soviet Union (Dynesius and Nilsson 1994) and 85% of US rivers (Tharme 2003), and transform water quality, food web energy sources, connectivity, and physical habitats in lotic ecosystems (Poff and Hart 2002; Cooper et al. 2017; Auerswald et al. 2019). Environmental flows aim to help restore such ecosystem functions in part by mimicking the magnitude of historical extreme discharge levels (Yarnell et al. 2015; Pander et al. 2019). An advantage of this approach is that slight reductions in median flow can compensate for water release during brief peak flows, yielding little net cost in water availability for human activities. Simultaneously, peak flow events predominantly regulate the spatial distribution of sediments and can cause mass transport of organisms with river currents ('advective dispersal' hereafter), as commonly found in aquatic invertebrates (Brittain and Eikeland 1988; Gibbins et al. 2007; Pander et al. 2019), immature fish (Platania and Altenbach 1998; Lechner et al. 2016; Pander et al. 2019), macrophytes (Pander et al. 2019), and molluscs (Kappes and Haase 2012; Thompson et al. 2016). Compared with other dispersal forms, such as elective larval drift at median flow, during advective dispersal currents can move organisms unable to resist peak flows out of preferred habitats and across longer distances. Consequently, implementing environmental flows could greatly intensify downstream transport in one or more life stages for a broad range of taxa.

In heavily degraded rivers, restoring peak flows present under pristine conditions might interact with habitat loss to accelerate loss of native taxa by consistently moving individuals out of remnant pristine habitats into degraded 'sink' areas ('washout' effect hereafter; Speirs and Gurney 2001; Lutscher et al. 2006). Loss of natural river habitats typically arises from reservoir construction, channelization, water depletion in riverbeds, or when intensified runoff from heavily developed terrestrial landscapes causes eutrophication and siltation (Allan and Flecker 1993). Such stressors typically arise in arid or agricultural regions where dams regulate flow to provide flood control, irrigation, and water storage (Poff and Hart 2002), and only some forms of habitat loss might quickly subside with flow restoration. Preserving threatened populations might, therefore, require restoring habitats and flow regimes simultaneously to avert washout effects.

The capacity of washout effects to undermine population persistence may depend on the magnitude of advective dispersal and the forms of habitat loss. Across taxa, this potential might be greater in shorter lived taxa (e.g., semelparous insects), for which larval stages vulnerable to peak flows comprise a greater proportion of the population. A greater vulnerability to advection at the population scale can then translate to reduced persistence under restored peak flows when combined with extensive habitat loss. Across systems, washout effects may also depend on the spatial scale of habitat loss: for instance, reservoir construction produces large, isolated subpopulations, whereas localized streambed channelization or siltation intersperses sink habitats, and subsequent washout effects, throughout the entire population. Within specific taxa, the potential magnitude of advective dispersal remains largely unknown, especially among endangered species. For example, freshwater mussels (Unionida order, > 300 mostly river-dwelling species) are considered the most imperiled faunal group worldwide (Lopes-Lima et al. 2018), with strong fragmentation and declines of populations primarily linked to long-term habitat loss (Downing et al. 2010; Geist 2011; Dobler et al. 2019). Mussels also have high conservation importance as environmental quality indicators, flagship, and umbrella species (Geist 2010, 2011). Although frequently discussed (Balfour and Smock 1995; Strayer 1999; Hastie et al. 2001) and found experimentally (Thompson et al. 2016) or anecdotally (Zajac et al. 2019), population studies do not consider advective dispersal of mussels by intense flows (e.g., Villella et al. 2004; Matter et al. 2013). At the same time, washout effects could strongly impact populations by amplifying mortality in juvenile or long-lived, critically important adult stages.

Here, we analyze the capacity for washout effects to reduce persistence in a wide range of taxa. For this, we develop a spatially explicit population model spanning distinct life histories that incorporates advective dispersal and habitat loss. In conjunction, we estimate advective dispersal in a mussel population subject to extensive habitat loss using a large-scale survey and intensive mark-recapture study of the federally endangered Texas hornshell (*Popenaias popeii*) in the Rio Grande River (Texas, USA). We then discuss systems and taxa where washout effects might most strongly affect population persistence, emphasizing implications for conservation, and evaluate specific approaches to detecting and quantifying advective dispersal across systems.

Methods

Spatially structured population model

We developed a general, spatially explicit population model to examine washout effects on population persistence across taxa and conservation scenarios (Fig. 1). We modeled space discretely to capture the spatial clustering seen in most riverine faunal groups among discrete habitat patches (Townsend 1989), between which animals disperse actively during reproduction or passively by advection, and within patches species may experience extirpation from habitat loss. The spatial scales (i.e., length along river) of habitat patches and

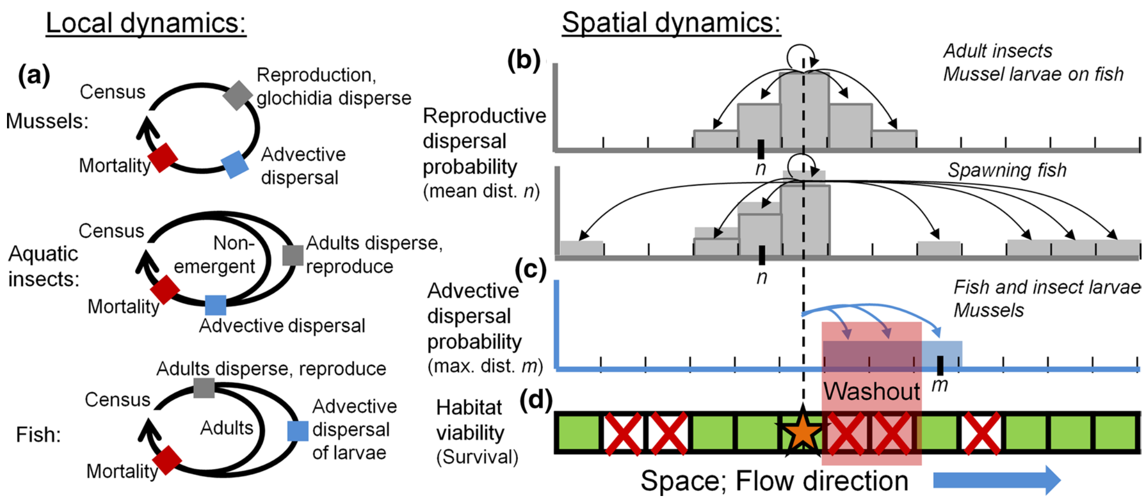


Fig. 1 Local dynamics of modeled life histories differ in stages affected by advection (all individuals for mussels and insects versus larval recruits only for fish; **a** Across space, recruits from a focal patch are dispersed to adjacent patches (**b**, upper plot), but fish readily detect and avoid spawning in degraded habitat patches (**b**, lower plot). Advective dispersal then transports vulnerable organisms downstream (**c**), and dispersal to degraded habitat patches (red crosses in **d**) produces washout effects

habitat loss we considered exceed the distance that individuals vulnerable to advection can actively move; this feature makes washout effects relevant, because organisms transported into degraded patches by peak flows cannot move to better habitats. Given that molluscs can move much shorter distances (10–100 m, Zajac et al. 2019) compared to insect and fish larvae that can electively drift downstream (1–5 km, Brittain and Eikeland 1988), individual patch sizes implicit in our models differed among life histories accordingly.

Our model tracks $N_{i,t}$, the abundance of mature individuals in patch i (with patch $i = 1$ being farthest upstream) in year t, in a population distributed across L habitat patches in a river. Abundance in patch i next year ($N_{i,t+1}$) is the sum of (1) recruits produced in surrounding patches and actively dispersed into patch i, (2) individuals in patch i now ($N_{i,t}$) that remain after natural mortality d and advective dispersal ρ, and (3) individuals arriving from upstream patches via advective dispersal after surviving dispersal-induced mortality μ. We assume reproduction precedes natural mortality and advection, with each mature individual producing r recruits on average. That is, r is the product of fecundity, the probability of surviving active dispersal during reproduction (potentially low for adult insects), and the probability offspring survive early life stages to become insect larvae, mature mussels, or mature fish. Whilst this formulation assumes mussels and fish mature in 1 year, we consider delayed maturation in Online Resource 1.

Throughout, we measure dispersal distances in units of habitat patch size. Active dispersal spans a mean absolute distance of n patches and is represented by the matrix $\boldsymbol{F}$, where $\boldsymbol{F}_{ij}$ is the proportion of individuals in patch i dispersing to patch j. To calculate $\boldsymbol{F}$ we integrated a continuous Gaussian distribution with mean 0 and variance $n^2\pi/2$ (Fig. 1b) over the river length spanned by patch j (scaled to 1 in our models) to calculate $\boldsymbol{F}_{ij} = \boldsymbol{\Phi}\left(|i-j| + 0.5, n^2\pi/2\right) - \boldsymbol{\Phi}\left(|i-j| - 0.5, n^2\pi/2\right)$ using the Gaussian cumulative density function $\boldsymbol{\Phi}$. This $\boldsymbol{F}$ form ignores a bias in some taxa to disperse upstream, a feature we consider in Online Resource 5. To model downstream advective dispersal $\boldsymbol{D}$ we use a simplifying assumption that individuals moved by flows out of patch i are evenly deposited across m successive patches downstream of i (i.e., maximum dispersal distance m), so that $\boldsymbol{D}_{ij} = 1 - \rho$ for $i = j$, $\rho(1 - \mu)m^{-1}$ for $1 \leq i - j \leq m$, and 0 otherwise (Fig. 1c). Finally, the habitat quality vector $\vec{E}$ denotes each patch i as either suitable ($\vec{E}_i = 1$) or degraded ($\vec{E}_i = 0$), with degraded areas having 100% mortality and occurring in a proportion H of all patches (i.e., habitat loss H is the average of $1 - \vec{E}_i$ over all patches). We note that our models apply equally for less extreme habitat loss (i.e., $\vec{E}_i < 1$) and consider temporary habitat loss such as droughts where $\vec{E}$ depends on t in Online Resource 3.

To examine the possible effects of habitat loss and advective dispersal on persistence, we modeled several qualitatively distinct life histories (Fig. 1a). In all models annual dynamics follow the form $\vec{N}_{t+1} = \boldsymbol{P}\vec{N}_t$, where $\boldsymbol{P}$ is the spatial population projection matrix (Rogers 1966) and its leading eigenvalue is low-density population growth λ. In the case of iteroparous species such as mussels, the change in population before advection is the sum of survivorship from the previous year $(1 - d)\boldsymbol{E}\vec{N}$ and new recruits (after dispersal by fish) $r\boldsymbol{F}\vec{N}$, where $\boldsymbol{E}$ is a diagonal matrix with $\boldsymbol{E}_{ii} = \vec{E}_i$. Advection $\boldsymbol{D}$ then affects all individuals, yielding adult abundance dynamics

$$\vec{N}_{t+1} = \boldsymbol{D}((1-d)\boldsymbol{E} + r\boldsymbol{F})\vec{N}_t. \tag{1}$$

Aquatic insects experience similar dynamics except adults are semelparous and advection only affects larvae. Our model, therefore, tracks abundance of larvae, of which a proportion γ annually emerge as winged adults to disperse and reproduce while the rest stay and do not reproduce:

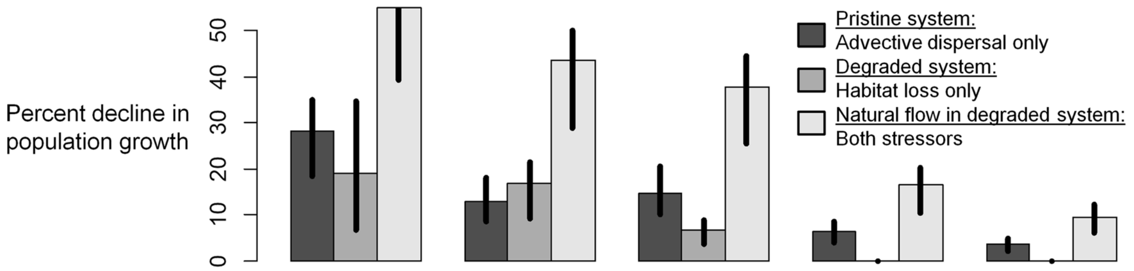
$$\vec{N}_{t+1} = \boldsymbol{D}((1-d)(1-\gamma)\boldsymbol{E} + \gamma r\boldsymbol{F})\vec{N}_t. \tag{2}$$

Finally, we modeled fish populations in which only larval recruits experience advective dispersal, while surviving adults reproduce in and annually move among only viable patches. First, to model that adult fish avoid degraded patches where all individuals die, we set active dispersal probabilities into and out of degraded patches to zero in the modified matrix $\boldsymbol{F'} = \boldsymbol{F} \circ \vec{E}\vec{E}^{T}$, where T indicates vector transpose and ∘ denotes element-wise multiplication. Zero entries in $\boldsymbol{F'}$ reflect that each year (1) adults which start in a viable patch move only to viable patches and (2) recruits displaced into degraded patches by advection over the preceding year die. Second, we assumed that adults in isolated, viable patches with no viable habitats nearby disperse to any viable patch in the river. To model this, we divide the columns of $\boldsymbol{F'}$ by their sums $\vec{1}_L\boldsymbol{F'}$ using the diagonal matrix $\boldsymbol{M} = \left(\vec{1}_L\left(\boldsymbol{F'} + \varepsilon\right)\right) \circ \boldsymbol{I}_L$, where $\vec{1}_L$ is a length-L unity vector, $\boldsymbol{I}_L$ is the identity matrix, and $\varepsilon = 10^{-9}$ is an arbitrary, small constant preventing infinite values in the inverse. This yields the full adult fish abundance dynamics

$$\vec{N}_{t+1} = \left((1-d)\boldsymbol{F'}\boldsymbol{M}^{-1} + \boldsymbol{D}r\right)\vec{N}_t. \tag{3}$$

Washout effects on persistence across taxa

First, we examined the extent to which washout might reduce population growth λ across different life histories (Fig. 2). Specifically, we modeled populations of aquatic insects (*Hydropsychidae* sp.) and shorter vs. longer lived species of fish (*Alburnus alburnus* and *Abramis brama*) and freshwater mussels (*P. popeii* and *Margaritifera margaritifera*, representing *r*- and K-strategist mussels following Haag 2013). This taxonomic range captures life histories differing in the life stage affected by advective dispersal and the relative abundance of recruits at low densities (greater for shorter lived species). For each life history, we compared the percent decline in population growth λ in the presence of: high habitat loss (85% of patches degraded), moderate levels of advective dispersal in the vulnerable life stage (Fig. 2; parameter details in Online Resource 2), and habitat loss and advective dispersal together. In this comparison we assume that habitat loss happens locally (i.e., is patch-specific) and randomly throughout a river of $L = 100$ habitat patches.



	Insects	Mussels	Long-lived mussels	Short-lived fish	Long-lived fish
Example taxa	Hydropsychid caddisflies	*Popenaias popeii*	*Margaritifera margaritifera*	Common bleak	Common bream
Mean longevity (years)	0.5 (Merritt and Cummins 1996)	10 (this study)	20 (Hastie et al. 2000)	2.4 (Blanck et al. 2007)	4 (Blanck et al. 2007)
Population growth factor	1.25	1.25	1.1	1.25	1.1
Advective dispersal stage; frequency	Larval; 0.5	All; 0.37 (this study)	All; 0.37	Larval; 0.5	Larval; 0.5
Factors controlling washout effect	*H* (51%), *ρ* (41%)	*H* (63%), *ρ* (33%)	*ρ* (59%), *H* (39%)	*ρ* (51%), *H* (27%), *r* (20%)	*ρ* (48%), *r* (29%), *H* (21%)

Fig. 2 Independent and interactive effects of advective dispersal and permanent habitat loss (85% of patches uninhabitable) on the decline in population growth relative to conditions ideal for persistence (i.e., no advective dispersal or habitat loss) across life histories. For caddisfles, mean longevity denotes the average duration of juvenile stages preceding mortality or emergence. Vertical segments denote 25th and 75th percentiles of model results in the global sensitivity analysis varying all model parameters within ± 50% of their default values over 4000 replicates (restricted by y-axis range for insects). Factors controlling washout effect denote parameters having the greatest effect on the decline in growth under both advective dispersal and habitat loss (advective dispersal frequency ρ, extent of habitat loss H, or per capita recruitment r; percentages denote relative importances). See Table 1 and Online Resource 2 for model parameterization

To test the sensitivity of possible washout effects to the qualitative form of habitat loss, we also considered large-scale habitat loss (e.g., reservoir construction or intense pollution) that produces demographically isolated populations (Fig. 3). For this, we examined how the number of adjacent, viable remnant habitat patches affects λ across levels of advective dispersal. In Online Resource 3, we also considered habitat loss from intermittent disturbances such as droughts using stochastic implementations of our model. Although we model alternate forms of habitat loss using *P. popeii* parameters, qualitatively similar results arise for other life histories.

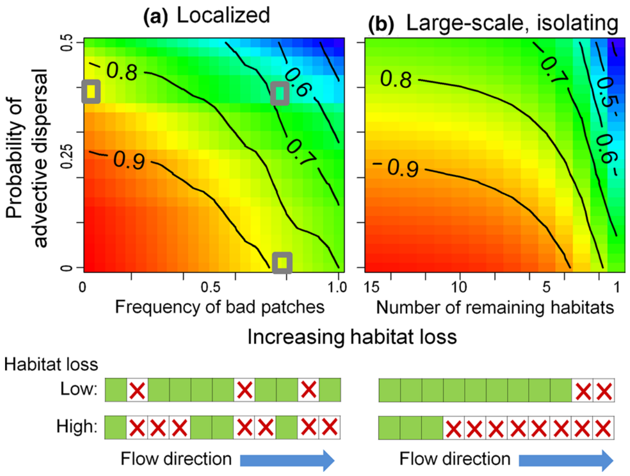


Fig. 3 Due to washout effects, advective dispersal (ρ, y-axes) reduces modeled population growth more strongly under high habitat loss (x-axes) that happens either locally in individual patches throughout the system (**a**) or at large scales by reducing the number of remaining patches in a population (**b**). Colors and contours both denote population growth relative to ideal conditions without advection or disturbance. Life history parameters reflect our *P. popeii* study population (see Table 1). Boxes in (**a**) highlight parameters used for *P. popeii* scenarios in Fig. 2. Insets below panels exemplify spatial distribution of habitat loss (red crosses) for each scenario

In quantifying washout effects across life histories, we combine empirically measured estimates of demography with a robust global parameter sensitivity analysis. We determined demographic parameters d, ρ, and γ based on published studies and our own results (Table 1). Given that per capita reproduction estimates are rare and vary widely among species and systems, we set r values that, under ideal conditions without advective dispersal or habitat loss ($\rho = 0$, $H = 0$), yield an annual population growth of 25% for shorter lived taxa and 10% for long-lived species with delayed maturation. This range of λ values occurs, for example, in recovering mussel populations (Jiao et al. 2008). As we did not find any studies on advective dispersal distance and mortality associated with peak flows, we chose m values based on organism mass ($m = 1$ for mussels and > 1 for larvae) and $\mu = 0.3$ as the proportion of mussels deposited outside the streambed and the proportion of larvae killed by physical abrasion. Given high uncertainty and system-specific variation in such parameters, we ensured robustness of our results using a global sensitivity analysis (Fig. 2). For this, we varied each parameter over a uniform distribution spanning ± 50% of the default value, randomly drew 4000 parameter sets from this multivariate distribution, and for each parameter set re-calculated percent decline in λ under habitat loss, advective dispersal, and both stressors. We then summarized the distribution of these outcomes across parameter sets (vertical bars in Fig. 2). Additionally, we identified parameters that predominantly control washout (the decline in λ with habitat loss and advection) by summarizing our sensitivity results using a random forest approach. This standard sensitivity analysis calculates the importance

Table 1 Description and default values of model parameters

	Parameter description	Aquatic insects	Short-lived mussels	Long-lived mussels	Short-lived fish	Long-lived fish
r	Number of recruits produced per adult**	1.43	0.4	0.125	0.5	0.26
γ	Proportion of larvae emerging to reproduce	0.8				
g	Proportion of juveniles maturing (stage structured model only, Online Resource 1)		0.6			
d	Proportion dying to natural mortality	0.5	0.1	0.025	0.25	0.15
ρ	Proportion advectively moved downstream**	0.5	0.37	0.37	0.5	0.5
μ	Proportion dying during advective dispersal	0.3	0.3	0.3	0.3	0.3
H	Proportion of habitat patches degraded**	0.85	Varied	0.85	0.85	0.85
L	Number of patches in the overall population	100	Varied	100	100	100
m	Maximum distance of advective dispersal	2	1	1	4	4
n	Average distance of recruit dispersal	0.35	2	2	5	5

All proportions denote fractions of individuals affected by the process each year. Dispersal distances are measured relative to the mean distance between adjacent habitat patches. For parameter sources and derivation see Online Resource 2

**Denote parameters predominantly controlling the strength of washout effects in the sensitivity analysis (Fig. 2) of each parameter to the model outcome (*see* Harper et al. 2011).

Case study: habitat distribution of *P. popeii*

To resolve *P. popeii* habitat distribution in the Rio Grande River, we surveyed 150 km of the river around Laredo (Texas; Fig. 4) in 2011–2012. Previously in this system Karatayev et al. (2018) found *P. popeii* almost exclusively in narrow gaps beneath large sandstone rocks resting atop bedrock. In this study, we first searched for these distinctive *P. popeii* habitats, which were found in discrete sections ('patches') along the river; sampling from an airboat at low water allowed us to easily detect all patches > 10–20 m long. For each habitat patch, we estimated patch area, mussel density using 3–15 0.25 m^2 randomly placed quadrats or detailed area searches covering 4–35 m^2 (depending on bed area), and measured the length of all mussels found. We then tested for significant variation in *P. popeii* density, abundance, and mean mussel length across these habitat patches using an analysis of variance.

Case study: demography and spatial dynamics of P. *popeii*

To quantify *P. popeii* demography and spatial dynamics we conducted an intensive mark-recapture study at the La Bota Ranch site in Laredo in 2011–2014. We sampled the downstream 1000 m^2 area of the mussel bed, from which the nearest downstream mussel bed was 1.5 km and the nearest upstream bed was 8 km (Fig. 4). Using a Barker robust design approach, we annually sampled the local population on three consecutive days in March–May to account for detection levels in our abundance and demographic estimates and unequal sampling intervals (White and Burnham 1999; Table 2). This approach incorporates dead as well as live recaptures to estimate mortality separately from permanent advective dispersal downstream. As live mussels could not burrow to avoid detection or secure themselves to counter strong currents, we assumed equal probabilities of detection and advective dispersal among live and dead individuals (we note that greater advection of dead mussels might inflate survival and advection estimates to a limited extent). We compared 32 parallel models that assumed constant, year-specific, and/or mussel length-specific survival and capture probabilities. To test for advective dispersal specifically, we compared models with versus without advective dispersal. We obtained aggregate demographic estimates by averaging across estimates from all models, weighted by each model's Akaike Information Criterion score adjusted for sample size (AICc). We then estimated year-specific immigrant frequency I_t as the increases in estimated abundance N not explained by survival S_t, recruitment b_t (age 3 frequency; see below), or advective dispersal ρ_t estimates: $I_t = 1 - b_t - \left(1 - \rho_t\right)S_t N_{t-1} N_t^{-1}$, and approximated uncertainty in I_t by assuming additive variance in N, S_t, and ρ_t. To test whether our analysis could produce plausible survival estimates without advective dispersal, we also evaluated our best-fitting model (Table 4.1) with advective

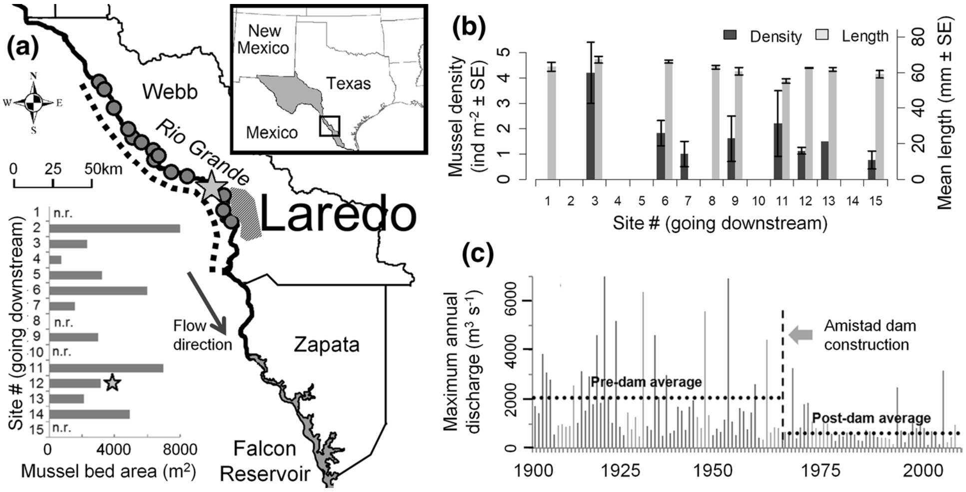


Fig. 4 Distribution of *P. popeii* habitats (gray points on map) in 150 km section of the Rio Grande surveyed (**a**, dotted line), distribution of habitat patch areas (**a**, inset bar graph), variation in mussel density and mean size across habitats (**b**), and historic levels of peak annual discharge on the Rio Grande near Laredo, TX before and after the Amistad dam construction (**c**, maxima across daily readings; IBWC 2016). In (**a**), starred habitat denotes the mark-recapture site, the hashed area denotes the city limits of Laredo, and "n.r." denotes "not recorded". In (**b**) absence of bars for some sites indicates density or length measurements were not recorded, and sample sizes in each site j N_j are number of mussels collected: $N_1 = 11$; $N_3 = 21$; $N_6 = 12$; $N_7 = 4$; $N_8 = 31$; $N_9 = 12$; $N_{11} = 65$; $N_{12} = 973$; $N_{13} = 77$; $N_{15} = 24$. Stream gage measuring data in (**c**) located 900 m below our sampling site furthest downstream (#15)

Table 2 Estimated demographic rates, abundance, and annual maximum discharge rates (across daily readings, International Boundary and Water Commission Water Data 2016)

Time period	Detection probability	Per-capita recruitment to age 3, b_t	Estimated abundance N_t	Maximum discharge ($m^3 s^{-1}$)[a]	Advective dispersal probability ρ_t	Resident survival probability $1-d_t$	Frequency of immigrants I_t
March 8–11, 2011	0.11 ± 0.02	0.03	986 ± 145				
2011–12				235	0.160 ± 0.099	0.88 ± 0.05	0.48 ± 0.11
March 19–21, 2012	0.12 ± 0.01	0.02	1463 ± 134				
2012–13				451	0.441 ± 0.060	0.93 ± 0.03	0.32 ± 0.12
May 1–3, 2013	0.12 ± 0.01	0.03	1178 ± 122				
2013–14				945	0.509 ± 0.063	0.96 ± 0.02	0.33 ± 0.13
April 1–3, 2014	0.17 ± 0.02	0.04	884 ± 82				

All uncertainties denote standard errors

[a] Maximum discharge was not a covariate in mark-recapture models

dispersal fixed at zero. For further mark-recapture methods, see Online Resource 4.

To independently validate our model-fitted survival and advective dispersal estimates, we additionally measured mean mussel longevity based on the size distribution of dead mussels and the magnitude of interannual variation in population size and age structure, which may reflect high levels of downstream migration. For this, we determined a size-age relationship by fitting a growth model (with growth rate K and size at zero growth L_∞; von Bertalanffy 1938) using least squares regression to growth observed in recaptured individuals and growth estimates based on early (ages < 5) growth increments evident as growth annuli in mussel shells < 60 mm (Fig. 5b). Annuli-based growth estimates agreed well with observed growth, and were excluded in the few individuals with obscure annual rings or worn periostracum. In rare cases, when length exceeded L_∞ we conservatively assigned the minimum predicted age at L_∞. We then estimated age distributions using the relation $\text{Age} = -K^{-1}\log(1 - L_\infty^{-1}\,\text{Length})$, and used the mean age of dead *P. popeii* (i.e., longevity) estimate survival as $\exp(-\text{Longevity}^{-1})$. Finally, flow-induced migration can also lead to unexpected changes in population structure. To test for this, we compared the magnitude of year-to-year size structure changes found here to those in a long-term study of *P. popeii* in the Black River (NM), which experiences 20-fold lower maximum discharge (Inoue et al. 2014; Fig. 5). In all cases, we adjusted size distributions for length-dependent detection estimated in our mark-recapture analysis (Fig. 5a).

Results

Washout effects on persistence across taxa

Washout effects reduced population growth in every life history model (Fig. 2), including models that explicitly accounted for juvenile and adult stages (Online Resource 1). In pristine systems with all patches intact, advective dispersal alone reduced population growth by 5–25% due to dispersal mortality and a gradual loss of the population from upstream habitats. Importantly, for insects and mussels, the decline in persistence with advective dispersal only can be largely counteracted by a bias towards upstream dispersal during reproduction (Online Resource 5). In degraded rivers with little advective dispersal, habitat loss alone reduced persistence of taxa that cannot avoid poor habitats during biological dispersal, for instance winged insects or mussel larvae parasitizing fish (8–18%). However, when intense flows and habitat loss co-occur, advection throughout the system transports individuals into degraded areas, producing the washout effect that reduced survival of affected stages and therefore overall population growth to a much greater degree than either stressor alone. Overall, washout effects were stronger in taxa vulnerable to advection over most of their lifespan (e.g., mussels and insects, 40–60%), but washout also affected fishes where advective dispersal affects only juveniles (10–20%) because young individuals are disproportionally more abundant in recovering populations, for instance short-lived fish with high recruitment.

The strength of washout effects was consistent across large (50%) deviations from estimated parameters, and depended predominantly on advective dispersal frequency, habitat loss, and per capita recruitment rather than poorly resolved parameters (i.e., advective dispersal distance and mortality; Fig. 2). We found washout effects under both small-scale habitat loss (Figs. 2; 3a) and when large-scale habitat loss constrains populations to contiguous but small river stretches (Fig. 3b). Washout also occurs when localized, intermittent habitat loss happens less frequently in some habitat patches (Fig. 3.1a) because flows move individuals from better to less protected locations, such as shallower pools vulnerable to drought (Fig. 3c).

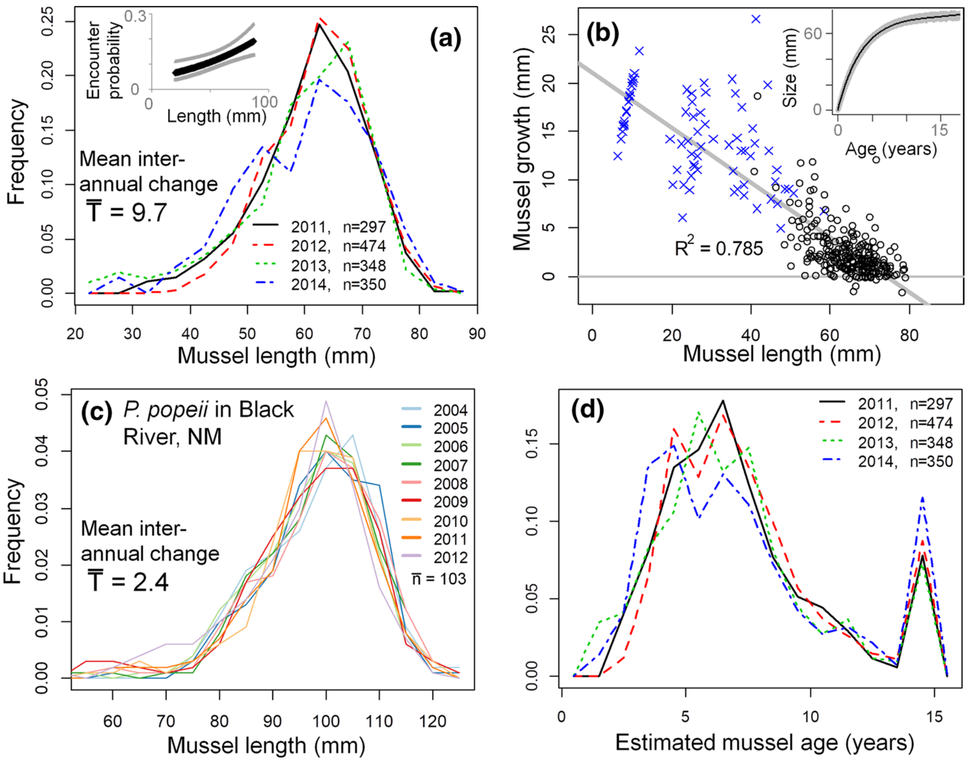


Fig. 5 Presence of advective dispersal of adult mussels is supported by large interannual variations of frequency distributions in size (**a**) and growth-based estimates of age (**d**) classes compared to variation in size-frequency distributions over a long-term *P. popeii* study in a river with lower discharge (**c**; Inoue et al. 2014). **b** Denotes estimates of mussel age from length based on annual growth observed during study (circles) and juvenile growth estimated from shells (crosses), and the inset shows size-at-age (black) ± 1 standard error (gray region) based on uncertainties in K and L_∞ (slope and x-intercept of regression in b, respectively; $N = 319$). Numbers in legend of (**a**, **c**, **d**) indicate sample sizes used in size and age distributions (all mussels captured in a year). Inset in (**a**) shows the model averaged relation between mussel length and detection probabilities (gray lines indicate standard error) used to adjust the size-frequency distributions. $\bar{T}$ in (**a**) and (**c**) is the mean Cramer-von Mises test statistic for difference in size distributions computed over consecutive years. The peak at 15 years in **d** represents individuals longer than L_∞, which were ≥ 15 years old and for which age could not be estimated. In (**c**) $\bar{n}$ denotes the average number of mussels collected each year

Habitat and population distribution of *P. popeii*

Along the surveyed 150 km river stretch we identified 15 suitable habitat patches (Fig. 4a). Total area of all patches corresponded to approximately 3% of the surveyed riverbed, and individual patches were separated by 1–5 km river stretches with a flat bedrock substrate where no *P. popeii* were observed. We note that other mussel species were rare inside *P. popeii* habitat patches but occurred in other parts of the river (Karatayev et al. 2012). Habitat patches varied in area (3,589 ± 785 m^2) but had very similar substrates, water depth, and hydrologic features (i.e., discharge flow rate and water velocity; Fig. 4b). All habitat patches contained live mussels at consistent densities (1.77 ± 0.38 m^{-2}, $F = 1.07$, $P = 0.44$, d$f = 6$, one way ANOVA) and similar mean length ($P = 0.21$, $F = 1.62$, d$f = 7$), suggesting that demographic rates at our study site were representative of the overall population. The farthest downstream inhabited patch was immediately upstream from the Laredo Sewage Plant wastewater discharge. In the 40 km surveyed area downstream of this site, rocky habitat patches with apparently suitable substrates contained no live *P. popeii*, likely due to organic pollution causing prominent biofilm layers.

Estimates of advective dispersal in *P. popeii*

At local scales, several lines of evidence indicated high levels of dispersal among tagged mussels (predominantly age ≥ 4, Fig. 5d) in our intensively studied mussel bed at La Bota. First, all mark-recapture models which received any AICc weight assumed high levels of advective dispersal after accounting for interannual variation in survival and capture probabilities (Table 2, Table S4). Annual survival estimated by these models was consistent with our (conservative) survival estimates based on growth rates and the sizes of dead mussels (proportion surviving 0.87 ± 0.07). In contrast, when assuming the death of all mussels experiencing advective dispersal our best-fitting model estimated much lower survival (proportion surviving 0.74 ± 0.05 *versus* 0.92 ± 0.03 in Table 1, $p < 0.001$, t test) and longevity (3.8 years versus 12.5). Second, high magnitude and variability in net migration explains the strong, significant interannual changes observed in mussel abundance (Table 2) given consistently low recruitment (i.e., frequency of individuals age ≤ 3), survival, and capture levels throughout our study. Finally, very strong interannual variation in *P. popeii* population age and size structure (Fig. 5a, d) indicated the presence of immigration from upstream habitats rather than a demographically closed, gradually aging local population. Size structure of mussels newly marked each year differed significantly among sampling events spanning 2 years with the highest maximum discharge levels (2011–2012: $T = 2.9$, $p = 0.63$; 2012–2013: $T = 22.6$, $p = 0.008$; 2013–2014: $T = 16.0$, $p = 0.04$, Cramer von Mises tests, sample sizes 297–474). For the whole population, interannual variation in *P. popeii* size structure was threefold higher in our system than in the Black River (Fig. 5c), where low peak discharge made advective dispersal unlikely (26 vs. 540 $\mathrm{m}^3\ \mathrm{s}^{-1}$).

Discussion

Our results suggest that in rivers with high habitat loss, restoring natural flow regimes alone could accelerate local extirpation across taxa with distinct life histories (Fig. 1, 2). This unintended consequence can potentially arise if restored peak flows increase advective dispersal, thereby intensifying washout of threatened populations out of the remaining suitable habitats. Washout predicted by our model can occur regardless of whether habitat loss manifests at localized scales throughout the range of a population (e.g., local pollution or channelization; Fig. 3a), at large scales by isolating subpopulations to short river stretches (e.g., reservoir construction; Fig. 3b), or temporarily as short-term disturbances (e.g., droughts; Fig. 5a).

Our findings build on extensive theoretical work on population responses to perturbations in rivers (Anderson et al. 2005; Nisbet et al. 2007; Diehl et al. 2008) by showing that the effects of environmental (here, on persistence) can be qualitatively robust to variation across taxa and the qualitative form of environmental heterogeneity. Populations constrained to small areas are less likely to persist as both advection and active dispersal during reproduction move many individuals outside suitable habitats ('critical domain size', Speirs and Gurney 2001; Fig. 3b). Our modeling suggests that in patchy environments persistence analogously declines when the proportion of habitable patches is low (Fig. 3a; see Lutscher et al. 2006). Conversely, in pristine systems where many patches are habitable (> 50%, Fig. 3a) we suggest that frequent downstream advection has limited impact on population persistence because dispersal from downstream habitats promotes recruitment in upstream patches, even without upstream dispersal bias.

Avoiding the adverse effects of restoring natural flow regimes predicted here may require restoring habitats in conjunction with the flow regime when advective dispersal strongly affects threatened species. Our empirical study is the first to suggest high levels of advective dispersal in adult (age ≥ 4) unionid mussels, supporting recent experimental predictions (Thompson et al. 2016). The specific levels of advection found here (16–51% of population annually, Table 2) indicate a high potential for spatial dynamics and vulnerability to washout effects (Fig. 2) of freshwater mussels, a particularly threatened, umbrella taxon. Across taxa, restoration efforts could alleviate washout by creating or maintaining long, contiguous stretches of high-quality habitats wherein washout effects occur only in downstream patches (Fig. 3b). The required area of suitable habitat increases with the magnitude of advective dispersal (Fig. 3b), and patch size will likely depend on the imperiled species (see "Methods" section and below). Conversely, protection of subpopulations isolated in small river stretches by itself may not prevent local extirpation if elevated peak flows carry most individuals to downstream, degraded habitats.

Evidence for advective dispersal under peak flows

A common theme of emerging empirical studies across taxa is that advective dispersal of vulnerable life stages can be common and occurs primarily under peak river flows. Most studies explicitly tracking flow-driven movement resolve only localized 'behavioral' drift (e.g., < 200 m, Brittain and Eikeland 1988) at low discharge levels. However, field studies spanning flood events find mass advection of aquatic insects (Brittain and Eikeland 1988; Gibbins et al. 2007), juvenile fish (Lechner et al. 2016), and molluscs (Kappes and Haase 2012; Sousa et al. 2012; see Online Resource 2). In turn, peak flow conditions can also determine the spatial distribution of organisms (Brittain and Eikeland 1988): for instance, Gangloff and Feminella (2007) found that bankfull shear stress predominantly governed spatial mussel distribution across eight streams. Finally, site-specific studies find lower retention of marked individuals in years of higher discharge (Villella et al. 2004), a pattern also seen in our results (Table 2) and restoration efforts in which floods washed away reintroduced mussels out of entire habitat patches (Ahlstedt 1980; Layzer and Gordon 1993). These results suggest a strong influence of peak flows on the spatial dynamics of many organisms, paralleling foundational ideas in hydrology that spatial dynamics of sediments and organic matter predominantly depend on peak discharge (Yarnell et al. 2015).

Field studies also find direct evidence for advective dispersal over long distances in relatively sessile organisms moved predominantly by river currents. Spatial surveys in systems with concurrent mark-recapture studies have found individual adult mussels living long distances (1–10 km) downstream from tagging sites (Alderman, Dunn, Schueler, Welte, personal communication, see Online Resource 2) or molluscs established in previously unoccupied habitats following floods (gastropods: Rosa et al. 2014; mussels: Hastie et al. 2001). Unfortunately, studies monitoring abundance alone cannot resolve movement among inhabited patches if immigration balances emigration (e.g., 2012–2014 in our study, Table 2). Similarly, in single-site mark-recapture studies that do not consider migration the presence of advective dispersal can explain anomalously low mussel survival estimates (0.50, Villella et al. 2004; 0.49 ± 0.04, Matter et al. 2013; 0.58 ± 0.06, our estimates ignoring advective dispersal) that contradict the persistent, adult-dominated populations observed in these systems. However, such single-site results represent at best indirect evidence for population-level effects of advective dispersal in mussels and cannot measure dispersal distances, and other multi-year studies in systems with unconsolidated or soft sediments (where mussels can burrow, see below) find persistent mussel beds despite floods (Sansom et al. 2018).

Focusing on a bedrock system with a high peak annual discharge (500–1500 $m^3 s^{-1}$, Fig. 4c), our results suggest that (1) peak flows can in some systems move a large proportion of adult mussels among habitat patches, and (2) this spatial dynamic does not greatly reduce population persistence in pristine systems (e.g., 4%, Fig. 3a). Water velocities under peak flow conditions near our study site (2.6–10.5 $m s^{-1}$, coarse estimate based on discharge and 90 m^2 cross-sectional area) fall on the same order of magnitude as velocities found to entrain adult mussels in experiments (0.9–1.5 $m s^{-1}$, Thompson et al. 2016). As we found *P. popeii* exclusively under large rocks, the strongest refuges from flow in the bedrock-lined riverbed, advection of adult mussels among separate habitat patches appears likely in the Rio Grande. Advective dispersal estimated here also reflects system- and stage-specific studies showing that peak flows can concentrate mussels in flow refugia (Gangloff and Feminella 2007), move adult mussels out of these habitats (Strayer 1999), and transport juvenile mussels to downstream refugia (Daraio et al. 2012; Irmscher and Vaughn 2018). Additional mark-recapture studies spanning mussel beds 1–5 km apart or telemetric mussel tagging (e.g., Zajac et al. 2019) would help fully resolve the frequency and distance of advective dispersal in our system. Nevertheless, the role of peak flows in dispersal indicated here emphasizes future studies relating flow rate to advection across taxa.

General approaches to quantifying advective dispersal

Although our mark-recapture results demonstrate a large potential for advective dispersal at the population level, the realized magnitude of this process can strongly vary across systems and taxa. For mussels, advection found in our system may amplified by high discharge (Fig. 4c) and < 5 cm sediment depth atop bedrock that prevents burrowing. Burrowing is a common behavior in rivers with softer substrates (Zieritz et al. 2014) that can increase water velocities needed to entrain adult mussels by ~ 50% (Thompson et al. 2016). Similarly, insect and fish can avoid intense flows by sheltering under rocks, attaching to vegetation, or moving to better protected habitats with reduced flow rates (e.g., floodplains). On the other hand, such behaviors depend on substrate availability, habitat complexity, and reliable flow intensity cues (e.g., temperature) which can decline with habitat and flow regime degradation (Tuomainen and Candolin 2011). Finally, the seasonal occurrence of young life stages highly vulnerable to advection may be separated from peak flow timing.

Within specific systems demography-based approaches could estimate advective dispersal, but may require intensive studies at limited spatial and temporal scales. Advective dispersal may be directly measured by tracking tagged or isotopically marked individuals (Hershey et al. 1993; Bilton et al. 2001). Such efforts can be hampered by low detection rates (e.g., mussels, Table 2, but see Zajac et al. 2019) or high mortality of organisms affected by advection (e.g., juvenile fish, Franzin and Harbicht 1992). An alternative approach is to quantify mortality separately from dispersal by accounting for recovery rates of dead individuals in mark-recapture studies (as we have done here) or estimating mortality from changes in population age or size structure. Advective dispersal is then the difference between observed changes in abundance and those predicted by mortality and recruitment alone. Unfortunately, detailed demographic studies span limited spatiotemporal scales and might underestimate dispersal when they fail to span high-flow areas or infrequent (e.g., decadal) peak flows that have disproportionally strong population effects, especially on long-lived species (Haag 2013).

We suggest that resolving the magnitude of advective dispersal and resulting washout effects may be best achieved using approaches which synthesize hydrodynamic studies and field surveys. Hydrodynamic models and experiments are increasingly used to resolve the potential for flow-driven movement of organisms across taxa and observed flow rates in a given system (Strayer 1999; Gibbins et al. 2007). When this potential for advective dispersal is strong, hydrodynamic models can predict local peak flow intensity across occupied and unoccupied habitats using broad substrate and streambed characteristics (Morales et al. 2006; Daraio et al. 2012). Evaluating the extent to which peak flow characteristics vs. other habitat requirements explain the spatial distribution of vulnerable populations (e.g., Gangloff and Feminella 2007) could then estimate realized advective dispersal. A particular strength of this approach is the potential to predict advection across long river stretches, historic floods, and the target flow regime. Field surveys comparing population distribution before vs. immediately after peak flow events could further supplement efforts to quantify advective dispersal. Where they identify intense advective dispersal (e.g., below dams), joint modeling and empirical approaches can directly prioritize habitat restoration in river stretches with the greatest potential for washout.

When restoring peak flows might reduce local persistence

Our results suggest that restoring peak river flows could reduce local persistence when (1) advection affects a large portion of a population and (2) extensive habitat degradation spans sufficiently large spatial scales. The prevalence of advective dispersal in a population depends on the relative abundance of life stages vulnerable to drift under peak flows (Fig. 2) and the frequency of peak flow events. However, for long-lived species even infrequent (e.g., decadal) peak flow events can cause washout effects in each generation. Additionally, we predict reduced persistence even in taxa where only young stages are vulnerable to advection and washout because the structure of recovering populations can be skewed towards younger stages.

Washout effects in a given taxa additionally require that habitat loss spans spatial scales (e.g., river length) greater than the distance larvae or molluscs can actively move. In this case organisms displaced by flow cannot reach suitable habitats before dying. Reflecting this, we assume among-patch movement only via advection or during reproduction and patch-scale habitat loss in order to compare the potential for washout effects among taxa. However, within a given system threatened species can greatly differ in movement capacity. For instance, mussels actively move only short distances and can experience washout even from fine-scale (~ 100 m) habitat loss. In contrast, insect and fish larvae which electively re-enter river currents and drift to more suitable downstream habitats (Townsend 1989) may only be affected by washout into larger (e.g., 1–5 km) sections of degraded habitats. These areas might include river stretches with adverse food, predation, or abiotic regimes such as reservoirs (Hofer and Kirchhofer 1996; Platania and Altenbach 1998; Jager et al. 2002), river channels with low substrate complexity, or areas of intense pollution (Jager et al. 2002). Fishes with semibuoyant eggs may be particularly susceptible due to washout effects reducing both egg and larval survival, which may. This increased susceptibility, combined with flow modification and habitat fragmentation (Platania and Altenbach 1998), may explain the extirpation of several pelagic-broadcast spawning minnows in the middle Rio Grande and the Upper Pecos River. Finally, species declines can propagate through communities, for instance mussels that rely on specific fish hosts for reproduction (Lee et al. 1998). Altogether, potential washout effects may be strongest in taxa which are sessile or rely on high annual recruitment (e.g., insects and short-lived fishes, Fig. 2).

For tractability, our population models make several simplifying assumptions about spatial structure that can affect the magnitude of washout effects. First, we model habitat loss as independent of flow, whereas reducing hypoxia and substrate siltation is a common goal of restoring river hydrology, and peak flows in particular (Yarnell et al. 2015). If flow restoration alone can improve habitat conditions quickly relative to the annual rate of advective dispersal, it may have a positive net effect on population persistence. Second, we consider flow intensity only as advective dispersal probability averaged over the population. In regulated rivers, advection peaks below dams and would intensify washout if the best habitats also occur below dams (e.g., lower siltation or drought amelioration by constitutive water release) by moving individuals into lower-quality habitats further downstream. Conversely, washout may be limited if habitat degradation also peaks below dams, for instance if releases of cold hypolimnetic water prevents mussel and fish reproduction (Platania and Altenbach 1998; Vaughn and Taylor 1999). Finally, we assume habitat loss is homogeneous across space. If some degraded habitats can still sustain populations, advective dispersal to such poorer-quality 'sink' habitats might promote populations if density dependence (not modeled here) in the highest-quality habitats is intense (sensu source-sink dynamics, Pulliam 1988). Furthermore, whilst we model randomly distributed disturbance, habitat loss might have limited impacts on persistence if sufficiently large, contiguous habitats remain. For instance, despite the loss of *P. popeii* from 75% of its historical range in the Rio Grande, relatively large sections of suitable habitats remain (~ 15–28 patches, Karatayev et al. 2018). However, such constricted populations are particularly vulnerable to further habitat loss, such as dessication during droughts or organic pollution that occur in our study area (Karatayev et al. 2018). Analogously, tributaries with reduced discharge and advective dispersal may also provide refugia from washout effects and possible sources of re-colonization. In these cases, flow restoration places greater importance on protecting existing habitats.

Conclusions

Natural resource managers increasingly rely on environmental flow regulation to restore ecosystem processes and native populations. We predict a potential to accelerate rather than reverse species loss when restoring peak flows to natural levels in a system that has also lost a large proportion of suitable habitat for a particular species of concern. This adverse impact is due to advective transport of the species from remnant suitable habitats into degraded areas. We suggest system-specific studies integrating hydrodynamics and field surveys to detect both the potential for advective dispersal under proposed flow regimes and, using dynamical models developed here as a basis, its population consequences. Where this potential is strong, we recommend a multi-faceted conservation approach concomitantly restoring flow regimes and long, contiguous stretches of natural habitats.

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Author contribution statement VAK conceived the model and conducted data analyses. VAK and LY analyzed the model. LEB, AYK, and TM conceived and conducted the field study.VAK wrote the manuscript, with input from LEB, AYK, and LY.

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