



# Floodplain Rehabilitation as a Hedge against Hydroclimatic Uncertainty in a Migration Corridor of Threatened Steelhead

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**Abstract:** *A strategy for recovering endangered species during climate change is to restore ecosystem processes that moderate effects of climate shifts. In mid-latitudes, storm patterns may shift their intensity, duration, and frequency. These shifts threaten flooding in human communities and reduce migration windows (conditions suitable for migration after a storm) for fish. Rehabilitation of historic floodplains can in principle reduce these threats via transient storage of storm water, but no one has quantified the benefit of floodplain rehabilitation for migrating fish, a widespread biota with conservation and economic value. We used simple models to quantify migration opportunity for a threatened migratory fish, steelhead (*Oncorhynchus mykiss*), in an episodic rain-fed river system, the Pajaro River in central California. We combined flow models, bioenergetic models, and existing climate projections to estimate the sensitivity of migration windows to altered storm patterns under alternate scenarios of floodplain rehabilitation. Generally, migration opportunities were insensitive to warming, weakly sensitive to duration or intensity of storms, and proportionately sensitive to frequency of storms. The rehabilitation strategy expanded migration windows by 16–28% regardless of climate outcomes. Warmer conditions raised the energy cost of migrating, but not enough to matter biologically. Novel findings were that fewer storms appeared to pose a bigger threat to migrating steelhead than warmer or smaller storms and that floodplain rehabilitation lessened the risk from fewer or smaller storms across all plausible hydroclimatic outcomes. It follows that statistical downscaling methods may mischaracterize risk, depending on how they resolve overall precipitation shifts into changes of storm frequency as opposed to storm size. Moreover, anticipating effects of climate shifts that are irreducibly uncertain (here, rainfall) may be more important than anticipating effects of relatively predictable changes such as warming. This highlights a need to credibly identify strategies of ecosystem rehabilitation that are robust to uncertainty.*

**Keywords:** anadromy, ecosystem restoration, Endangered Species Act, recovery, salmonid

Rehabilitación de Planicies Inundables como Cerco contra la Incertidumbre Hidroclimática en un Corredor Migratorio de *Oncorhynchus mykiss*, Especie Amenazada

**Resumen:** *Una estrategia para recuperar especies en peligro durante el cambio climático es restaurar procesos de los ecosistemas que moderan los efectos de los cambios. En latitudes medias, los patrones de tormentas pueden modificar su intensidad, duración y frecuencia. Estas modificaciones amenazan con inundar comunidades humanas y reducir ventanas de migración (condiciones favorables para la migración después de la tormenta) para peces. La rehabilitación de planicies inundables históricas, en un principio, puede reducir estas amenazas por medio del almacenamiento transitorio del agua de las tormentas, pero no se ha cuantificado el beneficio de la rehabilitación de las planicies para los peces migratorios, una biota extensa con valor económico y de conservación. Usamos modelos simples para cuantificar la oportunidad migratoria para un pez migratorio amenazado, *Oncorhynchus mykiss*, en un sistema ripario con alimentación constante de*

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*lluvia, el río Pájaro en el centro de California. Combinamos los modelos de flujo, los modelos bioenergéticos y las proyecciones existentes de cambio climático para estimar la sensibilidad de las ventanas de migración a los patrones alterados de las tormentas bajo escenarios alternados de rehabilitación de las planicies inundables. Generalmente, las oportunidades de migración no fueron afectadas por el calentamiento, fueron afectadas débilmente por la duración o la intensidad de las tormentas, y fueron afectadas proporcionalmente por la frecuencia de las tormentas. La estrategia de rehabilitación expandió las ventanas de migración en un 16-28% sin importar los resultados climáticos. Condiciones más cálidas incrementaron el costo energético de la migración, pero no lo suficiente como para tener importancia biológica. Los hallazgos novedosos fueron que menos tormentas parecían ser una mayor amenaza para la especie migratoria que tormentas más pequeñas o más cálidas y que la rehabilitación de las planicies aminoraba el riesgo de menos tormentas o tormentas más pequeñas a lo largo de todos los resultados hidroclimáticos. Esto sigue los métodos de reducción de escalas estadísticas pueden caracterizar erróneamente el riesgo, dependiendo de cómo resuelvan los cambios totales de precipitación a cambios en la frecuencia de las tormentas, en oposición al tamaño de la tormenta. Además, anticipar los efectos de las modificaciones climáticas que son irreduciblemente inciertas (en este caso, la lluvia), puede ser más importante que anticipar los efectos de los cambios relativamente predecibles como el calentamiento. Esto resalta la necesidad de identificar certeramente estrategias de rehabilitación de ecosistemas que son propensas a la incertidumbre.*

**Palabras Clave:** Acta de Especies en Peligro (ESA), anadromía, restauración de ecosistemas, salmónido

## Introduction

Many conservation efforts intend not simply to protect endangered species but to restore their viability. This intention is at the heart of the U.S. Endangered Species Act, which mandates preparation of recovery plans, the goal of which is to reestablish conditions for species viability so legal protection becomes unnecessary. Active recovery of species typically requires the repair of ecosystems modified by people. This is particularly true for species dependent on river ecosystems, which have been widely modified to provide water, dispose of wastewater, and control floods (Reisner 1993). Species that use rivers as migration corridors are especially vulnerable because stream networks typically do not provide alternate routes when human modifications block a migration corridor. Migration barriers may block dispersal within metapopulations or movements of species requiring multiple habitats, such as anadromous fishes that mature in the ocean but migrate up rivers to spawn. Dams are a familiar migration barrier, but in small or episodic rivers the primary barrier is often shallow streamflow, such that migration can occur only after storms transiently raise flows (Jonsson et al. 2007; Barnett & Spence 2011; Otero et al. 2011). Human strategies for water provisioning and flood control appear to exacerbate flow-related barriers by diverting water, accelerating run-off during storms, and reducing streamflows between storms. Species recovery needs strategies to reverse these effects.

For the foreseeable future, the recovery of species migrating in rivers will coincide with rapid climate change and rapid human cultural adaptation to climate change. At intermediate latitudes, intrinsically uncertain but potentially large shifts in hydroclimate may have the same level of effect as warming (Milly et al. 2008). For example, in

California (U.S.A.), a modest expected loss of 10% annual precipitation (i.e., mean prediction) tends to overshadow a large range of plausible outcomes between  $-50\%$  and  $+50\%$  shifts in annual precipitation (95% confidence limit [CL]) (Dettinger 2005). Such annual summaries may also hide substantial shifts in the duration and intensity patterns of storms (Dettinger 2011). Uncertain changes in precipitation will drive the flow regimes and migration opportunities of the future, and these changes create a need for strategies of ecosystem repair that perform well across an array of plausible future climates (Levin & Lubchenco 2008; Schindler et al. 2008). Similar reasoning applies to human strategies for water provisioning, disposal, and flood control, which also must change to address shifts in precipitation patterns (Dettinger 2005; Milly et al. 2008; Hallegatte 2009).

Some frameworks that address climate change emphasize restoration of ecosystem processes that confer resilience to both biodiversity and to ecosystem services needed by people (Bohensky et al. 2006; Brauman et al. 2007; Nelson et al. 2009), and these naturally attract the interest of conservation biologists (Schindler et al. 2008; Waples et al. 2008). Ideally, these restored processes would generate similar outcomes (natural habitats, ecosystem services) in different future climates; that is, they would be robust to uncertainty and resilient to change. But not all ecosystem processes are robust and restorable. Which processes, restored to what degree, will both improve habitat and sustain ecosystem services under a broad array of possible future climates?

A promising strategy for rivers is rehabilitating former floodplains that have been disconnected from their rivers by human activity. Rehabilitation is the partial restoration of key ecosystem processes and is playing a prominent role in the worldwide movement to improve natural

function of impaired river systems (Brierley & Fryirs 2008). Rehabilitating a floodplain typically means re-designing levees to allow some portion of the former floodplain to once again flood and generate natural areas whereas other portions stay unconnected from the river system to accommodate conventional human use. This improves floodplain, riparian, and aquatic ecosystems, which benefits local biodiversity; creates transient water storage during storm events, which lowers flood hazard for human communities; and promotes infiltration of storm water into the ground, which improves ecosystem function and water provisioning. It also seems likely that rehabilitated floodplains would benefit species that use rivers for migration because transient storage of floodwaters would tend to extend the time window after storms when flow is deep and slow enough for individuals to migrate. The benefit should be robust to hydroclimate uncertainty because transient water storage could only lengthen these migration windows, regardless of future storm patterns.

However, we have found no quantitative studies linking floodplain rehabilitation to migration opportunity in databases of peer-reviewed literature or in technical summaries such as DeVries et al. (2007). The benefit could be trivially small or not robust, depending on quantitative details of river function and species performance. We conducted a case study of migration by steelhead (*Oncorhynchus mykiss*), a threatened species, in the Pajaro River (Fig. 1a) in central California to evaluate the cascading effects of climatic, hydrological, and biological response to climate change, each of which is substantially uncertain. We assembled a dynamical model calibrated to existing data on the river and species and examined whether current understanding suggests that a proposed floodplain rehabilitation project would expand migration windows by a biologically meaningful amount. We determined whether modeled windows are robust to hydroclimatic uncertainty, modeled as changes in the intensity, duration, frequency, and temperature of a standardized design storm (temporal pattern of rainfall), and whether predictions are sensitive to uncertainty in other key parameters of the model.

Steelhead are an anadromous salmonid that matures in the Pacific Ocean but migrates up coastal rivers to spawn. Suitable migration conditions in California central coast rivers are unreliable and occur briefly during storms (Barnett & Spence 2011). Levees, constructed in the 1950s for flood control, line the active channel of the lower Pajaro river. The levees disconnected the river from nearly the entire floodplain, smoothed and simplified the riparian zone and channel, and increased movement of floodwaters, which led to incision of the active channel. A proposed rehabilitation (Andrews et al. 2003, scenario PWA2) sets levees back from the channel approximately 90 m; excavates benches between the

levees so they will flood 1 year out of 2; restores woody vegetation to banks; and adds gravel and cobbles to the channel (currently sand and gravel) (Fig. 1b). The intent is to secure riparian ecosystems while reducing flood hazard outside the levees by transiently storing water during storms (Schaaf 2002; Andrews et al. 2003).

## Methods

### Storm Traits and Climate Projections

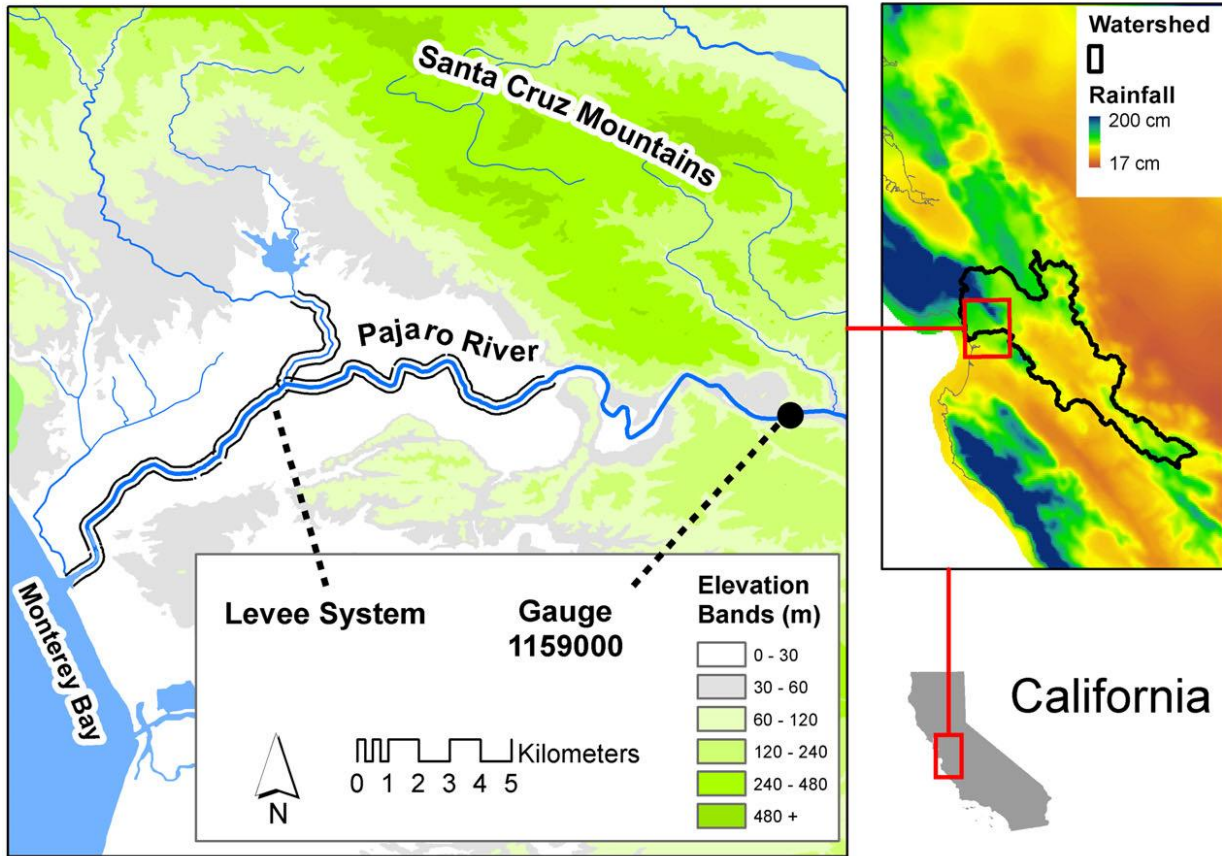
To model uncertainty about future climate shifts, we used 112 climate projections (Maurer et al. 2007) to estimate exceedance curves for prospective monthly climate in the Pajaro Basin. Exceedance curves are similar to cumulative-probability distributions. They showed the probabilities that various shifts in temperature or precipitation would be reached or exceeded during a given period. We estimated exceedance curves for each quarter century from 1975 to 2100 by combining the 112 projections in a statistical metamodel (details in Supporting Information). We also used monthly means and standard errors to estimate stationary curves for 1975–1999 historical climate (Maurer et al. 2007). The exceedance curves provided a climatic context for interpreting the sensitivity of modeled migration windows to shifts in storm traits.

We assumed the relation between migration windows and annual rainfall was mediated by 4 storm traits—duration, intensity, frequency, and temperature—that potentially affect river flow or steelhead migration differently. Reasoning that historic rainfall patterns are a rough guide to how future shifts in rainfall might manifest as storm traits, we examined the historical relation among annual rainfall, number of storms per year, and mean duration and intensity of storms per year. Hourly precipitation data were obtained from the National Climate Data Center for a coastal, mountain-top, and 2 inland-valley weather stations in or near the Pajaro watershed (see Table 1 for lat/long). We divided the time series into discrete storms separated by at least 24 h of dry conditions; computed annual precipitation, number of storms, mean duration, and mean intensity of storms; and estimated a covariance matrix for traits across years. Storm temperature was estimated as rainfall-weighted mean air temperature during storms, computed from the weather data described by Maurer et al. (2002).

### Bioenergetic Models of Steelhead Migration

For the model, we assumed migrating steelhead integrate the effects of altered temperature and storm traits via the bioenergetics of swimming upstream (Farrell et al. 2008). Following Trudel and Welch (2005), the energetic cost

(a)



(b)

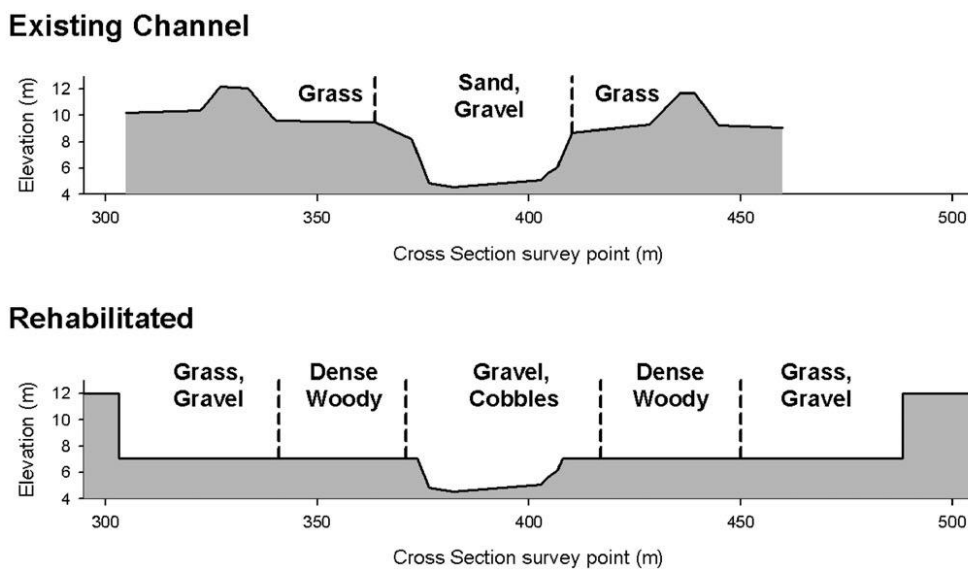


Figure 1. (a) Schematic representation of the current levee system (constructed during the 1950s) in the lower Pajaro River in a low alluvial valley between the Santa Cruz Mountains and the coast. The U.S. Geological Survey's gauge 1159000 is in the Pajaro Gap, a narrow valley the river traverses through the mountains. (b) A typical cross section of the current levee system and the proposed rehabilitation (i.e., alteration of the floodplain and surfaces of the banks and channel bed).

**Table 1.** Interannual correlations (below the diagonal of each matrix) and  $R^2$  (above the diagonal) for annual storm characteristics and annual precipitation in the Pajaro River basin, 1973–2010.<sup>a</sup>

	Mean annual storm characteristics			
	intensity	duration	no. of storms	annual precip.
Coastal site <sup>b</sup>				
intensity	-	25%	0%	0%
duration	-0.50	-	4%	34%
no. of storms	0.03	0.20	-	68%
annual precip.	-0.03	0.59	0.83	-
Inland valley site, Morgan Hill <sup>c</sup>				
intensity	-	16%	12%	14%
duration	-0.40	-	2%	28%
no. of storms	-0.34	-0.16	-	30%
annual precip.	-0.37	0.53	0.55	-
Inland valley site, Hollister <sup>d</sup>				
intensity	-	34%	4%	7%
duration	-0.58	-	6%	27%
no. of storms	-0.19	0.24	-	79%
annual precip.	-0.26	0.52	0.89	-
Mountaintop site <sup>e</sup>				
intensity	-	0%	1%	8%
duration	0.02	-	1%	38%
no. of storms	0.10	0.12	-	54%
annual precip.	0.27	0.62	0.74	-

<sup>a</sup> Observations prior to 1973 were excluded due to changes in instrumentation that affected the way discrete storms were identified.

<sup>b</sup> Sunset State Beach, 36.8975°N, 121.8347°W, elev. 80.

<sup>c</sup> 37.13639°N, 121.6025°W, elev. 375.

<sup>d</sup> 36.84833°N, 121.4213°W, elev. 275.

<sup>e</sup> Ben Lomond Mountain, 37.14222°N, 122.1963°W, elev. 2175, just north of Pajaro watershed.

of swimming is

$$\ln(R) = \alpha + \beta \ln(L) + \phi T + \nu U + \varepsilon, \tag{1}$$

where  $R$  is oxygen consumption,  $L$  is fish length,  $T$  is water temperature,  $U$  is swim speed relative to water flow, and  $\alpha$ ,  $\beta$ ,  $\phi$ ,  $\nu$ , and  $\varepsilon$  are estimated parameters, the latter an error term drawn from a normal distribution with mean 0 and variance  $\sigma^2$ . Trudel and Welch (2005) found that Eq. 1 explained existing data better than models with interactions terms for  $T$  and  $U$ .

Brodersen et al. (2008) argue that the upstream swim speed chosen by fish depends on whether they have been naturally selected to minimize travel time versus energetic cost. We assumed the Pajaro’s short, unreliable migration corridor favored a strategy to minimize travel time, which implies continuous swimming at the critical swim speed ( $U_{crit}$ ), the fastest speed sustainable through aerobic metabolism (Brett 1964; Farrell 2008). Fish can swim faster anaerobically but only briefly (Kolok 1999). Because  $U_{crit}$  is closely related to energy consumption (Farrell et al. 2008), we assumed length and temperature effects as in Eq. 1. However, energy available for activity goes to zero in *O. mykiss* as water temperatures approach 25 °C, probably due to a physiological constraint (Farrell 2002). We added a factor forcing this downward bend in  $U_{crit}$  near 25 °C, with the sharpness of the bend set by

parameter  $b$ :

$$\ln(U_{crit}) = (\alpha + \beta \ln(L) + \phi T)(1 - e^{-b(25-T)}) + \varepsilon, \tag{2}$$

where  $\phi$  describes steelhead’s ability to maintain critical swim speed at temperatures well below 25 °C, and  $b$  quantifies the domain near 25 °C where this ability breaks down.

Parameters in Eqs. 1 and 2 are posterior distributions from a Bayesian analysis of data from Trudel and Welch (2005) for Eq. 1 and Peake (2008, his Table 39) for Eq. 2. More specifically, we made Markov-chain Monte-Carlo simulations in R (Plummer 2011; R Development Core Team 2011; Su & Yajima 2011) with likelihood equations derived from Eqs. 1 and 2 and vague, normally distributed prior distributions  $[N(0, 1000)]$ . Posterior distributions were represented numerically as 75,000 random draws from the Markov chains after convergence (as judged by Gelman’s R; Gelman et al. 2004) and thinning (20:1, yielding effective samples of 18,000–75,000). From these random draws, we estimated quantiles of interest, such as medians and 95% CLs.

The model applied bioenergetic patterns of laboratory fish in steady flows to a more turbulent field situation. Turbulent flow can raise the energy cost of swimming (Enders et al. 2003), but steelhead also reduce energy cost by exploiting vortices (Liao et al. 2003) or seeking

slower-than-average water velocities in the flow field (known as “flow-refuging”; Liao 2007). We assumed the simplified river channel had negligible vortices and migrants used flow-refuging.

### Hydrodynamic Models

To project migration opportunity as a function of storm intensity and duration, we combined the bioenergetic model with the Pajaro flow model, a 1-dimensional hydrodynamic model previously developed and calibrated by Schaaf (2002) using HEC-1 and HEC-RAS simulation software (HEC 1998; Brunner 2010). The HEC-1 model simulates runoff from hourly precipitation data for 32 subwatersheds of the basin, on the basis of synthetic unit hydrographs estimated from watershed characteristics (Cronshey et al. 1999; Feldman 2000). Unit hydrographs define response of subwatersheds to a standard unit of rainfall, which are then dynamically rescaled for hourly rainfall inputs. Runoff from different subwatersheds is combined via a simple routing model that also accounts for storage in 4 dammed reservoirs and 2 natural lakes.

The HEC-RAS model takes output from HEC-1 for a flow gauge in the Pajaro Gap (U. S. Geological Survey [USGS] gauge 11159000) and simulates more-detailed river flow in the 25.8-km river downstream to the ocean, which includes the rehabilitation site. HEC-RAS is based on laws of conservation of mass and momentum. These laws are applied to predict unsteady streamflow throughout the river on the basis of data on water inputs, channel geometry, and bed roughness (Brunner 2010). The model predicts water elevation, wetted cross section of the river channel, and mean water velocity for 348 channel cross sections, 133 of which were ground surveyed and the rest interpolated. For each cross section, we estimated slowest available water velocity for migrating fish by converting mean flows into a quasi-two-dimensional velocity field: lateral distribution of velocities was estimated from an empirical channel-roughness and flow relation applied to 10 lateral subsections of flow (Manning’s equation) (Brunner 2010). Vertical distribution of velocities in each subsection was estimated from a power law applicable to turbulent flow (Schlichting 1979).

Schaaf (2002) calibrated the Pajaro flow model to 6 annual peak flows (years 1994–1999) with hourly streamflow of 4-day duration from 8 gauges throughout the basin. He then compared predictions to daily flow at 5 stream gauges with 20–60 years of data, so as to assess fit for large flow events (2- to 200-year recurrence; Supporting Information). At Pajaro Gap, standard errors were mostly within 20%, which is comparable to accuracy of the gauge itself. Receding flows after storms (recurrence  $\ll$  2 years) were overpredicted. Therefore, we adjusted HEC-1 baseflow and loss parameters so that the 2-year event ended at January–May median flows, estimated from gauge data (1.47 m<sup>3</sup>/s, 72 years). This adjusted the modeled hydrographs by a trivial propor-

tion for large flows but a substantial proportion for small flows. The adjustment represented a typical year but was somewhat arbitrary because median flows vary markedly across years (Supporting Information), perhaps due to river banks storing water in wet years (Kondolf et al. 1987). Ultimately, the adjustment is important because it affects how quickly the river becomes too shallow for fish migration after a storm. We assessed sensitivity to this effect by varying the limiting passage depth (see below).

### Storm Traits and Migration Windows

Using Schaaf’s (2007) 2-year design storm as a reference point, we rescaled its hourly precipitation inputs to construct design storms of different magnitudes. Each hydrodynamic simulation had the 72-h reference storm or a single-design storm in which duration or intensity was rescaled between 10% and 200% (see Supporting Information for examples). Each simulation lasted 468 h, long enough for streamflow to recede after the storm and become impassable to steelhead. Rainfall temperatures were drawn from the climate projections.

Migration opportunity was quantified by duration of the migration window and mean energy cost (oxygen consumed) of migrating within the window. Indicators were estimated from a simple model of upstream steelhead migration with parameters from the bioenergetic models. Migration windows are the set of times when a fish starting at the river mouth finds flow sufficiently deep and slow to reach the top of the corridor. Fish swim upstream at  $U_{crit}$  along the slowest available water velocity (“flow-refuging”; Liao 2007), but could not use velocities closer to the surface or bed than half the limiting passage depth.

Fish migration was blocked at cross sections where the deepest flow subsection was shallower than limiting passage depth or where the slowest water velocity was faster than  $U_{crit}$  (called depth barriers and velocity barriers, respectively). Estimates of limiting passage depth usually range from 0.21 to 0.31 m (DeVries et al. 2007). We assessed 0.21 and 0.31 m to test sensitivity of model predictions, but otherwise we focused on 0.31 m to counteract potential biases in our model (shallowest reach may occur outside of surveyed cross sections; shallowest riffle may have substantial through-gravel flow). In a few cases, fluctuations in rainfall caused temporary depth barriers during the storm; fish were allowed to wait these out at resting swim speed and resume when flow increased. Depth or velocity barriers that lasted to the end of the simulation indicated a closed migration window.

### Channel Modifications

We quantified migration opportunity for both the current channel and a proposed rehabilitation in the lower 17.5 km of the river. The current channel has a gradient



of 0.12% from the gauge (USGS 11159000) to the start of the rehabilitation site 8.3 km downstream, 0.097% for another 11.9 km, and 0.019% for the last 5.6 km to the ocean. The channel at the site is incised and has an average width of 50 m. Its levees are set back around 25 m from the bank. We used Manning's  $n$ , an empirical surface-roughness parameter, in the hydrodynamic model to estimate water velocities (Brunner 2010). Manning's  $n$  averaged 0.036 in the channel (sandy and featureless with some gravel and vegetation) and 0.048 on banks (light brush and trees) (Chow 1959).

The modeled rehabilitation set levees back an average 85 m from banks (differed somewhat according to local land use) (scenario PWA2 in Andrews et al. 2003). Between the levees we modeled excavation to an elevation matching maximum water level during the 2-year reference storm, which created a 2.37-km<sup>2</sup> floodplain. These lowered benches were assigned roughness values corresponding to a 33-m-wide band of dense riparian vegetation along the banks (Manning's  $n = 0.12$ ) and gravel or grass elsewhere ( $n = 0.04$ ). The channel itself was gravel and cobble ( $n = 0.04$ ). The setbacks and lowered benches provide transient storage of floodwaters and the roughening slows down flow.

## Results

### Storm Traits and Bioenergetics

Below we use *low*, *median*, and *high* to refer to the 0.025, 0.5, and 0.975 quantiles of probability distributions, respectively. Climate models projected skewed warming outcomes in each month of migration season, with low, median, and high shifts of +1°, +2°, and +5.6 °C by the year 2100 (Supporting Information). Historic low, median, and high storm temperatures were 4.13°, 9.23°, and 13.98 °C, respectively (51 years, 677 storms). Storm temperature varied somewhat from mean air temperature of the month in which it occurred (mean difference of -0.17 °C [SD 1.93]).

Median projected shifts in precipitation were small, but the gap between low and high shifts by year 2100 was nearly twice as wide as a simple statistical projection (Supporting Information) and encompassed both a 55% decline and a 60% increase in mean monthly rainfall. Historic precipitation data showed year-to-year variation in annual precipitation was primarily due to variation in number of storms and secondarily to mean duration of storms (Table 1).

The bioenergetic models projected higher energy consumption by fish, 6.3%/1 °C of warming. Energy consumption doubled at +11.4 °C. Critical swim speed was almost independent of temperature up to approximately 22 °C (Fig. 2) due to a large estimate for  $b$  and a small estimate for  $\phi$  (see Supporting Information for parameter

estimates). Prediction intervals for  $U_{crit}$  were rather wide (Fig. 2) due to high residual error.

### Migration Window

A steady-flow simulation with HEC-RAS indicated the low and high estimates for limiting passage depth corresponded to flows of <4.3 and <6.3 m<sup>3</sup>/s, respectively, with large numbers of cross sections becoming impassable below 2–3 m<sup>3</sup>/s (Supporting Information). This is greater than median daily flow in migration season (1.47 m<sup>3</sup>/s for 72 years of flow data) and verifies prevalence of depth barriers.

Migration windows responded similarly to altered storm duration versus storm intensity, increasing slowly as storms got larger (Fig. 3). The net expansion of migration windows as storm size increased was less steep than if the same amount of precipitation manifested as shifts in storm frequency. For example, the reference storm (100%) generated a 9.4-day window, but two, 50% storms producing the same net rainfall would generate two, 7.6-day windows for a cumulative window 60% larger. This result suggests that migration windows tend to be more resilient to shifts in storm duration and intensity than to shifts in storm frequency (see 1:1 line in Fig. 3). In this comparison, we assumed a 1-to-1 response of total migration window to storm frequency, but at high frequencies storms would begin rescuing fish trapped by receding flows of the previous storm and thus expand windows even faster than 1-to-1.

Migration windows were sensitive to floodplain rehabilitation and assumptions about low-flow and limiting passage depth, but little else. Rehabilitation lengthened the migratory window by a mean of 2.22 days (SD 0.08), a 16–28% expansion of migration windows (Fig. 3). Changing the limiting depth from 0.31 to 0.21 m expanded the window by 4.5–6.5 days (63–66% longer). Migration windows were insensitive to fish size, uncertainty in  $U_{crit}$ , and uncertainty about future rain temperature (Supporting Information).

### Energetic Cost

Energy cost of migration was not sensitive to storm size and channel modifications, except for a few outliers. For 60-cm fish at the mean historical temperature (9.23 °C), oxygen consumption in all parts of the window in all storms and channel scenarios was nearly identical (4.075–4.077 g), except for 4% of simulations (up to 13.8 g) where temporary velocity or depth barriers made fish wait.

Energy cost was more sensitive to rain temperature, and 2 extreme climate-warming scenarios (14.9 and 19.6 °C) roughly doubled the energetic cost relative to the historic median rain temperature (Table 2). Thus,

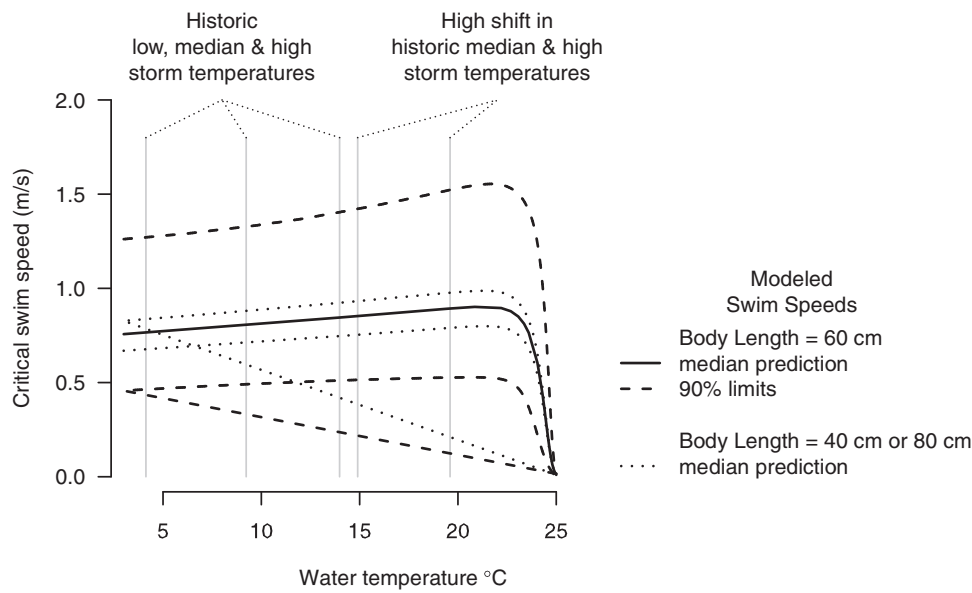


Figure 2. Fitted model of critical swim speed used to describe the sustainable swim speed of steelhead migrating up the Pajaro River. Historic storm temperatures and projected shifts in storm temperatures are derived from exceedance curves in Supporting Information, as described in Results.

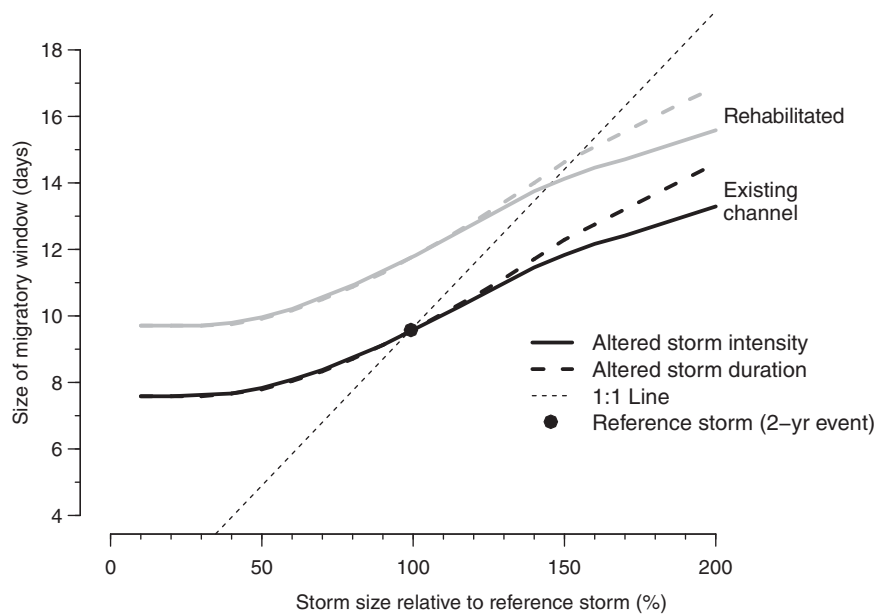


Figure 3. Duration of migratory windows in existing channel system and in rehabilitated channel system as a function of varying storm intensity and duration. Duration of windows was estimated from the hydrodynamic and bioenergetic models (1:1 line, null model in which rainfall and migration window are directly proportional).

the cost of migrating 26 km in the extreme warming scenarios was about the same as migrating 52 km in the current climate, well within the capability of steelhead.

**Discussion**

The model suggests that steelhead migration is generally resilient to warming climate and shifting storm duration and intensity but sensitive to altered number of storms. Past variation in rainfall was mostly linked to number of storms, indicating a possible threat if future shifts play out similarly. If the future is drier, windows will shrink less if storms are smaller rather than fewer. If the future is wetter, the benefit for steelhead is the opposite: windows will expand more if storms are more numerous rather than bigger.

Theoretical and empirical considerations suggest a future with a larger proportion of rainfall packaged into fewer, larger storms (Trenberth 1999, 2011; Dettinger 2011). The popular delta downscaling method assumes only a shift in storm intensities (Tabor & Williams 2010). Our results suggest that the delta method, by omitting shifts in storm frequency, misses a key vulnerability (fewer storms rather than smaller storms), and overlooks the benefit of floodplain rehabilitation.

Floodplain rehabilitation expanded migration windows for storms of all sizes, even those too small to flood the benches. This is because the slightly rougher substrate in the rehabilitated channel (gravel and cobble vs. current sand and gravel) slowed down flows enough to raise water levels and ease depth barriers in all storms (Supporting Information). The benefit of lowered benches is thus indirect. Their ability to store floodwater



**Table 2.** Energetic cost of migration (grams of oxygen consumed) for different water temperatures and 3 fish sizes (body lengths of 40, 60, and 80 cm).

Length of migrants (cm)	Prediction error (percentile)	Historic rain temperatures			Climate change	
		low (4.1 °C)	median (9.2 °C)	high (14.0 °C)	high response of historic median (14.9 °C)	high response of historic high (19.6 °C)
		40	2.5th	0.9	1.1	1.5
	50th	1.2	1.6	2.2	2.3	3.1
	97.5th	2.0	2.8	4.0	4.2	6.2
60	2.5th	2.1	2.8	3.8	4.0	5.4
	50th	2.9	4.1	5.6	5.9	8.1
	97.5th	5.7	8.2	11.9	12.8	19.0
80	2.5th	4.0	5.4	7.3	7.6	10.4
	50th	5.8	8.1	11.2	11.9	16.3
	97.5th	12.2	18.1	27.3	29.4	46.1

reconciles flood protection with a rougher channel that creates deeper, slower water at all but the highest flows. This is what makes it a robust strategy: it moderates extreme climate events while reliably improving ecological function otherwise.

Similarly, ability of steelhead to maintain critical swim speed up to 22 °C made migration robust to extreme warming. This result was based on data from respirometry studies, mostly of hatchery fish (see references in Trudel and Welch 2005 and Peake 2008). Prediction error was wide (Fig. 2), but our results were insensitive to it (Table 2 & Supporting Information). The robustness had an energy cost and ultimately a temperature limit; thus, it would tend to break down in species with similar response profiles but long, energy-intensive migrations during the summer. In this situation, evolution tends to tailor thermal tolerances and metabolic efficiencies to particular temperature profiles, creating sensitivity to warming (Crozier et al. 2008; Eliason et al. 2011). In the Pajaro, summer is a time of juvenile rearing rather than adult migration, so it is in juvenile growth and survival that one would expect adaptation to thermal extremes and sensitivity to further warming.

The key sensitivity in our study was the limiting passage depth. This limiting factor suggests evolution would favor fish that can traverse exceptionally shallow flows and that there would be large benefits from rehabilitation strategies that slow down the recession of flows after storms. Results of the sensitivity analysis suggest that it would be more important to improve and validate models of depth barriers than velocity barriers, which had little effect in our simulations.

In general, species experience some aspects of climate directly, whereas other aspects are mediated by the ecosystem. In our case study, species performance (migration) was robust to the aspect of climate experienced directly (rainfall temperature) but vulnerable to the aspect mediated by the ecosystem (flow depth after

storms). This combination made ecosystem rehabilitation a promising recovery option despite climate change and could be looked to for other endangered species. The promise of the option depended on a strategy (floodplain rehabilitation) whose effect on the species was robust to hydroclimate uncertainty, and identifying credible, robust strategies in other modified ecosystems would be valuable, perhaps by carefully combining empirically derived dynamic models as we have endeavored to do here.

Hydroclimate in California may be fundamentally unpredictable because atmospheric water participates in positive feedback loops (Dessler & Sherwood 2009) and affects California through a relatively small number of events annually (approximately 13 storms/year in the Pajaro). Positive feedbacks produce intrinsically uncertain outcomes (Roe 2009), and small numbers of events are subject to irreducible random variation, so both are general warning flags of irreducible uncertainty. It is tempting to focus on aspects of climate change that have greater predictive certainty, such as warming. But our results show it may often be more important to plan for uncertain climate shifts of likely consequence than to anticipate likely shifts of little consequence and to know which are which. Assessing consequence, however, depends on scientific insight into the likely responses of individual ecosystems and species to unprecedented change.

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## Supporting Information

Information on design storms, limiting passage depths, and exceedance curves are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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