FEATURE

All Fish, All the Time: A Good General Objective for Fish Passage Projects?

Bret C. Harvey | USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521. E-mail: bret.harvey@usda.gov

Steven F. Railsback | Humboldt State University, Department of Mathematics, Arcata, CA | Lang Railsback and Associates, Arcata, CA

Cutthroat Trout *Oncorhynchus clarkii*.
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Better understanding of the degree of "passability" needed to sustain robust sub-populations upstream of barriers could help address and perhaps eliminate perceived trade-offs between fish passage and other resource management goals. We used spatially explicit, individual-based modeling to explore the population-level consequences of various levels of upstream passability by (1) adult resident trout, and (2) juvenile salmon. In simulations of a stream network with widespread barriers, adult trout allowed to move upstream during only the highest 4% of streamflows sustained the distribution and abundance of the population to the same extent as in a no-barrier scenario. In simulations of salmon production in a reach fully accessible to spawning adults, the number of barriers to upstream movement by juvenile salmon did not affect the production of large outmigrants. Passage objectives less ambitious than "all the fish, all the time" may sometimes suffice to maintain populations of resident trout and anadromous salmon.

INTRODUCTION

Improving fish passage in human-altered river networks can efficiently increase the diversity, distribution, abundance, and persistence probability of native fishes. However, in some cases, the desire to improve fish passage will create trade-offs with other goals, particularly with imposition of the requirement to allow passage for "all fish, all the time." For example, a requirement to provide upstream passage for small fish during low streamflows at weirs in experimental watersheds could compromise efforts to measure streamflow precisely and accurately. A requirement for upstream passage for small fish during low flows at beaver dams and beaver dam analogs in meadows could decrease the effectiveness of those dams in providing habitat for fish and amphibians or in shifting hydrologic processes toward more natural conditions. In some settings, barriers modified to allow passage by small fishes over a broad range of streamflows could favor non-native over native fishes (Silva et al. 2018).

The extent of "passability"—a term that commonly incorporates both the species and lifestages under consideration and the range of streamflows that allow their passage—is an important issue in frameworks for prioritizing passage projects (Kemp and O'Hanley 2010). Upstream movement by juvenile fishes has received considerable attention (e.g., Forty et al. 2016) and many prioritization schemes simply use passability ranging from 0 to 1 as a multiplier in quantitative methods of prioritization (e.g., Lin et al. 2020). However, alternative approaches seek to link degrees of passability to their population- and community-level consequences (Kemp and O'Hanley 2010). In some settings, partial passage—by some fish some of the time—may be adequate to fully maintain upstream sub-populations. Better understanding of the effects of fish passage on population dynamics will increase the efficiency of efforts to improve passage and allow resource managers to better address trade-offs with other goals.

However, evaluating the effects of partial passage on fish population dynamics exemplifies the kind of problem difficult, if not impossible to address with empirical observations alone. Here, we use spatially explicit, individual-based modeling to address this question, focusing on resident trout and anadromous salmonids because of their broad importance in resource management.

METHODS

We applied a spatially explicit, individual-based model of stream salmonids to evaluate partial passage scenarios in two situations: (1) a resident trout population in a stream network and (2) anadromous salmon spawning in a single river reach. Railsback et al. (2009) describe the formulation, software, and application of the resident trout model in detail. Railsback et al. (2013) provide information about the adaptation of the model to anadromous populations. Additional information on the model and the opportunity to download it is available: ecomodel.humboldt.edu. Here we cover features of the model especially relevant to this application.

Simulation of Habitat

The model explicitly represents stream reaches as sets of habitat cells, delineated to capture habitat heterogeneity important to fish and to cover all the wetted area at the highest streamflows included in the simulations. Habitat cells vary in size and shape. The simulations presented here used habitat cells commonly between 4 and 16 m^2. Daily streamflow data and hydraulic modeling yield daily estimates of depth and velocity in each cell. The model incorporates additional characteristics of habitat cells important to fish, including the availability of cover that can reduce predation risk, velocity shelter that can allow especially efficient drift feeding, and spawning gravel. The model also relies on daily reach-scale records of temperature and turbidity, which influence various modeled processes important to fish (e.g., bioenergetics, feeding efficiency, predation risk). Reaches can be linked to form stream networks, such that from the perspective of simulated fish the habitat cells of linked reaches abut.

Habitat Selection and Movement

Adult fish individually select habitat cells on each daily time step by maximizing a fitness measure; the estimated probability of surviving to the end of a sliding time horizon that extends a fixed time into the future (in this case, 90 days). The fitness measure also includes a term that motivates juvenile fish to grow. In this formulation (Railsback et al. 1999), fish must consider both food acquisition (to avoid starvation) and a variety of short-term risks (particularly predation) in selecting habitat. Characteristics including depth, velocity, and the availability of velocity shelter determine net energy intake in habitat cells. Characteristics including depth, velocity, and the availability of cover determine relative predation risk. The formulation causes virtual fish to reproduce many commonly observed individual- and population-level patterns exhibited by real stream salmonids (Railsback and Harvey 2002; Railsback et al. 2002; Harvey and Railsback 2009), such as habitat shifts with changes in food availability, habitat shifts and feeding mode changes in response to elevated turbidity, and changes in size distributions with altered habitat.

Daily habitat selection to maximize the fitness measure determines fish movement; the model does not impose directional movements such as spawning migrations. In the model of anadromous salmon used here, we model daily habitat selection by juveniles while they reside in the stream, but not their downstream movement after the decision to outmigrate. The model assumes fish can perceive conditions in nearby habitat

and that this ability increases with fish size; parameter values used here yielded the assumption that a 10-cm fish assesses habitat within 20 m and a 20-cm fish assesses habitat within 80 m. The combination of individual movement capability and habitat selection results in realistic distributions of fish at the reach and stream network scales and rarely leaves high-quality habitat unoccupied, even as the distribution of such habitat varies over time with variation in streamflow, temperature, and turbidity.

To represent the dominance hierarchies commonly observed in salmonid fishes (e.g., Hughes 1992), on the scale of individual habitat cells, resources used by individuals become unavailable to smaller fish. Therefore, events such as the consumption of a large fish by a terrestrial predator or the outmigration of a large smolt have significant consequences for the resources available to remaining individuals. Small fish in heavily populated cells have few resources; the model commonly produces density-dependent growth.

Barriers

The original version of the model (e.g., Harvey and Railsback 2012) included only absolute barriers to upstream movement. For the simulations presented here, we added the capability to allow fish in adjustable size categories to pass upstream barriers within specified ranges of streamflow, while retaining the distance constraint on daily movement described above. Simulation of upstream movement over barriers did not involve the imposition of movement; instead, habitat cells upstream of barriers passable to certain fish were included among possible destinations for those fish, as they selected habitat on each time step to maximize fitness. The process could be thought of as model fish moving up over barriers on days when flows allowed, evaluating the habitat there, then either remaining upstream or returning downstream if none of the habitat available to the fish above the barrier was superior to the habitat below. We did not alter the simulation of downstream movement in the original version of the model. Fish within range of a barrier moved downstream over it when no habitat cells upstream of the barrier within the fish's perceptive range offered a value of the fitness measure greater than an assumed value for cells available downstream. This assumed value for downstream cells was low, so fish moved downstream over a barrier only when they expected low probability of surviving upstream of it.

Spawning/Reproduction

In contrast to the process of daily habitat selection, simulated fish receive substantial direction about when and where to spawn. Fish must exceed minimum size and condition thresholds to spawn. Spawning can occur only within a defined time window, within a specified range of water temperature, when streamflow is both not excessive and relatively steady. To produce a realistic distribution of spawning, whether a fish eligible to spawn on a particular day actually does so is determined by whether a random number between 0 and 1 exceeds a daily spawning probability parameter.

While the model takes a mechanistic approach to daily habitat selection, as described above, to limit model complexity spawning site selection is determined empirically; this is the one piece of the model that uses the traditional concept of habitat suitability. Spawners use the product of empirically determined suitability functions for depth and velocity and the amount of available spawning gravel to select habitat cells. The placement of redds matters because they are subject to de-watering. The model also includes representation of redd scour and superimposition.

Outmigration

For anadromous salmon, we used the representation of outmigration of Railsback et al. (2013). Juvenile salmon outmigrate when none of the habitat cells available to them offer expected fitness higher than the expected fitness from outmigration. A juvenile's expected fitness from outmigration is a logistic function of length, to incorporate the likely positive relation between juvenile size and the probability of successful migration, ocean survival, and spawning. Very small juveniles outmigrate only if expected fitness in their reach (or accessible adjacent reaches) is very low, especially due to conditions that do not allow weight gain. With increasing juvenile size, predation risk becomes more important in determining expected fitness and the probability of outmigration. Larger juveniles remain in the stream network only under favorable energetic conditions and high survival probability. This approach has produced simulated outmigrant size and timing that closely match empirical observations (Railsback et al. 2013).

Specifics of these Simulations

We constructed an artificial stream network for simulations of a resident population of Cutthroat Trout *Oncorhynchus clarkii* by linking physical simulations of three actual segments of varying drainage area in the Little Jones Creek watershed, a tributary of the Smith River in northwestern California. Harvey and Railsback (2012) provide details on the simulation of these segments. The artificial network in this study included a lower reach consisting of two copies of the largest stream segment, three middle reaches each consisting of two copies of the intermediate-sized segment, and six upstream "tributaries" each consisting of two copies of the upstream-most segment (Figure 1). All three segment types represent reaches persistently occupied by multiple size classes of Cutthroat Trout in the actual stream network, although streamflows in the upstream-most segments approached zero in the dry seasons of some years. In the simulations, food availability (as concentration per cubic meter of water for drift and area-specific productivity for food captured by search feeding) and the parameter describing maximum predation risk did not vary across the three stream sizes. However, predation risk still varied strongly among the three because habitat features such as depth modify risk. We did no model calibration for the simulations presented here. Instead, we used values for the standard calibration parameters that describe food availability and predation risk similar to those used in previous studies. We completed 30-year simulations, first using streamflow, temperature, and turbidity input for October 1, 1960 to September 30, 1990 derived from observations from a streamflow gage on the lower Smith River, continuous records of streamflow, temperature, and turbidity at Little Jones Creek from 2000 to 2015, and strong relationships among physical variables among sites. To generate nine additional "replicate" simulations that reflect natural variability at an annual scale, we randomly shuffled the water years in the dataset, without replacement. To generate flow frequency information for use in the development of partial barrier treatments, we used a 78-year streamflow record from

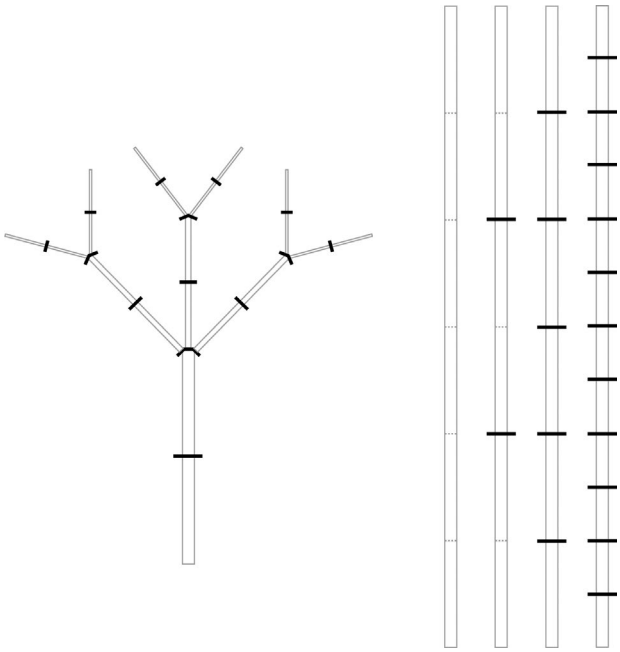

Figure 1. Left: the simulated stream network work used to explore the effects of partial upstream passage on the distribution and abundance of a resident trout population using an individual-based model, including one lower "mainstem" segment, three intermediate segments, and six upstream "headwater" segments. The network represented a total of 1,922 m of stream: 368 m of mainstem creek, 678 m of intermediate-sized stream, and 876 m of headwaters. Right: the barrier treatments (0, 2, 5, and 11 barriers) used in the simulation of a single 1.1-km stream reach used for spawning by anadromous salmon. The simulation of anadromous fish assumed barriers prevented upstream movement by age-0 but not adult fish. Adults were evenly distributed throughout the reach at the beginning of each simulation.

the Smith River gage and relationships between flows at that gage and those at the three Little Jones Creek segments we simulated. We took an adaptive approach to the development of treatments, by first allowing movement only by relatively large fish during only a small fraction of streamflows, and planned on developing additional treatments as necessary to achieve minimal differences in population-level responses between partial barrier treatments versus the no-barrier scenario. We present the first set of treatments we developed, which allowed fish 13-cm FL and longer (approximately equal to fish age-2 and older in the population we simulated) to move upstream over barriers during 2, 4, or 8% of streamflows. We also present for comparison the results from a no-barrier treatment and one with full barriers that prevented upstream passage by all fish. We used the extent of network occupation and the abundance of age-1 and older fish after 30 years as response variables.

For the simulations of a spring-spawning anadromous salmonid, we did not use a stream network, but instead a chain of segments with stream size typically used for spawning by salmon. We linked six copies of the lowest segment in Little Jones Creek to create a reach of about 1.1 km. In all simulations, 40-cm-long anadromous adults were initially evenly distributed among the six segments, although because of the ability of adults to move over barriers, random initial positioning of individuals within segments, individual habitat selection, and variation in the timing of spawning, the distribution of spawning often became somewhat uneven among the six segments. We used 10 randomly selected water years from a 78-year streamflow record to begin replicate simulations of outmigrant production from 1 year of spawning. Because the fish model incorporates the effects of streamflow on the probability of redd scour and desiccation, and on habitat suitability for spawning (which affects the timing of spawning), replicates had the potential to vary significantly. Treatments varied in the number of barriers in the spawning reach that prevented all upstream movement by age-0 fish; we included treatments with 0, 2, 5 and 11 barriers (Figure 1). To address the possibility that barrier effects depended on the density of spawning fish, we conducted simulations across three densities of returning adults. We tracked variation among treatments in the number of large outmigrants (≥8 cm fork length). Benefits of passage could be hidden in the simulations if we included the large numbers of smaller outmigrants with relatively low probability of returning to spawn. Large outmigrants also better represent the juveniles that stay longer and make most use of the stream, and hence are more likely to benefit from barrier passage.

RESULTS

In the 30-year simulations of resident trout, the no-barrier scenario yielded full occupation of the stream network and modest annual variation in abundance. Full barriers to upstream movement reduced the distribution of fish because the six smallest upstream segments in the network usually did not sustain isolated sub-populations (Figure 2A), although successful reproduction at least occasionally occurred in them. The effect of full barriers on total abundance was limited because the larger downstream segments supported most of the fish and retained self-sustaining sub-populations (Figure 2B).

Very limited upstream movement over barriers by adult fish sustained the simulated resident trout population (Figure 2A). Adult fish given the ability to move upstream during only 4% of the highest streamflows in the 30-year dataset maintained the network-wide distribution of the population over 30 years. Beyond the maintenance of fish distribution, some partial-barrier scenarios yielded greater overall abundance of fish than the no-barrier scenario (Figure 2B).

Barriers to upstream movement of juvenile fish had no detectable effect on the production of large outmigrants in the simulations of anadromous salmonids (Figure 3). The number of spawners did not influence this result. One of the 10 spawning years randomly selected for simulation yielded relatively few outmigrants due to redd scour, but this also did not influence the similarity in results across barrier scenarios for that year.

DISCUSSION

The simulations presented here yielded no improvement in population-level outcomes with increased upstream passage by juvenile salmonids to upstream reaches where spawning occurred. In fact, some of the simulations predicted higher abundance of post-age-0 fish in a resident trout population under some partial barrier scenarios in comparison to the no-barrier scenario. Results from prior simulations of complete barriers in a similar stream network (Harvey and Railsback 2012) suggest the explanation for this result involves benefit from limiting tributary entry by

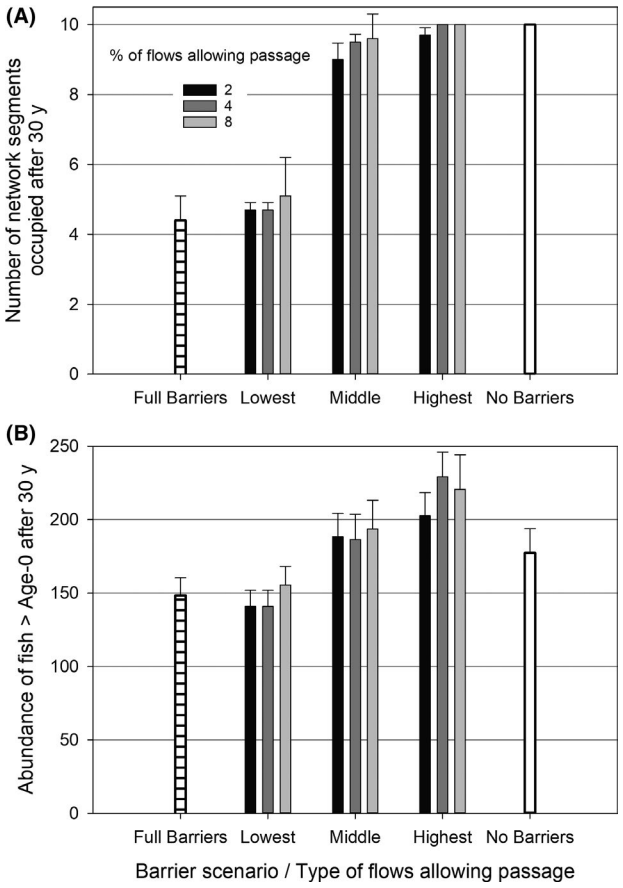

Figure 2. The distribution **(A)** and abundance **(B)** of resident trout resulting from 30-year simulations under various barrier passage scenarios. Distribution is summarized as the number of segments occupied in the 10-segment network. The "full barrier" scenario prevented upstream movement by all fish. Partial barrier scenarios allowed upstream movement only by adult fish. "Lowest," "Middle," and "Highest" refer to the segments of the distribution of streamflows allowing passage. For example, in the "Highest, 2% scenario" only the highest 2% of daily mean streamflows over the period simulated allowed upstream movement by adult fish. Error bars indicate 1 SE.

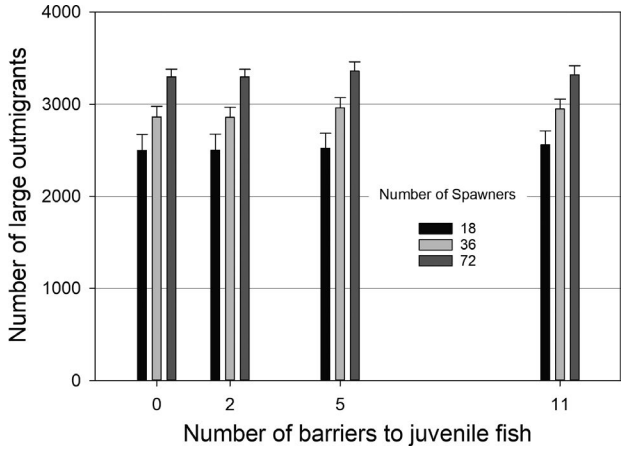

Figure 3. The production of large outmigrant anadromous salmonids, in simulations with varying densities of barriers to upstream passage by age-0 fish and three densities of spawning adults. (Barriers did not limit upstream movement by adults.) Error bars indicate 1 SE.

older fish when such movement could lower their survival probability. In the simulations presented here, lower abundances when older fish were allowed to move into tributaries only at low flows suggest that the limitations on movement distance we assumed can trap older fish in tributaries where they are exposed to low food availability and high predation risk as flows decrease. In contrast, the highest abundances occurred when older fish were allowed to enter tributaries specifically during high flows, and therefore at times of the year most likely to allow them to successfully retreat to larger stream channels. Another likely contributing factor to higher abundances under partial barrier scenarios is that, while present in tributaries, older fish have significant negative effects on the survival, growth, and reproduction of smaller individuals. While one might anticipate real fish avoiding being trapped in drying tributaries through timely long distance movement, in fact this kind of mortality has been consistently observed in real salmonid populations (e.g., Quinn and Buck 2001; May and Lee 2004).

Why did rare movement by adults in the simulations of a resident population sustain its distribution and abundance? That level of movement allowed two fundamental conditions to be met: (1) through a combination of local reproduction and downstream movement, all reaches were supplied with enough young that multiple age classes took full advantage of all available habitat; and (2) when local extinction of upstream reaches occurred, highly limited upstream movement by adults still allowed re-establishment of upstream sub-populations.

In retrospect, the success of modest barrier passability in sustaining upstream sub-populations and network-scale abundance of salmonids makes sense. High variability in the abundance of age-0 fishes in comparison to older fish is common in resident trout populations, and salmonid populations commonly exhibit density-dependent growth (Grossman and Simon 2020). These patterns suggest that resident trout populations are rarely limited by the number of young and that upstream immigration by young fish to spawning areas will only benefit populations in rare circumstances.

The simulations of the anadromous population also suggested that upstream movement by juvenile fish to upstream spawning areas may not always benefit populations. It seems reasonable to assume that the fecundity of anadromous fish, density-dependent growth, and limited amounts of highly productive habitat in most natural settings will likely often combine to produce this result. Any age-0 anadromous salmonids that move upstream to areas where spawning occurred will most likely encounter many other age-0 fish using all the resources that can support relatively high survival and growth.

We considered spatially explicit, individual-based modeling a particularly appropriate framework to address the population-level consequences of fish passage, in part because rare fish passage events involving very few individuals can have important consequences for populations, which play out over long timespans. While such situations are readily addressed in an individual-based modeling framework, they are difficult or impossible to address with empirical observations (or even "expert judgement"). Of course, the specific results of the simulations depend on a large number of

assumptions and other specific characteristics. For example, results presented here certainly depended on the assumed movement capabilities of individuals and the lengths of the stream-network segments simulated, particularly the upstream-most segments. While the individual-based model we employed is complex, it is also mechanistic, so at a minimum it helps us think about natural mechanisms and understand the consequences of the assumptions we put in it. We have confidence in the general patterns illustrated by the specific results presented here, because they make ecological sense in retrospect.

In conclusion, the simulations presented here give reason to question whether complete passage of "all fish, all the time" should be routinely assumed superior to "some fish, some of the time." In many settings, highly limited barrier passability may produce population-level outcomes equal or greater than "all fish, all the time." However, a variety of studies have identified situations where upstream passage by juvenile fish may be important to population-level outcomes (e.g., Ebersole et al. 2006). In some settings, habitat accessed via upstream movement by juveniles may provide them with favorable hydrologic or thermal conditions, or perhaps exceptional food availability or reduced exposure to predation by large fish. But determining the value of upstream movement at the population level is always likely to be challenging, particularly where such movements increase non-zero densities of juvenile fish, because juveniles already in the habitat might have benefitted from a lower density of conspecifics. Clearly, efforts to translate barrier passability into population-level outcomes will benefit from careful consideration of site- and species-specific conditions and processes. For salmonids at some sites, passage of adults only (and only some of the time for resident trout) may be as valuable as allowing passage of all fish, all the time. While the results presented here cannot be extrapolated to other taxa, they do indicate that re-consideration of the population-level consequences of complete versus partial barrier passability may be warranted for other fishes.

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